Food and Agriculture
Organization of the
United Nations

ICARDA
Science for Better Livelihoods in Dry Areas

CROP ECOLOGY, CULTIVATION AND USES OF CACTUS PEAR

Advance draft prepared for the
IX INTERNATIONAL CONGRESS ON CACTUS PEAR AND COCHINEAL
CAM crops for a hotter and drier world
Coquimbo, Chile, 26-30 March 2017

CROP ECOLOGY, CULTIVATION AND USES OF CACTUS PEAR

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Published by
the Food and Agriculture Organization of the United Nations
and
the International Center for Agricultural Research in the Dry Areas
Rome, 2017

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Foreword

Climate change is one of the biggest challenges the world must meet today and in the future. Prolonged droughts and desertification are among the issues faced by many countries, especially in Africa and Asia, where the rural poor and smallholders are most heavily affected. If people are to survive in these ever harsher conditions, their crops need to withstand drought, high temperatures and poor soils.

Cactus crops are gaining increasing interest across the globe, in particular cactus pear (*Opuntia ficus–indica*), because of its unique characteristics which provide resilience to the above mentioned harsh conditions. Cactus pear is able to grow on land where no other crops are able to grow; it can be used to restore degraded land and in many countries, such as Ethiopia, it is the only crop that can be relied on when everything else fails. The crop originates in Mexico – still the largest producing and consuming country in the world – but other countries, including Morocco, Ethiopia, South Africa, Kenya, India and Pakistan, are increasing their production and use.

In addition to its resilience as a crop, cactus pear is also increasingly appreciated for its multiple purposes. The fruit and young cladodes can be consumed by humans, and there is growing interest in its use as fodder. In Brazil, a plantation of over 400 000 ha in the northeast region serves as a key component in supporting livestock production in the country's semi–arid regions. The cultivation of cactus pear for use as fodder is also being adopted in sub–Saharan Africa and South Asia. Furthermore, its medicinal properties and industrial uses are being researched and promoted.

The FAO–ICARDA International Technical Cooperation Network on Cactus (CactusNet) was established in 1993 to support the promotion of this underutilized crop. The first edition of this book, *Agro–ecology, cultivation and uses of cactus pear*, was published in 1995. During the last 20 years much knowledge on cactus pear has been generated, and this is reflected in this extensively revised edition in 2017.

The dedication of all the experts who have contributed to this edition is greatly appreciated and it is hoped that the book will become a useful resource in those countries interested in developing or increasing cactus production. Further, we acknowledge the excellent work of CactusNet, and encourage others to join and contribute to expanding the outputs generated by the Network and its partners.

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Acknowledgements

It was August 1993 when the International Cactus Pear Network (CactusNet) was established following initial discussions in Santiago, in September 1992, during the International Prickly Pear Congress organized by Fusa Sudzuki and Carmen Sáenz at the University of Chile. Eulogio Pimienta, one of the editors of the first edition of this book, was also the first General Coordinator of the Network. In 1995, the International Society for Horticultural Science (ISHS) Working Group on Cactus Pear and Cochineal was established and has made a tremendous contribution to the development of the knowledge of this crop and its utilization. Papers presented in the *Acta Horticulturae* of the Working Group symposia and in refereed journals have had a valuable impact on the advancement of cactus pear. Now, 25 years later, we are back in Chile, proud to present the second edition of *Crop Ecology, Cultivation and Uses of Cactus Pear*. The first edition was a miracle, considered a "milestone in the literature of cactus pear". We were at the earliest stage of the Web. No emails available! Only floppy disks and airmail! Twenty–six authors from 18 universities and research institutions in Chile, Germany, Israel, Italy, Mexico, Peru, South Africa and the United States of America contributed. Similar to the first edition, the second is the result of international cooperation. Some of the authors of the first edition are still involved: Giuseppe Barbera, Carmen Sáenz, Candelario Mondragón, Giovanni Granata, Maria T. Varnero, Helmuth Zimmermann. We thank all of them for the long run we have made together. But we also thank all the authors for their devotion to this crop and their enthusiastic contribution to this book. In total, we have brought together 30 authors from 10 countries, surpassing the first edition.

During the last 25 years we have had the dedicated support of the Food and Agriculture Organization of the United Nations (FAO) and the International Center for Agricultural Research in the Dry Areas (ICARDA), and we have grown considerably. Enrique Arias, from 1992 until he retired from FAO in 2012, was for CactusNet like a lighthouse in the storm. He guided us and served science and technical development for the rural poor with devotion and daily commitment. Umberto Menini in the early years, and later Alison Hodder, both of the Plant Production and Protection Division, FAO, also leant their full support. Today, we have the good fortune to share our work with Makiko Taguchi who has led this edition of the book. We are deeply indebted to her for her "firm" kindness and determination. ICARDA became a partner of our Network when Ali Nefzaoui became the General Coordinator; the FAO–ICARDA partnership created the conditions for further development of CactusNet activities. This book was made possible by support from FAO and ICARDA, with timely contributions from the German Agency for International Cooperation (GIZ).

We thank all the members of CactusNet. We are proud to belong to this community and to share science and friendship within it. Indeed, this book is dedicated to Enza Chessa, a member of our community who passionately championed science along with friendship and loyalty. She was able to smile until the end, and we smile back to her in our soul.

Let us finish with the same words used for the first edition which we firmly believe are still valid: *We sincerely hope that this book will play an important role in increasing the knowledge and usage of cactus pear, given its potential in the agriculture and economy of the world's arid and semi–arid zones.*

The Editors

Acronyms

ADF	Acid detergent fibre
ADG	Average daily gain
ADL	Acid detergent lignin
AFLP	Amplified fragment length polymorphism
AGR	Absolute growth rate
ANADEC	National Association of Cactus Development (Morocco)
ARS	Agricultural Research Service (United States of America)
a_w	water activity
BCE	Before the Common Era [BC]
CactusNet	International Cactus Pear Network (FAO)
CAI	Cladode area index
CAM	Crassulacean acid metabolism
CBTA	Agricultural Technology School (Mexico)
CECCAM	Center for Studies for Change in the Mexican Countryside
CENARGEN	National Research Center for Genetic Resources and Biotechnology
CEZA	Agricultural Centre for Arid Zones (Chile)
CFU	Colony–forming units
CIF	Forage Research Center (Bolivia)
CIREN	Natural Resources Centre (Chile)
CIRNO	Research Center for the Northwest Region (Mexico)
CMC	Carboxymethyl cellulose
CNERNA	Coordination of Studies and Research on Nutrition and Food (France)
CNR	National Research Council (Italy)
CNRS	National Center for Scientific Research (France)
CONACYT	National Council of Science and Technology (Mexico)
CONICET	National Scientific and Technical Research Council (Argentina)
CP	Crude protein
cp–SSR	Chloroplast simple sequence repeat
CREZAS	Regional Center for Arid and Semi–arid Zones (Mexico)
CRUCEN	Regional Center North Center University (Mexico)
DB	Dry basis
DE	Dextrose equivalent
DESA	Department of Economic and Social Affairs (United Nations)
DM	Dry matter
DNA	Desoxyribonucleic acid
DW	Dry weight
EC	Electrical conductivity
EDW	Estimated dry weight
EPDM	Ethylene propylene diene terpolymer
EST	Expressed sequence tag
FAUANL	Faculty of Agronomy of the Autonomous University of Nuevo León (Mexico)
FDP	Fruit development period
FI	First flush (flowers)
FIA	Foundation for Agrarian Innovation (Chile)

FII	Second flush (flowers)
FM	Fodder machine–sliced (cladodes)
FOB	Free on board
FW	Fresh weight
GA	Gibberellic acid
GAE	Gallic acid equivalent
GDH	Growing degree hours
GIZ	German Agency for International Cooperation
GRIN	Germplasm Resources Information Network
HDPE	High density polyethylene
HI	Harvest index
HTST	High–temperature short–time
IADIZA	Argentine Dryland Research Institute
IBA	Indole–butyric acid
ICARDA	International Center for Agricultural Research in the Dry Areas
IFAD	International Fund for Agricultural Development
IIZD	Institute for Desert Area Research (Mexico)
IMZ	Imazalil
INCA	National Institute of Agricultural Sciences (Mexico)
INEGI	National Institute of Statistics and Geography (Mexico)
INIFAP	National Institute for Forestry, Agricultural and Animal Husbandry Research (Mexico)
INRAT	National Institute of Agricultural Research of Tunisia
IPCC	Intergovernmental Panel on Climate Change
IPM	Integrated pest management
IQF	Individually quick frozen
ISHS	International Society for Horticultural Science
ISPA	Institute of Sciences of Food Production (Italy)
ISSR	Inter–simple sequence repeat
ITS	Internal transcribed spacer
Kc	Crop factor
KC	Knife–chopped (cladodes)
LAI	Leaf area index
LPG	Liquefied petroleum gas
ME	Metabolizable energy
MF	Microfiltration
NAFTA	North American Free Trade Agreement
NALPGRU	National Arid Land Plant Genetic Resources Unit (United States of America)
NCRE	Non–conventional renewable energy
NDF	Neutral detergent fibre
NEMA	National Environment Management Authority
NF	Nanofiltration
NGO	Non–governmental organization
nrITS	Nuclear ribosomal internal transcribed spacer
NTU	Nephelometric Turbidity Unit
OD	Osmotic distillation
ODEPA	Office of Agricultural Studies and Policies (Ministry of Agriculture, Chile)
OEP	Office of Livestock and Pasture (Tunisia)
OM	Organic matter

OP	Oviposition period
PAR	Photosynthetically active radiation
PCR	Polymerase chain reaction
PDO	Protected designation of origin
PEP	Phosphoenolpyruvate
Pn	Net photosynthesis
PPFD	Photosynthetic photon flux density
PPO	Polyphenol oxidase
PROAGRO	Sustainable Agricultural Development Program (Bolivia)
PUFA	Polyunsaturated fatty acids
PVA	Polyvinyl alcohol
PVC	Polyvinyl chloride
RAPD	Random amplified polymorphic DNA
RCPs	Representative Concentration Pathways
RH	Relative humidity
RNA	Ribonucleic acid
RO	Reverse osmosis
ROS	Reactive oxygen species
RUE	Rain–use efficiency
SAGARPA	Secretariat of Agriculture, Livestock, Rural Development, Fisheries and Food (Mexico)
SAI	Stem area index
SC	Separate concentrate (feed)
SFA	Saturated fatty acids
SFR	Spring flush removal
SIAP	Agricultural and Fishery Information System (Mexico)
SINAREFI	National System of Plant Genetic Resources for Food and Agriculture (Mexico)
SLP	San Luis Potosí
SNICS	National Service Seed Inspection and Certification (Mexico)
SOMECH	Mexican Society of Horticultural Sciences
SSR	Simple sequence repeats
TBZ	Thiabendazole
TDM	Total dry matter
TMR	Total mixed ration (feed)
TN	Total nitrogen
TSS	Total soluble solids
UF	Ultrafiltration
UFRPE	Federal Rural University of Pernambuco (Brazil)
UNAM	National Autonomous University of Mexico
UNDP	United Nations Development Programme
UNSO	Office to Combat Desertification and Drought
USDA	United States Department of Agriculture
UV	Ultraviolet
VFA	Volatile fatty acids
WBT	Wide–band tracheid
WUE	Water–use efficiency
w_w	Weight of water

01

History and economic and agro-ecological importance

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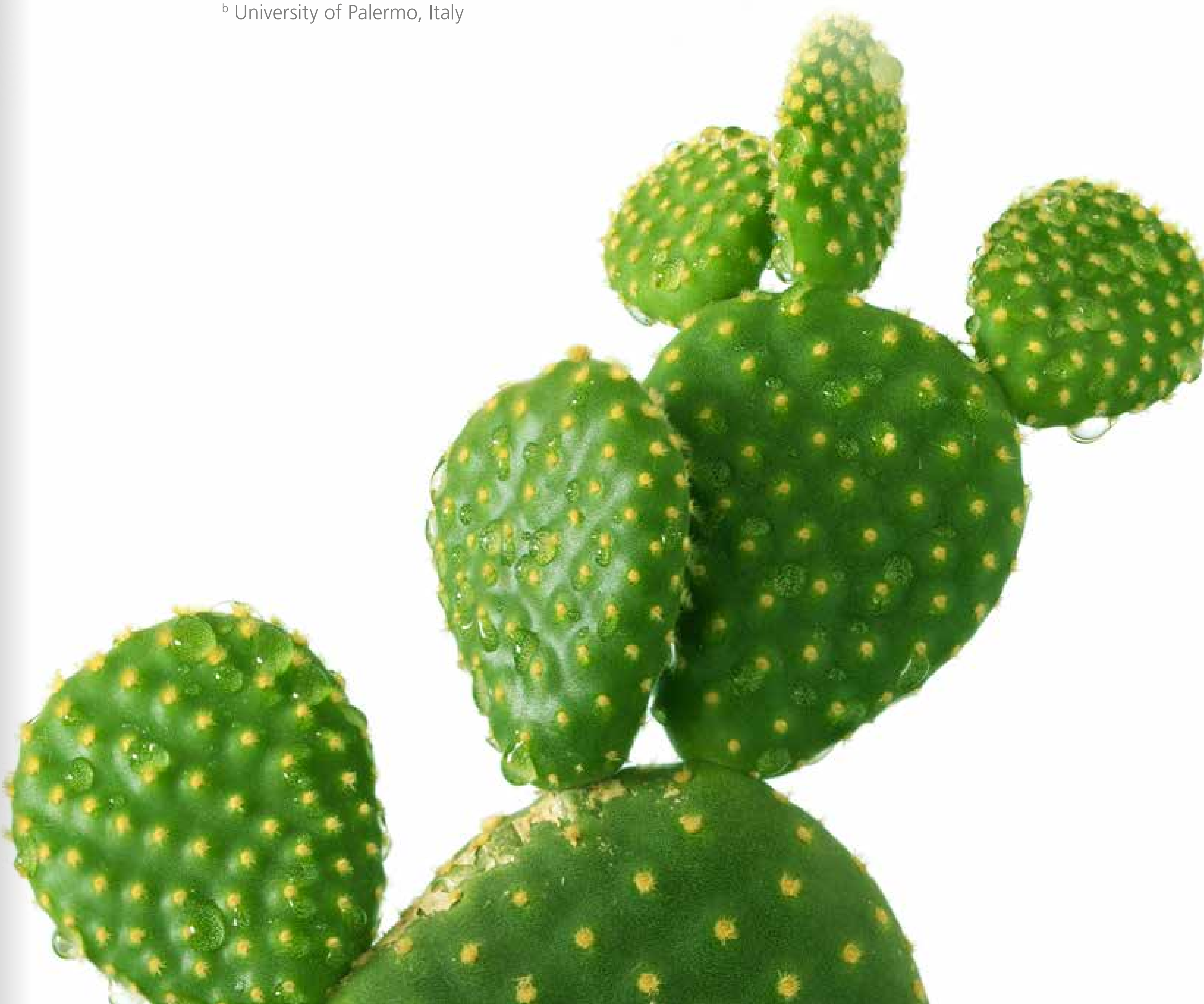

01

History and economic and agro-ecological importance

INTRODUCTION

"The most important thing since the creation of the world ... is the discovery of the Indies." These words, addressed in 1552 to the Emperor Charles V by Francisco Lopez de Gomara, author of the famous *Historia General de las Indias* (General History of the Indies, 1552), testify to the European conquerors' awareness of the possible outcomes of the encounter between the Old and the New World. According to Crosby (l972), the consequences of the "Columbian exchange" were particularly significant for the flora and fauna of the various regions of the planet and especially for the agriculture. Throughout the centuries, this exchange has continued and does not cease to amaze us. During the decades immediately following Columbus' first trip, the rate of exchange of animals and plants between the two Worlds varied. The conquistadors quickly imposed their traditional crops in America: they had the scientific and technological edge and wished to recreate the conditions and habits of their homeland. Transfer in the opposite direction took longer, since the Europeans were mainly interested in products capable of bringing immediate profit. When they did eventually become interested in the local flora, it was through scientific curiosity or a taste for the exotic; they were not aware of the potential of those plants as food or as goods of economic relevance. On the contrary, the Spaniards were initially suspicious of the culture of the peoples they had conquered, and they approached their food habits with much caution and out of mere necessity (Doria, 1992). For these reasons, it was centuries before opuntias – one of the most relevant economic plants of the Aztec civilization – were fully appreciated in the various regions of the world.

Figure 1
Representation of Tenochtitlan's emblem the Codex Mendoza, the cactus pear as centre of the universe

HISTORY

When the Spaniards arrived in 1492 on Hispaniola Island (now Haiti and the Dominican Republic) in the Caribbean Sea, the natives introduced them to *Opuntia* red fruits, then called "tuna", from the Caribbean word *tun*. An amusing anecdote recorded by the chronicler refers to how the newcomers, upon observing the colour of their urine, thought they had been poisoned and were bleeding to death (Kiesling, 1999a). The first Europeans to land on the American continent appreciated the important role – both cultural and economic – of opuntias in the complex pre–Hispanic world. When the first conquistador, H. Cortés, reached the Mexican Plateau in 1519, they could not fail to notice the presence everywhere of *nopalli* (the Nahuatl word for the plant), and on entering Tlaxcala (Diaz del Castillo, 1991), they were welcomed with cactus pear fruits (*nochtli*). Cactus pear was part of the Aztec culture: the Aztec army flag shows an eagle over a cactus pear eating a snake; and the empire capital was called Tenochtitlan, i.e. "Cactus pear over a rock" (now Mexico City). This same scene is depicted on the first page of Codex Mendoza, representing the centre of the universe (Berdan and Anwart, 1992) **(Figure 1**).

The conquistadors began to eat the fruits. Oviedo and Valdés – the first author to describe the fruit and the plant – wrote that his fellows "knew and ate that fruit with pleasure" in Hispaniola in 1515. He also recorded an accurate description (in particular in a later work, written in 1535) of the morphology of the plant. According to this description, the plant grew not only on Hispaniola, but also on other islands and in other areas of the Indies. Moreover, "its seeds and skin are like those of the fig and are tasty too".

Other authors mention the success of the fruit with both the local populations and the Spaniards (Donkin, 1977). In particular, Oviedo y Valdés, Toribio de Motolinia and Galeotto Cei (1539–1553) all described various species, often highlighting the various uses in addition to food: as herbs (the "welding tree" variety was used to treat fractures), as a water source and as barriers or fences. The presence of different species is underlined by Toribio de Motolinia, who mentions "many species", and by Bernardino de Sahagun and Francisco Hermindez (around 1570), who cite 13 and 9 species, respectively. Despite this interest, there was no real economic assessment of the fruits.

On the other hand, the highly prized red dye, *nocheztli*, was greatly appreciated by the Spaniards, who called it *grana cochinilla*. The dye is rich in carminic acid and is extracted from the body of the *Dactylopius coccus* cochineal that lives in the cladodes (Reyes Agüero *et al.*, 2005). The red dye was highly rated for its commercial qualities, and was probably shipped in small quantities to Europe early on. It is certain that Spain was requesting it by 1521 and that in 1544, according to Cervantes de Salazar, "a great quantity at a high cost is imported by Spain" (Donkin, 1977).

The new product was successful because of its intense red colour. It was the most desired import commodity from America at the end of the sixteenth century, surpassed only by precious metals. The precise nature of the powder (*grana*) was for a long time the subject of debate, until Hartsoeker (1694), Van Leenwenhoek (1704) and De Ruuscher (1729) specified its animal origin (Donkin, 1977).

However, despite the economic importance of *grana*, the host plant was not introduced into Europe. There was a ban on exporting the infested cladodes and the Spanish maintained a monopoly for two centuries, until a French doctor, Thiery de Menonville, brought the insect to the French dominions (Haiti) in 1777. The insect was reported in India in 1795 and in Europe at the beginning of the nineteenth century, where attempts to breed it failed in France, Spain and Italy. In 1853, however, there were 14 breeding plants in Algeria, and in 1850–1860 the Canary Islands were already exporting twice the quantity coming from America (Donkin, 1977). Hence, since the plant was not introduced for economic reasons, it may be concluded that the Europeans were mainly attracted by its shape, which was completely new to them.

Indeed, European travellers went in search of unusual plants (Europe was in the period of the "Cabinet of Curiosities" and *Wunderkammem*) and cactus pears fitted the bill. The first depictions of cactus pear and other columnar cacti, are found in the *Historia Natural y General de las Indias* (Natural and General History of the Indies), written by the Spanish officer Gonzalo Fernando Oviedo y Valdés in 1536 (**Figure 2**) (written information had been recorded earlier on Colon´s second Caribbean trip). Oviedo y Valdés wrote: "I cannot make up my mind whether it is a tree or one of the most frightful monsters among trees." Neither his words nor his paintings, however, are adequate to provide an accurate description: "Maybe Berreguete or other great painters such as Leonardo da Vinci who I met in Milan, or Andrea Mantegna would better draw it..."

Their introduction to Europe is not documented; however it did take place before 1552, when Lopez de Gomara wrote about the "nopal", taking for granted that it was already well known in Spain (Donkin, 1977). The plant was *O. ficus–indica* or – as maintained by Berger (1912a) – *O. amyclaea*. The first opuntias probably grew in the vicinity of Seville or Cadiz, the terminus for traffic with the Indies (Donkin, 1977); they then spread to the lush estates of aristocratic mansions and to botanic gardens. It is reported to have been present in Italy around 1560, in Germany and the Netherlands in 1583, and in England in 1596 (Donkin, 1977).

It was immediately well received as a curiosity and decoration. Pier Andrea Mattioli – who in 1558 was the first to provide a drawing based on plants grown in Europe – wrote that "this plant rightly deserves to be included among the miracles of nature". The 1568 edition of his Discorsi included two tables testifying to the general curiosity surrounding the species. The fruits were probably not appreciated – they could barely ripen in northern Italy – and Mattioli reported the words of Oviedo y Valdés citing one of its supposedly terrible effects: on eating them, the urine turns red.

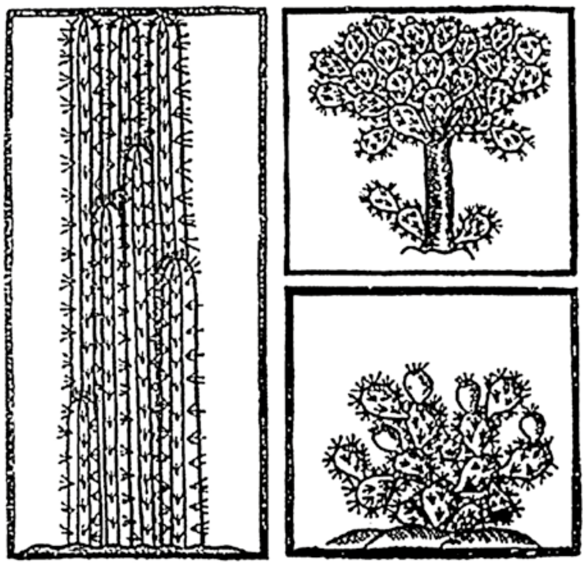

Figure 2
Drawings of columnar cacti and two species of cactus pear by Oviedo Valdés, 1535

The Spaniards took the cactus pear – and most likely also *Dactylopius coccus* – to Peru, although other cochineal were used for dying before the Hispanic period (De Acosta, 1590). In Argentina, red fabric dye, clothes and "ponchos" (De Acosta, 1590) were made using native cochineals. The medical use of cacti and its derivates was documented in *Medicina en el Paraguay natural* (Medicine in Natural Paraguay), 1771–1776, written by José Sánchez Labrador; he described the use of *cochinilla gusano de la grana* (cochineal red worm) for fevers and insanity, how the fruit was used as refreshment and seeds as an astringent (Ruiz Moreno, 1948).

A John Arrowsmith publication (London, 1842) about the topography of Plata and its provinces indicates the Santiago del Estero province in northern Argentina as a great grana producer (**Figure 3**).

In 1580, Gian Vettori o Soderini recalled the fruit's Mexican origin and how it roused the same wonder as peacocks. Towards the end of the century, Agostin del Riccio named cactus pear as a plant ideal for a king's garden (Tangiorgi Tomasi e Tosi, 1990). Numerous works of art incorporate the cactus pear. A wonderful watercolour painting of the *Iconographia Plantarum* by Ulisse Aldrovrandi also dates from the end of the sixteenth century. In 1600, the Bishop of Eichstatt commissioned the Hortus Eystehensis to comprise all the plants of the palace garden, and it includes a drawing of the species. Bruegel the Elder's "Land of Plenty" (1567, now in the *Alte Pinakhotek* of Munich) also includes an *Opuntia*. In Rome's magnificent Piazza Navona, in 1648–1651, Gian Lorenzo Bernini sculptured the Fours Rivers Fountain, designed by Borromini, depicting cactus pear cladodes beside the Rio de la Plata. By the seventeenth century, there is evidence of the presence of *Opuntia* in Europe: a xylograph by A. Switzer (1650, now in the National Central Library in Florence) shows the cactus pear among other plants in the Garden of Eden; and in 1650/1651, J. Bahllin wrote: "it is grown in the pensile gardens of noblemen's mansions".

In northern regions, cultivation was indeed only possible in privileged spaces, since to survive the winter the plants had to be well sheltered or placed in greenhouses. In Mediterranean regions, on the other hand, the climate was ideal and opuntias soon naturalized, becoming one of the most common and representative elements of the landscape. The plant spread along the Mediterranean coast: birds ate its fruits, the Moors returned to North Africa from Spain, and it was also shipped to combat scurvy (caused by lack of vitamin C), as cladodes easily tolerate long journeys without losing their ability to take root (Kiesling, 1999a). During the eighteenth century, opuntias spread to South Africa (1772), India (1780), China (1700) and Indochina, although it is also possible that the plant was introduced in these countries before that time (Donkin, 1977). The iconic use of the plant became very popular during the nineteenth century in arts, cartoons, marketing and even in politics (Barbera and Inglese, 2001). Numerous artists, including Diego Rivera, Frida Kahlo, Roy Lichtenstein, Felice Casorati and Renato Guttuso, used it in their works.

CURRENT SITUATION

Opuntias are now part of the natural environment and agricultural systems, and *Opuntia ficus–indica* (L.) Mill. is the most important economic cactus species worldwide (Kiesling, 1999a). It is cultivated in America, Africa, Asia, Europe and Oceania (Casas and Barbera, 2002). It can be found from Canada to Patagonia, Argentina, from sea level to 5 100 m asl in Peru (Bravo Hollis and Scheinvar, 1995). When first discovered by the European explorers, opuntias were distributed from Mesoamerica to Cuba and other Caribbean islands

Figure 3
Geographical atlas of Santiago del Estero

In the greatest deserts you can find an abundance of cactus species where insectcochinillas live, around 10 000 pounds of this colour are exported.

(Griffith, 2004). It became invasive in areas with a wet season characterized by high temperatures, for example, in South Africa and Australia (Wessels, 1988a; Zimmermann *et al.*, 2009). In Mediterranean climates, natural invasion is limited by the humidity and cold winter temperatures that contrast the warm, dry conditions of summer (Barbera, 1995).

The traditional and popular uses of cactus pear in a wide range of countries and its multiple functions have caught the imagination of farmers, cattlemen and the scientific community.

AMERICAS

Argentina

Argentina has a cactus pear production surface area of 1 650 ha; 80% is in the northeastern region, the remainder scattered in the centre and Cuyo (Targa *et al.*, 2013). The main cultivar is a local selection called 'Amarilla sin espinas' (yellow without spines) (Ochoa, 2003). Production goes to the national markets in Córdoba and Buenos Aires. In the last 5 years, during the dry season, producers have introduced *Opuntia ficus–indica* as forage. Research institutions have begun incorporating cactus pear in their programmes and research projects.

Bolivia

Opuntia ficus–indica is well known in Bolivia, where is has multiple uses. Cactus pear production was developed in Cochabamba, Chuquisaca, Sucre, Tarija and La Paz, in areas with 350–640 mm year^{-1} rainfall and at altitudes of 1 500–3 000 m asl.

In recent years, cactus pear has been promoted in the districts of Pasorap and Cochabamba, supported by the Forage Research Center (CIF) and San Simón University, Pasorapa City, under the Sustainable Agricultural Development Program (PROAGRO). In the valley region and Chaco, cactus pear production is currently being increased to meet the demand for forage for livestock in arid and semi–arid zones of Bolivia (M. Ochoa, personal communication).

Brazil

Brazil has a production area of 500 000 ha (J. Dubeaux, personal communication) in the northeast region in the states of Paraiba, Pernambuco, Sergipe and Alagoas, and recently extended to other states, such as Bahia, Río Grande del Norte and Ceara. There are a large number of small growers and the majority of the production is destined for forage. Brazil boasts the largest cactus pear system in South America, and it has the highest level of production and technology in intensive forage production. In this area, *O. ficus–indica* reaches the highest level of fresh and dry mass production in the world.

Chile

Cactus pear production zones in Chile cover 934.4 ha, with no significant changes in the last decade. The main areas of fruit production are the Metropolitana area and the regions of Coquimbo and Valparaíso (ODEPA, 2016). *Opuntia ficus–indica* gives two crops per year without technical intervention: the first in February–April, the second in July–September. The second crop produces just one–third the volume of the first, but it reaches higher prices (Sudzuki Hills *et al.*, 1993; Sáenz *et al.*, eds, 2006). Production is destined mainly for fresh fruit consumption on the national market. As a result of projects in recent years, there is growing interest in the use of cladodes as food – marmalades or *nopalitos* – in the Chilean diet.

Peru

At present, 60% of cactus pear farming is destined for cochineal production and 40% for the fresh fruit market. In recent years, the processing industry has grown with fruits transformed into nectar juice.

The Peruvian cactus pear crop is grown mainly for domestic consumption rather than export. Cochineal red dye is produced on 10 000 ha under intensive (80% of the area) and semi–wild plantations in Huarochirí and Ayacucho districts. In 2012, the association for cactus producers and cochineal in Huarochirí produced more than 5 000 tonnes of cactus pear fruits for local markets; 'Blanca' and 'Morada' are the most important cultivars.

Mexico

Opuntias in Mexico have the highest degree of genetic diversity and the greatest level of consumption (Reyes Agüero *et al.*, 2005). The main species utilized in Mexico are: *O. ficus–indica*, *O. joconoxtle, O. megacantha and O. streptocantha*. In addition, *O. robusta, O. streptacantha, O. leucotricha, O. hyptiacantha and O. chavena* are harvested in the wild on 3 million ha in arid and semi–arid zones with poor soil in Sonora, Baja California, Baja California Sur, Sinaloa, Chihuahua, Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosí, Jalisco, Guanajuato, Querétaro and Hidalgo.

The first modern farming techniques with the best cactus pear varieties were established in the 1940s and 1950s in the states of Mexico, Zacatecas, San Luis Potosí, Aguascalientes, Jalisco and Guanajuato. This system peaked in 1985, as a result of social programmes launched towards the end of the 1970s (Pimienta Barrios, 1990). Today, cactus pear production is distributed among various states mainly in Federal District, State of Mexico, San Luis Potosí, Zacatecas, Tamaulipas, Aguascalientes and Guanajuato (SIAP, 2014). Cactus pear is the sixth fruit crop in Mexico, after orange, avocado, banana, mango and apple; it is more important than peach, guava or table grapes (SIAP, 2014).

The recent history of cactus pear as a crop in Mexico presents vicissitudes. During the 1970s and early 1980s, the crop was heavily subsidized by government programmes and promoted extensively as an alternative to dry beans and corn. Extension was intense and experimental, based on the limited technical developments available. Many farmers began planting and producing fruits without proper market development. In this period, the predominantly national market was subject to extreme vagaries in prices. In 1985, the Government promoted farmers' organizations based on the assessment of crop needs and the evaluation of problems, involving all the actors in the production chain: growers, wholesale and retail vendors, and agro–industry leaders. Research increased, but was held back by the recurrent lack of proper funding. These developments were in line with a general trend: the Mexican grower entered global markets and was exposed to open competition from foreign growers while in a position to exploit export markets.

In the semi–arid regions of central Mexico, cactus pear is now the most reliable and even profitable option for utilizing rainfed semi–arid lands. In areas exposed to drought, it is the crop of choice over corn or dry beans, while in slightly more benign sites, cactus pear supplements the income obtained from these staples. The available figures illustrate its importance: the planted area covers 53 876 ha; it is the fifth fruit crop in the country; about 20 000 families obtain income from cactus pear cultivation; and gross annual production has reached 428 763 tonnes year^{-1} (Gallegos Vázquez *et al.*, 2013). Vegetable production – characterized by the utilization of small tracts of land – accounts for an additional 12 000 ha of planted area.

The last two decades have seen significant **changes in cactus pear production** in Mexico:

- Slow but steady adoption of drip irrigation in semi–arid areas – a practice unheard of in the last century.
- Introduction of cactus pear to more benign areas, with less limiting rainfall patterns and better quality soils – located in the central highlands and some subtropical regions in the central south and western part of the country.
- Increased utilization of mechanical fruit–cleaning technologies.
- Use of improved packing materials and novel commercial presentations – given the widespread presence of cactus fruits in supermarkets in large and medium–sized cities and the renewed interest in the export market.

A keen interest in the nutritional properties of cactus pear and the positive effects on human health attributed to the regular consumption of fruits and tender cladodes has resulted in a myriad of scientific studies since the beginning of the century. Forage production, on the other hand, has proven beneficial at experimental and semi–commercial level, but has not taken off – perhaps because of the abundance of standard feedstuffs, the low revenue of traditional livestock production systems and the loss of rangelands.

Cactus pears in family gardens or *nopaleras de solar*

These gardens are found in rural environments, since cactus pear fruits are an important component of the diet in the Central Plateau and the north. *Nopaleras de solar* are grown in Zacatecas, San Luis Potosí, Guanajuato and Aguascalientes, mostly for self–consumption or sale on local markets.

Vegetable *nopalitos* production

The farming of *nopalitos* – young tender cladodes for human consumption used in Mexican cooking – depends on a selection of the best varieties. The biggest cultivation area is in Mexico City in the Milpa Alta borough, where research programmes have supported and developed production since 1950. This area is the most important in the country in terms of high production levels and quality. *Opuntia ficus–indica* (L.) Mill. is the most important species for *nopalitos* production.

United States of America

In the United States of America at time of the colonization of California, the Franciscan friars established the first plantation. At the beginning of the twentieth century, selections created by Luther Burbank were widely used in the diets of both men and animals. Today cactus pear is cultivated for fruit production in California, where there are 120 ha under intensive production ("D'Arrigo Bros" trademarked cactus pears in 1928) (P. Felker, personal communication). In Texas, Arizona and parts of California, *O. lindheimeri* are often used as emergency forage (Russel and Felker, 1987a). There are also some small industries based on fruit processing for jelly.

Stephen D'Arrigo emigrated to the East Coast in 1911 at the age of 17. He began growing vegetables such as broccoli and fennel (common in his homeland but not easily available in America) in San Jose, and became a distributor shipping cactus pears east in the late 1920s.

In 1930, he registered a trademark, "Andy Boy", with a logo depicting his 6–year–old son, Andrew. When Stephen died in 1951, Andrew took over the family business; he still heads the company today, aged 87, and takes a particular interest in the firm's cactus pears. Cactus pear cultivation in the Santa Clara Valley went through several cycles of contraction and expansion during the Depression, the Second World War and the post–war years. As the area developed and land became more valuable, Marco and Sal LoBue, the grandsons of Rancadore, moved most of their production south to Gilroy. In 1968, the LoBue family was ready to give up growing cactus pears, but Andrew D'Arrigo stepped in and bought the business, including the production orchards.

A few years later, D'Arrigo changed the name of the product from "prickly pear" – which he thought sounded off–putting – to "cactus pear". As labour became scarce, he discontinued the traditional practice of wrapping each fruit in tissue paper. In the 1980s, he moved his plantations to the Gonzales area southeast of Salinas.

This fertile valley, with its equable maritime climate, is best known as the summer "salad bowl" of America, and it might seem curious that cactus, most associated in the public mind with broiling deserts, would fare well here. Moreover, the main season for cactus pear in Mexico is summer, when the country exports large quantities of inexpensive fruit to the United States of America. However, in the cooler northern climate, and with the aid of the old Sicilian practice of *scozzolatura* (meaning "take the berries away"), involving the removal of flowers from the spring flush, D'Arrigo harvests from October to March, obtaining higher prices when there is less competition. The D'Arrigo Brothers recently selected some new cultivars, thanks also to the work of R. Bunch and P. Felker

AFRICA

The introduction of cactus to North Africa was furthered by the Spanish expansion during the sixteenth and seventeenth centuries and also by the return of the Moors to their homeland when they were finally deported from Spain in 1610 (Diguet, 1928). They took with them the "Indian fig tree" with its succulent fruits and planted them around their villages (Diguet, 1928).

Algeria

Historically, the introduction of the cactus in Algeria was similar to that in Morocco and Tunisia. Today, the area devoted to the cultivation of *Opuntia* extends over 30 000 ha, 60% of which in the municipality of Sidi–Fredj (45 km north of Souk Ahras) and the remainder in Ouled Mimoune, Taoura, Dréa and Ouilène (Huffpost Algeria, 2015). The area was originally extended by the High Commission for Steppe Development, the Directorate of Agricultural Services and Forest Conservation in order to control desert progress (Belgacem, 2012).

In the north, *O. ficus–indica* is used as a fence around houses and small towns; fence plants are also used for fruit production and, in the dry season, as a source of forage. Fruits are harvested from wild plantations and are used for human consumption or sold on local markets. The *Opuntia* cladodes in the south are used as emergent feed for small ruminants and camels.

As in other African countries, the crop is gaining in interest in Algeria, which now has its first cactus pear processing unit. The infrastructure – based in Sidi–Fredj and covering 5 000 m^2 – can transform about 2 tonnes hour[1]. Its principal functions are the packaging of cactus pear and the production of essential oils, pharmaceuticals, juice, jam and livestock feed. The processing plant represents an important means of income improvement for the inhabitants of the wilaya of Souk Ahras (Agence Ecofin, 2015).

Ethiopia

On the Eritrean border, the Ethiopian region of Tigray cultivates cactus pear, known as *beles*. The crop has an important economic and cultural role, reflected in traditional songs and sayings: "Oh my beles you spare me this summer till barley has cheerfully come to rescue me." More than 85% of the population of Tigray derive their livelihood directly from agriculture. Given the ever–increasing pressures of humans and livestock on the land, combined with a decline in soil productivity and recurrent episodes of drought and famine, there is increasing reliance on cactus pear to minimize risk and ensure crop and food security. Cactus pear has a crucial economic role: it is a source of food, animal feed and fuelwood; in some cases, it is a means of additional income, increasing the efficiency and economic viability of small and low–income farmers. Tigray covers about 80 000 km^2 and is estimated to have about 360 000 ha of cactus pear, two–thirds of which are spiny plants. Approximately half the existing area of opuntias was planted; the remainder has been invaded by naturalized cacti. Various projects have been developed to raise awareness of the uses of cactus by local communities; however, the introduction of *Dactylopius coccus* created serious problems when it became aggressive to the wild stands. Cactus pear is mainly used for fruit production, although not in any intensive or rational way. Food and Agriculture Organization of the United Nation (FAO) cooperation projects in the area, carried out by International

Cactus Pear Network (CactusNet) members, have led to increased use of *nopalitos*.

Morocco

In Morocco, cactus was introduced in 1770 and it is now well represented throughout the national landscape. As a result of drought, the cactus area has evolved significantly in the past two decades: from 50 000 ha in 1998 to > 120 000 ha at present. The region of Guelmin–Sidi Ifni accounts for over 50% (> 50 000 ha) of the national surface area, followed by Haouz–El Kelaa of the Sraghnas with 30% (about 33 000 ha). Khourigba is in third place, Doukkala in fourth. This increase in cactus area over the last two decades is the result of abundant planting operations carried out by farmers in collaboration with development agencies and extension services as part of national drought control programmes (Arba, 2009a). Currently, the modernization of Moroccan agriculture (Green Morocco Plan) encourages cactus plantation as an alternative crop in less favourable regions. Each year, over 4 000 ha are planted in the centre and south of the country (Ait Hamou, 2007). In the past 10 years, several firms and cooperatives of rural women have been created for the transformation of cactus. The main products manufactured are: jam, vinegar, silage, flour and seed oil. However, the main interest is in its role as a source of forage for livestock during the frequent dry years (M. Ochoa, personal communication).

A recent threat to cactus in Morocco and throughout the Mediterranean Basin is the advance of cochineal (*Dactylopius opuntiae*). The origin of the infestation is hard to establish, but it probably came from Spain where it was reported in Murcia in 2006 and in Almeria in 2013. The cochineal is today present in Sidi Bennour, Rhamna and Youssoufia; if no action is taken, it will proliferate, destroy Moroccan plantations and migrate to Algeria and Tunisia. The authorities carried out an emergency intervention, uprooting and incinerating all cactus plantations on more than 400 ha at Sidi Bennour in Doukkala (Abdelouahed Kidiss, 2016). A control strategy has been put in place in collaboration with the International Center for Agricultural Research in the Dry Areas (ICARDA).

South Africa

Cactus pear, *Opuntia ficus–indica*, was introduced in the Cape well over 300 years ago. The plant was carried by settlers to all the arid and semi–arid parts of the subcontinent, where it was cultivated as a living fence and for its delicious fruit. The plants gradually reverted to the spiny forms over a period of about 150 years, contributing significantly to its invasive properties and resulting in dense impenetrable thickets in certain regions, mainly in the Eastern Cape (Beinart and Wotshela, 2011). The cacti invaded > 2 million ha in the early twentieth century in South Africa alone, with serious consequences for agriculture, despite its utilization as fruit and forage. In the cooler parts of the country, the cactus was less aggressive and farmers adopted it extensively (Walters *et al.*, 2011).

To solve the problem of uncontrollable invasions of cactus pear, South Africa relied on biological control. About 80% of the infestations were brought under control as a result of the serious damage caused by two cactus–feeding insects of American origin: the cactus moth, *Cactoblastis cactorum* and the cochineal, *Dactylopius opuntiae* (Zimmermann *et al.*, 2009). An estimated 1 500 ha are cultivated for fruit and another 3 000 ha exclusively for forage. An estimated 150 000 ha of the original cactus pear infestations are now also extensively utilized, mainly for their fruit, which are sold on informal markets.

Germplasm banks have been established in the Limpopo, Free State, Eastern and Western Cape provinces, with 42 varieties or types of *O. ficus–indica* established for research purposes. Research originally focused extensively on the use of cactus as drought fodder (Menezes *et al.*, 2010). However, the focus has recently shifted to the intensive production of cactus for animal feed and human consumption.

Tunisia

Beginning in 1920–1930, cultivation for fodder production has been gradually established in Tunisia, based mainly on *Opuntia ficus–indica* f. *inermis*. For example, prior to the expansion of irrigated farming in the 1950s and 1960s, the dairy operations around Tunis and other cities in North Africa used fresh cactus as green stuff (particularly in summer and autumn) in addition to hay, straw and cereal grain. Fodder plantations were systematically developed following the expertise provided by Griffith to the Government of Tunisia in 1932 (Le Houérou, 2002). In the early 1930s, under the colonial land allotment in Sidi Bouzid (central Tunisia), where average rainfall is 250 mm, land ownership was only granted by the Government on condition that contracting beneficiaries, *inter alia*, planted 10% of the land allocated to spineless cactus as an emergency fodder crop reserve. This was a very wise decision, considering the frequent droughts faced by farmers (Le Houérou, 1965). With the support of international organizations (World Food Programme [WFP] and FAO), large areas (70 000 ha) in arid Tunisia were planted with cactus during the 1960s and 1970s to serve as fodder reserves (Le Houérou, 2002). Meanwhile the Tunisian Government provided support, based on state incentives and soft bank loans, to boost cactus plantations. In addition, in 1990 the country launched a national strategy for rangeland improvement; 142 000 ha of cactus were planted in this period (OEP, 2016).

The current area covered by cactus is around 600 000 ha under different forms: defensive hedges, groves surrounding rural houses, consolidation of erosion control structures, extensive fruit production and, more recently, intensive fruit production in favourable agroclimates. Most of these plantations are located in arid areas with < 300 mm rainfall and production is destined for fodder and fruit. In the last decade, in intensive cactus orchards where all required inputs are applied, the practice of *scozzalatura* has been adopted to produce fruits for both the local market and export. In winter, the price of cactus fruits reaches double that of apple, pear or banana. Tunisia uses the varieties used in Sicily ('Rossa', 'Gialla' and 'Bianca'); indeed, it was Italian farmers who introduced *scozzolatura* in the early 1990s. In recent years, the agro–industry of cactus pear transformation has expanded. Several enterprises, such as "Nopal Tunisia", specialize in the production and export of organic cactus pear fruit, cosmetics (seed oil, soap and shampoo), foods (jam, frozen pulp and juice) and dried flour made from cactus pads.

WEST ASIA

In most West Asian countries, cactus is long established, mainly for fruit production and as hedges around houses. In recent years, there has been a growing interest in the crop, but as a secondary crop planted in marginal lands and only for fruit production. However, given the low input requirements and the high level of adaptation to harsh environments, governments and farmers are becoming increasingly interested in growing cactus as a high water–use efficiency crop to enhance local fruit consumption. Nevertheless, despite the severe feed shortages and the negative effects of climate change in these countries, cactus is still not recognized as a good source of fodder, capable of making a significant contribution to alleviating the feed gap. On the other hand, cactus was recently promoted in Syria for feed production, and a high level of adoption was observed.

Jordan

In Jordan, spiny cactus plantations were started 60 years ago as hedges around homes and orchards. The spineless cactus was later introduced and planted extensively under a sole cropping system in the semi–arid areas in the middle of Jordan. In general, in addition to the local spiny and spineless Khadri cactus, most available cultivars are imported to Jordan. The current area under cactus is approximately 300 ha, comprising extensive production systems, hedges and mixed plantations (Nasr, 2015). Extensive production systems are located mainly in Madaba, where farmers grow cactus for fruit production in rows using supplementary irrigation. Cactus is also planted under mixed plantation systems, intercropped with other fruit trees, such as fig and olive; however, due to the negative effect of cactus spines on the fruits, this system is gradually disappearing. In the high rocky areas of Jordan, spiny cactus are still planted, while spineless varieties cannot survive in these environments (Nasr, 2015). Given the severe livestock feed shortage in Jordan, more effort is required to raise awareness of cactus as fodder.

Lebanon

In Lebanon, cactus pear was introduced long ago in coastal and internal areas at altitudes of 0–900 m asl. Cactus pear is destined mainly for fruit production, but it is also grown as a natural fence for the production of "arak" (unsweetened anise–flavoured distilled alcoholic drink). Cactus plantations are common under mixed plantation systems growing alongside other fruit trees, as well as in family gardens for self–consumption. Extensive production systems for commercial fruit production exist in a very limited area in south and north Lebanon (Chalak *et al.*, 2012). Cactus pear cultivars grown in Lebanon are 'Baldi' (spiny cactus) and imported cultivars from Europe, Brazil etc. The imported cultivars include both spiny and spineless ones (Chalak *et al.*, 2012).

Syria

In Syria, as in Jordan and Lebanon, cactus pear has long been cultivated, planted extensively in the rural areas of Damascus mostly for fruit production. At a later stage, and as a consequence of research projects, many cultivars were introduced to Syria from North African countries. However, these accessions were kept in research nurseries and not disseminated on farms for two main reasons. First, there was a lack of awareness of the importance of this crop; second, the Ministry of Agriculture was focused on the improvement and breeding of barley as the main livestock feed resource. In the last 2 years, with the Syrian crisis and the shortage of fodder, interest has increased in cactus cultivation in relatively stable parts of the country, such as Swidaa, Homs and the coastal areas. Cultivars sent by ICARDA were planted as mother plants in two research stations in the coastal area and the Damascus rural area; the new pads are now being distributed to farmers. A recent International Fund for Agricultural Development (IFAD)–funded project for "livestock development" planted 100 ha for feed and fruit production. The results are very promising, with a huge demand for pads and a high level of adoption.

Gulf countries and Yemen

Within the framework of its regional programme in the Arabian Peninsula, ICARDA introduced 38 cactus accessions from Tunisia in 2005 and established a mother nursery in Oman. The pads of these accessions were then introduced in research stations in the Gulf countries and Yemen. Studies on production performances and adaptation to agro–ecological conditions in the Arabian Peninsula were conducted in Oman, Qatar, Saudi Arabia, the United Arab Emirates and Yemen. Since 2012, dissemination has been underway. In 2016, a total of 47 farmers adopted spineless cactus: 15 in Qatar, 10 in Oman, 9 in Yemen, 7 in Saudi Arabia and 6 in the United Arab Emirates.

Israel

In Israel, *O. ficus–indica* has been the subject of several projects, including investigations to induce blooming and ripening in summer, autumn and winter. Today, fruit is sold almost year–round, and at high prices when off–season (Y. Mizrahi, personal communication). 'Ofer' is cultivated on 350 ha in the Negev and Arava valley areas, close to the Egyptian border in the south and near Jordan in the west. In these regions, fruit ripens from late June to late August. Adoption of appropriate cultural techniques produces a second bloom, with fruits ripening between December and April. There is also a limited production of dried flowers harvested after pollination and sold as natural medicine for non–malignant prostate growth (Jonas *et al.*, 1998).

AUSTRALIA

Australia has a long and interesting history relating to the commercial use of *Opuntia*, which was first introduced in the early 1840s for cochineal production and for fencing. Cochineal insects were imported, but they did not thrive because of the abundance of bird and insect pests; the fledgling cochineal industry failed. Nevertheless, *Opuntia* thrived thanks to the suitable climate and the lack of natural *Opuntia* pests and grazing animals. By 1925, the introduced species had naturalized and covered 24 million ha. Biological pests were introduced and they successfully eradicated the vast feral populations.

The modern cactus pear industry in Australia is very small with no more than 200 ha currently grown in the whole continent. Most production and varietal diversity is found in home gardens among Australians of Mediterranean heritage (S. Prowse, personal communication).

EUROPE

Italy

Italy, in particular Sicily, represents an atypical example of the appreciation of *Opuntia ficus–indica*. Cactus pear has been exploited since the eighteenth century, when its multiple uses included fences in farming systems and emergency fodder. It was known as "bread for the poor" (Barbera *et al.*, 1991).

On the coast and close to the main cities, fruit production was exported to the continent. This economic success was reinforced by the *scozzolatura* technique, developed by the Italians to be able to harvest in autumn, producing better quality fruit than in the regular August season. In 1975, modern plantations where established for the fruit industry. Cactus pear production thrives in environments that are environmentally too poor for other crops.

In Italy, cactus pear cultivation is concentrated on the island of Sicily, which accounts for 90% of total production (3 500 ha of specialized area, 15 000 ha in total). There are four important regions: San Cono, Mount Etna, Roccapalumba and Santa Margherita Belice; rainfall is 600 mm year^{-1}. The cultivars, 'Gialla', 'Rossa' and 'Bianca', are grown; summer fruits account for 10% of production, while the winter harvest (August–November) accounts for the remaining 90%. Under irrigation, yield can reach 25 tonnes ha^{-1} (Basile, 1990).

Portugal

In Portugal, the private sector has recently begun to plant commercial plantations of cactus pear for fruit production in the semi–arid areas of Alentejo and Algarve. More than 200 ha have been planted and 500 ha will be planted in the coming years, thanks also to a programme to help unemployed young people who want to work in agriculture (Gonçalves, personal communication).

Spain

In Spain – Andalusia, Murcia, Almeria and the Balearic Islands – cactus pear is only found on family plantations. Lanzarote (Canary Islands) has a small production of red dye.

PERSPECTIVES

"Green gold", "fruit for the poor", "treasure under its spines", "world vegetable dromedary", "future plant", "sacred plant" and "monster tree" are just some of the epithets used for the plant and the fruit (Arias Jiménez, 2013a). These names convey the importance of opuntias in the work and lives of people, because of their resistance to drought and high temperatures and their adaptability to poor soils. However, there is still much scope for **development and improvement**:

- **Greenhouse effect**. The increasing concentrations of CO$_2$ and other gases in the atmosphere will lead to a greater distribution of the species and increased productivity surpassing all previous levels (Nobel and

García de Cortázar, 1991). Moreover, the increase in cactus pear plantations could be part of a strategy to lessen the accumulation of CO_2 in the atmosphere. Cactus pear plantations can function, not only as a water reserve, but as a carbon reservoir in arid and semi–arid regions, where climate is more erratic. More research is required.

- **Plant diversity**. Based on the current understanding of the evolutive patterns of opuntias, further investigation is needed to address issues of generic delimitation and species identity. The integration of molecular, morphological and biogeographical data will generate a clearer picture of the relations between the genus and produce a more stable and reliable source of biological information about the diversity of this exceptional plant family (Chessa, 2010).
- **Marketing.** Since the sixteenth century, opuntias – mainly *Opuntia ficus–indica* – have been used in subsistence gardening in many communities of Africa, Asia, Europe and America. However, fruit consumption remains limited to local ethnic markets and there is little export. Cactus pear benefits from good marketing strategies only in Italy, Mexico, the United States of America and South Africa (Inglese *et al.*, 2002a). Marketing and promotion campaigns are therefore needed, as well as consumer–education strategies at local and international level (Caplan, 1990).
- **Fruit quality.** How can people be encouraged to consume cactus pear? Despite the efforts of the last 20 years, current knowledge remains scarce and only limited scientific information is available to growers (Inglese *et al.*, 2002a). It is essential to do away with the common belief that cactus pear needs few inputs for good performance. This misconception has led to bad management of cactus pear plantations and poor fruit quality. The Italian experience has shown that rational orchard management gives better returns and higher quality fruit with low management costs. To improve productivity and fruit quality, there must be greater awareness of the influence of the environment and orchard management on fertility, fruit growth and ripening (Ochoa, 2003). It is also important to establish fruit quality standards and implement proper orchard design and management.
- **Glochids and seeds: marketing obstacles to overcome**. The glochids on the rind can be removed effectively after harvesting and consumers need to be informed accordingly. Reduced seed content, on the other hand, is a major challenge: there have been no important developments in recent decades, although some selections of the 'Bianca' and 'Ofer' cultivars (El Behi *et al.*, 2015; Weiss *et al.*, 1993a) are available; further research is required.
- **Cladodes as food.** *Nopalitos* offer good prospects for the future, but they are currently used only in Mexico and further efforts are required for their dissemination. CactusNet has introduced *nopalitos* in regional diets and gastronomy, and in Ethiopia the "Mums for Mums" project promotes the use of *nopalitos*.
- **Multiple uses.** There is clearly vast potential for non–food uses of cactus pear, exploiting its biofunctional, medicinal, nutraceutic and cosmetic properties. Many products have been patented in recent years (http://www.bionap.com/it/).
- **Forage.** The exploitation of *Opuntia* for forage must respond to the economic needs of each country and technologies must adapt to livestock requirements; Brazil is a clear example of progress in this regard.

The legacy of Park S. Nobel on the environmental biology of opuntias, combined with the cooperation and technical assistance of the FAO–ICARDA International Cactus Pear Network (CactusNet – created in 1993), paved the way for the current understanding of the potential of the species and its prospective role in marginal semi–arid areas. The last 25 years have seen: the publication of technical and scientific books, leaflets, acta and proceedings; the organization of International Society for Horticultural Science (ISHS) symposia, regional congresses and seminars; and the implementation of projects, thanks to the efforts of the Network, its coordinators and FAO and ICARDA officers. It is vital to continue moving towards these clear objectives for the benefit of the poorest regions in the world. Cactus pear is the "world vegetable dromedary" and one of the most valuable legacies given to the world by America's native population over five centuries ago.

02

Origin and taxonomy of *Opuntia ficus–indica*

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02

Origin and taxonomy of *Opuntia ficus–indica*

INTRODUCTION

Opuntia ficus–indica is the cactus species of greatest agronomic importance, due to its delicious fruits, but also to its stems, which are used as fodder for livestock or as a vegetable for human consumption (Alkämper, 1984; Kiesling, 1999a; Casas and Barbera, 2002). The use and cultivation of opuntias dates back to prehistoric times, long before the Spaniards arrived in the Americas. The Indian chroniclers were the first to record these plants and its fruits, which were carried to Spain and initially used as ornamental plants (Casas and Barbera, 2002). It is probable that opuntias were brought back after the first or second visit of Columbus to the Caribbean, although the first definitive record is from Mexico in 1515 (in the chronicle of Fernández de Oviedo, reproduced by López Piñeiro *et al.*, 1992). The long history of the use, cultivation and domestication of *O. ficus–indica* and related species resulted in taxonomical and nomenclatural problems, summarized in this chapter.

ORIGIN AND TAXONOMY OF *OPUNTIA FICUS–INDICA*

The spineless form of *O. ficus–indica* – common in agriculture today – is the result of a long selection process in cultivation and it is absent in wild stocks. According to Bravo Hollis and Sánchez Mejorada (1991), its domestication began about 8 000 years ago. Reyes Agüero *et al.* (2005) maintain that domestication took place in the south of the meridional Mexican highlands. Archaeological references indicate that the opuntias used 8 000 years ago cannot be associated directly with *O. ficus–indica*. Callen (1965) studied the food habits of pre–Columbian Mexican Indians and found epidermis remnants of *Opuntia* in coprolites on the floor of caves, indicating that the consumption of *Opuntia* dated back thousands of years to at least 5200 BCE. According to Casas and Barbera (2002), archaeological remains of opuntias were found in caves of the Ajuereado phase (14000–8000 BCE). Several taxa are mentioned as putative ancestors of *O. ficus–indica*, in particular *O. megacantha* Salm–Dyck and *O. streptacantha* Lemaire. These and several other taxa and names are often confused due to ambiguous descriptions and a lack of types (Leuenberger, 1988).

Griffiths (1914) considered *O. megacantha* Salm–Dyck to be the wild thorny form of cultivated *O. ficus–indica* (in the narrow sense, or *O. ficus–indica f. ficus–indica*); this was later corroborated by molecular studies (Griffith, 2004). However, the most likely explanation is that they have a common ancestor. Both arose from natural hybridization and multiple sporadic interbreeding. Benson (1982) considers *O. megacantha* as a cultivated taxon and a synonym of *O. ficus–indica* in the "spiny form", and discards the category of variety or form. Other authors (e.g. Gibson and Nobel, 1986; Brutsch and Zimmermann, 1993) follow this reasoning. According to Kiesling (1999a), *O. megacantha* is a reversion to spined plants from escaped, spineless *O. ficus–indica* (see below).

One of the few authors mentioning *O. ficus–indica* solely in the spineless form is Bravo Hollis (1978), who uses only morphological characters for the delimitation; however, she contradicts herself more than once (1978: 288, 322). In the same book she lists six *variedades hortícolas* (which correspond to the concept of cultivar) based solely on the fruit characters. Scheinvar (1995) accepts three separate species: *O. ficus–indica*, *O. streptacantha* and *O. amyclaea*, but also considers *O. ficus–indica* as a

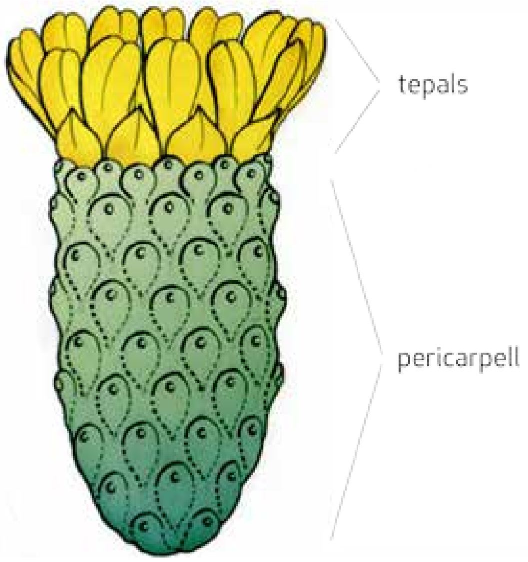


Figure 1
Opuntia ficus-indica

cultivated form originating from *O. streptacantha* and keeps it separate at a specific rank for practical reasons (L. Scheinvar, personal communication).

Several names of the series *Streptacanthae* and *Ficus–indicae* (Britton and Rose, 1919) correspond to minor morphological variations of *O. megacantha*. A description by Britton and Rose (1919) of the series *Ficus–indicae*, which includes the more or less spineless forms of the group discussed here, stated: "None of the species is definitively known in the wild state, but all doubtless originated from tropical ancestors, and they may all represent spineless races of plants here included in our series *Streptacanthae*."

On the other hand, others maintain that there are enough differences to keep the series *Streptacanthae* and *Ficus–indicae* separate. Colunga Garcia *et al.* (1986) wrote: "Thus, these two groups can be differentiated based on cladode size and areole length, fruit and seed length, as well as the length and weight of pulp of the fruit (the edible portion of the fruit). In our opinion, the cladode size, the weight of fruit pulp, as well the areole form may differ caused by the selection process that aims to improve the quality for use as animal fodder or for human consumption."

The spines – presence and size – represent another very variable character. Although the development of spineless forms was encouraged during the domestication process, the opposite – from spineless to spination – is also possible. Such reversions, where some branches of spineless forms produce spines after drought stress or other sorts of stress, are mentioned by several authors (Griffiths, 1912, 1914; Le Houérou, 1996a; Kiesling, 1999a). Moreover, when seeds of the spineless form are sowed, a small percentage of the seedlings develop spines; and vice versa, sowing of seeds from spiny plants results in a small proportion of spineless plants (Berger, 1905; M. Ochoa, personal communication; I. Chessa, personal communication; authors' experience). The reversion of spineless cultivars to spiny plants was also observed in South Africa and Sicily (Zimmermann, 2011; Leuenberger and Arroyo Leuenberger, 2014). The presence of spines is not a valuable character in *Opuntia* taxonomy, because the formation of spines is not independent of environmental factors (Labra *et al.*, 2003).

CHROMOSOME NUMBERS

Determination of chromosome number and ploidy level is a useful tool in plant taxonomy. The basic chromosome number in the cactus family is $n = 11$, and the number in somatic cells is mostly $2n = 22$. In the subfamily Opuntioideae, 64.3% of the taxa are polyploid (Pinkava *et al.*, 1985). Several karyotypic studies show tetra–, hexa– or octoploids in the putative relationship of *O. ficus–indica* (spiny form as *O. megacantha*) $n = 44$ (Pinkava *et al.*, 1973); *O. streptacantha* $n = 44$ (Pinkava and Parfitt, 1982); *O. streptacantha* $2n = 88$ (Palomino and Heras, 2001); *O. amyclaea* and *O. megacantha* $2n = 88$ (Sosa and Acosta, 1966); *O. polyacantha* $2n = 44, 66$ (Stockwell, 1935). Octoploids ($2n = 88$) are also reported for other taxa of the series *Streptacanthae* (including ser. *Ficus–indicae*) (Segura *et al.*, 2007; Majure *et al.*, 2012a). Polyploidy is favoured by hybridization. Natural, interspecific hybridization in the genus *Opuntia* has been proved by several studies (e.g. Benson and Walkington, 1965; Grant and Grant, 1982; Griffith, 2003; McLeod, 1975) and hybridization in cultivation is common. The occurrence of higher ploidy levels of cultivars in comparison with wild relatives is obviously true for cultivated *O. ficus–indica* (Mondragón Jacobo and Bordelon, 1996). For *O. ficus–indica* alone, many chromosome counts show that both the spiny and the spineless forms are octoploid (Pinkava *et al.*, 1973, 1992). Cultivated plants of *O. ficus–indica* in Italy were found to be octoploid (Barbera and Inglese, 1993). However, this species is also reported as hepta–, penta–, hexa– and diploid, so there exists a variation of chromosome numbers, depending on the provenance (Spencer, 1955; Weedin and Powell, 1978; Pinkava, 2002; Majure *et al.*, 2012a) – unless the different numbers are the result of misidentified study material or anomalies in the meiosis. McLeod (1975) indicates the presence of hybrid specimens with $2n = 77$, in between *O. ficus–indica* megacantha (octoploid: $2n = 88$) and *O. phaeacantha* var. *major* Engelm. (hexaploid: $2n = 66$). Carpio (1952) mentions also $n = 44$ for *O. ficus–indica*. He suggests that the anomalous meiosis and the existence of tetravalentes show that *O. ficus–indica* is either an allopolyploid originating from two species with $2n = 44$ or an autopolyploid. Allopolyploidy of *O. ficus–indica* is confirmed by Griffith (2004).

MOLECULAR STUDIES

Given that morphological studies resulted in different taxonomic hypotheses, greater insight was expected from molecular studies (mainly of DNA) concerning variability, relationship and origin of the *Opuntia* species and *O. ficus–indica* in particular. Although several studies focus mainly on the genetic diversity of cultivars (e.g. Bendhifi *et al.*, 2013; El Finti *et al.*, 2013; Ganopoulos *et al.*, 2015), some give insight into the differentiation of *O. ficus–indica*. Wang *et al.* (1999) studied five cactus fruit cultivars from Mexico and Chile, two ornamental Texas accessions, and one vegetable accession from Mexico. The DNA analysis revealed significant differences between the market accessions, but only slight differences between the fruit cultivars (including spined and spineless forms). The genetic diversity of cultivated cacti seems to be low in general, probably because they originate from a narrow germplasm base (Boyle and Anderson, 2002).

In the study by Labra *et al.* (2003), molecular data revealed a high genetic similarity between *O. ficus–indica* and *O. megacantha*. The only (morphological) difference between the units is the presence of spines. The authors conclude that *O. ficus–indica* should be considered a domesticated form of *O. megacantha*.

Griffith (2004), when studying the origin of *O. ficus–indica* using molecular data, found a well–supported clade including *O. ficus–indica*, *O. streptacantha*, *O. tomentosa, O. leucotricha* and *O. hyptiacantha*, all from southern and central Mexico (diversity centres of Opuntia – Barthlott *et al.*, 2015). The analysis supports the hypothesis that the centre of domestication was central Mexico and *O. ficus–indica* may be polyphyletic, i.e. descended from different lineages. This could be due to hybridization (in nature or during cultivation), derivation of multiple unique clones from various parental stock, or lineage sorting of multiple internal transcribed spacer (ITS) copies in an ancestral population from which *O. ficus–indica* and closely related species may have descended (Griffith, 2004). Caruso *et al.* (2010) studied the genetic diversity of *O. ficus–indica* cultivated genotypes. Their analysis supports the hypothesis that *O. ficus–indica* consists of a group of multiple unrelated clones, derived from different parental species and selected for different agronomical features.

Majure *et al.* (2012b) concluded that *O. ficus–indica* is one of several species originating from allopolyploidization events caused by the hybridization of species belonging to different clades. The *O. ficus–indica* samples studied by Caruso *et al.* (2010) did not cluster separately from other species (*O. amyclaea, O. megacantha, O. streptacantha, O. fusicaulis* and *O. albicarpa*), indicating that the current taxonomical position and the genetic patterns do not fit very well. Lyra *et al.* (2013a) studied characteristics of cultivars of four species (*O. ficus–indica*, *O. albicarpa, O. streptacantha* and *O. robusta*), but with the used marker (ITS) it was not possible to assign the samples of these species to separate clades. This difficulty may arise from the fact that the samples are of hybrid origin or have a common ancestry. Valadez Moctezuma *et al.* (2015) advanced this latter assumption when *O. ficus–indica*, O. albicarpa and O. megacantha proved impossible to separate in different clades. Similarly, Samah *et al.* (2015) could not detect clear boundaries between *O. ficus–indica*, *O. albicarpa, O. megacantha, O. streptacantha, O. lasiacantha* and *O. hyptiacantha*. Astello Garcia *et al.* (2015), in a study of the molecular composition of five *Opuntia* species, could not verify a proposed domestication gradient for *O. ficus–indica*, when different cultivars of this species clustered within different groups. While the study failed to identify the ancestor, *O. hyptiacantha* could be related with the majority of the *O. ficus–indica* samples studied. Srikanth and Whang (2015) compared three taxa of Opuntia cultivated in Korea and found that the Korean *O. ficus–indica* is closely related to *O. engelmannii* and *O. ellisiana*, but not to the *O. ficus–indica* samples taken from the GenBank database. Molecular studies reveal the faultiness of the current taxonomy for the species and cultivar complex of *O. ficus–indica*, and question whether these problems are caused by hybridization, adaptive genetic responses, phenotypic plasticity, epigenetic bases or other factors (Valadez Moctezuma *et al.*, 2014).

DISTRIBUTION AND NATURALIZATION

While its ancestors originate in central Mexico (Griffith, 2004), *O. ficus–indica* has been taken by humans to other areas of the world with warm climates. Following the introduction of *O. ficus–indica* in Spain around 1500, the species (and others of the same genus) spread and naturalized throughout the Mediterranean area, soon becoming a characteristic element of the landscape. It was already widespread in Europe in 1550 (Mottram, 2013). Therefore, it is not surprising that one species, *O. amyclaea* Ten., was described in 1826 as coming from Italy, where it had been found near the town of Amyclæ (today Monticelli). It corresponds to the spiny form of *O. ficus–indica*. O. amyclaea was considered a form of *O. ficus–indica* by Schelle (1907); for this reason, in the taxonomic rank of form its previous name was *O. ficus–indica f. amyclaea* (Ten.) Schelle. Berger (1905, 1912b) also assumed that this *Opuntia* established in Italy must be the original form of *O. ficus–indica*, i.e. an ancestral form. A form of *O. ficus–indica* from Argentina was also described as a new species (*O. cordobensis* Speg.), and similarly a form from Bolivia (*O. arcei* Cárdenas) (Kiesling, 2013). At the beginning of the twentieth century, the American botanist and agronomist David Griffiths studied and cultivated opuntias in Texas for taxonomic and agronomic evaluation (Benson and Walkington, 1965; Walkington, 1968). He described several species from cultivated specimens, and some of these species – better treated as cultivars – are considered synonyms or hybrids of *O. ficus–indica* today (e.g. *O. fusicaulis* Griffiths, 1908; Kiesling *et al.*, 2008). In the eighteenth century, *O. ficus–indica* was introduced to other continents by navigators who – given its vitamin C content and low perishability – used it as a vegetable to prevent scurvy (Diguet, 1928). They also transported it to:

- meet the demand for carmine dye from cochineal, which feeds on Opuntia;
- use as fodder;

- incorporate in the human diet; and
- make living fences.

Adapted to harsh and dry conditions, opuntias could easily escape and naturalize in arid areas of Africa, Asia and Australia. *O. ficus–indica* had already been introduced to South America by the Spanish conquerors, for example, in Bolivia (Hoffmann, 1955). Opuntias spread rapidly in many regions, sometimes becoming invasive: a threat to native biodiversity and to agricultural land use (Brutsch and Zimmermann, 1993; Barbera and Inglese, 1993: 11). Today *O. ficus–indica* is naturalized in 26 countries outside its native range (Novoa *et al.*, 2014).

In all tropical arid countries where it is cultivated or naturalized, *O. ficus–indica* has undergone genetic alterations and phenetic modifications, resulting in new forms that have been distinguished and formally named. Sometimes they are classified as species or varieties, even when a classification and naming as cultivars of the two forms (*O. ficus–indica* f. amyclaea and *O. ficus–indica* f. ficus–indica) would be more appropriate (Brickell *et al.*, eds, 2009).

While there are numerous recordings of the introduction of the spineless *O. ficus–indica* f. ficus–indica to different countries, it should be noted that there are almost no references concerning the introduction of the spiny form.

VERNACULAR NAMES

Given the importance of *O. ficus–indica* and its numerous benefits, it has been given many names in its native range and in the regions where it has been introduced (Reyes Aguero *et al.*, 2005). Some of these names are a good illustration of the origin of introduction and distribution.

The name “tuna” is of Caribbean origin (Bravo Hollis and Sánchez Mejorada, 1991: 505) and was used by the first Spaniards to arrive in the Americas. To be precise, it is a Tain name (Moringo, 1966). It usually refers to the fruits, but is also used for the vegetative parts of the *Opuntia* species. The name is currently in use in a very extensive area, which suggests that it was the first name known by the Spaniards, even before the Mexican names (since they reached the Caribbean islands before the mainland).

“Nopal” is a Mexican name derived from the Nahuatl *Nopalli* (Bravo Hollis and Sánchez Mejorada, 1991: 558; Moringo, 1966: 424), and is used for several species. *Tenochtli* is the original name used in large parts of Mexico.

The first Spanish name is *higo de las Indias*, a reference to its origin, the New Indies; it gave rise to the first scientific name: *Cactus ficus–indica* Linné. The epithet, *ficus–indica*, was used as a “diagnostic phrase” long before Linné, to designate several more or less similar species. In other languages, similar vernacular names are used: *figo da India* (Portuguese); Indian fig (English); *figuier d’Inde* (French); *Indianische Feige* (German); *fico d’India* (Italian) (Reynolds and Arias, 2001).

Another widely known name is *tuna de Castilla* (or *nopal de Castilla*), obviously derived from the name of the former Spanish kingdom of Castilla, from where Opuntia was distributed to other countries. Le Houérou (1996a) mentions Andalusia as the first propagation centre in that continent – the region Christopher Columbus returned to after his voyages. Following the dissemination of *Opuntia* in Spain, it was introduced to North Africa, where it was called *higo de los cristianos*. The spiny form is currently widespread in Morocco, where it is called *tapia* (from the Spanish word for fence), a reference to its use as a hedge (A. Prina, personal communication). The name “sabra” – a word used to refer both to the native people and to the prickly pear plant – illustrates the extent of its distribution in the Mediterranean area. Indeed, the species is frequently used to illustrate postage stamps in several countries around the Mediterranean Sea.

In 1769, the Franciscan missionaries took the cultivated form from Mexico to California, where it is called “mission cactus” (Benson and Walkington, 1965; Walkington, 1968). However, it is not certain whether the natives already cultivated this species before the arrival of the Franciscans. Walkington (1968) used the name *O. ficus–indica* in a wide sense.

The species is very important for the economy of northeast Brazil, where it is mainly used as forage throughout the year and is called *palma forrageira*. It is not known when it was introduced to that country (Domingues, 1963). *Palma–de–gado* is another common name for *O. ficus–indica* in northeast Brazil. Several other vernacular names beginning with “palma” are applied to the species in regions of the Brazilian state Bahia, where the pads are used as forage and the fruits, mucilage and roots have several uses in human nutrition and medicine (Andrade, 2008).

THE ROLE OF COCHINEAL

The cochineals of the genus *Dactylopius* parasite on many cactus species, including those of the genus *Opuntia*. *Cochineals* have great species–specificity. Dactylopius coccus, also known as grana, has an absolute preference for *O. ficus–indica* and for taxa that are considered its synonyms or are closely related (e.g. *O. megacantha, O. streptacantha, O. cordobensis*). José de Acosta (1590, cited after Di Lullo, 1944) wrote about tunales domésticos in High and Low Peru (today, Bolivia and Peru), and his observations are in line with current knowledge of *O. ficus–indica*; it can therefore be deduced that this cactus was probably present in those areas in that early period. In Peru, the use of *grana* dates to the pre–Hispanic period, probably as far back as the time of Christ (Marín, 1991; Sáenz *et al.*, 2002a); however, it is not clear whether it was D. coccus or another cochineal species. Fester (1941) and Fester and Lexow (1943) mentioned a spectrometric analysis of the colours of pre–Hispanic tissues (Paracas, from Peru) and of tissues from northern Argentina, demonstrating that the red colorant probably originates not from *D. coccus* in Mexico and Central America, but from other species of *Dactylopius*.

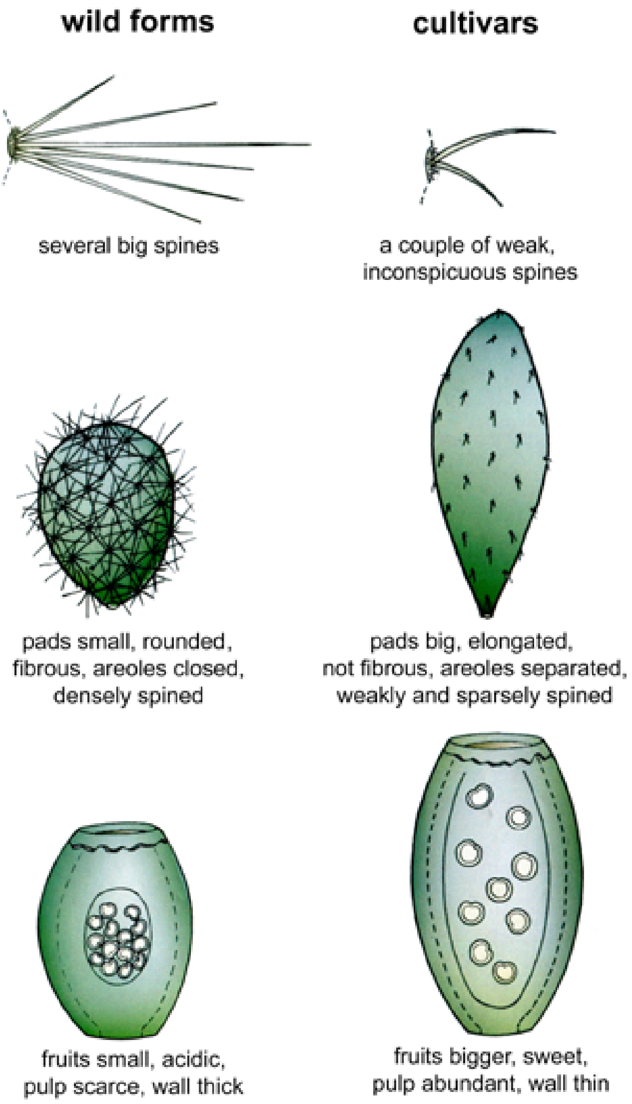
The economic importance of cochineal production in the nineteenth and twentieth centuries led to the introduction of both host plant and parasite into several countries outside their native distribution area. According to Piña (1981), *D. coccus* was introduced to Peru in the nineteenth century, before the country began to export *grana* in 1830.

For Argentina, Lafone Quevedo (1927) described how *grana* was harvested from *quiscaloro* (vernacular name for the wild species *Opuntia sulphurea* and *O. anacantha*, among others). According to the Argentinean entomologists, Claps and de Haro (2001), five wild and red–dye–producing species of *Dacytylopius* parasite on several cactus species native to Argentina. A sixth species is *D. coccus*, found on cultivated and naturalized *O. ficus–indica*. During the 1980s, the former President Menem introduced D. coccus to encourage the production of *grana* in Argentina. While this attempt at *grana* production was not successful, naturalized *D. coccus* was recorded for the first time in 1999 in La Rioja, Argentina (De Haro and Claps, 1999). Later, there were also recordings in Salta (Van Dam *et al.* 2015). Hence, it is plausible that the red colorant extracted in the past was obtained from other *Dactylopius* species. The same researchers state that while the native cochineal live on different Cactaceae species, they live neither on *O. ficus–indica* nor on *O. cordobensis* – a strong indication in favour of its species–specificity. According to Van Dam *et al.* (2015), D. coccus is a domesticated form, as is also assumed for *O. ficus–indica*.

From the known records it can be deduced that *D. coccus* was not present in Andean South America before the arrival of the Spanish conquerors.

TAXONOMICAL AND NOMENCLATURAL CONSPECTUS

The different entities considered and denominated under several scientific names as species correspond to a single biological entity. In the strictest sense, *O. ficus–indica* is not a natural species (Kiesling, 2013), rather a complex of cultivars and naturalized clones.



O. ficus–indica can be distinguished from other species by several characters. The receptacle of the flower and later the fruits have many areoles (≥ 38), with a very small number of cultivars having fewer (Pinkava *et al.*, 1992; Kiesling, 1999a); the areoles are situated mostly on very notable tubercles. Other *Opuntia* species have fewer areoles at the flowers and fruits, situated on less prominent tubercles.

The name *Opuntia ficus–indica* has priority over other names given to this species (Kiesling, 1999b). Nomenclatural types based on herbarium specimens, which determine the application of names, were not designated for *O. ficus–indica* until 1991, and for *O. streptacantha* and *O. megacantha* until 2010 (Leuenberger, 1991; Scheinvar *et al.*, 2010), although all three names were published in the eighteenth or nineteenth century and widely used afterwards. The specimen chosen as nomenclatural type (lectotype) of *O. ficus–indica* (Leuenberger, 1991) corresponds to a plant without (or with very small) spines. However, the presence/absence of spines is not a useful character for distinguishing *O. ficus–indica* from other species, and the spiny and spineless forms must be considered different phenotypes of one species. Nevertheless, this character is used here to separate the spiny and spineless plants of *O. ficus–indica* formally in the rank of form (the lowest level of the taxonomic categories), even if both forms can arise from each other.

Opuntia ficus–indica (L.) Mill., Gard. Dict. ed. 8, Nr. 2; 1768

Basionym: *Cactus ficus–indica* L., Sp. pl.: 468. 1753. 1753.
Plants are shrubby or tree–like, up to 6 m high, usually with well–developed trunks. Stem segments are variable, broadly obovate or oblong to spatulate, flattened, 20–50 cm long, 20–30 cm wide, about 2 cm thick, matt green, covered by a very thin waxy layer, areoles 2–5 cm apart. Glochids falling away early, spines absent or 2 (–7) per areole, 0.5–1.0 cm long, weak whitish. Flowers yellow, rarely orange, 6–8 cm long and 5–10 cm in diameter during anthesis. Fruit with numerous (approx. 30–40) areoles, with glochids, rarely with spines, tuberculate, ovoid to oblong, 6 (–8) cm long, 3 (–5) cm in diameter, yellow, orange, pink–green or reddish.

Opuntia ficus–indica f. *ficus–indica*

Synonyms: *Opuntia ficus–indica* var. *gymnocarpa* (F.A.C. Weber) Speg., Anales Mus. Nac. Buenos Aires ser. 3, 4: 512. 1905. *Opuntia ficus–indica* var. *decumana* (Haw.) Speg., Anales Mus. Nac. Buenos Aires ser. 3, 4: 512. 1905. *Opuntia ficus–barbarica* A. Berger. Monatsschr. Kakteenk. 22: 181. 1912. *Opuntia tuna–blanca* Speg. An. Soc. Cient. Arg. 99: 107. 1925.

Areoles without spines or with only small and weak spines.

Opuntia ficus–indica f. *amyclaea* (Ten.) Schelle, Handb. Kakteenkultur: 51. 1907

Basionym: *Opuntia amyclaea* Ten., Fl. Neap. Prod. App.: 15. 1826.
Synonyms: *Opuntia ficus–indica* var. *amyclaea* (Ten.) A. Berger, Hort. Mortol: 411. 1912. *Opuntia megacantha* Salm–Dyck, Hort. Dyck.: 363. 1834. *Opuntia streptacantha* Lem., Cact. Gen. Sp. Nov. 62. 1839. *Opuntia cordobensis* Speg., Anales Mus. Nac. Buenos Aires ser. 3, 4: 513. 1905. *Opuntia arcei* Cárdenas, Cact. Succ. J. (Los Angeles) 28: 113. 1956.
Areoles with notable spines.

CONCLUSIONS

Based on the facts presented and biological knowledge, the following conclusions can be drawn:

- *O. ficus–indica* f. *ficus–indica* is the result of a long–lasting selection process during cultivation. A result of this process is the development of polyploid (up to octoploid) and more vigorous forms or cultivars, more convenient for human use than their wild relatives. The selection of less spiny plants has led to spine–free forms. Fruit size and quality also influenced the selection process, which had begun before the arrival of the Spaniards in Mexico. Intraspecific as well as interspecific hybridization suggests a polyphyletic origin.
- The cultivated, spineless form was introduced to Spain, probably a few years after the discovery of America (c. 1500), and initially used as an ornamental plant and a curiosity in the gardens of the nobility. From there it was taken to other countries in the Mediterranean as well as to South America, South Africa, India and Australia. Navigators increased its distribution by taking it as a fresh vegetable to guard against scurvy. The main reasons for the further dissemination of *O. ficus–indica* by humans were the production of fodder in arid areas, the use of the fruits or pads for human consumption, and cochineal production.
- In several countries with a suitable warm and arid climate, the species was introduced and cultivated, spreading by vegetative and generative reproduction until it became naturalized. This process happened independently and more than once in several places, in different countries, and on all continents, in the native as well as the new distribution areas. This resulted in new centres of infraspecific differentiation, with the emergence of cultivars and subsequently naturalized clones and hybrids. The naturalized forms developed slightly different morphological and physiological characters compared with the cultivated clones. Spiny forms emerged repeatedly from the spineless plants.
- *O. ficus–indica* is considered a species, or a group of multiple unrelated clones derived from different parental species. The native distribution area of the ancestral taxa is central Mexico.

03

Morphology and anatomy of *Platyopuntiae*

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03

Morphology and anatomy of *Platyopuntiae*

INTRODUCTION

The species of *Opuntia*, particularly those in the subgenus *Platyopuntia*, have developed anatomical, morphological and physiological adaptations to grow and survive in arid environments where severe water stress hinders the survival of other plant species (Beccaro *et al.*, 2015). This chapter describes some of the most important anatomical and morphological adaptations present in the root, shoot and reproductive structures of *Opuntia ficus–indica* (prickly pear) – the *Opuntia* species with the largest economic value.

ROOT SYSTEM

Cactaceae roots receive little attention. They differ from those of other plants, as they develop xeromorphic characteristics that enable the plant to survive prolonged periods of drought. Roots can **contribute to drought tolerance** in various ways:

- Restriction of the root surface and decrease in their permeability to water – fine roots are covered with a layer relatively impermeable to water, or roots abscise at a cicatrization layer in order to avoid water loss to dry soil.
- Rapid absorption of the small quantity of water supplied by light rains – "rain roots" develop within a few hours after a shower and disappear as soon as the soil dries up, or there is a reduction in the root surface from which water flows off.
- Decrease in shoot transpiration due to root high negative potential.

The above characteristics mean that these drought–resistant water savers can have high hydraulic resistance (Passioura, 1988); this, in turn, decreases water flow to the shoot.

Opuntia ficus–indica has a shallow and fleshy root system, which spreads horizontally. Root distribution may depend on the type of soil and cultural management (Snyman, 2005). Under favourable soil conditions, a tap–root develops, penetrating nearly 30 cm into the soil. Under drought conditions, such as those found in arid and semi–arid regions, fleshy side roots develop from the tap–root to take up soil moisture at a greater depth. Nevertheless, in all kinds of soil, bulk masses of absorbing roots are found in the topmost centimetres, at a maximum depth of 30 cm, but spreading outwards 4–8 m. It has also been observed that plants periodically fertilized with manure develop succulent and unbranched roots, while they usually develop more lateral roots that soon develop a surface layer of loose exfoliating cork (North and Nobel, 1992).

According to Snyman (2004, 2005), the root system of *O. ficus–indica* is very complex and can exhibit **four kinds of roots**:

- **Skeletal roots**: formed from a primary skeleton of scarcely fibrous roots, 20–30 cm long, which very soon increase in thickness by secondary growth to form a periderm. When the root skeleton is kept dry for some time and then remoistened, absorbing roots are formed from latent buds within a few hours to quickly respond to the advent of moisture (North *et al.*, 1993; Dubrovsky *et al.*, 1998). The initiation of lateral roots is always endogenous from parenchyma cells belonging to the secondary phloem. Research into the regularities of adventitious root formation in *O. ficus–indica* has shown that the fine lateral roots on the tap–root die off with age. This process stimulates cell division in the parenchyma root tissues and the formation of meristem spots with adventitious roots (Gibson and Nobel, 1986). This fine and fragile mass of roots is formed from short and branched rootlets, completely covered with root hairs. Also, different kinds of ectomycorrhizae, mostly the vesicular–arbuscular type, grow together with the short and branched rootlets.
- **Absorbing roots**: formed within a few hours as the lateral buds rapidly respond to the advent of moisture. Gibson and Nobel (1986) named these absorbing roots "rain roots". They develop from the hidden latent bud in the cortex of the older roots. These rain roots die off as soon as the soil dries.
- **Root spurs**: developed from the bulkiest mass of roots as clusters (Boke, 1980). The spur base of *O. ficus–indica* exhibits a crown of appending–like bracts and, contrary to Boke's description, the roots developed from the spur in *O. ficus–indica* are of two classes: short, gross and fleshy, with plenty of root hairs; and two or three slender and long ones, similar to absorbing roots. It is not known whether the short roots die off or mature with time.
- **Roots developing from areoles**: developed when the areoles are in contact with the soil. At the onset of their development, they are gross and without

root hairs; they have a prominent calyptra, with the epidermal cells forming bract–like appendages. The growth of the young roots is very rapid; they become slender with a cortex 3–4 cells thick, and are covered with root hairs. In some of these cells, water deficit induces the formation of a higher number of endodermal cells with Casparian bands closer to the root tip (De Micco and Aronne, 2012).

CLADODE

O. ficus–indica is a CAM (crassulacean acid metabolism) plant, commonly considered drought resistant, because it stores considerable amounts of water in its shoots (Nobel, 1994, 1995). The morphology and anatomy of the shoots have evolved to serve this function.

According to Buxbaum (1955), Cactaceae are broadly characterized by short shoots ("areoles", bearing hairs and spines), a succulent stem with a green cortex, and the absence of foliage leaves. According to Hunt and Taylor (1986), the areoles of Opuntioideae, in addition to or instead of spines, develop short hair–like prickles called glochids. In *O. ficus–indica*, the stem–like organs, known as cladodes, are succulent and their shape is typically oblong to spatulate–oblong, usually 30–40 cm long, sometimes longer (70–80 cm), and 18–25 cm wide. Anatomically, the cladode in a cross–section is a eustele, formed by: skin; cortex; vascular tissue, in a ring and made from collateral bundles separated by parenchyma tissue; and pith, which is the major succulent tissue.

Skin

The skin consists of one layer of epidermal cells and 6–7 layers of hypodermal cells, with thick primary walls resembling a laminar collenchyma tissue. The epidermal cells are flat, thin and shaped much like paving stones. The epidermis and hypodermis provide an effective barrier to prevent physical damage and maintain mechanical integrity. The thick cells of the hypodermis are very strong and act as the first line of defence against fungi, bacteria and foraging by small organisms. The skin remains intact for a long time and is eventually replaced by bark (periderm).

The **periderm** is formed from epidermal cells, either as part of the natural ageing process, or from the deeper tissues of cortex when injury causes the skin to break. When bark forms from the thick cell walls of the hypodermis, it breaks off.

The **epidermis** constitutes the outermost layer of cells in the cactus body. It is a continuous protective cell layer, which also bears the stomata (**Figure 1**). The epidermis has three major functions:

- Regulate the movement of carbon dioxide into – and oxygen out of – the plant.
- Retain water within the plant body.
- Protect the plant from fungi, insects and intense sunlight (Mauseth, 1984).

The outermost wall of the epidermis is impregnated and covered with wax of a fatty substance called cutin. The cuticle of cactus, in comparison with the cuticle of most plants, is relatively thick and in *O. ficus–indica* can reach 8–20 μm. In chemical terms, cutin is not a pure product like cellulose; it is a mixture of fatty acids, which polymerize spontaneously in the presence of oxygen. Not only is cutin water–resistant, it is also one of the most natural chemicals known (Mauseth, 1984).

Examination of the surface of *O. ficus–indica* cladodes, using scanning and transmission electron microscopy, reveals a slender aggregate coating of a basic wax structure of semi–vertical plates. This coating gives the cladodes their glaucous appearance. According to Metcalf and Chalk (1979), the epicuticular wax present in *O. ficus–indica* corresponds to the basic group III type classified as plates and scales.

The waxy, rough surface around the epidermal cell serves a number of functions. As far as water equilibrium is concerned, the cuticle prevents the escape of water vapour from the plants and repels surface water. The white cuticle reflects solar radiation, resulting in a reduced stem temperature (Gibson and Nobel, 1986).

According to Mauseth (2006a), the epidermis in most Cactaceae persists for decades as a living, transparent tissue capable of facilitating gas exchange. This is in contrast with the ephemeral stem epidermis in most seed plants, which lasts only as long as a plant lives or dies when bark is formed on perennial plants. The epidermis in cactus is present and alive, as long as green colour is visible in the underlying cortex.

Mauseth (2006a) also mentions the fact that the epidermis in Cactaceae presents a folded surface, rather than a smooth one, affecting the shoot's strength, flexibility and ability to swell without tearing. A plicate surface means that, as water is absorbed and shoot volume increases, the rib bases spread and the volume of the rib is increased without requiring any increase in surface area. As the rib bases widen, the inner cortex can also expand. As a result, there is a change in the volume – but not the surface area – of the shoots, and there is no damage to the epidermis or hypodermis (Mauseth, 2000).

Stomata are abundant in the stem epidermis of most other Cactaceae and are evenly distributed over both sides of the entire stem surface (Sajeva and Mauseth, 1991). In *O. ficus–indica*, they are randomly spread, not great in number and are usually 15–35 mm^2 (Mauseth, 1984). The guard cells do not differ from other flowering plants; they are 40 µ and sunken, so the pore is hidden from the stem surface. A prominent substomatal canal, through the sclerenchymatous hypodermis tissue, forms a passageway for gas exchange between the atmosphere and the photosynthetic tissue below the hypodermis; the endostomatic chamber is in the chlorenchyma layer (**Figure 2**). The pair of guard cells are surrounded by 3–4 rows of subsidiary cells. The epicuticular surface brightens these cells, and the stomata can therefore be observed with low magnification. Within the epidermal cells and hypodermis lies a very conspicuous crystal aggregate of calcium oxalate, named drusas (**Figure 1**).

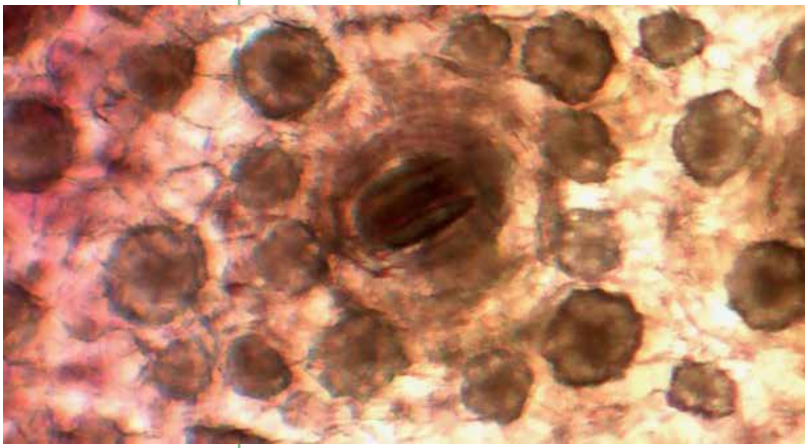

Figure 1

Stomata in the epidermis of a fully developed cladode. Also druses present in the hypodermic are shown, surrounding the stomata.

According to Mauseth (2006a), in *O. ficus–indica*, epidermis cell walls tend to be thin, not thickened and not lignified. The epidermis is often thinner than expected for a xerophyte and long, multicellular uniseriate trichomes are abundant at every node, but the internode epidermis has almost no outgrowth. A hypodermis of several layers of cells, with extremely thick and hard walls, is present (Gibson and Horak, 1978; Mauseth and Ross, 1988; Mauseth, 1996, 1999b; Mauseth and Kiesling, 1997; Terrazas Salgado and Mauseth, 2002; Loza Cornejo and Terrazas, 2003; Terrazas Salgado and Arias, 2003).

Areoles

Areoles are oval, 2 mm below the skin surface. Under appropriate environmental conditions, new cladodes, flowers or roots will arise from the meristem tissue of the areoles. In *O. ficus–indica*, the areoles are distributed in a helical formation, and they develop spines (rather than leaves, as most plants do). When the cladode is young, the areole forms at the base of the podarium (cladode). The podarium holds a small subulate short–lived green structure, which soon shrivels and falls off. This ephemeral structure corresponds to a leaf (**Figure 3**). The podarium is prominent in the first stage of cladode development, and becomes lost as the stem ages. The areole begins to form at the very base of the short apical meristem, and very soon the spines develop from the basal meristem (Mauseth, 1984); the number of spines varies, but there are often one or two long central spines and another shorter lateral spine. The long central ones grow for a longer period than the others; they are thicker because they are produced by more robust primordia (Gibson and Nobel, 1986) and have elongate cells with lignified cell walls. As they grow, glochids also appear.

Spines and glochids

The presence of spines is the particular characteristic of the areoles and their morphology has potential taxonomic significance (Robinson, 1974). It is possible to distinguish two types: spines and spine–hairs (glochids). According to Boke (1944), glochids and spines are best regarded as morphological equivalents of leaves and the differences between them are quantitative; both types are derived from tunica and corpus, as are leaf primordia.

The number and duration of the spines and glochids in *O. ficus–indica* depend on the type. Usually, spines are present in the first stage of cladode growth, and most of them fall off as the temperature rises, only occasionally remaining at the base of the cladodes for a long period.

According to Robinson (1974), it is very easy to distinguish the subfamily Opuntioideae by the rough surface of the glochids and spines. In *O. ficus–indica*, the spines have a rough, and the glochids a smooth surface; the glochids are arranged in clusters of 7–12 in the cavities of the areoles. Spines are white; one or two are long (1.0–1.5 cm); two smaller ones accompany each of them. As the tops of the spines harden, the basal meristem continues to lengthen. According to Gamong, cited by Buxbaum (1950), the spines are formed in series. Glochids are tiny, short and multicellular; it is suggested that the first two spines of the areole could be stipules, where the elongated smooth cells (14–16 in number) form a chain and do not become sclerified. They are brown, and give this colour to the areoles. The surface of the spine–hair is covered with calcium carbonate and pectic substances (Buxbaum, 1950). Glochids are grouped in 4–6 tight clusters, from which it is possible to distinguish 2–3 somewhat longer ones with a spine–like structure. They are hard, sclerified and pointed; their surface is covered with barbed scales, that permit them to lodge in the skin and which cannot usually be removed easily. While growing, the glochids are fastened to the areole, but a phellogen then develops in the outer cortical region around the base of each cluster. As a result, in *O. ficus–indica*, they are deciduous and easily removed when either touched or blown by the wind. Their precise function remains unclear, but they may condense water from the air (Buxbaum, 1950). Moreover, spines help to reduce daytime stem temperature, and their presence also diminishes light interception by the cladode.

Corte

Most Opuntioideae have a thick, chlorophyllous palisade cortex overlying a less or non–chlorophyllous inner cortex (Mauseth, 2005). Those with laterally flattened cladodes lack surface plications. In *Opuntia*, below the hypodermis lies the chlorenchyma, which constitutes the tissue between the hypoderm and the ring of vascular bundles. *Opuntia* chlorenchyma is thick and succulent and consists of a primary cortex, formed from a rather homogeneous mass of parenchymatous cells. It is chlorophyllous in the outer part and arranged in long radial rows to form a prominent palisade chlorenchyma, similar to a leaf palisade. The inner part is white and formed from spheroidal parenchymatous cells, similar to those of spongy mesophyll.

All species of Opuntioideae with flattened cladodes have wide (660–3 600 mm) canals filled with mucilage cells floating freely in extracellular mucilage, unattached by middle lamellas. The canals are lined with a multilayered epithelium. Mucilage–cell canals occur just outside the primary phloem, widening as inner epithelium cells detach and float into the lumen (Mauseth, 1980, 2005).
The green (chlorenchyma) and white (parenchyma) parts both contain idioblasts, filled with mucilage or with crystals smaller than those of the epidermal cells. While the green part containing the chloroplasts has the main function of photosynthesis, the white part is a simple water–storage bag. The parenchyma is the “chemical factory” that produces the hormones, alkaloids and other products formed during plant metabolism (Mauseth, 1984; Sajeva and Mauseth, 1991). It does not have chloroplasts, but does have other organelles – amyloplasts – for starch storage. It is made from homogeneous parenchymatous tissue, with small intercellular spaces.

The precise function of the mucilage is not known; however, it is generally believed that it helps to retain water inside the plant. Mauseth (1980) gives a detailed explanation of the development of mucilage cells. Very active dictyosomes produce small sacs or “vesicles” of mucilage along their sides, and this mucilage substance is deposited outside the cytoplasm as the amount of mucilage increases. Thereafter, the cytoplasm dies and the organelles break down, leaving only mucilage, where once there was a living cell. The mucilage cells are present in all types of tissue: hypodermic, cortical, vascular and pith. Mucilage is very slippery, complex and formed by indigestible carbohydrates (Gibson and Nobel, 1986).

Pith

The pith of *O. ficus–indica* is made from large spheroidal parenchymatous cells with thin cell walls, similar to those of the inner cortex. Most pith cells in close proximity to the vascular bundles contain numerous spheroidal starch grains or mucilage and some small druses. Surprisingly, the perimedullary zone (outermost pith adjacent to protoxylem and medullary rays) of some Opun-

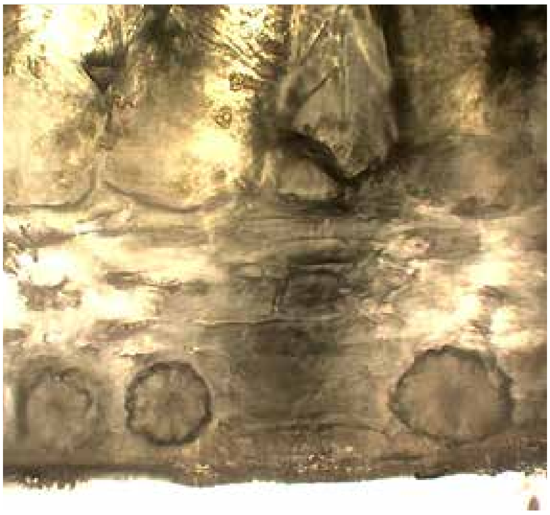

Figure 2

The epidermis with 4–5 layers of the hypodermis cells

Figure 3

Areole in the young cladode showing two spines, ephemeral leaf and several brownish glochids tioideae consists of wide–band tracheid (Mauseth, 2006b), a cell type associated with xylem rather than ground tissue, such as pith or cortex.

Vascular tissue

Beneath the cortex, *O. ficus–indica* has a ring of collateral vascular bundles with soft tissue between them (eustele), corresponding to fascicular cambium or medullary rays. The vascular bundles are connected to the meristematic tissue of the areoles, and form an elaborate, very fine fenestrate vascular tissue network of accessory bundles. As Freeman (1970) mentions for O. basilaris, anastomosing of stem bundles is common and results in the formation of a complex cylinder around the pith. A vascular network is formed at each node by the fusion of two sympodia and a leaf trace with an areole trace and numerous accessory bundles; a closed system is thus created. Between these bundles, large rhomboidal parenchymatous gaps are formed above the point at which each leaf trace diverges from the vascular network towards the areole.

The xylem is simple, and its vessel elements (75 µ wide) are greater in number than the scattered tracheary elements (40 µ wide). Primary vessels, as well as tracheary elements of vascular tissue, are characterized by helical and annular thickenings, with scalleriform or reticulate perforations in the secondary walls (Hamilton, 1970). Mucilage cells and spheroidal starch grains are abundant around the vascular bundles. Freeman (1969) puts forward the theory that mucilaginous canals or ducts are not actually formed; rather, there is a frequent lysogenic breakdown of the walls separating the mucilaginous cells.

All cactus stems, even the most flattened cladodes in Opuntioideae, have a single ring of collateral vascular bundles (a eustele, typical of all non–monocot seed plants). These primary vascular tissues have few or no unusual features in Cactaceae (Bailey, 1961; Gibson, 1976; Mauseth, 2004).

BARK

With few exceptions, cork cambium of cacti arises from epidermis cells (Mauseth and Ross, 1988; Mauseth, 1989, 1996, 1999a, b; Mauseth and Kiesling, 1997; Terrazas Salgado and Mauseth, 2002). Because the one and only cork cambium is superficial, cactus bark consists simply of alternating bands of cork cells and sclereids (both produced by the cork cambium); it never contains the hypodermis, cortex, primary or secondary phloem typical of bark in many seed plants. The water–storing cortex is never shed. Lenticels appear to be absent (Terrazas *et al.*, 2005).

WOOD

In Opuntioideae, wood has tremendous diversity: some species have ordinary fibrous wood, while others have wide–band tracheid (WBT) wood (Gibson, 1977, 1978a, b; Mauseth, 2006b). There are also two variations in WBT in Opuntioideae, since in some cases WBTs are located in the rays themselves. The distinction between those WBTs located in the ray system and those in the axial system is not clear because WBTs occur in both. Axial regions are defined by the presence of vessels (and by sieve tube members in corresponding regions of secondary phloem), and rays are areas with no vessels (and corresponding regions of secondary phloem lack sieve tube members). Ray WBTs can be distinctly larger than axial WBTs in the same shoot. In the other variation in Opuntioideae, WBTs occur only in rays, not in the axial system. Rays are very wide, consisting of WBTs and parenchyma. The fusiform initial–derived axial systems consist of just one or two rows of vessels and a few axial parenchyma cells.

FLOWER BUDS

The axillary buds in cactus are areoles, which have developed very early in the axil of the leaf primordia. The areole begins to evolve as a mass of cells, which rapidly become a regular shoot apical meristem with all the proper zones: tunical, central mother cells, peripheral zones and pith rib meristem. The spines and glochids develop at a very early stage. After a period (variably long or short), the meristem at the centre of the depression of the areoles goes dormant. When it becomes active again and grows as a long shoot instead of a short shoot, it forms a branch with leaves and areoles or produces a kind of super–modified long shoot, which is the flower (Pimienta Barrios, 1990).

A review by Reyes Agüero and Valiente Banuet (2006) on the reproductive biology of *Opuntia* indicates that, in contrast with all other Cactaceae, the meristem that can produce either a new cladode or a flower will not produce again. Furthermore, 74% of floral buds in *O. ficus–indica* grow on 1–year cladodes, with most vegetative buds sprouting from 2–year cladodes. *O. ficus–indica* develops 20 or more floral buds per cladode, and during flower development, the pericarp maintains its photosynthetic activity and areolar development of glochids, spines and leaves. When the floral bud of *O. ficus–indica* is 0.5 cm long, the gynoecium and the androecium can be distinguished microscopically. Stamens rapidly differentiate into pairs of anthers, each having two pollen sacs. The same authors mention that in *O. ficus–indica* the ovary has many carpels, varying in number from 6 to 12 (usually 8), that grow together at the base and become separated at the stigmatic region. The unilocular ovary contains up to 270 ovules or seed primordia weighing 0.44–3.01 mg. In *O. ficus–indica,* flower anthesis occurs after noon, and flowers close at sunset and open again the following day. At the onset of anthesis, stamens are grouped together around the style but become separated later. Anther dehiscence can occur 12 hours before or at the time of blooming.

Many characteristics make the **cactus flower unique** (**Figure 4**):

- Perianth segments, weakly differentiated as petals.
- Spirally arranged stamens.
- Pistil of four or more fused carpels, enclosed in a floral cup.
- Unilocular ovary with parietal placentation, apparently embedded in the end of a modified branch (Boke, 1980).

Furthermore, cacti are among the few plants in which the exterior of an inferior ovary, called receptacle, displays leaves and perfect areoles. This structure later becomes the peel of the fruit. As the bud emerges, it is possible to see whether it is vegetative or reproductive from its spatial volume. The reproductive bud is more spherical (**Figure 5**), while the vegetative is flatter.

The proportion of flowering to vegetative buds is 3 : 1, and 10% of the cladodes may have both kinds of bud in equal proportions (Sudzuki Hills *et al.*, 1993). The flowers are hermaphrodite and actinomorphic. They develop on the upper part of a 1– or 2–year cladode, and occasionally on a 3–year cladode. Both kinds of bud usually develop over the cladode surface with greatest exposure to light.

Floral differentiation occurs over a short period, from 50–60 days after the meristem starts to be active, through to anthesis, in contrast with many other fruit trees (apple, pear etc.) where floral differentiation begins the year before (Pimienta Barrios and Engleman, 1985). The sterile part of the flower is represented by the perianth and there are few differences between sepals and petals: the sepals are smaller, but both are oblong and fused at the base, with brilliant yellow or pink petals. The yellow flowers change colour to orange or pink after fecundation. The numerous stamens are base–fixed and inserted in the cavity of the receptacle in a fasciculate arrangement, developing centrifugally in such a way that the inner whorl is under the pistil and the upper one is at the altitude of the stigma. The filaments are free and the anthers produce a large amount of dry pollen grains, which shed before the ovules (protandry).

According to Pimienta Barrios (1990), the anthers have a thigmotropic movement. At the beginning of anthesis, the stamens are close to the style and the anthers are in contact with the base of the pistil. This process is known as cleistogamy, and the protandry of the flower explains the autogamous nature of *O. ficus–indica* (Rosas and Pimienta Barrios, 1986). Pollination is entomophilous when the flower is open; the stigma is placed above the stamens (Pimienta Barrios, 1990).

The pistil has a wide style at the base, and a prominent sectioned, granular and viscous stigma formed from ten septs and shaped like an anther. The ovary is syncarpous, unilocular, formed from five carpels and has a parietal placentation.

In *Opuntia*, the funicle is slender and relatively long; the ovules have true integuments (Archibald, 1935), with the inner one beyond the outer. The third integument is a modified part of one of the two normal integuments and it surrounds the ovule completely (Eames, 1961). Ovules are circinotropous, since the funicle surrounds the ovule and covers the

Figure 4

Longitudinal section of a fully developed flower, showing an inferior ovary with numerous ovules and the cortex, petals, stamen and pistil

Figure 5

Floral bud at the edge of a fully developed cladode.

micropyle like a thick third integument. It is possible to observe this structure in seeds of *O. ficus–indica*, where it is present with the micropyle pore quite free.

The inner surface of the funicle is covered with short hairs – "papillae" – especially at the point where the funicle touches the micropyle. The ovules are arranged in two rows in each ventral prominent suture. This situation may suggest that the carpel union is margin to margin, and dorsal bundles extend to the ovules (Boke, 1980).

POLLEN GRAIN

The pollen grain has a thick outer layer, the exine, which has a protective function. Its volume changes depending on the level of humidity (Eames, 1961). The inner layer is the intine; it is thin and readily adapts itself to changes in size. The patterns of exine have considerable taxonomic and phylogenetic value, as the wall may become very thick and complex in structure and the outer layer is sculptured with projecting ridges, spines and granules. In Opuntia, the pollen grains are spheroidal, reticulate and policolpate; they have 18 colpos – i.e. similar to the pollen grain of *O. fusicaulis* described by Scheinvar (1995), which has 20 colpos. There are a high number of pollen grains and it is possible to observe germinated pollen tubes over the glandular epidermal surface of the broad stylar canal 24 hours after anthesis. The fecundation of the ovules gradually begins 48 hours after anthesis and continues for 10 days. This pattern of fertilization was named by Rosas and Pimienta Barrios (1986) as "progamyc". The average number of fecundated ovules per flower depends on the cultivar (Rosas and Pimienta Barrios, 1986).

In *O. ficus–indica*, 18.4–30.1% of pollen grains deposited on the stigma germinate and form pollen tubes. Up to 397 tubes may be formed in this species, and they develop over the glandular epidermis of the inner channel of the style. Most tubes are initiated on the stigma and grow towards the base of the style. Pollen tubes reach the style base about 48 hours after pollination and ovule fecundation begins 72 hours later. After 4 days, 48% of ovules are fertilized (Rosas and Pimienta Barrios, 1986). Polyembryony of nucellar origin is common in *Opuntia*. This explains the development of two or three plants from only one seed. Archibald (1935) estimated that nucellar polyembryony, with the development of endosperm and without fertilization, occurs in *O. ficus–indica* and other cacti.

FRUIT

The fruit of *O. ficus–indica* is a simple fleshy berry formed from an inferior ovary sunk into the stem tissues of the receptacle. The peel originates in the receptacle and has the same morphology as the cladode:

- Epidermis with ephemeral leaves and perfects areoles; the glochids are more permanent than in the cladodes.
- Slender hypodermis and bulky cortex.
- Abundance of mucilage cells, but no crystals.

The **pulp** is formed from the outgrowth of the trichomes that originate in the epidermal cells of the funiculi and the funicular envelope (Pimienta Barrios and Engleman, 1985). Fruit size depends on the number of fecundated ovules and the number of seeds that abort (Archibald, 1935; Pimienta Barrios, 1990; Barbera *et al.,* 1994). It has not yet been established why seeds abort.

The fruits often have two kinds of sterile **seeds**, one of which sometimes predominates. The lack of viability of the seeds is related to an abortion of the ovule or of the young adventitious embryo (Archibald, 1935). In the latter case, the nucellus continues to grow, even after the embryo is formed, and at the time the funicle is formed, it changes into a hard lignified coat. In Chile, many fruits of *O. ficus–indica* have revealed a third kind of non–viable seed. It is an anomalous form, possibly also resulting from the transformation of the funicle into a hard cover, but with the active development of the nucellus, which eventually emerges through the micropylar pore that was not blocked by the ovule. In *O. ficus–indica* cultivars, the presence of a high number of normal seeds in the fruit is considered an obstacle for its commercialization. Italian cultivars have an average of 273 seeds per fruit, of which 146 are normal and 127 sterile. Israeli cultivars have an average of 268 normal seeds per fruit and Mexican cultivars 203 normal seeds per fruit (Reyes Agüero and Valiente Banuet, 2006).

The equatorial diameter best represents the fruit's fresh and dry **weight**. Comparisons between the development of the peel and the edible portion reveal that the growth of the peel is greater during the first weeks after flowering, whereas the edible portion begins to expand more in the last 5–6 weeks before ripening. According to the review of Reyes Agüero and Valiente Banuet (2006) on the reproductive biology of *Opuntia*, *O. ficus–indica* fruit grows vigorously in terms of length, width, weight and volume in the first 20–30 days after anthesis; it stops growing approximately 59–90 days after anthesis. The peel grows fastest during phase 1 of fruit growth, the seed has maximum growth in phase 2, and maximum pulp growth occurs during phases 2 and 3. Fruit weight is affected by the order of production of the flower bud and the number of fruits on the cladode. Thus, floral buds that sprout earlier usually become heavier fruits. Furthermore, the heaviest fruits are obtained from cladodes with only six fruits.

04

Ecophysiology and reproductive biology of cultivated cacti

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04

Ecophysiology and reproductive biology of cultivated cacti

INTRODUCTION

Cactus pear – *Opuntia ficus–indica* (L.) Mill. – is a CAM (crassulacean acid metabolism) plant cultivated in a wide range of environments, resulting in major differences in plant survival and development, and in crop potential. The ecological success of opuntias, specifically *O. ficus–indica*, is due largely to their peculiar daily pattern of carbon uptake and water loss, both of which occur mostly at night. Like other CAM plants, cactus pear opens its stomata at night to fix CO_2 and accumulate and store malate in the vacuoles of the chlorenchyma cells. Since night–time temperatures are lower than diurnal ones, and relative humidity is generally higher, the transpiration of CAM plants is three to five times lower than that of C_3 and C_4 plants (Nobel, 1988). The result is a tremendous increase in water–use efficiency and in the plant's ability to thrive in semi–arid environments characterized by a restricted water supply (200–300 mm of annual rainfall) or where long periods of drought and relatively high temperatures occur. The mechanisms of adaptation to aridity are not necessarily valid in relation to high temperatures. Although they occur at night, CO_2 uptake and acid accumulation are strongly influenced by environmental variables such as air temperature, light, plant water status, nutrients and soil salinity (Nobel, 1988). Indeed, in the native area of the Central Mexican Plateau (1 800–2 200 m asl), rainfall is < 500 mm, the mean annual temperatures range from 16 to 18° C, and the daily maximum temperature for the hottest month does not exceed 35° C (Pimienta Barrios, 1990).

In the Mexican mesas (tablelands), the dry season coincides with a cold winter, while the hot season, during which fruit and vegetative growth take place, is very humid and rainy; exactly the opposite occurs in the Mediterranean Basin, where the dry season coincides with the hottest days, when the fruit develops and vegetative growth occurs (Inglese *et al.*, 2002b). In Sicily, where *O. ficus–indica* is grown for fruit production, annual rainfall is around 500 mm and the mean annual temperature ranges from 15 to 18° C, with peaks of 37° C in August, during the fruit development period (Inglese, 1995). *O. ficus–indica* occurs extensively in northern Africa (Monjauze and Le Houérou, 1965a), in the highlands (2 000–2 500 m asl) of Tigray, Ethiopia and in South Africa. In contrast, it is absent in regions with rainfall < 350 mm and daily summer maximum temperatures > 42° C, such as the Sahelian belt, the Mojave Desert in California, or the Rajasthan Desert in India (Felker and Inglese, 2003). Le Houérou (2002) describes plantations in Aziza (Lybia) where the maximum temperature may exceed 50° C. *O. ficus–indica* cladode cannot survive at 70° C (Nobel, 2002).

The fruits of *O. ficus–indica* can be harvested from July to November in the Northern Hemisphere – Mediterranean Basin, California, and Mexico – and from January to April in the Southern Hemisphere, depending on the genotype and genotype × environment interaction. Natural or induced reflowering may extend the ripening period to January–February in the Northern Hemisphere and to September–October in the Southern Hemisphere. Almost continuous flowering has been reported in Salinas, California (Bunch, 1996), resulting in an extended fruit ripening period.

CAM CYCLE

Originally attributed to the Crassulaceae family, CAM represents a mechanism of concentration of CO_2 which has evolved in response to dryness in terrestrial environments and deficiency of inorganic carbon in water environments (Keeley, 1998).

CAM occurs in 16 000 species (6–7% of plant species), belonging to over 300 genera from around 40 families, ranging from the deciduous tropical forest to desert platyopuntias and columnar cacti. The vast majority of plants using CAM are angiosperms. Most of them are either epiphytes (e.g. orchids, bromeliads) or succulent xerophytes (e.g. cacti, cactoid *Euphorbias*); but CAM is also found in lithophytes, terrestrial bromeliads, the halophyte *Mesembryanthenum crystallynum*, one non–succulent terrestrial plant (*Dodonaea viscosa*) and one mangrove associate (*Sesuvium portulacastrum*).

Characteristics of CAM and succulence

- Separation of CO_2 uptake and decarboxylation – temporally or spatially.
- Reduction of transpiration due to night–time stomatal opening – and water storage organs contain 90–95% water compared with 40–70% of non–succulent wood.
- Reduced water loss – CAM plants lose 20–30% of the water lost by C_3 o C_4 plants for the same degree of stomatal opening during daytime CO_2 uptake.

- Low root: shoot ratios and fast root growth during wet conditions.
- Suberization of cortical cells, with the formation of root–soil gaps during soil drying.
- Internal recycle of water from parenchyma vs chlorenchyma – maintains turgor of the photosynthetic tissue over a wide range of water content.
- Supply of water and solutes to fruit through phloem (phloem osmotic pressure is relatively low: 0.94 MPa (2–3 times less than for most other vascular plants).

The CAM pathway can be summarized as follows (**Figure 1**):

- **Phase 1.** At night, CO_2 fixation occurs when stomata open and CO_2 diffuses into the mesophyll's intracellular spaces and then into the cytosol, where it is bound to phosphoenolpyruvate (PEP), a 3–C compound, through PEP carboxylase. The enzyme catalyzes the formation of oxaloacetate, which can be transformed into malate by NAD^+ malate dehydrogenase. To avoid inhibition, malate is actively transported from the cytosol to the vacuole, where it is converted into malic acid, leading to a noticeable increase in acidity. The vacuoles of the cells of the chlorenchyma occupy more than 90% of the cell volume because of nocturnal accumulation of organic acids.
- **Phase 2**. Early in the morning, the transition takes place from PEPc to Rubisco activity.
- **Phase 3**. During the day, plants close their guard cells, stomata are tightly closed and the pH increases. Malate diffuses out of the vacuole and is decarboxylated. CO_2 is released (rising from 0.2 to 2.5%) in the cytosol and fixed into the Calvin cycle in the chloroplasts by the ribulose–1,5–bisphosphate carboxylase/oxygenase (Rubisco) leading to the synthesis of starch or other glucans.
- **Phase 4.** In the late afternoon PEPc becomes active. Under very dry environmental conditions, this may be the only phase of the CAM cycle that takes place.

Measurements of gas exchange in *O. ficus–indica* began in the early 1980s, when Nobel and Hartsock (1983) measured CO_2 uptake on single cladodes. At optimal temperature and intercepted radiation, instantaneous values of net CO_2 uptake of 1–year cladodes may reach 18 μmol m^{-2} s^{-1}, with a total daily CO_2 uptake of 680 mmol m^{-2} (Nobel and Bobich, 2002). However, although individual–cladode net photosynthesis (Pn) determinations are useful for estimating gas exchange rate per unit area, they have limitations when used to scale up to whole canopy gas exchange, because there may be wide variability in carbon assimilation within the canopy, due to differences in cladode age (Samish

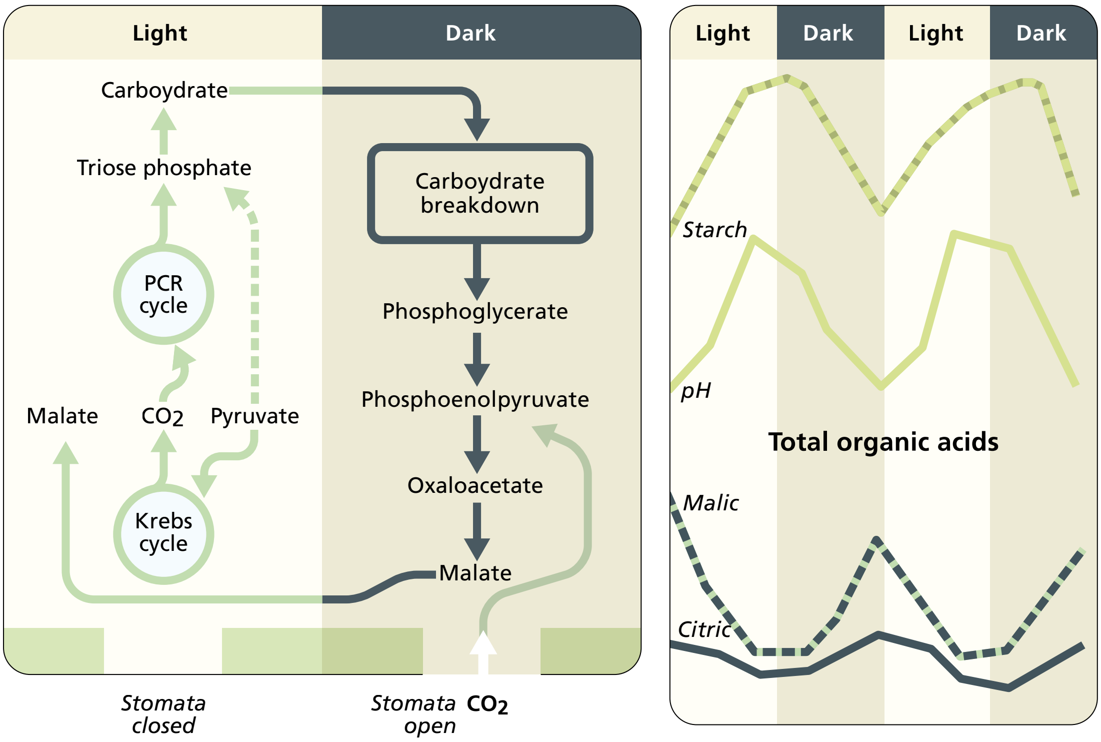


Figure 1
Crassulacean acid metabolism (CAM)

and Ellern, 1975), intercepted radiation (Nobel, 1988), crop load (Inglese *et al.*, 1994b), source–sink relationships (Pimienta Barrios *et al.*, 2005) and response to abiotic stress (Nobel and Bobich, 2002).

Few data are available on cladode net CO_2 uptake according to cladode age. Samish and Ellern (1975) noted that titratable acidity decreases linearly with increasing age, and 1–year cladodes have a level of acidity three times higher than 2–year cladodes, located in a basipetal position. Carbon translocation from 2–year cladodes to meet the photo–assimilate demand of 1–year fruiting cladodes has been hypothesized (Inglese *et al.*, 1994b; De la Barrera and Nobel, 2004), and carbon partitioning between mother and daughter cladodes changes depending on the cladode developmental stage and environmental conditions (shading, water availability) (Luo and Nobel, 1993; Pimienta Barrios *et al.*, 2005). CO2 uptake of 2–year cladodes throughout the season can be 40% lower than for 1–year cladodes (Liguori *et al.*, 2013a).

CAM–related statistics

- *O. ficus–indica* may assimilate 344–680 mmol m^{-2} day^{-1} of CO_2 (C = 35%).
- Maximum instantaneous values of CO_2 uptake by cladodes = 18 µmol m^{-2} s^{-1}.
- Fruit 2 weeks after bloom may reach a net CO_2 uptake of 42 mmol m^{-2} day^{-1}, i.e. 20% of the cladodes at the same place and time of the year.
- 10–30 stomata mm^{-2} in CAM plants vs 100–300 mm^{-2} in C_3 plants.
- Root: shoot ratio ranges from 0.12 (Nobel, 1988) to 0.09 (Inglese *et al.*, 2012) and 0.20 (Inglese *et al.*, 2012) on mature irrigated trees.
- Wax layer in the epidermis is 10–50 µm vs 0.2–2 µm in leaves of C_3 or C_4.
- The chlorenchyma of *O. ficus–indica* can reversibly lose 70% of its water content at full turgor and the parenchyma can lose 82%, both still being able to fully recover.
- After a 15–week drought period, the parenchyma loses 60% of its water content and the chlorenchyma 25% (Goldstein *et al.*, 1991).

Sunny better than cloudy

- Light and CO_2 uptake are shifted in time and nocturnal stomata opening depends on daily rather than instantaneous PPF values.
- Compensation point at PPF = 3 moles m^{-2} day^{-1}.
- Saturation point at PPF = 30 moles m^{-2} day^{-1}.
- At PPF = 22 moles m^{-2} day^{-1}, CO_2 uptake is at 90% of its maximal.

SOIL SUITABILITY IN THE CULTIVATION OF CACTUS PEAR

The species grows in all types of soil. It frequently adapts even to soils limited by continuous hard rock in the first 25 cm, which rest on materials with a calcium carbonate content > 40% or which contain < 10% by weight of fine soil (Nobel, 2002). Generally, *O. ficus–indica* is very versatile, but it is adverse to high salinity and to water-

TABLE 1 Functional characteristics and classes of soil capacity for *O. ficus–indica* cultivation

Functional characteristics		**Classes**			
		S1 *Most suitable*	**S2** *Suitable*	**S3** *Less suitable*	**N** *Not suitable*
Minimum temperature	°C	> 3	> 3	> –3; < 3	< –5
Medium temperature	°C	18–23	15–18	10–15	< 10
Annual rainfall	mm	> 400	> 400	200–400	< 100
Texture		sandy to mixed		clay–silt	clay–silt
Skeleton		indifferent	indifferent	indifferent	abundant
Depth		indifferent	indifferent	indifferent	indifferent
Carbonates		indifferent	indifferent	indifferent	indifferent
Reaction	pH_{KCl}	5–8	5–8	5–8	< 5; > 8
Organic matter	%	< 0.5	< 0.5	> 0.5	> 0.5
Ca available		elevated	elevated	mean	insufficient
K available		elevated	elevated	mean	insufficient
EC_e[a]	dS m^{-1}	< 2	2–4	4–7	> 7
Subsuperficial groundwater		absent	absent	absent	present

[a] EC_e = electrical conductivity of the saturate extract of the soil

logging, since the root system is very sensitive to anoxia (**Table 1**). For commercial production of the species, the salt concentration threshold of the soil solution is 50 mM NaCl (Nobel, 2002). A concentration of 30 mol m^{-3} (1.76 ppt NaCl) reduces growth by 40%, compared with the non–saline control, while a concentration of 100 mol m^{-3} (5.85 ppt NaCl) reduces growth by 93% (Gersani *et al.*, 1993). It tolerates well high air capacities (high textural or structural macroporosity) and a modest or meagre organic content. With regard to the edaphic requirements, ample availability of calcium and potassium is advantageous for a good crop.

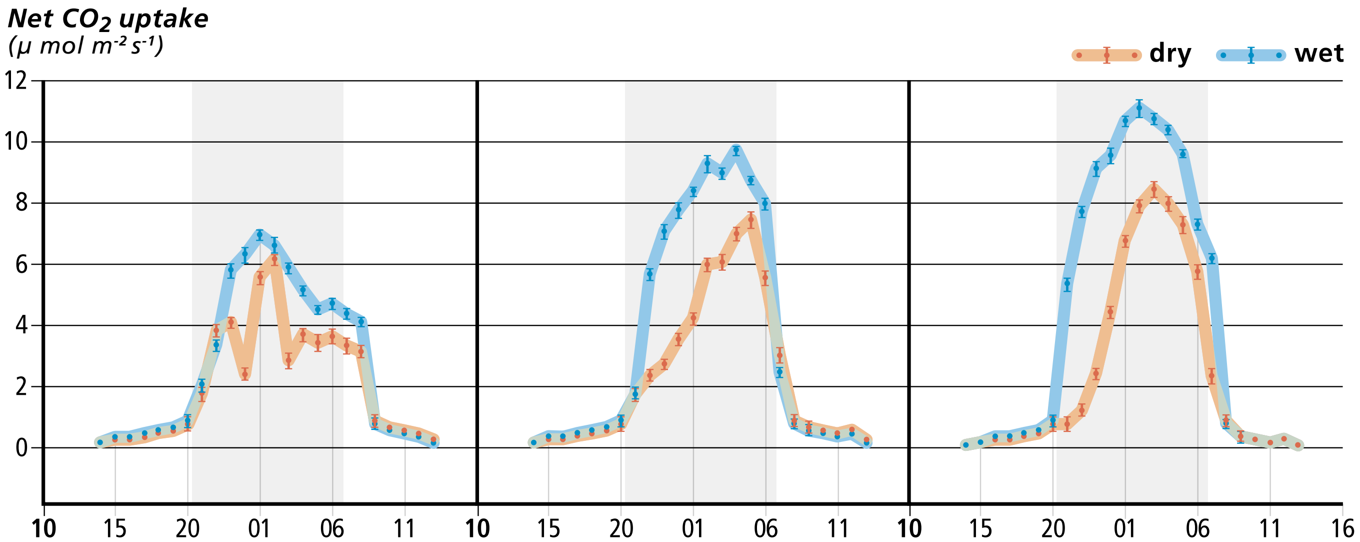
CO_2 UPTAKE AND WATER AVAILABILITY

O. ficus–indica water–use efficiency (WUE) reaches values of approximately 3.3–4.0 g dry matter (DM) kg^{-1} water (De Kock, 1980; Le Houérou, 2002). In young cladodes, water initially moves through the phloem, while xylematic water uptake starts about 1 month after their appearance (Wang *et al.*, 1997). Sink–to–source transition is also accompanied by an inversion of water potential difference between young and mother cladodes. Specifically, water potential is initially higher in the very young than in the mother cladodes, and it becomes lower in the young cladodes after 4 weeks of growth (Luo and Nobel, 1993; Wang *et al.*, 1997). Cladode succulence acts as a buffer to maintain turgor in the photosynthetic tissue (chlorenchyma), making it possible for the cladode to continue photosynthesizing during dry periods.

Long drought periods have several physiological effects on cactus pear. Under optimal conditions (25/15° C day/night) and light saturation, *O. ficus–indica* may assimilate 3.44 g m^{-2} day^{-1} CO_2; Nobel and Hartsock (1984) showed that 3 weeks of drought are required to halve single cladode net CO_2 uptake over 24–hour periods; after 50 days of drought, net CO_2 uptake of cladodes is around zero (Acevedo *et al.*, 1983). Moreover, 3 months of drought decrease nocturnal acid accumulation by 73%, essentially abolish transpiration, and lead to a decrease in the fresh weight (FW) of the parenchyma equal to 61%, while the chlorenchyma lose only 27% of water (Acevedo *et al.*, 1983; Goldstein et al., 1991). Optimal temperatures for cladode nocturnal net CO_2 uptake are reduced if plants are under drought conditions (Nobel and Hartsock, 1984), especially when water deficit is prolonged (Nobel, 2001). After prolonged drought, relative water content, cladode (parenchyma) thickness and chlorophyll content of single cladodes decline sharply (Pimienta Barrios *et al.*, 2007). In conditions of water stress, the parenchyma is barely distinguishable from the surrounding chlorenchyma (Barcikowski and Nobel, 1984; Liguori et al., 2013a). The ability of the parenchyma tissue to store water and to transfer it to chlorenchyma provides, under conditions of water stress, an efficient "buffer" effect in response to different physiological needs (Nobel, 2002). Parenchyma and chlorenchyma osmotic pressure is little affected after 3 months of drought, whereas turgor pressure is reduced by 86% compared with well–watered conditions (Goldstein *et al.*, 1991).

Diel fluctuations in cladode thickness may also represent an early indicator of dehydration stress. Young cladodes show more pronounced diel thickness fluctuations compared with older cladodes, and therefore serve as a suitable model for assessing plant responses to environmental factors. Under well–watered conditions, diel fluctuations of cladode thickness are directly related to temperature variations, but not under severe drought stress (Scalisi *et al.*, 2015). In addition, cladode growth is extremely responsive to rehydration after long periods of drought, suggesting that a regulated reduction of irrigation would not significantly affect plant biomass.

Surprisingly, measurements integrating whole–tree gas exchange prove that *O. ficus–indica* trees continue their photosynthetic activity 60 days after irrigation is stopped and when soil water content is < 5% (**Figure 2**). At this stage, current–year and 1–year cladodes of non–irrigated trees have become flaccid, but daily net CO_2 uptake of the whole tree still maintains the same rate as at the beginning of the experiment while, during the season, well–watered trees double their net CO_2 uptake. Eventually, the whole–tree daily CO_2 uptake, which integrates cladodes of different age and photosynthetic capacity, is well below values measured for individual cladodes under similar conditions (wet or dry) (Nobel and Bobich, 2002; Pimienta Barrios *et al.*, 2005) – indication of the different contribution of single cladodes to whole–tree photosynthesis. The capacity of *O. ficus–indica* trees to substantially maintain their photosynthetic activity, even when they have lost most of the water from the parenchyma, is probably related to water movement (from mother to daughter cladodes) and intertissue water transfer (from parenchyma to chlorenchyma) resulting in reduced water loss of the photosynthetic tissue (Barcikowski and Nobel, 1984; Nobel, 2006). According to Goldstein et al. (1991) and Nerd and Nobel (1991), following a 15–week drought period, cladode water content decreases by around 60% and the water–storage parenchyma loses a greater fraction of water (65%) than the chlorenchyma (27%), which most likely helps maintain nocturnal acid accumulation in the tissue of the chlorenchyma. The chlorenchyma of *O. ficus–indica* can reversibly lose 70% of its water content at full turgor, while the water storage parenchyma can lose 82% (Andrade *et al.*, 2009); indeed, when rainfall occurs following a long dry period, re–watered cladodes show complete recovery in terms of fresh and dry weight and gas exchange rate pattern (Pimienta Barrios *et*



A
Daily PPF: **27.3 mol m^{-2} d^{-1}**
Day/Night temp: **26°/19°C**
Soil water content:
- irrigated: **18%;**
- non irrigated: **6%**

B
Daily PPF: **35.1 mol m^{-2} d^{-1}**
Day/Night temp: **28°/20°C**
Soil water content:
- irrigated: **18%;**
- non irrigated: **5%**

C
Daily PPF: **39.2 mol m^{-2} d^{-1}**
Day/Night temp: **28°/23°C**
Soil water content:
- irrigated: **19%;**
- non irrigated: **2%**

Measurements made with open chambers covering three single trees for each treatment (dry and wet) (a: June, b: July, c: August). Dotted bar coincides with the night–time period.

Figure 2
Daily net CO_2 uptake in irrigated and non–irrigated O. ficus–indica potted trees

al., 2005). The accumulated C, in the absence of fruit, is partitioned in well–watered cladodes to the parenchyma of 1– and 2–year cladodes and the current–year growth. On the other hand, dry matter accumulated during the drought period is likely to be destined to older stems and the root system, which are responsible for plant recovery following a long period of drought (Nobel, 1988). The roots of 18–month non–irrigated *O. ficus–indica* trees incorporate 23% more carbon from the basal cladodes than do well–watered ones (Luo and Nobel, 1993). Shifting the carbon allocation pattern in favour of the roots contributes to drought resistance in perennials and woody trees and facilitates their recovery after long periods of water stress (Da Costa and Huang, 2009; Faust, 1989). Moreover, the soluble sugar content usually decreases with drought, associated with an equivalent increase in polysaccharides, presumably starch, in the water–storage parenchyma, but not in the chlorenchyma (Nerd and Nobel, 1991).

In areas where no rains (< 30–50 mm) occur during the fruit development period or where annual rainfall is < 300 mm (Gugliuzza *et al.*, 2002a), *O. ficus–indica* requires supplementary irrigation to obtain adequate yields and good fruit quality (> 120 g FW) (Barbera, 1984; Gugliuzza *et al.*, 2002a; Van der Merwe *et al.*, 1997). Fruit size is reduced by water deficit long before the tree shows any symptoms of water stress (Gugliuzza *et al.*, 2002a). Indeed, the plant is able to recycle internal water and supply water to the fruit through the phloem (Nobel, 2002). Nerd *et al.* (1989) report that in the Negev Desert, where the annual rainfall is < 300 mm, winter irrigation regulates plant fertility and spring burst timing in spring. However, irrigation alone cannot counteract the effect of very high temperatures, which affect carbon exchange rate more than transpiration and always result in reduced fruit growth and advanced maturity, even under irrigation. Consoli *et al.* (2013) – in areas with no summer rains (June–September) and with annual rainfall of 500 mm – measured Kc values of 0.45–0.50.

RESPONSE TO TEMPERATURE

Dry but not too hot: this could be the motto for *O. ficus–indica*. CAM metabolism enables the plant to reach maximum photosynthetic productivity with daylight temperatures of 25° C and nocturnal temperatures of 15° C. Higher day or lower night temperatures produce a sharp decrease in carbon assimilation, leading to poor plant growth, reduced production (Nobel, 2002) and eventually low crop value.

Temperatures > 30° C cause reductions of up to 70% in photosynthetic activity; they affect fruit shape when occurring during the initial stages of fruit growth; and they shorten the third stage of fruit growth, when most of the growth of the edible flesh occurs, leading to advanced and early ripening, and reduced fruit size, firmness and sugar content. High temperatures during fruit development enhance fruit sensitivity to low temperatures (< 8° C) during post–harvest storage (Inglese *et al.*, 2002b). On the other hand, daily temperatures < 15° C slow down fruit growth, delay fruit ripening time and result in thicker fruit peel and lower soluble solid content and poor peel colour (Inglese, 1995; Liguori *et al.*, 2006; Nerd *et al.*, 1991a). Temperatures < 0° C, even for 4 hours, produce irreversible damage to the cladode tissue and the fruit. High temperatures are a major constraint for the production of high quality fruits in areas with a hot and dry summer. As a matter of fact, the optimal daily temperature for CO_2 uptake decreases from 17° C under wet conditions to 14° C after 7 weeks of drought (Nobel, 2002). The number of days required to reach commercial harvest maturity changes with the time of bloom and with prevailing temperatures during the fruit development period, but the thermal time measured in terms of growing degree hours (GDH) from bloom to harvest does not change (40–43 × 103) (Inglese *et al.*, 1999; Liguori *et al.*, 2006). Nerd and Mizrahi (1995a) found that detached cladodes that experienced low winter temperatures produce the most fruit buds the following spring. Similar results were reported by Gutterman (1995), who examined 18 light/temperature combinations of detached cladodes and found that detached cladodes produce significantly more fruit with 8 hours of light grown outside in cool temperatures than with 8 hours of light in a heated greenhouse. Nobel and Castañeda (1998) indicate an increase in fruit production on detached cladodes held at 15/5° C compared with cladodes left at 25/15° C day/night temperature.

Potgieter and Smith (2006) report a strong environmental influence on fruit yield, with the highest fruit yield obtained in areas of South Africa with warm summers and cool winters. They also report a strong genotype × environment interaction, indicating variation in the plasticity of cultivars in terms of temperature requirement for optimal fruit production. However, cactus pear produce fruits in the Valley of Catamarca, northwest Argentina, and in the Canary Islands, where no more than 100 chilling units accumulate in winter; it is also able to reflower several times in the same season – naturally, in the case of Chile or California, artificially induced, in the case of Italy and Israel (Inglese, 1995; Liguori *et al.*, 2006). These out–of–season blooms appear to have no relation with endodormancy; the rest period could result from ecodormancy rather than true rest or endodormancy. In *O. ficus–indica*, another flush of fruits may take away the first spring flush of flowers and cladodes (Inglese *et al.*, 2002b). Temperature affects plant reflowering aptitude. In fact, plant response to the spring flush removal (SFR) is greatly affected by the prevailing temperatures at removal time (Barbera *et al.*, 1991; Brutsch and Scott, 1991; Nieddu and Spano, 1992). High temperatures (> 30/20° C day/night) produce more new cladodes than fruits; lower temperature (< 20/15° C day/night), on the other hand, may not result in rebudding.

RESPONSE TO LIGHT

Fruits of *O. ficus–indica* do not generally grow on shaded cladodes (García de Cortázar and Nobel, 1992), probably because in such conditions cladodes do not accumulate sufficient dry weight to support reproductive development. Net assimilation rate of cladodes of *O. ficus–indica* becomes negative for a total daily photosynthetically active radiation (PAR) of 5 mol m^{-2} day^{-1} and reaches 90% of the maximum at 20 mol m^{-2} day^{-1} (Nobel, 1988). Shading affects flower evocation, as was clearly demonstrated by Cicala *et al.* (1997) and Deidda *et al.* (1992). At least 80% of flowering seems to be inhibited if light is withheld the last 2 months before bloom – indication that flower evocation occurs close to bud sprouting. Sufficient light intensity during the winter rest period is therefore essential for a regular bloom. Shading applied within 5 days after the removal of the spring flush also inhibits the return bloom (Barbera *et al.*, 1993a).

Shading also affects fruit quality, depending on the extent of shading and sucrose exchange within the tree. Shading completely the main source of photo–assimilate for the fruit for 45–75 days after bloom has no influence on fruit weight, quality or ripening time. On the other hand, a short period (15 days) of imposed shade during earlier stages of fruit growth significantly affects fruit weight, but not the total soluble solids content or fruit firmness and ripening time. The fruits do not fully recover to maximum growth, even when the fruiting cladode is shaded for a short period before bloom. As with other fruit trees, such as peach and apple, fruit size at harvest seems to be related to the fruit growth rate attained in the early stages of fruit development. At this stage, photo–assimilate supply from the fruiting cladode becomes crucial to support fruit growth, probably because of the competitive demand of different and actively growing vegetative and reproductive sinks (Inglese *et al.*, 1999).

This is in line with the fact that thinning is most effective in increasing fruit size when applied no later than 3 weeks after bloom (Inglese *et al.*, 1995a). Since net assimilation of heavy shaded cladodes is negligible, fruit growth in cladodes shaded for long periods during the fruit development period must depend on extensive photosynthate translocation from non–shaded branches (Inglese *et al.*, 1994b; Luo and Nobel, 1993). This mobilization of storage carbohydrates makes fruit growth only partially dependent on reduced photosynthetic photon flux density (PPFD) – wavelengths of 400–700 nm – at fruit canopy location. Fruit ripening in shaded cladodes occurs later than in sunlit ones. The pattern of PPFD distribution within the canopy enhances the variability in fruit quality in terms of size, and fruits located in the lower part of the canopy are smaller than those at the top. Fruit ripening varies within the plant and the fruiting cladode, mainly because of a different time course of flower bud formation, development and flowering (Barbera and Inglese, 1993). The pattern of PPFD distribution within the canopy enhances this variability, since shade delays fruit ripening according to the length of the shading period.

In conclusion, the wide within–tree variability of fruit quality and ripening time that occurs in cactus pear (Barbera and Inglese, 1993) can be partially explained in terms of PPFD distribution within the canopy.

REPRODUCTIVE BIOLOGY

Fruit production by *O. ficus–indica* is extremely variable. Yields of 20–30 tonnes ha^{-1} are reported in Israel and Italy (Barbera and Inglese, 1993; Nerd and Mizrahi, 1993) and 10–30 tonnes ha^{-1} in South Africa (Wessels, 1988a; Brutsch and Zimmerman, 1993). The wide variability in yield depends on orchard design (plant spacing), cultural practices, environmental conditions and cultivar fertility. Plants begin to yield 2–3 years after planting; they reach their maximum potential 6–8 years after planting and remain productive for 25–30 years and even longer, depending on pruning and overall orchard management.

Cladode fertility

For a mature plant, most (80–90%) 1–year cladodes bear fruits accounting for 90% of the annual yield. However, they show a wide fertility range, depending on plant age, environmental conditions and their state of growth. The average number of flowers produced by a single, 1–year cladode is 6–9, with peaks of 30–35. Two-year cladodes are generally responsible for vegetative renewal and a small proportion (10–30%) produce fruits, but with reduced fertility compared with 1–year cladodes. The number of fruiting cladodes occurring on a plant every year depends on plant spacing, and ranges from 100–120 for 350–400 plants ha^{-1} to 20–30 for 1 000–1 200 plants ha^{-1}. A mature cactus pear tree *O. ficus–indica* (L.) Mill. produces new fruits and cladodes at a ratio of 4 : 1 every year (Barbera and Inglese, 1993). Cladode fertility is related to the amount of dry weight accumulated per unit surface area (García de Cortázar and Nobel, 1992). Cladodes become productive when their estimated dry weight (EDW) exceeds the minimum dry weight for a particular surface area by at least 33 g. Values of EDW become positive after 60–70 days of cladode development and in November they reach 13.1 ± 2.4 g and 10.6 ± 1.2 g, respectively, for spring cladodes and cladodes from the second flush of the previous season.

Flower buds emerge during the spring (Pimienta Barrios, 1990; Gutterman, 1995; Nerd and Mizrahi, 1995a). Photoperiod and/or low winter temperature may be the environmental signal for such bud initiation. In addition, nutrients can also affect bud initiation, since exposing plants to nitrogen fertilization (using ammonium nitrate) can increase the number of buds per plant (Nerd *et al.*, 1993a). Most of the flowers occur on 1–year terminal cladodes, and new cladodes usually develop on 2–year or even older cladodes (Inglese *et al.*, 1994a). Vegetative and reproductive buds appear contemporarily in spring or early summer when the spring flush is removed to induce reflowering (Barbera *et al.*, 1991). The flowers generally develop from the areolae disposed along the crown of the cladode, but production of flowers from the areolae on the planar surface exposed to the sun is not infrequent. A cladode can produce 35–40 flowers; during abundant flowering in conditions of high potential evapotranspiration, each can lose ≤ 3 g of water day^{-1}, equivalent to 15% of its weight at the moment of the anthesis (De la Barrera and Nobel, 2004).

Floral biology

Flower buds develop quickly, starting with a meristem covered by polycellular trichomes above the petiolar scar (Nieddu and Spano, 1992). When the flower bud reaches a length of 0.5 cm (Wessels and Swart, 1990), the gyneaceum and the androecium become visible inside. The ovary, which is inferior and unilocular, is multicarpellate (6–12 carpels, usually 8 growing together at the base and separating at the stigmatic region) (Nieddu and Spano, 1992). The stamens differentiate two techae with two pollen sacs each; another dehiscence occurs before anthesis (Nieddu and Spano, 1992). Pollen is presented in a spherical, apolar radio–symmetrical form with a reticulated and poly–panto–porated surface, with a circular polygonal perimeter (6–8 sides) (El Behi *et al.*, 2015).

Aguilar and Chavez (1995) reported that the hormone gibberellic acid (GA) promotes floral bud development and indole–butyric acid (IBA) stimulates vegetative sprouting. In subtropical regions, *Opuntia* floral buds start when the mean monthly temperature exceeds 16°C – in March or April in the Northern Hemisphere and in September or October in the Southern Hemisphere (Nerd and Mizrahi, 1995). The floral bud production period fluctuates between 3 and 5 weeks (Reyes Agüero *et al.*, 2006). Floral development from bud to anthesis requires 21–47 days, but can last as long as 75 days (Wessels and Swart, 1990). Generally, in the Northern Hemisphere, anthesis takes place between May and July, and in the Southern Hemisphere between February and August (Reyes Agüero *et al.*, 2006). Flowers are mostly hermaphrodite. Autogamic and xenogamic pollination both occur in *O. ficus–indica* (Nerd and Mizrahi, 1995a). Different bee species visit *Opuntia* flowers during pollination.

Apomixis occurs frequently in *Opuntia* (Pimienta Barrios, 1990; Mondragón and Pimienta Barrios, 1995). Gil and Espinoza (1980) obtained normal–sized parthenocarpic fruits containing empty seeds from fertilized flowers treated by gibberellin and auxin in pre–anthesis, but for some clones of *Opuntia*, the occurrence of pollination is not necessary to obtain seedless cactus pear fruits. In fact, Weiss *et al.* (1993b) reported vegetative parthenocarpy in some *Opuntia ficus–indica* (L.) clones.

El Behi *et al.* (2015), in a study of a seedless cultivar 'Bianca' from Sicilian germplasm, hypothesized that its seedlessness could be based on a partial stenospermocarpy, as reported for grape and *Citrus* (Vardi *et al.*, 2008). *Opuntia* fruits are unilocular and polyspermic. In *O. ficus–indica*, the unripened green peel has stomatal and photosynthetic activity, contributing 8–10% to fruit growth (Inglese *et al.*, 1994b). Fruit areoles always have glochids and may have spines and bristles or hairs, which can persist from the flower stage (Bravo, 1978).

Seed growth and ripening occur 30–70 days after anthesis; seeds are small and ovoid or lens–shaped (Bravo, 1978). Italian *O. ficus–indica* cultivars have an average of 273 seeds per fruit, of which 146 are normal and 127 sterile (Barbera *et al.*, 1991); Israeli cultivars have an average of 268 normal seeds per fruit (140–430) (Nerd and Mizrahi, 1995a) and Mexican cultivars an average of 203 normal seeds per fruit (10–448) (Reyes Agüero *et al.*, 2006).

Fruit growth

Fruit growth follows a double sigmoid pattern in terms of fresh weight; there is a pronounced gain in dry weight for the peel during Stage I, for the seeds during Stage II and for the core during Stage III of the fruit development period (FDP) (Barbera *et al.*, 1992b; Nerd and Mizrahi, 1997). The growth of fruits and daughter cladodes implies a substantial translocation of stored carbohydrates from the basal cladodes (Luo and Nobel, 1993; Inglese *et al.*, 1994b). In fact, when more than five fruits develop on a 1–year fruiting cladode, an extensive import of assimilates occurs, particularly during Stage III of fruit growth (Inglese *et al.*, 1994b).

Inglese *et al.* (1994b) and Luo and Nobel (1993) investigated the source–sink relationship on mature fruiting plants and found a massive carbon flux of assimilates among cladodes of different ages. Young developing cladodes apparently compete with fruits – as indicated by their higher absolute growth rate (AGR). However, they become a source of carbohydrates at an early stage of their development (Luo and Nobel, 1993), a time which coincides with the development of flowers or the earliest stage of FDP. Relative sink strength changes in line with the developmental stages of the seasonal growth of fruit and cladodes (Inglese *et al.*, 1999). Fruits become the major sink during Stage III – as indicated by the sharp reduction in cladode AGR at that stage.

Competition between fruit and cladode growth, as well as the reduction in the number of new cladodes following SFR can be sources of plant alternate bearing behaviour that also changes with genotype (Inglese *et al.*, 2002b). Alternate bearing of cactus pear depends on the reduction in the fertile cladodes following scarce vegetative activity the previous year. The number of flowers per fertile cladode becomes increasingly stable each year; it depends on the cladode age and is highest in 1–year cladodes. Fruit size varies between trees and depends on factors such as plant architecture and crop yield per plant and per cladode.

Out–of–season crop

The most powerful tool for achieving a longer fruit marketing season is the cladodes' ability to reflower several times within the same season, either naturally or after applying inductive practices (Nerd and Mizrahi, 1997). Double flowering occurs naturally in the Salinas area in California, where fruits are picked from September to March (Inglese, 1995), and in the central region in Chile, where the fruit harvest lasts from February to April and from July to September (Sudzuki Hills *et al.*, 1993). In Italy, a second flowering is obtained as a result of the complete removal of the spring flush of flowers and cladodes. SFR takes place when the main bloom occurs, between the end of May and the last week in June in the Northern Hemisphere, and in October in the Southern Hemisphere (Inglese, 1995). New flower buds develop on the fertile cladodes of the natural flush, and the reflowering index – defined by the ratio of second versus first flush flowers – is highest for cladodes with a natural fertility of 5–10 flowers, sharply decreasing with each additional flower that develops during the first flower flush. Removal time affects cladode reflowering rate (Barbera *et al.*, 1991; Brutsch and Scott, 1991). For instance, removing flowers at pre–bloom stage results in the highest reflowering rate, while removing the spring flush after petal shedding reduces reflowering by up to 50–70% (Barbera *et al.*, 1991; Inglese *et al.*, 1998). This decrease in reflowering that occurs when flowers are removed at full bloom or after petal shedding is related to an inhibitory effect on flower bud initiation (Barbera *et al.*, 1993a) of GA_3 diffused from the flowers to the mother cladode (Inglese *et al.*, 1998). Indeed, Barbera *et al.* (1993a) demonstrated that GA_3 applied within 6 days after SFR totally inhibits reflowering – indication that the flower bud, induced the preceding spring, is still reversible at that stage. Current–season developing cladodes also inhibit reflowering if they are not fully removed (Inglese *et al.*, 1994a). Pre–blooming fruits have the shortest fruit development period, and ripen 15–20 days earlier than full–bloom and 30–40 days earlier than post–bloom fruits.

The reflowering rate depends also on the prevailing environmental conditions at removal time (mainly soil water content and air temperature). Indeed, the extent of reflowering greatly differs from year to year and depends on orchard location (Barbera *et al.*, 1991; Brutsch and Scott, 1991; Nieddu and Spano, 1992). High temperatures during bud initiation induce vegetative rather than reproductive activity, resulting in a lower reflowering rate. Liguori *et al.* (2006) developed a strategy based on the potential of the plant to reflower even after a double spring flush removal: the first in early June with the removal of the spring flush and the second in late June with the removal of the second, induced flush. The rate of this second reflowering (third flush) is very uneven, ranging from 25 to 40%. The plant blooms during the first 10 days of August and the fruit ripens from December to March depending on covering time and environmental conditions. The length of the fruit development period increases from 100–120 days to 160–190 days for the out–of–season winter crop, depending on a longer third stage of fruit growth which occurs when temperatures are under the optimal values for fruit growth (**Figure 3**). However, winter temperatures inhibit fruit growth and ripening; it is therefore necessary to cover the plants with PVC tunnels to create appropriate conditions for regular fruit development. Winter fruit production occurs in the field in Israel (Nerd *et al.*, 1993a). In this case, the second crop follows the main one and occurs on current–year cladodes developed since May. After the harvest of the first crop, a second bloom is induced through extensive N fertilization and irrigation. The second bloom occurs in September–October and fruit develop from January to March. Fruit have a regular size but a reduced percentage of flesh (50–55%).

BIOMASS PRODUCTIVITY

High planting densities lead to an extremely high accumulation of dry matter in the vegetative growth, but deeply affect the allocation of resources to the fruit (García de Cortázar and Nobel, 1992). *O. ficus–indica* can have an annual dry matter productivity that exceeds that of nearly all

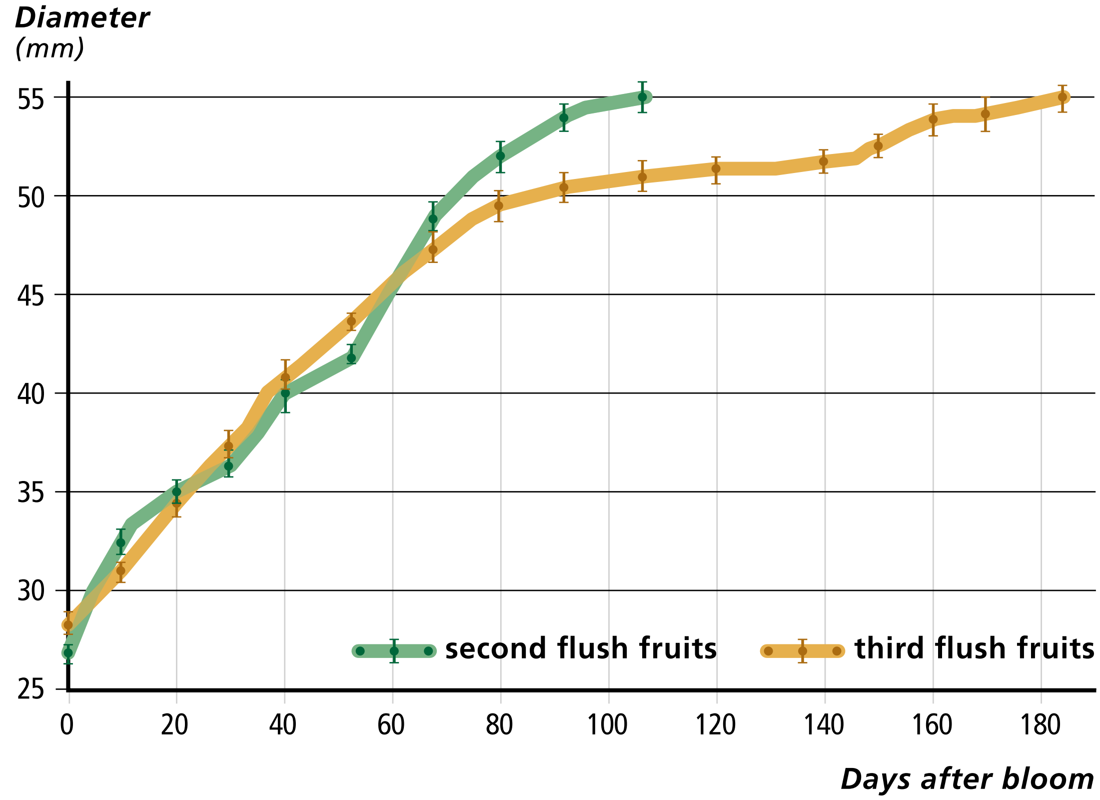


Figure 3
Cumulative growth curve for fruits of O. ficus–indica cv. 'Gialla' coming from the 2nd and 3rd flush of bloom

cultivated C_3 and C_4 species. For instance, a productivity of 47 tonnes dry weight (DW) ha^{-1} year^{-1} of cladodes (99%) and fruit (1%) has been predicted for high density plantings (24 plants m^{-2}), while a productivity of nearly 15 tonnes ha^{-1} was measured for lower spacings (0.24 plants m^{-2}), resulting in a lower vegetative vs reproductive growth, with early fruit cropping and an alternate bearing behaviour (García de Cortázar and Nobel, 1992). Acevedo *et al.* (1983) measured a cladode dry mass production of 1 kg m^{-2} ground area and 0.3 kg fruit m^{-2} year^{-1}. Recently Pinos Rodríguez *et al.* (2010) reported a dry mass production of 1.39 kg m^{-2} for *O. ficus–indica* grown to produce fresh biomass for cattle use. Inglese *et al.* (2012) – in commercial plantations for fruit production with a much lower plant density (333 trees ha^{-1}) – found very similar values to those found by Nobel (1988), but for a much lower total biomass and a commercial fruit weight (1.2 kg m^{-2} ground area, considering the first and second flush of fruits and cladodes). By the end of the first season of growth, current–year cladodes almost cover their final surface area, but they only reach 65% of the dry weight of 1–year cladodes. During the second year of growth, they show a marginal increase in terms of surface area, but a significant accumulation of dry weight (+30%). Thereafter, cladodes develop only marginally in terms of surface area, but continue to accumulate dry weight. The high specific dry weight of scaffold cladodes is twice that of 1–year cladodes. The absolute growth rate for cladodes and fruits can reach, respectively, 0.12 day^{-1} and 0.16 day^{-1}.

The fruit component (harvest index [HI]) has not been systematically studied in *O. ficus–indica*. García de Cortázar and Nobel (1992) showed that yearly variations in cladode vs fruit dry matter allocation also depend on planting densities. An increase in dry matter allocated to the fruit was accompanied by a reduction in cladode count and dry weight accumulation.

Light interception, CO_2 uptake and plant productivity depend on canopy architecture and stem area index (SAI) per ground area (taking account of both sides of the cladode for SAI) – SAI is the equivalent of the leaf area index (LAI) (Nobel, 1988). Despite their importance, SAI values for *O. ficus–indica* orchards have been poorly investigated. SAI values of 6.5–8.5 have been measured, considering all the cladodes in the canopy and the surface area covered by the tree canopy. Maximum productivity (2 kg DM m^{-2} ground area year^{-1}) has been predicted for SAI = 4–6; while for SAI < 3, with 20 000 and 6 000 plants ha^{-1}, the total net CO_2 uptake is about linear with SAI (Nobel, 1988). These calculations include all cladodes; they do not take into account that the single cladode contribution to CO_2 uptake changes with cladode age (Nobel, 1988), nor that optimal SAI definition must include fruit quality, which also depends on PAR interception by mother cladodes (Inglese *et al.*, 1999). For instance, the photosynthetically active canopy components of a commercial orchard for fruit production with 420 trees ha^{-1} (Liguori *et al.*, 2013a) account for 60% of canopy surface, with SAI–orchard = 2.6 and SAI–tree = 4.0 – i.e. values well below those reported by Nobel (1988). In these conditions, the HI was about 29%, considering both first and second flush, or 26% if only the reproductive and vegetative growth of the second flush are considered. Solar radiation (40%) is intercepted by the less photosynthetically efficient cladodes and by lignified scaffold. Carbon stock among canopy and root component shows that a mature plant can have 9–10 fruits m^{-2} of cladode surface area (current–year to 2–year cladodes), which means 1.1–1.4 kg fruits m^{-2}. A commercial orchard for fruit production can accumulate 7.5 tonnes DM ha^{-1} year^{-1}, which means 3.4 tonnes C ha^{-1} stored in the canopy components (including fruits). These values are similar to those reported for deciduous orchards (e.g. peach) and for evergreens (e.g. orange) (Tagliavini *et al.*, 2008).

POTENTIAL RESPONSES TO CLIMATE CHANGE

Agricultural, vehicular and industrial activities that rely on fossil fuels release greenhouse gases, mainly CO_2. Indeed, in just 150 years, the atmospheric concentration of carbon dioxide has rapidly increased from the pre–industrial level of 280 ppm to the current level of 400 ppm (IPCC, 2014). In turn, increased CO_2 leads to higher photosynthetic rates as a result of a steeper concentration gradient between the atmosphere and the sites of carboxylation in plant tissues. Also, given that higher partial pressures lead to a decreased carbon "demand" by leaves, a reduction in stomatal conductance is observed for plants exposed to elevated CO_2 (Smith *et al.*, 2009). Despite having an inherent mechanism for concentrating CO_2, which could make CAM plants insensitive to higher atmospheric concentrations of this gas, an actual fertilization effect has been observed. This is the case of *O. ficus–indica* exposed to doubled CO_2, either in controlled environmental chambers or in rooted plants kept in open–top chambers. In particular, plants accumulate 20–40% more dry mass under doubled CO_2 than under 350 ppm (Nobel and García de Cortázar, 1991; Nobel and Israel, 1994). In addition, plant development is enhanced by carbon fertilization. For instance, a doubling of the production of second order daughter cladodes is observed after 3 months of exposing mature cladodes to elevated CO_2 (Nobel and Israel, 1994). In addition, root elongation can increase up to 25% under elevated CO2 given optimal air temperatures averaging 30°C (Drennan and Nobel, 1998). These fertilization effects may be driven by anatomical

TABLE 2 RCPs considered in global climate change models

RCP	Equivalent previous IPCC scenario	Greenhouse gas emissions	Year 2100 (CO$_2$–eq.) (ppm)	Radiative forcing relative to 1750 (W m^{-2})	Temperature increase (°C)
RCP4.5	B1	Stringent mitigation	430–480	2.6	< 1.5
RCP6.0	B2	Intermediate	580–720	4.6	2–3
RCP2.6	n/a	Intermediate	720–1 000	6.0	3–4
RCP8.5	A2/A1FI	Very large	> 1 000	8.5	> 4

Source: IPCC (2014).

responses of *O. ficus–indica*, such as a chlorenchyma that is 31% thicker under doubled CO$_2$ than under ambient concentrations, despite a decrease in stomatal frequency of 20% and a 30% thickening of the cuticle that has more epicuticular wax (North *et al.*, 1995). This fertilization effect resulting from exposure to elevated CO$_2$ has also been observed for other cacti (e.g. the hemiepiphytic Hylocereus undatus). For this tropical crop, cultivated in over 20 countries, the photosynthetic rates increase by 34% under doubled CO$_2$ (Raveh *et al.*, 1995; Nobel and De la Barrera, 2004). However, high CO$_2$ concentrations can also lead to lower respiration rates, decreased maximum activity of cytochrome c oxidase, and lower mitochondrial numbers for *O. ficus–indica* individuals (Gomez Casanovas *et al.*, 2007). Thus, while the increasing concentrations of CO$_2$ can enhance plant productivity, this might be true up to certain levels when plant metabolism will be reduced.

In addition to the direct effects on plant physiology and anatomy, elevated greenhouse gas concentrations are likely to impact plant productivity by substantially changing the planet's climate. In this respect, four greenhouse gas emission scenarios are being considered by the Intergovernmental Panel on Climate Change (ICPP) that could lead to different climate outcomes during this century (**Table 2**). These so–called **Representative Concentration Pathways** (**RCPs**) consider scenarios leading to a given increase in radiative forcing relative to that from 1750 and differ from the previous emission scenarios (A1, B1, A2, B2) in that they explicitly consider international environmental and development policies (IPCC, 2014).

- RCP2.6 is the most optimistic scenario. With no previous equivalent considered by the ICPP, RCP2.6 relies on stringent mitigation policies that would result in a net removal of greenhouse gases from the atmosphere and could lead to a global temperature of ≤ 2 °C higher than the pre–industrial climate.
- RCP4.5 and RCP6.0 are intermediate and plausible emissions scenarios. Their previous equivalent IPCC scenarios are those of the B family, which consider the adoption of green technology with a consequent reduction in reliance on fossil fuels, while differing in the degree of international cooperation.
- RCP8.5 is the most extreme scenario, which assumes that despite reduction targets and international agreements, the world will still heavily rely on fossil fuels.

The extent of environmental change occurring during this century depends on compliance with the targets of reduction of greenhouse gas emissions agreed to by most countries in 2015, including the two main contributors (the United States of America and China).

This imminent climate change is likely to be detrimental to global agricultural productivity (Monterroso Rivas *et al.*, 2011; Lobell and Gourdji, 2012; IPCC, 2014; Ovalle Rivera *et al.*, 2015). However, for certain cultivated CAM plants, the new environmental conditions may result in an increase in the area suitable for their cultivation (García Moya et al., 2010; Lobell and Goudji, 2012). Naturally, a major adaptation of CAM plants to a warmer and often drier environment is the fact that gas exchange occurs at night when air temperature is lower. In addition, CAM plant productivity is predominantly driven by night–time air temperature (when gas exchange occurs), rather than by the diurnal temperature (when the stomata are closed) (Andrade et al., 2007). In most cases, the average nocturnal temperature leading to maximum CO$_2$ uptake by CAM plants ranges from 10 to 20°C (Nobel, 1988). Thus, as long as the nocturnal air temperature is appropriate, substantial CO$_2$ uptake can occur even under increasing diurnal temperatures. Indeed, given the expected increase in potential productivity of various species of Agave in the tropical and subtropical regions of the Western Hemisphere, their cultivation has been proposed for carbon sequestration, mitigation of soil erosion, and the production of biomass for use in biofuels (García Moya *et al.*, 2010).

Higher air temperatures could also be similarly advantageous for cultivated cacti. For instance, while the mean nocturnal air temperature resulting in maximum gas exchange by *O. ficus–indica* is about 12°C, this plant is able to adequately perform under a wide range of conditions; indeed, at least 80% of the maximum CO$_2$ uptake can be achieved between 6 and 20°C (**Figure 4**; Nobel, 1988; Nobel et al., 2002). The case of Hylocereus undatus is slightly different. For this tropical crop, a

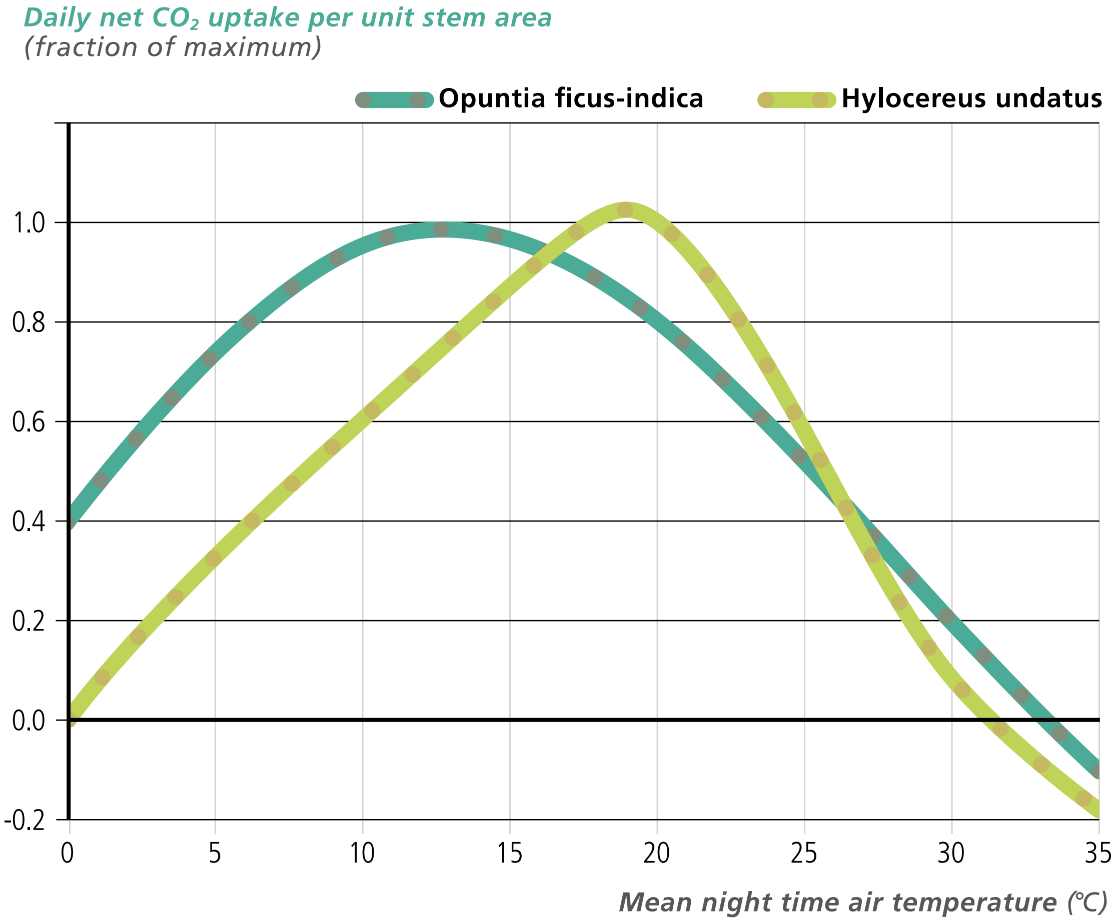


Figure 4
Responses of total daily net CO_2 uptake by the cactus crops Opuntia ficus–indica and Hylocereus undatus to mean night–time air temperatures
Used with permission of the California Botanical Society from Nobel et al. (2002).

higher air temperature will lead to more potential area for cultivation, as the optimum temperature for CO_2 uptake is approximately 20°C (**Figure 4**; Nobel *et al.*, 2002). However, for this plant, the range of nocturnal air temperatures leading to high gas exchange rates is rather narrow, especially compared with O. ficus–indica, as mean night–time air temperatures between 14 and 23°C are required to achieve at least 80% of maximum CO_2 uptake (**Figure 4**; Nobel *et al.*, 2002).

Mean changes in air temperature will determine the average productivity of crops, including cactus crops such as *O. ficus–indica* and *H. undatus*. However, the rate of warming and the severity of extreme weather events – i.e. infrequent heat spells, frosts, droughts or unusually heavy rains, which are likely to become more frequent and severe owing to climate change – will determine actual plant survival and limit crop cultivation (IPCC, 2014; Nobel, 1988). Whether a plant species will be able to fare increasingly frequent and severe episodes of high temperature depends on its temperature tolerance. For 18 species of cacti, the lethal high temperature is about 57° C (Nobel, 1988; Drennan, 2009). *O. ficus–indica* can usually survive exposure to temperatures up to 66° C, while *H. undatus* can only resist up to 55° C – the lowest high–temperature tolerance measured for a cactus (Drennan, 2009; Nobel *et al.*, 2002). For many species, the actual temperature tolerance is determined by the prevailing mean air temperature. Indeed, a 10° C increase in the air temperature to which plants are exposed leads to an average increase of 5.3° C for the lethal temperature of 18 species of cacti (Nobel, 1988; Drennan, 2009). For example, for *O. ficus–indica* individuals incubated under a mean temperature of 35° C, the lethal temperature is 62° C, but for plants incubated under 45° C, the lethal temperature is 66 °C; thus acclimation for this species amounts to 4.2 °C per 10° C increase in air temperature (Nobel, 1988; Nobel *et al.*, 2002). In contrast, the acclimation ability of H. undatus is the lowest measured for a cactus. For this neotropical vine, increasing the average air temperature from 20 to 30° C merely improves the high–temperature tolerance from 54.0 to 55.4° C; in addition, higher average temperatures lead to an inhibition of gas exchange and even plant death (Nobel *et al.*, 2002).

05

Nopal (*Opuntia* spp.) genetic resources

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05 Nopal (*Opuntia* spp.) genetic resources

INTRODUCTION

World population predictions for 2050 are grim, estimated to reach 9 billion at the current birth rate. Countries in arid and semi–arid areas have some of the fastest–growing populations; they are also the driest regions of the world, and water will be twice as scarce by 2050 (UN–DESA, 2015). Climate change will also affect the acreage of land under semi–arid conditions. Populations are expanding fastest in regions where it is most difficult to grow food. For this reason, governments must give immediate and sustained attention to the effects of climate change, whether their countries are already affected or potentially affected.

Effective water and land use, wise selection of cultivated species matching agroclimatic requirements to specific sites, sound strategies to increase yields, and improved plant and animal genotypes are among the tools for coping with this catastrophe. Multipurpose indigenous plants such as cactus pear (*Opuntia* spp.) may be included in the list of choice crops, given their drought tolerance and wide range of potential uses: as fruit, forage or vegetable crop, in addition to their utilization as living fences to protect family households in dry regions, or for erosion control (Mondragón Jacobo and Chessa, 2013). Germplasm resources are destined to be the cornerstone of all future applications of cactus pear; intensive exploration, effective *in situ* and *ex situ* conservation, dynamic evaluation on new sites and vigorous projects of germplasm exchange and improvement are needed to realize the full potential of this valuable resource. Scientists must identify the traits for use in intensive breeding programmes: old and new traits useful for coping with drought, frost, and indigenous and foreign pests and diseases, and for improving nutritional content.

This chapter summarizes the progress made in activities related to germplasm in those countries with the widest variability of cactus pear, whether native or introduced. It also describes the basics of *Opuntia* genetic resources exploration, documentation, *in situ* and *ex situ* conservation, and utilization.

GENETIC RESOURCES EXPLORATION

Before investing time and resources in the collection of cactus germplasm, it is necessary to put into perspective the prospect of finding real, useful genetic variability, the potential uses and – most important – the long–term costs of running a germplasm collection. It is then imperative to research bibliographical sources to understand the origins and dispersal routes, in order to verify the need for closer study before embarking on collection.

It is well documented that *Opuntia* originated and was domesticated in central Mexico, a country that still has the widest range of wild and domesticated species and varieties. It is also known that during the colonial period, domesticated cactus pear was introduced to Europe and then to North Africa, mainly to countries occupied by Spain, France and Italy. Other historical and economic events explain the presence of cactus pear in the Near East and central Asia and other parts of the world during the sixteenth to nineteenth centuries. Since the 1980s, there have been significant efforts by governments and non–governmental organizations (NGOs) to curtail the effects of desertification in North Africa and other areas; cactus pear cultivation is among the measures promoted to control erosion and boost vegetation recovery.

Germplasm variability

There is a direct connection between the above–mentioned historical events and germplasm variability: the earliest introductions were based on a restricted germplasm base, including mostly domesticated accessions, while recent introductions used an even more limited number of entries, considering only a few spineless varieties. Despite evidence of excellent adaptation in areas such as eastern Africa, cross–breeding of close genotypes does not yield new alleles immediately.

It is difficult to generate new variability in *Opuntia* germplasm. This is due to the high rate of apomictic seedlings and the length of the juvenile period (reported to be 4–7 years – Mondragón Jacobo, 2001); these biological features of cactus pear reduce the chances of cross–breeding to generate new genotypes through recombination. On the other hand, all domesticated genotypes and most wild genotypes are polyploid, a genetic feature that diminishes the likelihood of expression of natural mutations. The combination of these traits significantly reduces the potential for generation of new variability on sites other than the centre of origin and domestication.

Exploration of germplasm

For successful exploration, it is important to consider the following:

- Sources of local knowledge should be sought regarding the plant, local names, forms of utilization, integration of the plant into the local culture and history. It is always advisable to invite local guides to assist on field trips, not only extension agents, but also herders, wood collectors, and fruit and herb gatherers, who are usually better acquainted with the local flora.

- Knowledge of the phenology of cactus in the area of interest is crucial, since all descriptors are based on visual traits concerning all parts of the plant; however, roots, flowers and fruits are essential for accurate botanical identification. A common trait used to identify accessions and varieties is fruit colour, both internal and external. However, fruit colour is a dynamic trait – changing with the ripening phase, while the colour of the pulp changes at ripening – and for this reason the exploration should be guided by an experienced leader who is less likely to be deceived.
- An accurate geographical description of the area is indispensable: altitude, sunlight exposure and soil moisture all affect climate, and climate in turn can affect the ripening season. Lack of geographical knowledge is probably one of the main reasons for the presence of redundant accessions in *ex situ* collections. Accessions of early or late ripening, but collected in different locations, will flower and bear fruit at the same time when planted side by side.
- The presence or absence of spines is another interesting and important trait. Modern production systems demand mostly spineless cultivars; however, there is less variability in spineless cultivars compared with spiny, which probably arose as a mutation of spiny cultivars. Furthermore, the identification of spineless accessions is more difficult, since the process cannot be completed unless the plants have fruits.

The prospection of cactus genetic resources has been a topic of interest since the beginning of the twenty–first century. Germplasm studies have been conducted in Morocco (Arba *et al.*, 2002), Turkey (Bekir, 2006), Tunisia (Zoghlami *et al.*, 2007), Argentina and Ethiopia (Haile and Belay, 2002; Mondragón Jacobo and Tegegne, 2006), allowing the identification of accessions for local consumption mostly as fresh fruit. These studies have focused on domesticated and semi–domesticated stocks. Historical sources indicate a common origin for the cactus pears present in these areas; domesticated cactus pears brought from Mexico after the discovery of America were dispersed by the colonial activity of Italy, Spain and other European countries, and by Arab countries in North Africa and the Near East. Field observations support the hypothesis that the original pool was restricted mostly to domesticated accessions, which segregated and adapted to these new environments. For this reason, although reported to be ample, variability is actually relatively narrow compared with the known pool.

There have been extensive efforts in Mexico to collect domesticated and semi–domesticated cactus pears with the support of a federal government initiative focused on native crops: National System of Plant Genetic Resources for Food and Agriculture (SINAREFI). A more modest project was the collection of wild ancestors undertaken by the National Autonomous University of Mexico (UNAM); this collection can be visited at UNAM in Mexico City. Germplasm prospection reached a plateau and research teams then turned their attention to conservation and utilization.

What is left to collect? The Tigray region of eastern Africa certainly deserves a closer look; it covers part of Ethiopia and Eritrea and boasts the largest area of "naturalized" cactus pear in Africa, originated from introductions made during the nineteenth century; efforts to characterize the local variability are reported by Mondragón Jacobo and Tegegne (2006). Cactus pear spread to distant regions during its early dispersal, reaching such unlikely places as China, India and Madagascar, and it is necessary to explore and characterize the variability present in all locations, in order to compare with the genotypes available in germplasm banks and to evaluate the conservation needs and assess the presence of valuable traits for breeding.

Another case in point could be the recovery of the Burbank collection, acquired by South Africa at the beginning of the twentieth century. The collection contains most of the spineless varieties developed by Luther Burbank in California, as well as some accessions of Mexican origin, and is currently under the responsibility of the University of Free State, which has efficiently linked genetic resources studies to animal use and human nutrition.

Maintenance of germplasm

Maintenance of a cactus pear collection is expensive, considering that cactus pear is a perennial crop requiring a long time to stabilize productivity: 5–7 years in the case of fruit production. Several years are also required to obtain meaningful results with regard to forage and vegetable utilization; nevertheless, useful data on productivity and quality are already available after the second year.

Another important factor is the agroclimatic variability of production areas: for a thorough investigation, more than one experimental site is required, increasing substantially the cost of research or extension–research projects, and funds may not be readily available, depending on the country providing financial support. There is a global trend of long–term conservation projects *per se* becoming difficult to sell. Maintenance may be facilitated through a combination of goals and collaboration between interdisciplinary teams, using the same trials or collections for simultaneous purposes; nevertheless, uncertainty remains, as each donor agency sets its own terms and operations calendar.

GERMPLASM BANKS, CORE COLLECTIONS AND CULTIVAR TRIALS

It is advisable for all cactus–pear–producing countries to acquire, collect, conserve and evaluate genotypes that are different from those in commercial use. Such collections serve as exploratory sites and as reservoirs of new variability if needed. They are also a valuable source of information about the performance of individual accessions on specific sites, since adaptation and productivity are difficult traits to extrapolate.

The extent and nature of these collections vary: from cultivar trials to formal germplasm banks. Germplasm banks are not only recommended, they are mandatory in countries which are the centre of origin and secondary centres. Core collections are smaller in size and contain specific genotypes useful for breeding and preliminary agronomical evaluation. Cultivar trials should include promising new genotypes – whether strictly new or simply new to the area – and usually the design imposes the need for replicates. The extent to which germplasm evaluation is useful depends on several factors:

- Crop – how important is it?
- Site – how well does it represent the agroclimate?
- Extension services – how effective are the services linked to cactus pear production?

GENETIC RESOURCES DOCUMENTATION

The genetic resources maintained in a collection increase in value if complete and accurate data are assembled. In addition to adequate passport data, records of accession performance through the years may represent a valuable source of information for researchers and extensionists. Management and maintenance records must be kept in order to:

- monitor the status of conserved germplasm across all phases of conservation;
- optimize the efficiency of conservation programmes; and
- facilitate the exchange of materials and information among germplasm banks and collections.

The main concern about genetic resources management is the increase in the number of accessions usually associated with redundancy. To discard duplicates, and to prevent or reduce the addition of duplicative accessions to germplasm collections, comprehensive documentation for existing accessions and new entries is necessary.

The information associated with collected accessions is as important as the actual plant material held in gene banks (Given, 1994). For every accession, there should be descriptive information to optimize utilization, meet specific needs of the users, and support decisions concerning the choice of genotype.

As with major crops, characterization and evaluation of the available gene pool is essential for cactus pear breeding programmes. Phenotypic and genotypic characterization of germplasm provides opportunities to identify genetically diverse, agronomically superior accessions for the improvement of *Opuntia* species as a multiple–uses crop (Chessa, 2010).

Simplicity, speed and relatively low cost make morphological markers/traits the most widely used genetic markers for germplasm characterization. To facilitate and standardize characterization of collected accessions, a descriptors list for cactus pear is available, compiled (Chessa and Nieddu, 1997) according to the international format currently endorsed by Bioversity International. Characterization based on morphology has also been achieved, following descriptor lists and catalogues proposed to improve utilization of accessions of Mexican and South African collections (Gallegos Vázquez *et al.*, 2005; Potgieter and Mashope, 2009). A classification scheme for the identification of cultivated and wild variants of *Opuntia* species of Mexican origin was reported by Reyes Agüero *et al.* (2009). A statistical approach to identify the characters of differential diagnostic value has been considered to provide greater standardization between collections and to adapt the descriptor list to specific purposes (Erre and Chessa, 2013).

The identification and description of domesticated individuals present in low numbers in family orchards for domestic use has been undertaken by Mexican researchers. This particular subset is endangered by unusually harsh frosts and hail – probably linked to climate change – land–use changes, migration, and other social and economic factors. These landraces express the effects of long–term selection; they are also the carriers of valuable traits useful for immediate application by breeders. Assembling them in breeding collections may save valuable time in the process of genetic enhancement. A description of outstanding local and regional "varieties" as well as some restricted populations obtained from central Mexico is provided by Gallegos and Mondragón Jacobo (2011). Descriptions include data, pictures, distribution maps and brief information on the commercial traits of these "varieties". The data are valuable and of interest not only to researchers but also to farmers, merchants and consumers, on the assumption that the wider the audience, the greater the effect on conservation interest.

A common platform, based on the same traits, scales and units of measurement is needed on a global basis to facilitate exchange of information and plant material. The Germplasm Resources Information Network (GRIN) – a Web server (http://www.ars–grin.gov/) providing germplasm information about plants, animals, microbes and invertebrates – could be useful for cactus pear. The FAO database Hortivar (http://www.fao.org/hortivar/), involving the direct collaboration of users, focuses on commercial cultivars of horticultural crops; data on cactus pear cultivars have yet to be uploaded.

USING MODERN MOLECULAR TOOLS TO EXPLAIN CACTUS PEAR VARIABILITY AND REDUCE REDUNDANCY

Phenotypic identification based only on morphological markers can be misleading because of the complex genotype and environment interaction that governs most of the traits of interest. The first step towards the application of molecular tools to study cactus pear genetic resources – redundancy, phylogeny and inheritance of valuable traits – was the optimization of DNA extraction. Since the 1990s, protocols have been developed to extract DNA from cladodes and roots (De la Cruz *et al.*, 1997; Griffith and Porter, 2003; Mondragón Jacobo and Doudareva, 2000), circumventing the problem of mucilage. The adaptation of commercial kits has greatly facilitated the processing of large numbers of samples, as reported by Fehlberg *et al.* (2013), who evaluated the effectiveness of the commercial DNeasy Plant Mini Kit (QIAGEN, Valencia, California, United States of America) to extract DNA from the spines of eight species of cactus.

The best tool for the assessment of genetic diversity are markers based on DNA polymorphism. A wide range of molecular marker techniques have been developed and are commonly used for genotyping individuals and inferring information on the genetic structure of germplasm collections, discovery of synonymy, and kinship. However, in the case of minor crop species like cactus pear, the development and application of molecular markers are actually still limited.

The grouping of different *Opuntia* varieties and biotypes was achieved by means of isozymes banding pattern on pollen (Chessa *et al.*, 1997). Due to the low reliability of these markers, affected by environmental conditions, tissue type and plant stage, more informative polymerase chain reaction (PCR)–derived markers were applied.

Random amplified polymorphic DNA (RAPD) markers were successfully applied to verify the somatic origin within some Mexican accessions (Mondragón Jacobo, 2002). In order to identify fruit cultivars, vegetable and ornamental accessions, Wang *et al.* (1998) applied RAPDs combined with morphological and physiological data. The germplasm bank collection of the Faculty of Agronomy of the Autonomous University of Nuevo León (FAUANL) was characterized and duplicates were revealed by means of RAPD markers (Garcia Zambrano *et al.*, 2006); however, they were not confirmed using amplified fragment length polymorphism (AFLP) markers (Garcia Zambrano *et al.*, 2009). *O. ficus–indica* ecotypes from Tunisia were characterized by means of RAPD markers, and 13 main groups were identified with no relationship to different geographical regions (Zoghlami *et al.*, 2007).

Using AFLP, Labra *et al.* (2003) suggested that *O. ficus–indica* should be considered a domesticated form of the spiny *O. megacantha*. AFLP markers were also applied to investigate genetic relationships between species in three *Opuntia* collections in Tunisia (Snoussi Trifa *et al.*, 2009). The level of genetic diversity in cactus clones in Brazil was evaluated by ISSR (inter–simple sequence repeat) markers, revealing low genetic differentiation among them (Souto Alves *et al.*, 2009). In order to assess diversity, different molecular markers were applied, for example, RAPD–PCR and chloroplast simple sequence repeat (cp–SSR) (Chessa, 2010) and RAPD–PCR together with ISSR using DNA from seeds (Luna Paez *et al.*, 2007).

The evolutionary history of *O. ficus–indica* has been investigated with the use of Bayesian phylogenetic analyses of nrITS (nuclear ribosomal ITS) DNA sequences (Griffith, 2004).
Molecular evidence for the hybrid origin of various *Opuntia* species and the ease of introgression has been documented, and the polyphyletic origin of *O. ficus–indica* has been assumed (Griffith, 2003, 2009). The Griffith hypothesis considering *O. ficus–indica* as a group of multiple unrelated clones derived from different parental species and selected for common agronomical features was also supported by Caruso *et al.* (2010) by means of microsatellites. Six highly polymorphic simple sequence repeats (SSR) developed by Helsen *et al.* (2009) and two expressed sequence tag (EST)–SSR loci were used to fingerprint 62 *Opuntia* genotypes of Mexican, Israeli and Sicilian origin. A clear separation between cultivated accessions and cactus–pear–related species was documented.

Helsen *et al.* (2009) cite the usefulness of both molecular and morphological data in conservation planning – based on the relatively high morphological divergence found on the Galapagos endemic *Opuntia* species associated with low genetic variability – as evidence for divergent selection and adaptation to local environments. The same authors gave evidence that the current morphology–based taxonomic differentiation between the *Opuntia* taxa was not supported by molecular data.

The high variability and the codominant nature of SSRs have made them the marker of choice for DNA finger-printing in the characterization of *Opuntia* accessions in Italy (Sardinia). A novel set of microsatellite loci were isolated in different species and varieties of *Opuntia* (Erre *et al.*, 2013). Five out of the ten SSR loci developed were used to characterize two field collections from Italy and Argentina. The level of polymorphism and the relatively high number of alleles detected suggested that these markers can be used for both inter– and intraspecific studies, as well as to provide a more reliable tool in the classification of *Opuntia* species, based on their allelic profiles.

CONSERVATION OF CACTUS PEAR GENETIC RESOURCES

In situ conservation

In situ conservation should be encouraged at the centres of origin and diversity of cactus pear, with attention focused on wild ancestors and semi–domesticated types. Central Mexico is undergoing significant land–use changes, which directly endanger diversity hot spots; the main threats are incorporation of land to grazing, construction of new roads and growth of urban areas. Land tenure allows private individuals and communities to decide the actual or future fate of wild lands, complicating long–term conservation agreements.

Natural threats in the form of unusual frosts, snow and hail – believed to be associated with climate change – are also jeopardizing the survival of wild and semi–domesticated cactus pear plants, in particular frost–sensitive varieties. A late, harsh winter was recorded in spring 2016, and some of the most important states for wild cactus pear in north central Mexico were covered in snow and ice; the final effects are being assessed.

Different approaches to encourage conservation have been promoted in Mexico with varying levels of success: natural protected areas (federal, state and municipal level), nature tourism corridors, and other schemes of sustainable utilization. Such policies must balance the expected effects with the economic and social interests of the human groups involved. All these initiatives are under scrutiny due to budget cuts and political changes, risking the long–term protection of the resource.

Ex situ conservation

In the Eastern Hemisphere, *ex situ* conservation is the most active approach, with field collections in Tunisia, Morocco and South Africa. Italy has the largest and oldest collection outside Mexico. It was started in 1992 and acts as a germplasm bank and breeding collection; it hosts *Opuntia* and *Nopalea* specimens and the number of accessions is currently 2 200. The collection includes local varieties and selections, hybrids derived from open pollination, controlled crosses and embryo culture. In the Western Hemisphere, live collections are present in Argentina, Chile, Brazil and Mexico; the collection in Kingsville, Texas is no longer active, but the United States Department of Agriculture (USDA) has assembled a new collection under the umbrella of the National Clonal Germplasm Repository in Parlier, California.

While Brazil has oriented its conservation efforts towards forage accessions, other collections contain fruit, forage and double–purpose entries. Mexico, as the largest centre of diversity, maintains several sites varying in extension, age and number of accessions (**Table 1**). In 2010, it started a project on *in vitro* conservation of rare genotypes of immediate horticultural value. Brazil reports 1 417 accessions, including genotypes from several countries, as well as segregants and hybrids of controlled crosses. Italy reports around 2 200 entries obtained from Mexico, Chile, the United States of America, Morocco, Argentina and South Africa; they include wild types and ecotypes, local varieties, selections and hybrid populations of controlled crosses and plants derived from embryo culture.

In early 2011, the Mexican Government launched the National Research Center for Genetic Resources and Biotechnology (CENARGEN) in Tepatitlan, Jalisco, to serve as a national repository; its facilities are designed for the long–term storage of all crops and related organisms relevant to national agriculture, including cactus pear.

UTILIZATION: GERMPLASM ENHANCEMENT AND BREEDING

Attempts at cactus pear breeding go back to the late nineteenth century. Results have been mixed for two main reasons:

- Biological complexity – all opuntias of horticultural value are polyploid and present apomixes.
- Long–term juvenility – associated with the limited output of breeding programmes and costly projects (features directly related to funding).

As a result, breeding programmes are irregular, short–lived and poorly funded. Four programmes supported by the Mexican, Italian, Brazilian and American governments and one private company conduct breeding. They are briefly described below.

Italy

The Italian breeding programme has been involved in germplasm collection, description and documentation since 1992. It has performed crosses and pioneered the embryo culture of cactus pear. The products obtained include 12 selections of green, yellow and red peel (four of each) suitable for cultivation in Mediterranean countries.

Mexico

The programme started in 1995 and has conducted hybridizations and selections using the best Mexican genotypes for fruit production to obtain multipurpose varieties, and improve fruit quality and adaptation. To date, three improved varieties have been reported (Gallegos and Mondragón Jacobo, 2011). Since 2013, programme activities have been reduced due to lack of reliable funding.

Brazil

Located in the semi–arid tropical area of Pernambuco, the programme focuses on the development of improved varieties for forage production. Its inventory includes the varieties 'Gigante', 'Redonda' and 'Miuda', 1 061 clones of open–pollinated 'Palma Gigante', 171 clones of open–pollinated 'Palma Miuda', and 159 clones obtained from Chapingo, Mexico, plus 17 clones from CPATSA, 5 from Rio Grande do Norte and 4 from Petrolina, with a total of 1 417 accessions.

United States of America

D'Arrigo Bros., a private American company interested in cactus pear production and breeding in Salinas, California, has reported four improved varieties developed for private use: 'Sweet Emerald', 'Sweet Crimson', 'Sweet Purple' and 'Sweet Sunset' (http://www.andyboy.com/products/cactus–pear), reinforcing its line of fresh novel products.

The USDA Agricultural Research Service (ARS) National Arid Land Plant Genetic Resources Unit (NALPGRU) in Parlier, California maintains and evaluates plant germplasm adapted to arid conditions and high levels of salt, selenium and boron in soil. The result is four new cultivar patents, co–owned by Fresno State, Diener's Red Rock Ranch and the USDA. Red Rock Ranch intends to develop and market products in the form of juice and powder blends derived from the new plants (https://www.fresnostate.edu/jcast/cati/update/2013–fall/opuntia–study.html).

TOWARDS SUSTAINABLE UTILIZATION OF CACTUS PEAR

New varieties are the axis of any sustainable system; they are under development in Mexico, Brazil and Italy and to a limited extent in the United States of America. Since underdeveloped countries can benefit most from cactus pear cultivation, **international collaboration** needs to be encouraged, with countries sharing expertise, genetic resources and facilities. In order to achieve this, international centres must steer collaborative projects.

In the meantime, countries with native or naturalized stocks should intensify the collection, characterization and assessment of best entries, followed by propagation of outstanding selections under strict phytosanitary protocols. For other countries new to cactus cultivation, it is recommended to introduce selected genotypes, test them and propagate the best performers under local conditions before launching large–scale cultivation programmes.

TABLE 1

Inventory of Mexican germplasm banks of cactus pears, updated to 2014

Use	CRUZEN[a]		IIZD[b]	CBTA[c] 38	INIFAP–SLP[d]
Fresh fruit	357	16	302	136	908
Fruit and forage	5	–	–	–	17
Forage	7	2	3	3	47
Vegetable	39	5	30	3	86
Triple use	2	–	–	–	2
Not reported (n.a.)	–	23	–	–	28
Animal feed	–	–	–	–	29
Ornamental	–	–	–	–	4
Condiment	–	–	–	–	15
Total	410	46	335	142	1 021

[a] CRUCEN: Regional Center North Center University, Autonomous University of Chapingo, El Orito, Zacatecas, Mexico.

[b] IIZD: Institute for Desert Area Research, Autonomous University of San Luis Potosí, Mexico.

[c] CBTA: Agricultural Tech0,5ogy School, Ojocaliente, Zacatecas, Mexico.

[d] INIFAP–SLP: National Institute for Forestry, Agricultural, and Animal Husbandry Research – Experimental Field, San Luis Potosí, Mexico.

06

Fruit production and post-harvest management

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06

Fruit production and post-harvest management

INTRODUCTION

A worldwide expansion of cactus pear cultivation was predicted by Nobel in 1988. Predictions were partially based on the particular environmental biology of the cactus pear plant, which makes it possible to develop sustainable agricultural production systems in areas with limited water and poor soils (Inglese *et al.*, 1995a). Furthermore, there was an increased interest in cactus pear fruit production due to a greater demand for exotic fruit on the world's major markets (Inglese *et al.*, 1995a). In addition, limited irrigation water for expansion of mainstream crop production in arid and semi–arid areas has forced agriculturalists to look at alternative crops with improved drought tolerance and water–use efficiency (WUE). The plant is cultivated in a wide range of environments, resulting in differences in orchard practices (depending on the country), fruit quality and crop productivity (Inglese *et al.*, 2009; Liguori and Inglese, 2015). Fortunately, since the 1990s, much more information has become available on orchard management and other cultivation aspects of cactus pear (Felker and Inglese, 2003).

Currently, cactus pear cultivation for fruit production takes place in at least 18 countries in semi–arid areas in both hemispheres on more than 100 000 ha (Inglese *et al.*, 2002a); this figure does not include naturalized plants, nor plants cultivated for home consumption, commonly found in many countries (Inglese *et al.*, 2002a). The country with the largest area under cultivation of cactus fruit is Mexico (51 112 ha) (Reyes Agüero *et al.*, 2013), while other countries, such as Italy, Chile, South Africa, Argentina and Israel, also commercially cultivate the fruit (Inglese *et al.*, 2002a).

The innaccurate perception that cactus pear does not need to be cultivated like other crops and that little or no care still gives high productivity persists today to some degree. Even the early cactus pear researchers – Griffiths (1909) and Turpin and Gill (1928) – ascribed this theory to the ease with which the plant grows in virtually any environment. Today we know that this is untrue: in order to be profitable, the plant requires appropriate care.

ORCHARD PLANNING AND ESTABLISHMENT

Thorough planning is crucial when establishing a commercial cactus pear fruit orchard and many important decisions must be made prior to planting. Many aspects require consideration:

- meso– and microclimate of the growing site;
- physical and chemical soil analysis;
- cultivar choice;
- soil preparation;
- ordering of plant material;
- planting of windbreaks;
- determination of planting distances and row orientation; and
- installation of an irrigation system.

Site selection

The worldwide distribution of cactus pear is indicative of its extensive adaptability to various climatic and soil factors (Brutsch, 1979). Cactus pear plants can tolerate very high temperatures with no negative consequences (Nobel *et al.*, 1986); on the other hand, planting sites where the minimum temperature drops to below –5° C should be avoided, as most fruit cultivars are killed at these temperatures (Inglese, 1995). Low–lying areas where frost occurs in late winter to early spring may cause flower bud abortion (Wessels, 1988b; Inglese, 1995; Nerd and Mizrahi, 1995a) with partial to total crop failure. The optimal temperature range for nocturnal CO_2 uptake is 25/15° C day/night for cactus pear, because higher day or lower night temperatures result in reduced carbon uptake, leading to poor plant growth and production (Nobel 1994; Nobel and Bobich, 2002). Temperature patterns during floral budburst (late winter to spring) and fruit development period (FDP) have a particularly significant effect on productivity and fruit quality. Most *Opuntia* species are poorly adapted to long periods of cool moist weather (Brutsch, 1979).

In most countries characterized by predominant summer rainfall, cactus pear is grown under rainfed conditions; however irrigation is necessary where the dry time of year coincides with the FDP or where annual rainfall is < 300 mm (Inglese, 1995). Cactus pear is successfully grown in winter rainfall areas when provision is made for irrigation in the hot dry summer months. The maximum rainfall limit is 1 000 mm per year (Le Houérou, 1992, 1996a), but high rainfall is less ideal as it results in poor pollination, increased presence of fungal diseases, fruit cracking and reduced fruit quality (Wessels, 1989).

Given the succulence of the plant and fruit, it is easily damaged by hail, and commercial fruit production should be avoided where hail is a regular occurrence (Wessels, 1988a; Brutsch, 1997a). Physical damage as a result of hail facilitates the entry of pathogenic fungi into the plant (Granata, 1995; Swart *et al.*, 2003), and causes cosmetic damage making the fruit unmarketable.

Snyman (2004, 2005) showed that at 2 years, *O. ficus–indica* roots comprise only 7% of the total plant biomass – indication of the large difference between below– and above–ground biomass in the early years of plant growth. As a result, strong winds accompanied by rain may cause plants to lodge, especially when plants are young and the root system is not yet fully developed to keep it upright.

It is important to carefully examine the microclimatic features when selecting the most appropriate planting site for orchard establishment. For example, a north–facing site is warmer than a south–facing one (Southern Hemisphere), resulting in earlier harvest and improved fruit quality.

While cactus pear can be grown in a wide range of soil types (Inglese *et al.*, 2002a), it is important to select the best soils available for high productivity (Wessels, 1988a). Soils with a sandy to sandy loam texture are ideal (Vazquez–Alvarado *et al.*, 2006), but cactus pear can grow equally well on heavier soils. Wessels (1988b) noted that soil drainage rather than soil type is the conditioning factor. Cactus pear is very sensitive to a lack of oxygen in the soil (Brutsch, 1979; Le Houérou, 1992, 1996a), but very sandy soils have poor water–holding capacity and are more prone to leaching of nutrients (Wessels, 1988a). The plant prefers a neutral to slightly alkaline soil pH (water) (Wessels, 1988b; Zegbe *et al.*, 2015). Soil selected for planting should be at least 300 mm deep (Wessels, 1988a), although deeper soils (600–700 mm) are preferred for commercial production (Inglese *et al.*, 2002a). Most *Opuntia* species do not tolerate even moderate levels of dissolved salts in the rooting zone. Since net CO_2 uptake is inhibited, it negatively affects the vegetative growth of cacti in soils high in sodium chloride or calcium carbonate (Nobel, 1994, 1995). Gersani *et al.* (1993) report a 40% reduction in plant growth with a concentration of 30 mol m^{-3} (1.76 g $litre^{-1}$ NaCl), and a 93% reduction with a concentration of 100 mol m^{-3} (5.85 g $litre^{-1}$ NaCl).

Soil preparation

Pre–plant soil preparation is essential for successful cactus pear production and cannot be adequately performed after orchard establishment. Land clearing and levelling may be required (Inglese, 1995); irrigation supply lines may be installed and plant rows marked out. In areas where game and domestic animals can damage young plants, fencing is required.

Adverse soil conditions, such as impenetrable layers, perennial weed infestation and shallow soil depth, need to be addressed before planting (Wessels, 1988b; Inglese *et al.*, 2002a). Deep soil cultivation (at least 500 mm) with a ripper/subsoiler on the plant row is needed to break up any hardpan layers, and to improve drainage, aeration and water–holding capacity. In heavier compacted soils, deep cultivation across the rows may also be beneficial: it helps the plant survive during low rainfall years when it can utilize soil water from deeper soil depths (Inglese, 1995; Potgieter, 2001). On very shallow soils, ridging is recommended (Singh, 2003). It is important to remove perennial weeds before establishment – either mechanically or chemically – as they compete strongly with the cactus pear plant, particularly during the early stages of plant growth (Wessels, 1988b).

Pre–plant fertilization

Soil amendments to correct soil nutrient imbalances and soil pH must be carried out prior to establishment. A soil pH (water) of 6.5–7.5 is considered optimum (Wessels, 1988a, b; Singh, 2003). Fertilizer applications should be based on the results of soil analysis, which indicate the levels of plant nutrients in the soil (**Table 1**).

TABLE 1

Suggested optimum soil nutrient levels for cactus pear fruit production for rainfed cultivation in summer rainfall areas of South Africa

Element	Optimal soil level (mg kg^{-1})
P	20–30
K	80–100
Ca	> 400
Mg[a]	100–150

[a] Mg levels should not be higher than Ca levels.

Source: Potgieter, 2001, 2007 (adapted).

Representative soil samples of the topsoil (0–300 mm) and subsoil (300–600 mm) need to be taken for chemical and physical analysis. The secondary effects of soil pH on the availability of other plant nutrients are probably more important than soil pH *per se*. For example, P becomes less available to plants at a low soil pH (Nobel, 1988). Lime and P are relatively immobile in soils and as a result these need to be thoroughly mixed with the soil prior to planting. In addition to decreasing vegetative growth and dry mass (Berry and Nobel, 1985), high soil salinity also decreases water content of the cladode, uptake of K and Ca, and root–shoot ratio (Nerd *et al.*, 1991c). The addition of gypsum helps to neutralize excess salts in the soil solution. Cactus pear reacts very well to organic manures which also improve the soil structure, nutrient content and water–holding capacity (Inglese, 1995; Singh, 2003). As a general guideline, 6–10 tonnes ha^{-1} of well–composted animal manure needs to be incorporated into the soil before planting.

Windbreaks

In windy areas, it may be beneficial to plant live windbreaks to minimize the negative effects of wind in cactus pear orchards. Heavy rainfall accompanied by strong wind can cause young plants to lodge and can even cause branches and cladodes to break off (Felker *et al.*, 2005). Pollination and plant protection sprays are all negatively affected by high winds; it is difficult to perform orchard practices (pruning, fruit thinning, harvesting) under windy conditions as the glochids tend to become airborne (Wessels, 1989). When developing cladodes and fruit are too close together on a cladode, fruits can be damaged by chafing during windy spells. Live windbreaks must be adapted to the area of planting and they should receive water and plant nutrition to ensure that they do not compete with the orchard. A popular tree for live windbreaks in orchards is the Australian beefwood (*Casuarina* spp.).

Cultivar choice

The number of cactus pear fruit cultivars available varies significantly between countries. Mexico and South Africa have numerous cultivars, while in most other producing countries the cultivar choice is rather limited (Inglese *et al.*, 2002a). The choice of a fresh fruit cultivar depends primarily on the climatic conditions of the planting site and on market demand. *Opuntia* species and cultivars differ greatly with regard to their potential fruit yield, quality characteristics and adaptability to environmental conditions. Not all cultivars are equally adapted to a particular area; indeed, most cultivars exhibit strong genotype–environment interaction (G × E) (Potgieter, 2007). Cultivars must be chosen wisely; changing cultivar after establishment entails very high costs, because plants are self–rooted and grafting or top–working is not economically viable.

In addition, cultivar characteristics must be carefully considered (**Table 2**) before a final decision is made: there may be specific cultivar preferences for supplying a particular market. For example, cultivars with a red, pink, orange or yellow pulp are preferred on most European and North American markets, whereas white and green pulp fruit are favoured by South African (Wessels, 1988) and Mexican consumers (Mondragón Jacobo and Perez Gonzalez, 1994, 1996). If growers are contemplating exporting fruit, the cultivar choice becomes even more important as characteristics such as appearance, post–harvest resistance to handling and shelf–life play a major role in successful exports. Producers should take into account that some cultivar characteristics can be influenced by the environment or by orchard management practices. For example, although fruit mass may be genetically controlled, it can be influenced by fruit thinning, irrigation, fertilization and pruning. Annual variation in fruit yield and quality is also evident in most commercial orchards.

TABLE 2 Main cactus pear fruit cultivar characteristics in producing countries of the world

Cultivar name	Country	Species	Spininess	Peel/pulp colour	Ripening season	Fruit mass	Pulp	TSS	Post–harvest handling
				50% peel colour break	N. Hemisphere	g	%	°Brix	
Algerian	SA	*O. ficus–indica*	none	red/dark pink	Jul./Aug.	162	59.4	13.9	moderate
Gymno Carpo	SA	*O. ficus–indica*	none	Yellow/Orange	Aug./Sept.	170	61.7	11.2	moderate
Meyers	SA	*O. ficus–indica*	none	red/dark pink	Jul./Aug.	176	60.7	13.6	good
Morado	SA	*O. ficus–indica*	none	Green/White	Jul./Aug.	146	60.0	14.4	poor
Nudosa	SA	Unknown	slight	Red/red	Aug./Sept.	236	60.8	11.2	good
Roedtan	SA	*O. ficus–indica*	none	Yellow/Orange	Aug./Sept.	171	60.7	14.2	moderate
Turpin	SA	*O. ficus–indica*	none	Yellow/Orange	Jul./Aug.	181	55.0	13.6	moderate
Zastron	SA	*O. ficus–indica*	none	Light green/ White	Jun./Jul.	137	57.2	13.5	good
Reyna	Mexico	*O. albicarpa*	spiny	Light green/ light green	Jul./Aug.	120	63.7	16.4	poor
Cristalina	Mexico	O. albicarpa	spiny	Light green/ light green	Aug./Sept.	207	60.2	12.7	good

(Continued)

Cultivar name	**Country**	**Species**	**Spininess**	**Peel/pulp colour**	**Ripening season**	**Fruit mass**	**Pulp**	**TSS**	**Post–harvest handling**
				50% peel colour break	**N. Hemisphere**	**g**	**%**	**°Brix**	
Villanueva	Mexico	*O. albicarpa*	spiny	Green/light green	Jun./Jul.	129	60.9	14.4	poor
Burrona	Mexico	*O. amyclaea*	spiny	Light green/ light green	Sept./Oct.	217	59.8	12.7	very good
Roja San Martin	Mexico	*O. ficus–indica*	slight	Red purple/ purple	Jul./Aug.	116	44.5	13.7	poor
Naranjona	Mexico	*O. megacantha*	slight	Yellow/Orange	Aug./Sept.	170	51.7	13.1	very good
Roja Vigor	Mexico	*O. ficus–indica*		Bright red/red	Jul./Aug.	174			moderate
Dellahia	Morocco	*O. robusta*	none	Light green/ Light green		100	53.1	14.0	
Moussa	Morocco	*O. ficus–indica*	none	Yellow/Orange	Dec.	101	51.0	14.4	
Aissa	Morocco	*O. ficus–indica*	none	Yellow/Orange		96	50.0		
Gialla	Italy	*O. ficus–indica*	none			103	51.0	13.0	good
Rossa	Italy	*O. ficus–indica*	none						
Bianca	Italy	*O. ficus–indica*	none			112	53.6		
Amarilla sin Espinas	Argentina	*O. ficus–indica*	none	Yellow/Green				13.9	
Ofer	Israel	*O. ficus–indica*	none	Yellow/Orange					
Andy Boy	USA								
Verde (Criolla)	Chile	*O. ficus–indica*	spiny	Green/Green	Feb–Apr.	132	49.6	13.3	good

SA = South Africa; USA = United States of America.

ORCHARD LAYOUT AND DESIGN

Row orientation

Row orientation, unlike tree density, cannot be changed and is fixed for the lifespan of the orchard. According to Nobel (1982), cactus pear cladodes are inclined to face east–west, except at lower latitudes (> 27°) and in areas where vegetative growth occurs during winter. In these situations, row orientation is less important (Nobel, 1982). Once row orientation is decided, it is important to achieve optimal light utilization over the whole tree canopy during the day (García de Cortázar and Nobel, 1991; Stassen *et al.*, 1995). While the generally preferred row orientation is north–south to capture equal daily solar irradiance under sunlit and cloudy weather conditions, it can be adapted to suit the latitude, site and incidence of sunburn. There are other practical considerations, such as sloping fields, where it is recommended to plant on the contour to prevent soil erosion (Inglese, 1995; Stassen *et al.*, 1995).

Planting systems

Choice of planting design and planting distance depends on farm size, farm management, implements, climate, soil fertility, cultivar growth habit, plant training system and occurrence of pests such as cochineal (Wessels, 1988b; Inglese, 1995).

Hedgerow

Various planting systems can be employed for cactus pear fruit production, but in recent years, high–density hedgerows planted in a rectangular system have become the norm in large commercial orchards in South Africa (Unterpertinger, 2006), Israel (Nerd and Mizrahi, 1993), the United States of America (California) (Bunch, 1996) and Argentina (Felker and Guevara, 2001). Hedgerows have the advantage of lower input costs. They also enable more thorough spray coverage, and solar radiation capture is maximized, resulting in higher productivity.

Rectangular or square planting (free–standing trees)

In Italy, trees are usually widely spaced in a square or rectangular layout; however, similar fruit yields have been reported in Israel and Italy under different plant spacings (Inglese *et al.*, 1995a).

Spacing

Plant spacing for cactus pear fruit production varies greatly, depending on the hemisphere, country and environment. In Italy, planting distances are generally wide and vary from 6 × 6 m (278 plants ha^{-1}) to 4 × 6 m (416 plants ha^{-1}) (Inglese, 1995; Inglese *et al.*, 2002b; Tudisca *et al.*, 2015). In other parts of the Mediterranean, plants are spaced much closer. For instance, in Israel, 1.5 m in the row and 4 m between rows (1 666 plants ha^{-1}) is used to increase fruit yield in the early stages of orchard life (Nerd and Mizrahi, 1993). A plant density range of 500–2000 plants ha^{-1} has been reported in Jordan where plants in the rows are 1–2 m apart, with rows 5–10 m apart and usually positioned on the contour line (Nasr, 2015). In California, plant spacing is 1.5–4 m in rows 4–6 m apart (830–1 666 plants ha^{-1}) (Bunch, 1996). On large farms in Mexico, plants are spaced 4 × 5 m (500 plants ha^{-1}) (Pimienta Barrios, 1990). In the Southern Hemisphere, most new orchards in South Africa are established at 2 × 5 to 2 × 4 m in and between rows (1 000–1 250 plants ha^{-1}) in a hedgerow system. Targa *et al.* (2013) reports plant spacings of 1.5 m in row and 6 m between rows (1 111 plants ha^{-1}) as continuous hedgerows in Argentina.

Whatever spacing is used, it is important to keep open a working row of approximately 1.8 m for farm machinery movement (Wessels, 1988b; Gittens, 1993).

High–density planting

A general problem in cactus pear cultivation occurs when plants are allowed to become too large, resulting in "forests" rather than productive orchards. Large portions of these big trees, especially in the lower parts of the canopy, become completely shaded out (Liguori and Inglese, 2015). As a result, fruit–set is limited to the outside of the plant canopy and labour costs are high at harvest. Given the ever–increasing costs of land and production inputs, it is necessary to seriously re–evaluate planting systems, density and tree management in relation to fruit yield and quality (Stassen *et al.*, 1995; Liguori and Inglese, 2015). Low planting densities are not economically justified; nevertheless, there are two schools of thought on plant spacing:

- **Plant trees on an intensive scale and remove some as encroachment occurs.** The aim is to have an early heavy crop. Close spacing (1–1.5 m) within the row maximizes yield in the early years after planting, but may result in overshading after a few years. Therefore, further pruning and tree removal every few years is necessary to avoid a reduction in yield and fruit quality (Inglese *et al.*, 1995a; Inglese *et al.*, 2002a). Barbera and Inglese (1993) recommend more cuttings per planting station, spaced 4 m apart, resulting in a rapid SAI (stem area index) increase. This results in trees with most of the production on the outer cladodes. However, trees rapidly become 3–3.5 m high and 4–4.5 m wide, entailing higher pruning and harvest costs (Inglese *et al.*, 1995a). In addition to the problem of overshading, dense canopies also aid cochineal infestations and reduce pest control efficiency (Inglese, 1995b). High plant density (2 500 plants ha^{-1}) gives high fruit yield (> 30 tonnes ha^{-1}) from 3–year plants; however, more vegetative than reproductive growth occurs as the plant ages (García de Cortázar and Nobel, 1992).
- **Plant trees according to a realistic high–density spacing and utilize tree management systems to shape and contain the tree within the allocated space** (Stassen *et al.*, 1995). Close spacing within a row maximizes fruit yield in young plants as the number of fertile cladodes per unit area increase (Inglese *et al.*, 2002a). This approach is dependent on the use of manipulation techniques to maintain a specific plant volume. Tree height should not surpass 80% of the width between rows to avoid shading of the lower parts of the hedgerow (Stassen *et al.*, 1995), which makes these areas less fruitful. Provided tree management is done on an annual basis, this strategy is more efficient than lower plant densities. However, if tree management cannot for some reason be performed, it is advisable to maintain a low tree density.

ESTABLISHMENT

Cladode rooting and subsequent vegetative growth in the field depend on many factors. Observations in many commercial orchards have revealed a high degree of variability despite the use of vegetative plant material (Brutsch, 1979; Wessels, 1988a), indicating a need for careful selection of planting material.

Plant material selection and preparation

Cactus pear for fruit production purposes is primarily propagated by clonal means to ensure true–to–typeness (Wessels, 1988b). Where farmers do not have their own cactus pear plants, it is advisable to order plant material well in advance from producers that have good quality plant material. Both single and multiple cladode cuttings are used worldwide for orchard establishment.

Single cuttings

One– or two–year single cuttings (cladodes) can be used, although 1–year cuttings develop more and longer roots than 2–year cuttings (Arba, 2009b). In general, single, mature, large, terminal cladodes of uniform appearance, visually free of any defects, insects and diseases, should be selected as plant material (Potgieter, 2007). Barbera *et al.* (1993b) and Wessels *et al.* (1997) report that the surface area and dry mass of a cutting have a significant influence on successful rooting and budding in the field. A surface area of 500 cm^2 or dry mass of 70–100 g allows good plant growth. Inglese (1995) recommends placing two parallel cuttings spaced 0.4 m apart at a single planting station for rapid canopy development, or alternatively 3–4 single cuttings positioned in a triangle or square and spaced 0.3 m apart. Although this method has the advantage of faster canopy development, it results in wider within–row spacing and requires large quantities of planting material (Inglese, 1995; Mondragón Jacobo and Pimienta Barrios, 1995). Single cladodes as propagation units have the advantages of lower transport costs and easier handling during the planting process

Multiple cuttings

Cactus pear can also be propagated using mature attached (one, two or more) cladodes; this is common practice in Sicily where 2–3–year multiple cuttings are used (Tudisca *et al.*, 2015). Most of the basal cladode is placed underground to ensure plant stability (Inglese, 1995). Multiple cladode cuttings allow more rapid plant development and earlier fruiting than single cladodes after planting (Homrani Bakali, 2013; Nasr, 2015). However, due to their size and mass they are more difficult to handle and transport.

Cuttings can be cured for 4–6 weeks in partial shade on a dry surface to allow the cutting wound to callus (Potgieter, 2001; Inglese *et al.*, 2002a). Alternatively, various copper–based fungicides can be used to treat the cutting wound before planting (Inglese, 1995). To prevent the introduction of insects (e.g. cochineal and cactus pear moth) to new planting areas, it is recommended to disinfect cladodes thoroughly with a registered insecticide before planting. Immature stages of the cochineal insect are barely visible with the naked eye and unsuspecting producers may bring cochineal into an area where it did not previously occur with potentially devastating consequences. Cladodes should be washed with the insecticide mixture using a soft brush to destroy any possible insects.

Planting depth and methods

In sandy soils, cuttings need to be planted deeper than in heavier soils to prevent lodging; likewise, small cladodes should be planted deeper in order to ensure adequate rooting. There are three ways to plant cactus pear: upright; on the side at a 30–45° angle; or flat. The **upright** position is the most commonly adopted (Inglese, 1995) and is preferred for fruit production. Cuttings are planted upright (vertically) with the cut end pointing downwards into the soil. Plants root quickly and a sturdy plant develops (Arba, 2009b; Arba and Benrachid, 2013). Cladodes should be positioned with the flat sides towards the working row. To ensure proper contact between the cutting and soil, the soil needs to be firmed around the cladode after planting. The only disadvantage of this planting method is possible rotting at the cut end (Wessels, 1988b).

Planting time

Roots and cladodes reach their highest growth rate during late spring to early summer (Wessels, 1988b). In summer rainfall areas, newly planted cladodes benefit from rains that occur after planting (Pimienta Barrios, 1990; Singh, 2006). Planting can be extended to midsummer in areas with mild winters. The idea is for the plant to become well established and survive colder winter conditions. However, autumn planting is recommended in Morocco (Nasr and Jamjoum, 2002; Nasr, 2015) and Jordan (Homrani Bakali, 2013), where it resulted in well–established root systems in winter, strong growth in summer and earlier fruiting.

Care of newly planted cladodes

One or two light irrigations (10 litres plant^{-1}) in a small earthen dam around the plant promote root development, but care should be taken not to overirrigate young plants (Potgieter, 2001). Newly established cladodes may develop fruit soon after planting. Due to the high sink demands these fruit have on the plant, it is best to remove them in the establishment year (Wessels, 1988b; Inglese, 1995). From the first production year a light crop may be left to mature.

ORCHARD MANAGEMENT

Weed control

While cactus pear is well adapted to arid and semi–arid regions and can survive severe drought conditions, weed control has been shown to enhance productivity (Felker and Russel, 1988), especially in young plantations (Inglese *et al.*, 1995a). The plant's sensitivity to weed competition is due to the very shallow root system (Felker and Russel, 1988; Snyman, 2005), where it competes at the same soil level as weeds for nutrients and water. Nobel and De la Barrera (2003) showed that 95% of the roots of mature cactus pear plants develop at a soil depth of 40–470 mm, while Snyman (2006a) reports that roots can spread as far as 2.5 m from the stem of the plant in 2 years. Various methods of weed control can be used, but soil cultivation should be restricted to a minimum, in order to avoid damaging the shallow root system (Inglese, 1995). Weed control is best performed at an early stage of growth, when competition with the cactus pear crop is minimal (Wessels, 1988a; Inglese, 1995).

Chemical weed control

Due to high labour costs, chemical weed control is the norm in commercial fruit production. A range of herbicides may be used, but farmers are urged to only use products that are registered in their respective countries, especially when the fuit is produced for export. Weeds should preferably be controlled to 1–1.5 m on both sides of the planting rows (Potgieter, 2001); where the danger of soil erosion is limited, complete weed control between rows can be performed (Brutsch, 1979; Felker *et al.*, 2005). Because the early growth of cactus pear is extremely sensitive to herbicide sprays, spraying should be avoided on windy days. Where lower trunk sections contain chlorophyll, stems should be shielded during spraying to prevent herbicide damage.

Mechanical weed control

In a hedgerow planting system, in–row weed control by mechanical means is preferred when cactus pear plants are young due to their sensitivity to herbicides (Potgieter, 2007). However, in square planting systems with free–standing globe–trained plants, weed control remains manual because this training system makes it difficult to work with ordinary farm implements between trees (Inglese and Barbera, 1993). In smaller or more traditional farming systems with limited access to herbicides, the soil between the plant rows may be ploughed to clear the fields of weeds (Nasr, 2015; Tudisca *et al.*, 2015). Although mechanical weed control is not ideal, it is better than no weed control at all (Felker and Russel, 1988).

Permanent grass strips

Where orchards are planted along slopes, it is recommended that a regularly mowed grass strip be maintained between rows to prevent soil erosion (Potgieter, 2001). Weeds can be mowed and left on the soil surface as mulch to retain moisture and reduce weed growth (Inglese, 1995).

Pruning and training systems

The selection of an appropriate pruning and training system for cactus pear is closely related to the planting system, layout and spacing chosen in the planning phase. The main reason for pruning in cactus pear is to ensure maximum photosynthetically active radiation (PAR) interception by terminal cladodes. Most terminal cladodes exposed to adequate sunlight will produce flower buds (Nerd and Mizrahi, 1995b), while shaded cladodes are usually low–yielding or even infertile (Wessels, 1988a; Pimienta Barrios, 1990; Inglese *et al.*, 2010). Therefore, to ensure high CO_2 uptake and cladode fertility, it is important to prevent excessive cladode shading (Pimienta Barrios, 1990; Inglese *et al.*, 1994a) particularly during the last 8 weeks before spring floral budburst (Barbera *et al.*, 1993a; Cicala *et al.*, 1997). Other benefits of pruning include: controlled plant size, training of the plant into a hedgerow, increased fruit yield, improved fruit size, easier pest detection and control, easier harvesting and rejuvenation of old plants (Hester and Cacho, 2003; Inglese *et al.*, 2009, 2010). Between 20 and 50% of the terminal cladodes should be removed by pruning (Oelofse *et al.*, 2006). However, excessive pruning will reduce yield and contribute to strong vegetative growth the following season (Inglese *et al.*, 2002b). All diseased, small and damaged cladodes should be removed.

Formative pruning

Formative pruning begins in the first year of establishment and is changed to production pruning when the plants start bearing (Targa *et al.*, 2013; Nasr, 2015). The aim of formative pruning is to direct vegetative growth into the desired plant shape. In countries where high–density hedgerows are used, plants are pruned to a pyramidal shape (Potgieter, 2001). Where square planting systems with wider spacing are common, vase– or globed–shaped plants are formed (Inglese, 1995). These plants do not have main stems, resulting in large plants with a high number of terminal cladodes distributed around the outer portion of the canopy (Inglese *et al.*, 2002a).

Productive pruning

Productive pruning is used to maintain a good balance between vegetative and reproductive growth with an adequate number of new terminal cladodes for the subsequent year's blooming (Mulas and D'Hallewin, 1992). Environmental conditions, cultivar growth habit and plant spacing all affect canopy density (Inglese *et al.*, 2002a). Reduction of the canopy density through pruning facilitates orchard practices (e.g. fruit thinning, *scozzolatura*, harvesting) and contributes to improved fruit quality (Inglese *et al.*, 2002a, 2010). Plant height should preferably not exceed 1.8 m in order to avoid the use of ladders to perform orchard practices (Potgieter, 2001; Nasr, 2015).

Renewal pruning

In the case of old cactus pear plantations, senescence of the canopy and yield reduction with noticeable alternate yielding are common (Mulas and D'Hallewin, 1992). Rejuvenation of old plants can be achieved by cutting the plant back to a height of 0.5 m above soil level.

Only 3–4 well–spaced main scaffold branches should be left for development of the new plant. To prevent sunburn, the whole plant should be painted with white polyvinyl alcohol (PVA) paint, mixed 1 : 1 with water. With a large established root system, the plant resumes fruiting within 2–3 years after rejuvenation pruning (Wessels, 1988b; Mulas and D'Hallewin, 1992). The newly developing cladodes must be thinned to prevent cladode overcrowding.

Summer pruning

Complete removal of newly developing cladodes in spring is common practice in Sicily to reduce competition between fruit and vegetative growth. However, this practice may result in an alternate bearing pattern (Inglese and Barbera, 1993; Inglese *et al.*, 2002b). Summer pruning is not advisable in areas with cold winters, because cladodes developing late in the season would not have sufficient time to harden–off before winter when they would be subject to frost damage (Wessels, 1988b). However, in South Africa, thinning of some of the excess developing cladodes in spring and early summer is performed. Newly developing cladodes close to flower buds may cause chafing of the fruit epidermis, making it unmarketable due to cosmetic damage (Wessels, 1988b; Potgieter, 2001).

The best time to prune is after fruit harvest but not later than 2 months before floral bud break (Wessels, 1988b). Late pruning, especially in overcrowded trees, will result in cladodes not being exposed to sufficient PAR to make them fertile. In South Africa, pruning takes place from April to July (autumn/winter), when the plant is no longer actively growing (Wessels, 1988c; Potgieter, 2001). Similarly, in Mexico, Pimienta Barrios (1986, 1990) suggests pruning from November to March (winter).

Fertilization

Deficiencies in mineral nutrients affect cactus pear plant metabolism with a resultant negative impact on fruit yield and quality (Nerd and Mizrahi, 1992; Zegbe Dominguez *et al.*, 2014). In order to make fertilizer recommendations for cactus pear, it is essential to consider the plant nutrient status of the terminal cladodes as well as the available nutrient reserves in the soil.

Plant nutrition results reported for cactus pear fruit yield and quality are highly inconsistent and contradictory making fertilization recommendations challenging. Cactus pear plants differ from most other crop plants, both physiologically and morphologically; for this reason, fertilizer recommendations applied to other crops are of little use (Nobel, 1983, 1988; Magallanes Quintanar *et al.*, 2006). In the absence of agreement on cactus pear fertilization, **Table 3** provides growers with broad provisional soil and plant tissue analysis norms, while **Table 4** lays down general fertilization guidelines where no soil analysis results are available.

TABLE 3 Provisional soil and plant tissue norms for cactus pear fruit production

Soil parameter	Norm	Terminal cladode	Norm (% DM)
pH (water)	6.5–7.5	N	[b]
P (mg kg^{-1})	20–30	P	**0.1–0.3**
K (mg kg^{-1})[a]	80–100	K	**1.5–4.0**
Ca (mg kg^{-1})	> 400	Ca	**2.0–4.5**
Mg (mg kg^{-1})	100–150	Mg	**1.0–1.5**
Na (mg kg^{-1})	< 200	Na	**0.02–0.03**
Mn (mg kg^{-1})	30–70		
Ca/N	4.0		
K/N	3.4		
N/P	4.5		
Ca/Mg	3.0		

[a] If (Ca + Mg)/K > 8 (sandy soils) or < 5 (clay soils), apply K.

[b] Young trees (0–2 years): 0.6–0.8%. Mature trees (≥ 3 years): 0.9–1.3%.

TABLE 4 Provisional fertilizer recommendations for fruit production where no soil analysis results are available (plant nutrient amounts in kg ha^{-1} year^{-1})

Nutrient element	Year 1	Year 2	Year 3	> Year 4
N	50	50	70	100
P	10	10	20	30
K	20	20	30	50
Mg	10	10	20	40

Mineral nutrition research on cactus pear in various countries shows that fertilizer application, both organic and inorganic, is generally beneficial in fruit production. Nutrient elements influence vegetative and reproductive phenology, fruit yield and quality in cactus pear, with macroelements having the greatest effect on fruit production (Zegbe Dominguez *et al.*, 2014; Arba *et al.*, 2015b). Of all the plant nutrients, N is the most limiting nutrient in cacti (Nobel, 1983), with the highest N values found in young fertile cladodes (Nobel, 1988). However, very high N concentrations (> 2.2%) in 2– and 3–year old cladodes may result in excessive vegetative growth with accompanying higher input cost, reduced cladode fertility, poor fruit colour development and uneven ripening (Potgieter and Mkhari, 2000; Inglese *et al.*, 2002a). Reported P and K plant tissue concentrations range from 0.06–0.3 to 0.06–3.5%, respectively (Nobel, 1983, 1988; Arba *et al.*, 2015b). Ca and K are the most plentiful mineral elements in the cladodes, potentially more abundant than N (Galizzi *et al.*, 2004). Furthermore, Mg in young cladodes can reach levels of 1.47% (Magallanes Quintanar *et al.*, 2006). Therefore, N, P, K, Ca and Mg are all potentially limiting factors in cactus pear fruit production if cultivated in nutrient–deficient soils (Magallanes Quintanar *et al.*, 2006). Nutrient concentration in cladodes is affected by fruit crop load, cladode position, plant age, plant tissue analysed and season (Nerd and Nobel, 1995; Gugluizza *et al.*, 2002a).

In cactus pear, an additional flower flush can be induced with the application of N just after the removal of the summer harvest. According to Nerd *et al.* (1993b), the number of flower buds increases with increasing N levels up to 120 kg N ha^{-1}, while the N concentration in the cladode tissue is positively correlated to the number of flowers formed. Nerd and Mizrahi (1995b) further found that the autumn flower flush is higher in younger (< 6 years) than in older plants. However, high production systems with two fruit harvests in one year from the same plant may have additional nutritional requirements (Groenewald, 1996).

Due to the synergistic relationship between fertilization and irrigation, fertilizer application should take place when adequate rainfall or irrigation is available (Nerd *et al.*, 1989; Mondragón Jacobo, 1999). In countries with a Mediterranean climate, fertilization takes place in winter (Barbera *et al.*, 1992a; Inglese, 1995) with fertigation applied throughout the year in Israel (Nerd *et al.*, 1991b). Nerd *et al.* (1989, 1991b) and Ochoa and Uhart (2006c) report that the application of NPK fertilizer in winter increases the production of floral buds the following spring. However, according to García de Cortázar and Nobel (1991), the best time to apply fertilizer is during the warmer months due to higher photosynthetic photon flux density (PPFD) in summer. In Mexico, half the N and all the P and K are applied with irrigation at the onset of floral budburst, and the other half of the N is applied after harvest (Zegbe Dominguez *et al.*, 2014). Under rainfed conditions (summer rainfall), half the N and K and all the P can be applied directly after fruit harvest and the remainder towards the end of March (Wessels, 1988b), while liming is carried out at any time of the year, but preferably at least 1 month after N fertilization (Claassens and Wessels, 1997).

Irrigation

The exceptional drought tolerance and high WUE of cactus pear plants (Han and Felker, 1997; Zegbe–Dominguez *et al.*, 2015) are the primary reasons for its popularity as a rainfed crop in many areas of the world with low rainfall and a shortage of irrigation water. Although the plant can survive in areas receiving 200 mm year^{-1} (Acevedo *et al*, 1983), the optimal rainfall range for cactus pear production is 400–600 mm year^{-1}, but soil type also plays a role in the actual plant water requirement (Le Houérou, 1992, 1994). Although considerable fruit yields can be achieved under low rainfall, rainfed conditions (Potgieter, 2007), supplementary irrigation of cactus pear is advisable in summer rainfall areas where < 300 mm year^{-1} is received (Mulas and D'Hallewin, 1997; Van der Merwe *et al.*, 1997). In addition, irrigation during periods of unfavourable climate – such as dry spells during the rainy season, or when spring rains are late – is advantageous (Wessels, 1988d). In a Mediterranean climate, where most rainfall is in winter, supplementary irrigation in summer is indispensable for high yield and good quality (Mulas and D'Hallewin, 1997; Homrani Bakali, 2013). Irrigation of cactus pear is therefore common practice in Italy, Israel, Jordan, Morocco, Chile and the winter rainfall areas of South Africa.

There are definite advantages with supplementary irrigation of cactus pear, especially during certain critical phases of plant growth and development. García de Cortázar and Nobel (1992), Mulas and D'Hallewin (1997) and Liguori *et al.* (2013b) all report the beneficial effects of irrigation on vegetative plant growth, cladode number and canopy size. Fruit yield per plant is generally higher in irrigated than in non–irrigated plants, and researchers ascribe higher yield to higher average number of fruit per cladode rather than to increase in fruit size (Mulas and D'Hallewin, 1997; Mondragón Jacobo *et al.*, 1995).

According to Nerd *et al.* (1989), delay in irrigation during winter when annual rainfall is < 300 mm results in a substantial reduction of cladode fertility, and off–season winter crop water shortages, particularly during FDP, may adversely affect fruit quality. Application of 2–3 irrigations of 30–50 mm each during FDP increase fruit size and fruit pulp percentage of cactus pear (Barbera, 1984, 1994; Zegbe Dominguez *et al.*, 2015). However, irrigation alone cannot compensate for a reduced fruit size when there is a high number of a fruits per cladode, making fruit thinning essential to achieve good fruit size (La Mantia *et al.*, 1998; Gugliuzza *et al.*, 2002a).

Nobel (1995) points out that as little as 10 mm rainfall is adequate to wet the soil in the root zone of cactus pear, resulting in the plant being able to efficiently utilize small quantities of rainfall. Wessels (1988b) notes that due to the shallow root system of the plant, irrigation amounts of 20–25 mm at a time should be adequate. There is limited information on field parameters for appropriate irrigation scheduling, and the amount and timing of water application vary substantially between countries (Felker and Inglese, 2003). Recently, Consoli *et al.* (2013) determined the crop factor (Kc) for cactus pear within a range of 0.5–0.6. Drip irrigation of 150–200 mm water per year seems adequate for the main summer crop in Argentina, while 4–5 irrigations per year are given for a *scozzolatura* crop (Ochoa and Uhart, 2006a). Gugliuzza *et al.* (2002b) report that 2–3 irrigations (60–100 mm) applied during FDP increase productivity and improve fruit quality, while two 50–80 mm applications of water during FDP are essential to achieve export fruit size in the *scozzolatura* crop (Inglese *et al.*, 1995a). According to Homrani Bakali (2013), 3 and 6 irrigations per year produce more fruit than just 1 per year in Morocco. In South Africa, Haulik (1988) suggess ≤ 3 supplementary irrigations per year: beginning in August to stimulate the reproductive flush, then at anthesis, and again in the early stages of fruit development. Where *scozzolatura* is practised, the first irrigation is given at floral induction (40 days before budburst), the next after flowering, then ≤ 5 weeks after fruit–set and during fruit maturation (Targa *et al.*, 2013).

Different irrigation systems are used in cactus pear orchards with drip and microsprinklers common in modern orchards (Inglese, 1995). Microsprinklers covering a fairly large soil surface area with small volumes are very suitable for cactus pear with its shallow and widespread root system (Potgieter, 2001; Snyman 2004, 2005), and they positively influence fruit size and quality (Inglese *et al.*, 2010). Although traditional irrigation methods, such as basin irrigation, may be less efficient, such systems may provide an easy and cheap solution for cash–strapped farmers if irrigation is required only 2–3 times per season (Wessels 1988b).

Cactus pear is sensitive to dissolved salts in its rooting zone and therefore the quality of irrigation water needs to be tested to determine its suitability. Nerd *et al.* (1991c) recommend that $NaCl$ in irrigation water for cactus pear not exceed 25 mol m^{-3} to avoid salinity problems. Water harvesting and mulching to improve the productivity of cactus pear are sound agricultural strategies to be used in arid areas with limited scope for irrigation and to conserve soil water. Mondragón Jacobo (1999) showed that where small water microcatchments are made in the area between plant rows, a great deal of runoff is prevented, leaving more water available for the plant and consequently resulting in higher fruit yields.

Fruit thinning

Fruit size in cactus pear depends on water availability (Barbera, 1984), cultivar differences (Potgieter, 2007; Zegbe Dominguez and Mena Covarrubias, 2010b), length of FDP (Barbera *et al.*, 1992a), mineral nutrition (Ochoa *et al.*, 2002) and, most importantly, cladode fruit load (Brutsch, 1992; Inglese *et al.*, 1995a). In contrast with many other fruit crops, very few cactus pear flowers abscise and 95% of the flowers that set become fruit, unless damaged by late winter frost. However, if crop load is not reduced by fruit thinning, individual fruit size is low and whole branches and cladodes may even break off due to the excessive weight. Fruit prices on local and export markets generally depend on fruit size, with larger fruits selling for higher prices. However, heavy thinning to four fruits per cladode may substantially reduce total fruit yield by as much as 58% without any fruit size increase, and it could even cause a second reflowering (Zegbe Dominguez and Mena Covarrubias, 2010a). According to Brutsch (1992), thinned cladodes produce larger fruit than unthinned cladodes, regardless of the number of fruit per cladode. Thus, good fruit size is achieved with a high fruit–set per cladode followed by timely fruit thinning to reduce the crop load.

In addition to a higher individual fruit mass (Inglese *et al.*, 1995a; Nasr, 2015), fruit thinning has other **advantages**:

- easier harvesting (Wessels, 1989);
- prevention of branches from breaking due to a heavy crop load (Wessels, 1988a);
- reduction of alternate bearing (Wessels, 1988b; Hester and Cacho, 2003);

- regular and earlier ripening (Inglese *et al.*, 2002b);
- increase in total soluble solids (TSS); and
- higher percentage of first class fruits (Zegbe Dominguez and Mena Covarrubias, 2009, 2010a, b).

Fruit thinning can take place as soon as the spherical fruit buds are distinguishable from the elongated vegetative buds (Wessels, 1988), but no later than 3 weeks after anthesis, as later thinning does not improve fruit size (Inglese *et al.*, 1995b; La Mantia *et al.*, 1998; Gugliuzza *et al.*, 2002a).

Investigations showed that export–sized fruits (> 120 g) can only be produced if no more than 6 fruit per cladode are retained (Inglese *et al.*, 1994b). Since not all cladodes are the same size, the norm in the South African commercial sector is to thin fruit to approximately 50–70 mm between fruitlets, rather than to a specific number per cladode (Potgieter, 2001). Leaving adequate space between developing fruits ensures less damage to adjacent fruits during the harvesting process, especially where specialized harvesting secateurs are used. Fruits that develop on the flat sides of the cladode need to be removed as they tend to have a long "fruit stalk", making packing more difficult. Excess fruits can be removed by hand using a polyvinyl chloride (PVC) glove and a sharp knife or pruning secateurs.

Out–of–season cropping

Floral induction in most perennial fruit trees is largely synchronized, resulting in a single harvest at a specific time of the year (Liguori and Inglese, 2015). However, one of the most remarkable characteristics of cactus pear is the capability of the plant to reflower at different times in the same season (Inglese, 1995; Inglese *et al.*, 2002a), naturally or after inductive practices have been applied (Nerd and Mizrahi, 1997). These out–of–season fruit are sold at substantially higher prices than those of the normal summer season (Mondragón Jacobo *et al.*, 2009). Successful application of crop manipulation techniques, such as *scozzolatura* and winter production, has considerably increased the provision of fruit from 5 to 9 months of the year on the local fresh produce markets of South Africa, although the volume is limited from May to September. Nevertheless, cactus pear fruit marketing is generally highly seasonal, with cultivars available for approximately 4 months per season (Inglese, 1995; Liguori and Inglese, 2015). **Increased fruit availability** on markets could be achieved by:

- growing cactus pear in diverse agroclimatic areas (Mondragón Jacobo *et al.*, 2009; Liguori and Inglese, 2015);
- using cultivars with different ripening periods (Brutsch, 1992; Gallegos Vazques *et al.*, 2006);
- improving post–harvest technology (Liguori and Inglese, 2015); and
- adopting crop manipulation techniques (Barbera *et al.*, 1992a; Brutsch and Scott, 1991).

Scozzolatura

The *scozzolatura* technique – discovered by chance in the early nineteenth century (Coppoler, 1827, cited by Barbera *et al.*, 1991, 1992a) – has since become standard crop practice in the cactus pear fruit industry in Italy (Barbera, 1995). Complete removal of all newly developing flowers and cladodes of the spring flush results in a second reflowering approximately 12–16 days later with fruits ripening 6–8 weeks after the spring flush (Barbera *et al.*, 1988, 1991, 1992b; Brutsch and Scott, 1991). Although the second flush normally sets fewer flowers than the spring flush, fruit are marketed when prices are higher (Brutsch and Scott, 1991; Barbera and Inglese, 1993; Boujghagh and Bouharroud, 2015), which to an extent compensates for the lower fruit yield. *Scozzolatura* brings numerous **advantages**, including:

- increased prices;
- improved fruit quality – in particular, improved fruit size, lower seed–to–pulp ratio and higher pulp percentage (Barbera *et al.*, 1992b; Hammami *et al.*, 2015; Boujghagh and Bouharroud, 2015);
- greater flesh firmness and more intense pulp coloration (Mondragón Jacoboet *al.*, 1995);
- more complex and compact plant architecture in addition to more fertile terminal cladodes and higher fruit yield (when practised from an early plant age).

The reflowering index, as defined by the ratio of second flush to first flush flowers (FII : FI), may vary greatly depending on the timing of spring flush removal (SFR) and the environmental conditions at removal (Inglese, 1995). The number of cladodes produced with scozzolatura may be 10–40% less than the spring flush and fruit yield can be as much as 50% lower than in the summer season (Nerd *et al.*, 1991b; Inglese, 1995). Indeed, *scozzolatura* can also have **disadvantages**, including:

- reduced yield;
- higher peel percentage (Mondragón Jacobo *et al.*, 1995) – possibly due to reduced temperatures during FDP (Inglese, 1995; Hammami *et al.*, 2015);
- lower TSS;
- increased peel cracking;
- lower titratable acids; and
- poorly coloured fruit (Inglese, 1995; Mulas, 1997).

A maximum of 25% of the spring season cladodes should be kept on the plant after *scozzolatura*, as a higher percentage reduces the reflowering rate of the following spring and promotes biennial bearing (Inglese *et al.*, 2002b, 1994a).

Climatic conditions, cultivar response and timing of flush removal are important factors affecting *scozzolatura*. Environmental conditions at removal time influence the degree of reflowering and may cause large annual variation in the reflowering response (Barbera *et al.*, 1991; Nieddu and Spano, 1992). For example, a lower reflowering rate may be obtained if high temperatures coincide with bud initiation which will result in more vegetative than reproductive buds (Nerd *et al.*, 1989; Nobel and Castaneda, 1998). In some countries, *scozzolatura* is performed with irrigation (Inglese *et al.*, 2002a) and N fertilization (Flores Valdez, 2003), or farmers may apply a once–off fertigation at SFR (Nerd *et al.*, 1993b). It is essential to select the most suitable cultivar for the technique, as reflowering may be low or even absent in some cultivars (Mondragón Jacobo, 2001; Targa *et al.*, 2013). The timing of the SFR affects the extent of reflowering, the ripening time and fruit characteristics (Barbera *et al*, 1992b). Inglese (1995) reported reflowering rates of between 0.7 for pre–anthesis flower removal and 0.5–0.3 for post–anthesis flower removal. Pre–bloom removal produces the highest reflowering rate (Brutsch and Scott, 1991), but the latest stage of removal normally gives the highest economic returns, although fruit yield may be lower than for other SFR times (Mulas, 1992; Boujghagh and Bouharroud, 2015). In addition to Italy (Barbera *et al.*, 1991), scozzolatura is also regularly practised in South Africa (Brutsch and Scott, 1991), Morocco (Boujghagh and Bouharroud, 2015) and Tunisia (Aounallah *et al.*, 2005; Hammami *et al.*, 2015). In other parts of the world, *scozzolatura* produced poor results. For example, *scozzolatura* under Mexican conditions with 'Cristalina'and 'Reyna' gave negative results (Mondragón Jacobo *et al.*, 1995); similarly, Ochoa *et al.* (2009) reported a very low reflowering index of 0.05 in Argentina with 'Amarilla sin espinas'.

Following the *scozzolatura* performed at SFR, the process can be repeated with the complete removal of the first *scozzolatura* cladodes and fruit (Inglese *et al.*, 2010). Liguori *et al.* (2006) demonstrated that the double removal of new fruits and cladodes induced a third flush of flowers and cladodes in late August with fruit production ripening in winter (January–March) in the Northern Hemisphere. Winter fruits obtained by double *scozzolatura* and covered under PVC polymeric film in late autumn were regular in size and flesh percentage, but with slightly lower TSS. However, the rate of the second reflowering was low (20–40%) (Liguori and Inglese, 2015). Low temperatures in December stop fruit growth and ripening; for fuit to develop normally, it is necessary to cover the plants with PVC tunnels (Liguori *et al.*, 2006).

Winter fruit production

Flowering of the cactus pear plant is not restricted to spring. A smaller budburst occurs naturally in Argentina (Inglese, 1995), California (Curtis, 1977) and Chile (Sudzuki Hills *et al.*, 1993), as well as in the hot subtropical areas of Limpopo, South Africa (Groenewald, 1996; Potgieter, 2001). In addition to the natural out–of–season budburst in areas with mild winters, a second flowering flush can be obtained: Nerd *et al.* (1993b) and Nerd and Mizrahi (1994) showed that following the main summer crop harvest, immediate irrigation and N application at a rate of 120 kg ha–1 produced an autumn budburst; production of flower buds increased with increasing rates of N application and was highly correlated with the soluble reduced N content in the terminal cladodes (Nerd and Mizrahi, 1994).

Although the winter crop gives yields 50–80% smaller than the main summer crop (Nerd *et al.*, 1993b), higher prices are obtained (Mondragón Jacobo and Bordelon, 1996). Groenewald (1996) reported that even without irrigation, this technique can be successfully applied under rainfed conditions such as in summer rainfall areas of South Africa.

Furthermore, the flowering response to N is affected by the age of the plants. Floral bud production is much higher in young plants (≤ 6 years) than in older plants (Nerd and Mizrahi, 1994). However, this technique is only feasible where winter temperatures are sufficiently high for fruit development (Nerd *et al.*, 1993b). The peel–to–pulp ratio is higher in winter than in summer fruit, due to the thicker peel (Nerd *et al.*, 1993b; Groenewald, 1996). Producers should take note that cultivars producing high fruit yields in summer (e.g. 'American Giant') do not respond at all to the applied N (Groenewald, 1996). In addition, pruning needs to be delayed until after winter fruit ripening, by which time flower buds of the main summer crop have already appeared, making pruning difficult (Groenewald, 1996).

Orchard sanitation

Winter cladode prunings, cladodes that break off during normal orchard practices and fruitlets removed during thinning need to be removed from the orchard on a regular basis and destroyed. Pruned cladodes should not be dumped near the orchard, as detached cladodes and thinned fruitlets form roots and begin to grow, serving as host plants for cochineal, *Cactoblastis* and various other diseases, which results in increased plant protection costs (Potgieter, 2001).

Productivity

The fruit yield of cactus pear is extremely erratic and yields vary greatly, not only between and within countries, but within orchards of the same cultivar. Fruit yields vary from 1–5 tonnes ha^{-1} under traditional methods to 15–30 tonnes ha^{-1} with intensive orchard practices under rainfed conditions of 400–600 mm per year (Monjauze and Le Houérou, 1965a). Fruit yield is relatively low in most of the plantings in Mexico (2–8 tonnes ha^{-1} – Pimienta Barrios, 1990, 1994); however, some irrigated orchards may yield 25 tonnes ha^{-1} (Gallegos Vazques *et al.*, 2009). In Chile, fruit yields are generally low (6–9 tonnes ha^{-1} – Saenz, 1985), while in Argentina they range from 8–11 ha^{-1} (rainfed) to 22 tonnes ha^{-1} (irrigated) (Ochoa, 2003). Total fruit yields in excess of 50 tonnes ha^{-1} have been reported in the Karoo, South Africa (Brutsch, 1979) and Texas, the United States of America (Parish and Felker, 1997). In other rainfed areas of South Africa, such as the Free State Province, the highest mean fruit yield obtained was 17.44 tonnes ha^{-1} in a trial comparing 42 cultivars (Coetzer and Fouche, 2015). In Israel and Italy, yields of 20–30 tonnes ha^{-1} are regularly reported (Barbera and Inglese, 1993; Nerd *et al.*, 1993b).

If well managed, orchards can have a life span of > 100 years, as witnessed in North Africa (Le Houérou, 1994). Fruit yield is expected to increase yearly from planting through to approximately the fifth production year when plants have reached full maturity (Potgieter, 2007). Most of the flowers develop on 1–year terminal cladodes, while new cladodes usually develop on 2–year or older cladodes (Inglese *et al.*, 1994a; Wessels, 1988a). The fertility of the cladodes depends on environmental conditions, plant age and dry matter (DM) accumulation (García de Cortázar and Nobel, 1990; Inglese *et al.*, 2002b; Valdez Cepeda *et al.*, 2013). Cladodes with a higher than average DM content tend to produce more fruits (García de Cortázar and Nobel, 1992).

The possible reasons for high variability in fruit yield lie in four main areas: environmental conditions, genotype characteristics and their interactions, orchard planning and design, and orchard practices (Nerd *et al.*, 1991b; Inglese, 1995; Inglese *et al.*, 2002a; Potgieter 2007).

Environmental conditions

In contrast to vegetative growth, little is known about the influence of environmental factors on cladode fertility and fruit yield in cactus pear (Inglese *et al.*, 1995a; Nerd and Mizrahi, 1995b). According to Barbera *et al.* (1991), García de Cortázar and Nobel (1991), Nerd and Mizrahi (1995b) and Inglese *et al.* (2002a), cladode fertility depends on environmental conditions such as plant water status, temperature, photosynthetic photo flux density (PPFD) and soil nutrients. Wessels (1989) related **seasonal variation in fruit yield** to:

- differences in agroclimatic conditions (chill requirement, rainfall, temperature);
- differences in soil fertility status; and
- poor pollination and fertilization due to absence of pollinators and unsuitable climatic conditions during the pollination period (cold, rain).

Potgieter (2007) showed that soil P and soil N levels had the largest influence on fruit yield of 11 cactus pear cultivars. It is also well known that more than one crop can be obtained for the same environment by natural or artificially induced reflowering (Barbera *et al.*, 1991; Brutsch and Scott, 1991; Nerd *et al.*, 1993b; Sudzuki Hills *et al.*, 1993).

Genotype characteristics and interaction

Brutsch (1979), Pimienta Barrios (1990, 1994) and Wessels (1988a, 1989) indicated that cultivars differ in their reproductive vigour and cladode fertility. According to Wessels (1989) and Pimienta Barrios (1990), this **wide variation in productivity between cultivars** is due to:

- inherent genetic fertility differences;
- fertility of the mother plant; and
- cladode fertility of the mother plant.

On the other hand, **variation within a cultivar** is due to:

- variation in fertility of the mother plant; and
- fertility differences between cladodes according to position on the mother plant.

According to Barbera (1995), large variances in cactus pear fruit yield are due to inadequate understanding of **plant × environment interaction**. In an 8–year field trial with 11 cactus pear cultivars in three diverse agroclimatic areas in South Africa, Potgieter (2007) showed that there were significant differences between cultivars, diverse environments and production years in terms of fruit yield and its components. The variance observed in fruit yield was due first to soil P levels and second to applied N. The study results demonstrate clearly not only that environmental factors have a definite influence on fruit yield, but that there is strong interaction between the 11 cultivars tested and the environmental conditions. Broad cultivar adaptation was only seen in one cultivar and yielding ability in some cultivars is a genetic trait rather than a G × E response (Potgieter, 2007).

Orchard planning and design

Fruit productivity in cactus pear can be improved by increasing the number of fertile cladodes per plant and/or by increasing the plant population (Inglese *et al.*, 2002a). Extremely high fruit yields at an early plant age can be obtained at high plant densities. In Israel, spacing plants 1.5 m in the row and 4 m between rows (1 666 plants ha^{-1}) substantially increased the number of fertile cladodes in the early stages of orchard life, with fruit yields of 18 tonnes ha^{-1} for 4–year trees reported (Nerd and Mizrahi, 1993). According to Inglese *et al.* (2002a), to obtain an annual yield of 20 tonnes ha^{-1} – with an average fruit weight of 100–120 g and cladode fertility of six fruit per cladode after thinning – 28 000–30 000 fertile cladodes per hectare are needed. This implies 80–90 fertile cladodes per plant on free–standing plants spaced 6 × 5 m apart (335 plants ha^{-1}) or 28–30 fertile cladodes per plant for high–density hedgerow plantings with plants spaced 5 × 2 m apart (1 000 plants ha^{-1}) (Inglese *et al.*, 2002a). In order to further increase fruit yield, it would be necessary to increase the number of fertile cladodes rather than increase cladode fertility (Inglese, 1995).

Orchard practices

Large variations in fruit yield are regularly observed, even in well–managed orchards of the same cultivar (Potgieter, 2007). The low fruit yields reported in Mexico are partially due to the fact that a large percentage of growers do not use cultural practices such as fertilization and pruning, resulting in poor vegetative growth and low fruit yields (Pimienta Barrios, 1994). In comparison, the relatively high yields obtained in Sicily (14 tonnes ha^{-1}) are mainly due to irrigation, fertilization and thinning (Tudisca *et al.*, 2015).

Biennial or alternate bearing has been reported in cactus pear (Brutsch, 1979; Pimienta Barrios, 1990) and it is one of the reasons for large differences in annual fruit yield. Inglese *et al.* (1995) and Brutsch (1979) noted that the possible **reasons for alternate bearing** are:

- incorrect pruning;
- cultivar differences;
- plant age;
- competition between floral and vegetative growth; and
- bud induction timing.

Nevertheless, farmers prefer a cultivar that bears consistently – even if at a lower yield level – rather than a cultivar that bears well one year and poorly the next, as this pattern has a serious economic impact which negatively affects the cash flow position of the enterprise (Potgieter and Smith, 2006; Potgieter, 2007). Indeed, competition between reproductive and vegetative growth, as well as reduction in the number of new cladodes following SFR, are potential sources of plant alternate bearing behaviour (Inglese *et al.*, 2002b). Although Barbera *et al.* (1991) found that alternating plants in the off–year had the same number of 1–year cladodes as in the on–year, most of these cladodes were unfertile under scozzolatura conditions. Practical approaches for **reducing alternate bearing** are to:

- adopt appropriate pruning systems (García de Cortázar and Nobel, 1992);
- ensure fruit thinning regimes (Wessels, 1989; Hester and Cacho, 2003); and
- avoid *scozzolatura* and winter production on the same orchards every year.

HARVESTING

Quality is a very important factor in fruit production, since consumers prefer attractive fruit with a good taste and high nutritional and functional value. The overall quality is generally highest at harvest; it then declines at rates which vary according to genetic background, pre–harvest treatments, environmental conditions, degree of maturity at harvest, handling processes, post–harvest treatments, and storage and distribution conditions. Overall quality includes a very complex set of features not always positively correlated: depending on the targeted consumers, market destination and planned storage time, the importance of the various qualitative aspects varies. As the fruits mature, their nutritional value, flavour and taste improve, but the tissue's natural defence mechanisms against pathogens, susceptibility to some physiological disorders and potential life span all decrease. Therefore – as with other species (Crisosto and Valero, 2008) – for direct delivery to local markets, harvest should take place when the highest eating quality is reached; for delivery to distant markets, earlier harvesting is more appropriate to prolong the post–harvest life span.

In order to identify the best harvest time, objective and subjective maturity indexes have been developed, based on factors such as cultivar, producing country, fruit destination and utilization. The most popular harvest maturity indexes include:

- percentage of peel colour–break;
- total soluble solids (TSS) ≥ 13%;
- pulp firmness (measured with an 8–mm plunger) ≥ 8 kg cm^{-2} (Pimienta Barrios, 1990; Barbera *et al.*, 1992);
- reducing sugar level around 90% of that of full ripe fruit – however, in some cultivars the reducing sugars never exceed 50% of the total sugars (Pimienta Barrios and Mauricio, 1989);
- abscission of glochids;
- flattening of the floral cavity of the receptacle;
- percentage of pulp;
- peel thickness and ease of removal; and
- peel resistance to physical handling (Cantwell, 1995).

Cactus pears are particularly difficult to harvest because of the presence of glochids and spines, which can pierce the skin and enter the eyes and respiratory tract. Fruit are therefore harvested in the morning when humidity is sufficiently high to prevent glochids from dislodging and floating in the air. Pickers should be provided with protective clothing (gloves and safety glasses). Despite the plant's tough appearance and its ability to withstand harsh environmental conditions, the fruit are very tender and cannot withstand rough treatment (Wessels, 1992a).

For most cultivars, the physiological loosening of the articulation connecting the fruit to the mother cladode is low at harvest time, and injury at the stem end is inevitable if the fruit is harvested by snapping, pulling or twisting. Therefore, for commercial purposes, a knife must be used, a sharp cut made at the base of the fruit and a small piece of cladode left attached. Pickers usually collect the fruit in plastic baskets or lugs and empty them into plastic boxes holding 15–20 kg of fruit for transport to the packing house.

Physical damage during harvest and transport can markedly compromise fruit quality and storage length and increase fruit susceptibility to physiological disorders and decay. Bruises and wounds can occur due to finger pressure when cutting the fruit or impact when fruit are dropped into the baskets, and also during transport and handling in the packing house. Injuries are also inflicted by cutting and by glochids. The susceptibility of fruit to physical injuries increases with maturity. High cellular pressure can also cause cracks and microcracks of the peel, especially in second–crop fruit, which ripen in more humid environmental conditions.

Post–harvest handling

The presence of spines and glochids is one of the main constraints limiting cactus pear consumption and marketability; worldwide, their removal is the primary post–harvest operation before commercialization. In many countries, especially with fruit destined for the local market and consumed within a few days of harvest, despination is still done manually: the fruit are spread on the grass or areas covered with straw, and then the fruit are brushed with brooms (Cantwell, 1995). However, with fruit destined for distant markets, despination is done in packing lines.

Unlike other kinds of fruit, post–harvest operations of cactus pear are quite simple and restricted to despination, grading and packing. Regardless of the scale of the packing house, despination is generally accomplished by dry brushing. Given the limited post–harvest treatments, the production of several associated growers can be handled in a small–scale on–farm packing house with a **small, simple packing line** comprising the following components:

- dumping devise – fruit are dry–dumped before passing onto a series of rollers;
- tunnel – a series of brushes, each one rotating in the opposite direction to the next, remove the glochids, which are either vacuum–sucked out of the unit and deposited in a disposable bag or left to drop beneath the rollers;
- second set of rollers – fruit are conveyed onto a large round rotating table, where workers sort, grade and package them.

Larger packing houses comprise the following:

- dumping area;
- moving conveyer belt – workers preselect fruit;
- despining section – designed with the same criteria as for a small–scale packing house;
- sizing devise – either mechanical or electronic;
- delivery and packing devise – for final sorting and packing.

Fruit are usually packaged on the day of harvest and directly delivered to destination markets in refrigerated conditions. They can be transported alone or in combination with other commodities, by truck, ship or aircraft. When fruit are handled a few days after harvest, they can be stored at ambient conditions for curing or in storage rooms at 6–10 °C. In a small number of countries (e.g. South Africa), fruit are waxed to replace the natural waxes lost with despination, in order to reduce transpiration and enhance skin gloss. No synthetic fungicide is registered for post–harvest purposes; therefore, much care must be taken to avoid injuries and prevent microbiological decay.

In Italy, **fruit grading** is based on:

- cultivar ('Gialla' or 'Surfarina'; 'Red' or 'Sanguigna'; and 'Bianca' or 'Muscaredda' or 'Sciannarina');
- category (EXTRA and I); and
- weight (class B, 105–140 g; class C, 140–190 g; class D, 190–270 g).

Depending on the cultivar, peel shades can range from green to orange–yellow for the yellow cultivar ('Gialla'), from green to ruby–red for the red cultivar ('Rossa') and from green to straw–white for the white cultivar ('Bianca'). Depending on producing area, fruit destined for the fresh market must have the following characteristics:

- weight ≥ 120 g
- TSS ≥ 13–14% °Brix
- flesh firmness ≥ 6 kg cm^2

Larger fruit can be packed in one–layer plastic nest trays inserted in carton or plastic trays or directly in carton trays. Small fruit, generally destined for local markets, are packaged in plastic trays or punnets containing 6–8 fruits.

Post–harvest physiology

Cactus pears are classified as non–climacteric, as they do not exhibit a rise in respiratory activity during the ripening period. Respiration rates are generally considered quite low compared with other fruits (Lakshminarayana and Estrella, 1978; Cantwell, 1995). However, respiratory intensity is strongly affected by:

- genetic background (quite wide in cactus pear);
- ripening stage at harvest;
- crop type; and
- environmental conditions.

In a study of different varieties from the Mexican germplasm conducted by López Castañeda *et al.* (2010), respiratory activity ranged from 22 in 'Rojo Pelón' to 31 ml CO_2 kg^{-1} hour^{-1} in 'Sangre de Toro' and 'Alfajayucan'. In studies conducted in Italy with fruit from the first crop of 'Gialla', respiration intensity showed very pronounced variability from year to year, ranging from 4–14 mg CO_2 kg^{-1} hour^{-1} (Chessa and Schirra, 1992) to 13 ml CO_2 kg^{1} hour^{-1} (D'Aquino *et al.*, 2014) and 60–92 mg CO_2 kg^{-1} hour^{-1} (Piga *et al.*, 1996). As in other non–climacteric species, respiration declines gradually when fruit are held at warm temperatures (D'Aquino *et al.*, 2014), but when moved from cold storage to room temperature, respiration increases greatly (Schirra *et al.*, 1999b) in response to chilling temperature. Incipient infections from microorganisms, and physical or mechanical stresses caused by bruising, impact or wounds, can also lead to sudden increases in respiratory activity. Ethylene production is very low, generally 0.1–0.2 µl C_2H4 kg^{-1} hour^{-1} and, as for respiration, significant increases may occur after prolonged exposure to chilling temperatures, or because of pathogen infections or abiotic stresses (D'Aquino *et al.*, 2104; Schirra *et al.*, 1996, 1997).

As with most non–climacteric fruit, cactus pear does not contain starch. Therefore, after harvest, TSS, sugars and organic acids tend to decrease, depending on storage conditions, ripening stage and cultivars; the pattern of decline can be gradual or uneven. For example, in a comparative study with six cultivars of cactus pear stored at 9 °C for 1, 2 or 3 months plus 4 days at room temperature, the loss of TSS was very high in 'Amarillo Montesa', 'Copena T–5' and Copena–Torreoja', but gradual in 'Cristalina' and 'Pinochulo', while in 'Burrona' losses were highest during the first month of storage (Corrales Garcìa *et al.*, 1997).

Vitamin C content at harvest ranges from about 10 to 80 mg 100 g^{-1} depending on the cultivar (Butera *et al.*, 2002; Kuti, 2004). It can vary greatly from year to year (Sumaya Martìnez *et al.*, 2011), but also depends on the ripening stage. In fruit of yellow and orange cultivars of Opuntia megacantha harvested at 2–week intervals, 4 weeks before commercial maturity and then 4 weeks after commercial maturity, the vitamin C content increased constantly even when fruit were overripe (Coria Cayupàn *et al.*, 2011). In fruit stored at low temperature, the vitamin C content is quite stable despite the relatively high pH of the juice (Schirra *et al.*, 1996), but it declines rapidly at room temperature (D'Aquino *et al.*, 2014) or after fruit are moved from cold storage to warm temperatures (Schirra *et al.*, 1996).

Physiological disorders

Similar to most species of tropical origin, cactus pear is susceptible to chilling injury when exposed for prolonged periods to temperatures below 10–12° C. Indeed, the intrinsic **sensitivity of fruit to low temperature** is markedly affected by:

- environmental conditions;
- agronomic practices;
- crop type (summer or late crop); ripening stage at harvest; cultivar; and
- post–harvest treatment.

Generally fruit at an advanced stage of maturity are less susceptible to chilling injury than less ripe fruit, while pre–harvest treatment with gibberellic acid (Schirra *et al.*, 1999a) or calcium chloride (Schirra *et al.*, 1999b) do not affect or increase fruit susceptibility to chilling injury. Symptoms of chilling injury can manifest on the peel as scalded or bronzed areas varying in size and intensity, black–brownish pits and sunken brown spots (D'Aquino *et al.*, 2012). However, chilling injury can also cause metabolic alterations in addition to visible symptoms; likewise, the appearance and severity of peel disorders are accompanied by non–visible qualitative alterations. Indeed, peel alterations are usually a combination of disorders induced by low temperature and other causes (superficial wounds inflicted by glochids, excessive transpiration, dry rots) that can appear at non–chilling temperatures (D'Aquino *et al.*, 2012, 2014). Metabolic imbalances may alter the respiratory metabolism, induce the production of undesirable volatiles (acetaldehyde, ethanol) and ethylene, and lower the overall host defence mechanisms to pathogens (Schirra *et al.*, 1999a; D'Aquino *et al.*, 2014). As a result, chill–injured fruit may show peel disorders without any change in eating quality or chemical composition (D'Aquino *et al.*, 2014); or they may show negligible symptoms of chilling injury at the end of cold storage but become highly susceptible to decay when moved to warm temperatures (Schirra *et al.* 1996, 1997, 1999b; D'Aquino *et al.*, 2014).

Post–harvest decay

Fruit composition and tissue consistency make cactus pear highly susceptible to decay incited by various pathogenic fungi, yeast and bacteria. The stem end is the main site of infection due to wounding caused by harvesting operations. However, a curing treatment of 1–2 days at room temperature in ventilated conditions helps heal wounded tissue. Even a slight dehydration of the little piece of cladode left at harvest can effectively reduce the risk of decay (Cantwell, 1995; Inglese *et al.*, 2002a). Other sites of infection are the microwounds caused by glochids and microcracks in the peel, especially if second–crop fruit are harvested under wet conditions. The main filamentous fungi that cause decay are *Botrytis cinerea*, *Fusarium* spp., *Aspergillus* spp. and various *Penicillium* species, including *P. digitatum*, *P. italicum*, *P. expansum* and *P. polonicum* (Chessa and Barbera, 1984; Rodriguez Felix *et al.*, 1992; Granata and Sidoti, 2000; Swart *et al.*, 2003; D'Aquino *et al.*, 2015; Faedda *et al.*, 2015a). However, since fruit are generally not stored for long periods, the risk of decay does not represent a serious problem.

Post–harvest treatments

Despite limited treatments at commercial level and occasional refrigeration for short periods, the increasing worldwide demand for cactus pear – especially from markets located far from producing areas – will pose new challenges for the cactus pear industry in the future. In order to extend the market window beyond the harvest season and delay the decline in appearance, appropriate **post–harvest treatments and handling procedures** are required to:

- reduce transpiration and respiration rates;
- increase fruit tolerance to chilling temperatures; and
- prevent microbiological spoilage.

While refrigeration is undoubtedly the main means for prolonging the post–harvest life of fresh fruit and vegetables, the susceptibility of cactus pear to chilling injury poses limits to its use. On the other hand, as with other commodities, as storage life increases, the natural defence mechanism of tissue against pathogens declines and fruit become progressively more susceptible to microbiological attacks, especially when moved from cold storage to a warm environment.

Experiments conducted with post–harvest fungicides approved for other commodities revealed various degrees of effectiveness in reducing decay incidence in cold–stored cactus pears:

- Benomyl, captan or vinclozolin treatments were ineffective in controlling post–harvest decay (Gorini *et al.*, 1993).
- Imazalil (IMZ) and thiabendazole (TBZ) treatments prevented natural decay induced by *Penicillium* spp., *Botrytis cinerea* and *Alternaria* spp. in first–crop 'Gialla' fruit over a 2–month storage period at 8° C followed by 1 week of simulated marketing conditions at 20° C; chilling injury symptoms were also reduced (D'Aquino *et al.*, 1996). Sodium ortophenilphenate, either alone or in combination with TBZ or IMZ, was phytotoxic, resulting in increased decay and weight loss (D'Aquino *et al.*, 1996). TBZ efficiency was markedly increased when applied at 52° C even at a concentration six times lower than that applied at 20° C (Schirra *et al.*, 2002).
- Fludioxonil, a synthetic fungicide registered over the last decade to control a wide range of decay–causing fungi in different commodities, very efficiently controlled decay when applied at 20 or 50 °C before storage; on the other hand, its effectiveness was reduced when it was applied at the end of cold storage (D'Aquino *et al.*, 2015).
- Hot water – either as dip treatment at 50–55° C for 2–5 minutes (Schirra *et al.*, 1996, 2002; Rodriguez *et al.*, 2005; D'Aquino *et al.*, 2012) or by water brushing at 60, 65 or 70° C for 30, 20 or 10 seconds, respectively (Dimitris *et al.*, 2005) – inhibited the growth of pathogens naturally present on the fruit surface.
- Curing (at 38° C for 24, 48 and 72 hours in a vapour–saturated environment) not only controlled decay, but also improved fruit sensitivity to chilling temperatures (Schirra *et al.*, 1997). Yet, curing the fruit at 38° C with 75–80% relative humidity (RH) hastened detachment of the piece of mother cladode left at harvest. Additionally, the healing process of the stem–end scar with respect to curing at the same temperature but with 100% RH decreased decay incited by pathogens developing from the stem (D'Aquino *et al.*, 2014). High temperature conditioning delayed fruit ageing and weight loss, possibly due to melting and rearrangement of the epicuticular wax layers with consequent filling of microcracks separating wax platelets, the main fruit transpiration pathway (Schirra *et al.*, 1999a; López Castañeda *et al.*, 2010).

Other treatments which can delay loss of freshness and increase tolerance to low temperature are: controlled atmosphere storage (Testoni and Eccher Zerbini, 1990); intermittent warming (Chessa and Schirra, 1992); salicylic acid dip treatments (Al Qurashi and Awad, 2012); and film wrapping (Piga *et al.*, 1996, 1997; Shumye *et al.*, 2014), although the latter may induce anaerobic conditions and a build–up of undesirable volatiles (Piga *et al.*, 1996) if film permeability to gases does not match the O_2 requirement of packaged fruit.

READY–TO–EAT CACTUS PEAR

Over the last two decades, the fresh–cut fruit market has seen steady growth due to consumers' tendency to eat healthy and convenient foods at any moment and in any place. Ready–to–eat fruit and vegetables are attractive because the consumer requires no labour and generates no waste through peeling and coring (Rojas Graü *et al.*, 2011). This is particularly relevant in the case of cactus pear, where the presence of glochids makes the fruit difficult to peel, especially for people not familiar with it.

Fresh–cut fruit and vegetables are very perishable products; wounds caused by processing operations stimulate respiration and ethylene production rates, hastening the loss of respirable substrates, firmness and senescence.

Damaged tissues are also subject to oxidative browning due to the enzyme polyphenol oxidase (PPO) (Beaulieu and Gorny, 2004). The increasing demand for fresh–cut cactus pear has had a marked impact on companies involved in processing and distribution: more attention is paid to hygienic requirements and new packing solutions are adopted to meet logistics and consumer requirements (Timpanaro *et al.*, 2015a).

The main factors affecting the quality of fresh–cut cactus pear are loss of acidity, firmness, juice leakage and, above all, microbiological spoilage. Spoilage is a considerable hazard, especially when there is contamination by pathogenic microorganisms with potentially harmful effects on consumer safety (Yahia and Sàenz, 2011). When fruit are stored at the optimal temperature of 4–5°C, TSS are quite stable and sometimes increase; on the other hand, titratable acidity and juice pH are quite stable but may decrease (Piga *et al.*, 2000). Higher temperatures reduce the potential storage life, while increased O_2 requirements due to increased metabolic activity may not be matched by the packaging permeability to gases, leading to abnormal increases in titratable acidity, ethanol and taste alterations as a result of anaerobic respiration (Piga *et al.*, 2000).

Its low acidity and high sugar content make cactus pear – more than any other fruit – an ideal substrate for microbiological proliferation. In order to maintain bacteria and yeast populations below the legal limits of 10^7 and 10^8 CFU g–1 established in Spanish legislation (BOE, 2001), it is essential to use appropriate processing equipment and adopt an effective sanitizing programme, with personnel trained in hygienic processing and maintenance of low storage temperatures. Surface sterilization of the fruit surface prior to peeling is generally achieved by dip treatments in sodium hypochlorite; however, new alternatives that are safer for workers and consumers as well as environmentally friendly and cheap, such as electrolyzed water (Pannitteri *et al.*, 2015), are gaining in popularity.

Provided processing operations maintain low initial microbiological load, storage temperature is the main factor affecting the microbiological population. The recommended storage temperature range of 8–12° C to prevent chilling injury of the whole fruit is not optimal for storage of ready–to–eat cactus pear; indeed, the best results in terms of maintenance of overall chemical, sensory and microbiological quality are at 4–5° C (Piga *et al.*, 2000; Corbo *et al.*, 2004; Del Nobile *et al.*, 2007; Cefola *et al.*, 2014). The permeability of the film used for packaging and in–package gas composition have a minor impact on chemical composition and microbiological population when fruit are stored at 4–5° C. However, temperature increments and reduced levels of O_2, coupled with increased concentration of CO_2, may lead to anaerobic conditions and in turn induce production of undesirable volatiles, compromising the sensory quality and altering the microbiological population both quantitatively and qualitatively (Piga *et al.*, 2000; Del Nobile *et al.*, 2009).

Coatings based on sodium alginate, agar and fish protein gel did not affect yeasts and mesophilic bacteria but stimulated the load of lactic acid, psycrothrophic and coliform bacteria (Del Nobile *et al.*, 2009). When acetic acid was combined with chitosan, an overall decrease in the microbial population was achieved compared with the control fruit (Ochoa Velasco and Guerrero Beltrán, 2014). Coating fresh–cut cactus pear is not common at commercial level and the literature indicates no clear and consistent benefits from their application (Del Nobile *et al.*, 2009; Ochoa Velasco and Guerrero Beltrán, 2014; Palma *et al.*, 2015).

Storage response may also be affected by the stage of ripeness and the ripening time of the fruit. The overall quality of the summer crop declines faster than that of the *scozzolatura* crop, while fruit harvested at the commercial stage maintains its quality longer than fruit harvested later, when fully ripe, especially in the case of fruit coming from the *scozzolatura* crop (Allegra *et al.*, 2015). Both aerobic mesophilic bacteria and mould population are affected more – albeit in different ways – by the stage of ripeness than by the time of ripening, with fruit harvested at an advanced stage of maturity showing a higher load than fruit harvested at the commercial stage (Allegra *et al.*, 2015).

CONCLUSIONS AND FUTURE PERSPECTIVES

While there has been a general improvement in orchard practices over the past two decades, much remains to be done to convince producers that cactus pear can achieve high yields and good quality if it receives appropriate care and attention – just like any other crop. It is hoped that by providing the latest technical and scientific information on the cultivation and post–harvest management of the crop, productivity levels and especially fruit quality standards worldwide will improve, enabling the fruit to compete on an equal footing with other mainstream fruits on international markets. In order to attract new consumers to cactus pear fruit and create higher demand, consistent high–quality fruit must be available on the market. Increased fruit productivity is easier to achieve than improved fruit quality; special attention should be therefore given to all horticultural practices potentially affecting fruit quality, both pre– and post–harvest.

Figure 1
Cumulative growth cDespination of cactus pear fruit by rotating brushes: besides removing glochids the brushed make the fruit shiny.

Figure 2
Sorting table used to sort, grade and pack the fruit

Figure 3
Chilling injury as scald staining (a) and tissue depression underneath the peel around the receptacle scar (b).

Figure 4
Chilling injury symptoms in the form pits (a) and brownish scars (b).

Figure 5
Fruit splitting occurring in fruit stored at high humidity levels.

Figure 6
Soft rot on cactus pear starting from the stem end.

Figure 7
Decay caused by Penicillium spp. in cold stored cactus pear.

Figure 8
Dry rot (Alternaria spp.) develops slowly in cactus pears stored for long time.

Figure 9
Preparation of ready–to–eat cactus pears: fruit are first manually peeled and placed in plastic punnets (a) and then sealed with a polymeric film (b).

07

Forage production and supply for animal nutrition

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07

Forage production and supply for animal nutrition

INTRODUCTION

Livestock production remains the main source of income for rural populations living in drylands. It is a key component of resilient production systems and is an indicator of wealth. However, the sector faces many challenges including feeding constraints and climate change. Rangelands in semi–arid regions play an important role in livestock production systems, although their contribution to animal feeding is decreasing. Rangeland productivity is usually low (< 5 tonnes dry matter [DM] ha^{-1} $year^{-1}$) with low yields of consumable biomass (< 1 tonne DM ha^{-1} $year^{-1}$), leading to low carrying capacity (12–15 ha to sustain an adult cow) (Dubeux *et al.*, 2015a). Adapted perennial species are a potential option for improving fodder availability in dry areas. The global livestock population has steadily increased in recent decades, often resulting in rangeland degradation. Water scarcity is another important limiting factor in drylands, threatening the sustainability of livestock–based systems. Global projections indicate that water use will increase in the coming decades; there will, therefore, be less water available for agriculture and livestock production.

Figure 1
Wild cactus in San Luis Potosí, Mexico (photo credit: Ali Nefzaoui)

In this scenario, cactus becomes one of the most prominent crops for the twenty–first century. Cactus, a succulent and drought–tolerant species, can produce > 20 tonnes DM ha^{-1} $year^{-1}$ and provide 180 tonnes ha^{-1} $year^{-1}$ of water stored in its cladodes, representing a cost–effective option for livestock watering (Dubeux *et al.*, 2015b). At such levels of productivity, it is possible to produce sufficient forage to sustain five adult cows per year – at least a 60–fold increase over rangeland productivity. With small, intensively cropped cactus orchards, it is possible to produce feed and reduce the pressure on overstocked rangelands. The potential of cactus, however, remains underexploited. Major cactus species used as fodder include *Opuntia ficus–indica* Mill. and *Nopalea cochenillifera* Salm–Dyck., with several varieties released in different countries.

There are reports of the successful use of cactus as a feed source in countries ranging from Brazil and Mexico to South Africa and Tunisia, usually supported by strong research and extension programmes. To achieve success, it is essential to involve all stakeholders in the livestock production chain, including producers, suppliers, retail stores, research and extension institutions, and policy–makers. The livestock feed market is growing, and it involves fewer risks than the fruit and vegetable market, representing, therefore, potential for entrepreneurial activity. In some countries, cactus cladodes from pruned fruit orchards can be used as livestock feed, complementing the farmer's income. In general, the forage potential of cactus in semi–arid areas is underutilized. There are tremendous opportunities to develop cactus–based livestock production systems, promoting human livelihood and reducing the pressure on natural rangelands.

CACTUS–BASED FOR AGE PRODUCTION SYSTEMS

Given the lack of information on cactus surface areas in different agro–ecologies, it is not possible to make a full assessment of the importance of cactus within the various production systems. For example, data on native cactus or the role of cactus in defensive hedges and copses are important, but rarely reported.

Native

The largest area of native cactus is located in Mexico and covers an estimated 3 million ha. Livestock often go to graze in these areas and no special treatment is applied. In some countries, cactus species may become invasive and plantations are used in a similar way to native plantations – for example, in Tigray, Ethiopia, livestock graze directly the thorny cactus.

Defensive hedges and copses

Little is known about this form of cactus plantation, but it clearly has an important role in many countries, especially in North Africa and parts of Italy and Spain, where many farms are protected by biological fences using thorny cactus.

In addition to their efficient defensive role, these hedges have traditionally played an important part in landscape organization and the local socio–economy as evidence of land rights and land ownership in countries or regions where collective land ownership is prevalent, such as in North Africa. Cactus hedges are often planted as proof of land ownership. Moreover, they contribute to erosion control, particularly when established along contours (Le Houérou, 2002).

Cactus plantations also take the form of a copse around rural houses. This kind of “close–by” plantation is a source of feed for family livestock, as well as providing fruit for self–consumption and shelter for family poultry.

Mixed fruit–forage

This is the most common and most widespread system. It is prevalent in almost all countries where environmental conditions allow cactus growing and cropping cactus is part of the local knowledge and tradition. There are two main types of plantation: intensive specialized fruit orchards, where the production objective is to produce good quality fruits for the local market or export; and orchards with low inputs, where fruits are mainly for self–consumption or the local market. In both cases, pruning provides large amounts of cladodes that are sold and/or utilized at farm level to feed the livestock.

Rangeland rehabilitation

Rangeland improvement using spineless cactus has been practised mainly in North Africa since the early 1930–1940s. Le Houérou (2002) reports that fodder plantations were systematically developed, in particular in Tunisia, on the basis of the research conducted by Griffiths and collaborators in Texas, United States of America. In 1932, the Government of Tunisia invited Griffiths and applied his 30 years of experience on the use of cactus as fodder in central Tunisia to mitigate the effects of drought on livestock. Furthermore, land allotment was authorized in central Tunisia on condition that the contracting beneficiaries, inter alia, planted 10% of the land allocated to spineless cactus to act as an emergency buffer and standing fodder crop reserve. This proved a wise decision, because the country faced 3 years of severe droughts during 1946–1948, when 70–75% of livestock were decimated – but not on farms with cactus plantations (Le Houérou, 2002).

From an agronomic view point, in order to rehabilitate or improve rangeland, shrubland, bushland or poor farming areas characterized by shallow, stony, steep or sandy soil or where the climate is too dry for practical farming, an appropriate planting strategy must be adopted: density of 1 000–2 000 single or double cladodes per ha, with a spacing of 5–7 m between rows and 1–2 m within rows. In general, no special treatments (e.g. fertilizer application, pruning and treatment against pests and diseases) are applied. Supplemental irrigation may be applied during establishment – but only if the first year is too dry. Plantations are exploitable after 3–4 years and fully grown after 7–10 years; if rationally managed, they can remain productive for > 50 years.

The productivity of a rangeland planted with cactus can be increased by a factor of between 1 and 10 when very degraded and between 1 and 5 when in good condition (Le Houérou, 2002); similar results are reported by Nefzaoui and El Mourid (2009). Impressive results are obtained with fast–growing shrubs (*Acacia cyanophylla*) or cactus (*Opuntia ficus–indica*) in central Tunisia (**Table 1**).

TABLE 1 Productivity of natural and improved rangelands in Tunisia (Nefzaoui and El Mourid, 2009)

Rangeland type	Productivity (forage unit per hectare and per year)[a]
Natural rangeland in Dhahar Tataouine, Tunisia (100 mm rainfall)	35–100
Private rangeland improved by cactus crop in Ouled Farhane, Tunisia (250 mm rainfall)	800–1 000
Cooperative rangeland improved through Acacia cyanophylla, Guettis, Tunisia (200 mm rainfall)	400–500

[a] One forage unit is equivalent to 1 kg barley grain metabolizable energy (12.4 MJ kg^{-1} DM)

Few plant species are able to increase land productivity at such a high rate, especially on marginal lands characterized by low rain–use efficiency (RUE, measured in kg DM ha^{-1} $year^{-1}$ mm^{-1}), for example (Le Houérou, 1984):

- degraded Mediterranean rangelands: RUE = 1–3
- rangelands in good condition: RUE = 4–6
- desert rangelands: RUE = 0.1–0.5

Cacti, however, have a high RUE. Rangeland rehabilitated with *O. ficus–indica* exhibits a RUE of 10–20 kg of above–ground DM ha^{-1} $year^{-1}$ mm^{-1} in arid areas where rainfall is 200–400 mm $year^{-1}$.

Alley cropping

Expansion of cereal cropping into rangelands and reduction in fallow practice are among the main reasons for declining soil fertility and wind erosion. One way of combating degradation resulting from cereal monocropping is the introduction of adapted forage legumes, fodder shrubs/trees and cactus in cropping systems (Nefzaoui *et al.*, 2011).

Alley cropping is an agroforestry practice where perennial crops are simultaneously grown with an arable crop (barley, oat etc.). Shrubs, trees or cacti are grown in wide rows (e.g. 10–15 m) with a crop in the interspace. Alley cropping is a variation of hedgerow intercropping. Leguminous and fast–growing tree or shrub species are preferred (Saraiva, 2014). Legume trees improve soil attributes (e.g. nutrient recycling, biological N_2–fixation), suppress weeds and control erosion on sloping land. Alley cropping allows the farmer to continue cultivating the land while the trees or shrubs planted in intermittent rows help maintain the quality of the soil. Cactus can act as a windbreak, resulting in improved grass and cereal yields. Wide alleys allow animals to graze the biomass strata or cereal stubbles in the summer, and cactus cladodes may be harvested, chopped and given directly to grazing animals as energy supplement to the low–quality stubbles (Nefzaoui *et al.*, 2011).

If properly managed, alley cropping can provide income at different time intervals for different markets in a sustainable, conservation–oriented manner. Alley designs can also make better use of the space available between trees and add protection and diversity to agricultural fields.

There is a low adoption rate of cactus orchards as monoculture for various reasons, from the technical design of plantations and mismanagement to competition for land often dedicated to cereal crops. However, alley cropping overcomes some of these constraints because it:

- improves soil fertility;
- increases crop yield;
- reduces weeds; and
- improves animal performance.

Properly managed alley cropping allows diversification and farmers can benefit from several markets. It also promotes sustainability in both crop and livestock production by increasing land productivity and reducing weather risks compared with cultivation of annual crops only. The benefits of cactus–barley alley cropping were evaluated in Tunisia (Alary *et al.*, 2007; Shideed *et al.*, 2007). Compared with barley alone, the total biomass (straw plus grain) of barley cultivated between the rows of spineless cactus increased from 4.24 to 6.65 tonnes ha^{-1} and of grain from 0.82 to 2.32 tonnes ha^{-1}. These results reflect the impact on the micro–environment created by alley cropping with cactus, in particular the beneficial "wind breaking" effect that reduces water loss and increases soil moisture. The barley crop stimulated an increase in the number of cactus cladodes and fruits, while the cactus increased the amount of root material contributing to the soil organic matter.

Tree legumes are another option for alley cropping with cactus. Tree legumes add N to the system, providing protein and fibre to cactus–based livestock diets. In Brazil, *Gliricidia* sepium or *Leucaena leucocephala* were used with cactus and a comparison was made with cactus planted in monoculture. Adding the legumes did not change the total biomass, but it did provide a diversified feed source (**Table 3**). Cactus and legumes can be grown locally in semi–arid areas, reducing dependency on foreign grain and increasing food security.

TABLE 2 Total biomass changes and barley crop yields in Sidi Bouzid (Tunisia)[a]

Treatment	Natural rangeland	Barley crop (alone)	Cactus crop (alone)	Alley cropping (cactus + barley)
Above ground biomass (tonnes ha^{-1})	0.51	0.53	1.87	7.11
Underground biomass (tonnes ha^{-1})	0.33	0.11	1.8	1.98
Barley grain yield, (tonnes ha^{-1})		0.82		2.32
Barley grain + straw + weeds (tonnes ha^{-1})		4.24		6.65

[a] Average rainfall in Sidi Bouzid is 250 mm $year^{-1}$. No fertilizers were applied to all treatments. Source: Alary *et al.* (2007).

TABLE 3 Biomass productivity in alley cropping with cactus and *Gliricidia sepium or Leucaena leucocephala*, Pernambuco, Brazil

Cropping system	Cactus biomass	Legume biomass	Total biomass
	tonnes DM ha^{-1} $year^{-1}$		
Cactus + *Gliricidia*	13.6[a]	4.2[a]	17.8[a]
Cactus + *Leucaena*	14.0[a]	2.6[b]	16.6[a]
Cactus	16.9[a]	–	16.9[a]
Standard error	1.0	0.2	0.8

[a,b] Means in the same column followed by similar small case letters do not differ by Tukey's test at 5%. Source: Saraiva (2014).

Figure 2
Example of alley–cropping technique using O. ficus–indica and maize (Photo credit: Jaime Mena)

Figure 3
Alley cropping with cactus and Gliricidia sepium, Pernambuco State, Brazil (tree legumes planted in rows, cactus planted between rows) (Photo credit: Jose Dubeux)

Intensive system (with or without irrigation, high density)

The intensive system for cactus fodder production is restricted to a small number of countries, prevalent mainly in northeast Brazil and a few areas in Mexico. Figure 4 illustrates an extreme example of intensification in Mexico, where cactus is cultivated under drip irrigation and fertigation on a dairy cattle farm (**Figure 4**).

Recent experiences in Brazil indicate that drip–irrigating 10 mm month^{-1} (2.5 mm week^{-1}) using water harvested through *in situ* water catchment increases productivity and enables the cultivation of cactus in areas where cactus growth was previously limited because of warm night temperatures and lack of soil moisture (Lima *et al.*, 2015).

Figure 4
Cactus plantation for fodder production (top); details of irrigation and fertigation equipment (bottom), Zacatecas, Mexico

AGRONOMIC PRACTICES

Ecological adaptation

Opuntias are native in a range of environments: from sea level in the Californian deserts to 4 700 m asl in the Peruvian Andes; from tropical areas of Mexico with temperatures always > 5° C to parts of Canada where temperatures reach as low as –40° C (Nobel, 1995). While cactus pear requires high soil fertility in order to reach its production potential, it also grows in poor soils. However, it does need well–drained soils and does not tolerate saline soils (Berry and Nobel, 1985).

Opuntias have a crassulacean acid metabolism (CAM) photosynthetic pathway: when exposed to water stress, cactus opens its stomata only at night to reduce water loss. Therefore, cooler nights (15–20° C) are beneficial for cactus development compared with warmer nights (> 25–30° C). Warmer temperatures increase the capacity of the air to hold water vapour, thus reducing relative humidity. Conversely, cooler temperatures increase atmospheric relative humidity and reduce the water loss from cactus. Nobel (1995) reported a reduction in atmospheric water–holding capacity from 39.7 g m^{-3} at 35° C to only 6.8 g m^{-3} at 5° C. Since night temperatures are also related to elevation, cactus grows better in highlands, because there is less water loss during the cooler nights. Rocha (1991) indicated that for every 100 m of elevation there is a reduction of 0.65° C in the average temperature.

Opuntia or *Nopalea* have the highest potential for fodder production compared with other species of cactus. Nopaleas often require greater rainfall (> 600 mm $year^{-1}$) than opuntias (> 400 mm $year^{-1}$). The interaction between rainfall and temperature at elevation affects the growth performance of cactus: at high elevation with cool nights, cactus requires less rainfall than on a site with warm night temperatures.

Establishment and varieties

Cactus is vegetatively propagated. Cladodes are used as propagative material and they preserve the genetic characteristics of the parent material. When establishing a cactus orchard, various factors should be considered, including: cactus variety, type of cladode used (i.e. primary, secondary or tertiary), number and position of cladodes, timing of planting, plant spacing, planting method, weed control, fertilization, and pest and disease occurrence. Management practices usually interact and they should be carefully analysed in a system approach.

Varieties indicated for forage production and adapted to the specific environmental conditions should be used, and variety trials need to be carried out in different locations and regions to select high–performing ones. It is important to take into account the prevalence of pests and diseases in some areas and choose the best variety for the region. In Brazil, for example, common varieties include 'Gigante' and 'Redonda' (*Opuntia ficus–indica* Mill.), but an outbreak of cochineal (*Dactylopius opuntiae* Cockerell) led to a change in the variety recommendation. Producers in the region are currently planting varieties tolerant to this insect ('Orelha de elefante Mexicana' – *Opuntia* spp.; 'Miuda' – *Nopalea cochenillifera* Salm–Dyck.). This is an example of an integrated approach, taking into consideration the different environmental limitations when choosing the most suitable variety.

Once the best variety has been identified, site selection is key for achieving success. The ecological characteristics must be taken into account, and the site should have well–drained soils and balanced soil fertility (Dubeux and Santos, 2005).

Planting usually takes place in the last third of the dry season in order to reduce the occurrence of plant pathogens, which are more common during the rainy season (Inglese, 1995; Farias *et al.*, 2005). Cactus cladodes planted during the dry season are able to develop the initial roots after planting, thus reducing disease incidence in the wet season. When planting material is harvested, it is recommended to leave it in the shade to allow the cut portion to heal and reduce disease incidence. Mondragón Jacobo and Pimienta Barrios (1995) recommend placing cladodes in the shade for 4–6 weeks before planting to heal the cut and reduce disease incidence. In Brazil, it is common to place cladodes in the shade for 5–7 days to achieve good results (Farias *et al.*, 2005). Fungicide (e.g. Thiabendazol at 60% or "Bordeaux mixture") can be used to reduce fungus disease (Mondragón Jacobo and Pimienta Barrios, 1995; Farias *et al.*, 2005). Mature cladodes from the intermediate portion of the plant should be used for propagation (Tapia, 1983).

If mechanization is available, cactus can be planted in furrows 15–20 cm deep. It is common, however, to use a hoe and dig individual pits, particularly in small farming systems. In general, one cladode per pit (or furrow position) is recommended; planting more cladodes per position may result in higher yields, but the higher establishment costs do not always justify the use of two or three times more planting material (Mafra *et al.*, 1974). Likewise, a half cladode may be planted, but productivity is usually reduced, particularly in the first harvest (Medeiros *et al.*, 1997). Depending on the cultivar, cladode mass varies, ranging from 0.5 to 1 kg for most *Opuntia* varieties, although heavier cladodes are often found. Cladodes from *Nopalea* varieties are usually lighter (0.3–0.7 kg).

Cladode position affects establishment. Mafra *et al.* (1974) tested three positions: horizontal, vertical or diagonal. While no difference in biomass production was revealed, lodging was observed when cladodes were placed horizontally at planting. Therefore, the authors recommend planting in a vertical or diagonal position, with one–third of the cladode buried. The orientation – north–south (N–S) or east–west (E–W) – of the cladodes may also be important. In Mexico, Rodrigues *et al.* (1975) observed that cladodes facing N–S produced less than cladodes facing E–W, and they ascribed the results to the greater light interception with E–W orientation. In Brazil, on the other hand, studies indicated no differences between N–S and E–W cladode position. Young cladodes actually take different directions, leading to a unique plant architecture that optimizes light interception. It is important to follow contour lines, particularly on steep slopes; cactus should face the slope to reduce soil erosion.

The recommended plant spacing varies according to the production system and environment. Cactus can be planted as a sole crop or intercropped with cash crops. Farias *et al.* (1989) tested different plant spacings for cactus intercropped with sorghum (*Sorghum bicolor* L.). Cactus cladodes were spaced at 3 × 1 × 0.5 m or 7 × 1 × 0.5 m, and sorghum was planted between rows. Cactus produced less biomass in the wider spacing, but sorghum compensated for the loss. If mechanization is available, this too should be taken into account when choosing the optimal spacing, which may also vary with location. In dryer areas, spacing should be greater so that the individual plants can build greater root mass, reducing risks during drought periods (Dubeux *et al.*, 2011a, b).

Sites with better soil fertility and greater rainfall are more suited for hosting high–density cactus plantations. Souza (2015) observed a linear increase in Nopalea cocheniliifera dry matter yield as population density was increased: from 10 417 plants ha^{-1} at 1.2 × 0.8 m to 83 333 plants ha^{-1} at 1.2 × 0.1 m. Linear responses to plant spacing were also observed by Silva (2012) for *O. ficus–indica* with the plant population ranging from 20 000 to 160 000 plants ha^{-1}. Even greater responses were observed under higher organic fertilization (80 tonnes ha^{-1} of cattle manure).

Fertilization

Cactus (*Opuntia* and *Nopalea*) has a high productivity potential, but it is only reached with appropriate fertilization (Silva, 2012). Nutrient extraction from cactus fields dedicated to forage production is high because cladodes are removed from the area in cut–and–carry operations. The concentration of nutrients in cactus cladodes varies depending on the cultivar, environmental conditions and management. Considering an average concentration (DM basis) of 0.9% N, 0.16% P, 2.58% K and 2.35% Ca (Santos *et al.*, 1990) and an annual productivity of 20 tonnes DM ha^{-1}, the nutrients exported (kg ha^{-1} year^{-1}) via harvested material would be 180 kg N, 32 kg P, 516 kg K and 470 kg Ca, without considering other macro– and micronutrients (Dubeux and Santos, 2005). Therefore, this nutrient demand must be matched by fertilization in order for the system to be sustainable over time.

Cactus often responds better to organic fertilization than to mineral fertilization (Méndez Gallegos and Martínez Hernandez, 1988; Santos *et al.*, 1996). There is usually interaction between fertilization level, plant spacing and environmental conditions; the larger the plant population, the greater the necessary fertilizer inputs. Cultivar 'IPA–20' (*Opuntia ficus–indica* Mill.) presented linear responses up to 80 tonnes ha^{-1} of cattle manure applied, with a plant population of 20 000 to 160 000 plants ha^{-1}. Greater responses were observed with the combination of higher organic fertilization and higher plant population. Intensive systems like this may reach annual productivity of > 50 tonnes DM ha^{-1} (Silva, 2012). Producers in northeast Brazil, however, usually apply 20–30 tonnes ha^{-1} of manure. Indeed, smallholders may not have access to large quantities of manure and there may also be reduced availability of both time and labour.

Manure should be incorporated into the soil (Inglese, 1995; Mondragón Jacobo and Pimienta Barrios, 1995) or surface–applied at planting and after each harvest. Saraiva (2014) evaluated different organic fertilizer sources (cattle, sheep and goat manure, and broiler litter) on cactus (*Nopalea cochenillifera* Salm–Dyck) development. Organic sources were applied at the same rate (200 kg N ha^{-1}) – although, given that N concentration differs among sources, the total amount actually varied – and the authors observed no difference in cactus productivity. Berry and Nobel (1985) evaluated mineral stress in two cactus species (*O. ficus–indica* and *Ferocactus acanthodes*) and observed that these species do not require high Ca levels in the soil solution. In fact, their development was not affected when the soil pH was 4.5–8.5. High levels of Ca observed in cactus cladodes reflect the high Ca–oxalates. Potassium is the nutrient extracted in greatest quantities due to its high concentration in cactus cladodes. Therefore, it is essential to replenish soil K after each harvest to maintain cactus productivity.

A combination of organic and mineral fertilizers might be the best option when less manure is available. Dubeux and Santos (2005) estimated that a nutrient deficit occurred in cactus orchards with a high plant population (40 000 plants ha^{-1}) and high productivity (20 tonnes DM ha^{-1} year^{-1}) if only 20 tonnes ha^{-1} of cattle manure were applied. Nobel *et al.* (1987) observed increased productivity (Opuntia engelmannii Salm–Dyck) with 160 kg N ha^{-1} and 80 kg P ha^{-1}. The authors also observed that boron significantly increased cactus yield. Nobel (1995) indicated that N, P, K, B and Na are the nutrients that exert the most influence on cactus productivity. Baca Castillo (1988) ranked P, N, K, Ca, B, Mg, Fe and Mn in decreasing order of importance, considering them to be the nutrients with the greatest effect on cactus growth. In fact, Dubeux *et al.* (2006) observed a linear increase in the productivity of *Opuntia ficus–indica* Mill. up to 300 kg N ha^{-1} $year^{-1}$ on different sites in the semi–arid region of Brazil. They observed that N fertilization increased N concentration in cactus cladodes and improved rainfall–use efficiency. Phosphorus fertilization produced positive responses in yield only when soil P was < 10 mg kg^{-1}.

Saline soils are not suited for cactus (*Opuntia* and *Nopalea*) cultivation, as they reduce shoot and root growth (Nerd *et al.*, 1991c; Calderón Paniagua *et al.*, 1997). Berry and Nobel (1985) showed that roots of *O. ficus–indica* Mill. exhibit saline stress when NaCl concentration in the nutrient solution reaches 25 mM, reducing shoot development.

Weed management

Weed control is essential to increase cactus productivity. Cactus has shallow roots that spread horizontally. In favourable conditions, roots can grow to a depth of 30 cm and spread horizontally in a radius of 4–8 m (Sudzuki Hills, 1995). Therefore, weeds compete with cactus for nutrients, moisture and light. Farias *et al.* (2005) tested different weed control methods on the development of cactus *Opuntia ficus–indica* Mill. cv. 'IPA–20'. When weeds were not controlled, the cactus produced only 3 tonnes DM ha^{-1} after 2 years of growth, compared with 12 tonnes DM ha^{-1} obtained using the best treatment (Tebuthiuron applied as pre–emergence herbicide at 2 litres ha^{-1}). Thus, weed control resulted in a fourfold increase in cactus yield. Mechanical control was not as efficient as the pre–emergence herbicides: Diuron, Tebuthiuron, or a combination of Simazine and Ametryne. If the weeds are potential quality forage material, it is possible to avoid herbicide application and instead make hay to use when feeding the cactus to livestock. This approach, however, results in reduced cactus productivity (Farias *et al.*, 2005). Felker and Russel (1988) indicated that glyphosate can be used at 20 g $litre^{-1}$ for *O. lindheimeri* without causing damage. They also indicated that Hexazinone, Simazine and Tebuthiuron promote the best yields for that species. Plant spacing is important for mechanized weed control. In Brazil, plant spacings recently used for cactus forage production are 1.6 × 0.2 m for *Opuntia* and 1.2 × 0.2 m for *Nopalea* (Silva, 2012; Souza, 2015).

Harvest management

Cactus harvest management must take into consideration harvest intensity, frequency and timing. Interaction between these factors affects cactus regrowth. Several harvesting trials have been carried out in northeast Brazil to determine the best harvesting strategy to maximize growth (Li-

Figure 5
Harvest, transportation and utilization of cactus in Pernambuco State, Brazil (Photo credit: Jose Dubeux)

ma *et al.*, 1974; Santos *et al.*, 1996, 1998; Farias *et al.*, 2000). In general, increased harvest frequency requires reduced harvesting intensity, and these two factors interact with plant population. Residual photosynthetic area after harvesting is critical to increase plant regrowth, and this is the case also for cactus. Field trials often reveal a low cladode area index (CAI), which reduces light interception and plant growth. Nobel (1995) suggests a CAI of between 4 and 5 to increase cactus productivity. Both faces of the cladodes are taken into account when measuring the CAI. The larger the plant population, the higher the CAI, resulting in increased productivity when no other factors limit growth. Farias *et al.* (2000) observed that when cactus (*O. ficus–indica* Mill.) was harvested every 4 years, there was no difference between preserving primary and secondary cladodes. Harvesting every 2 years, on the other hand, required a less intense cut with the preservation of all secondary cladodes. This trial, however, was done on a cactus population of < 10 000 plants ha^{-1}; with a more intense plant population, more frequent harvesting might be possible because of the greater residual CAI after cut. Souza (2015) observed that productivity increased with greater plant population (≤ 83 333 plants ha^{-1}), harvesting every other year, and preserving primary cladodes. This intensive system, however, requires higher inputs of organic fertilizer.

Cactus is usually harvested in the dry season, when livestock feed is scarce. In more intensive production systems, cactus is considered a component of the livestock diet throughout the year, but year–round supply of cactus is not common in most regions. Producers usually take advantage of the rainy season for pastures and rangelands, leaving cactus for the dry season. During the rainy season, the moisture content of the cladodes increases and there is more chance of pathogen incidence on the cut surface of cladodes, resulting in more disease problems.

Irrigation

Irrigation is not a common practice in cactus orchards dedicated to forage production. In some regions where low rainfall associated with warm night temperatures limits cactus development, the application of small amounts of water has expanded the cactus planted area. Dubeux *et al.* (2015b) report that the use of drip irrigation (only 10 mm month^{-1}) resulted in annual dry matter yields of ≤ 19.6 tonnes ha^{-1} in a region where cactus (*O. ficus–indica* Mill.) would otherwise not grow well because of the low rainfall and warm night temperatures.

Salt concentration in irrigation water is a problem. Application of small amounts of water and use of organic fertilizer reduce any potential salinization problem. Snyman (2004) observed that an irrigation of only 13.6 and 11.6 mm for *O. ficus–indica* and *O. robusta*, respectively, was sufficient to fill the cladodes in plants subject to water deficit. In rainfed systems, rainfall–use efficiency (RUE) varies according to the environment and management practices. Dubeux *et al.* (2006) report an average RUE of 18 kg DM ha^{-1} mm^{-1}, with values ranging from 5 to 35 kg DM ha^{-1} mm^{-1}.

Productivity

Cactus can reach high productivity in rainfed semi–arid agro–ecosystems. A rainfed system in northeast Brazil achieved productivity of > 50 tonnes DM ha^{-1} year^{-1} in intensive cultivation systems including the use of high levels of manure (80 tonnes ha^{-1} year^{-1}) and high plant population (160 000 plants ha^{-1}) (Silva, 2012). However, the average productivity of small farming systems is inferior, due to lower fertilization, smaller plant populations and absence of weed control. The data reported by Silva (2012) reflect the potential yield of cactus in semi–arid regions. A cactus orchard productivity of 20 tonnes DM ha^{-1} year^{-1} (Santos *et al.*, 2000) is sufficient to sustain 4–5 cows per year. In the same area, 15 ha of rangeland is needed to sustain just one animal unit per year, meaning that cactus productivity is potentially 60–75 times higher. A small area of cactus can provide enough forage to sustain the herds while reducing the pressure on the rangelands' natural resources.

However, productivity in low input systems can be much lower. Farias *et al.* (2005) report productivity of 1.5 tonnes DM ha^{-1} year^{-1} with no weed control in a cactus field. Cactus intercropped with other crops often has diminished productivity. Farias *et al.* (2000) report cactus productivity of 2.2–3.4 tonnes DM ha^{-1} year^{-1} with 5 000 plants ha^{-1} intercropped with *Sorghum bicolor* (L.) Moench. In conclusion, productivity varies with inputs and systems; the producer must take into account land availability and the economic value of inputs and outputs when deciding what system best suits a particular condition.

FORAGE QUALITY

Nutrients

Cactus (*Opuntia* spp.) cladodes are high in water, sugars, ash and vitamins A and C, but they are low in crude protein (CP) and fibre (Ben Salem *et al.*, 1996; Le Houérou, 1996a; Batista *et al.*, 2003a, b). They exhibit a high Ca–P ratio and are highly palatable (Tegegne, 2001; Nefzaoui and Ben Salem, 2001). However, numerous authors (e.g. Le Houérou, 1996a; Azocar, 2001; Nefzaoui and Ben Salem, 2001; Tegegne, 2001) have demonstrated significant variability in the nutritive value of cladodes of different species and cultivars. Nutritive value also varies according to the season, agronomic conditions and the technical package adopted (soil texture, rainfall, fertilization etc.). According to Le Houérou (1996a), 1– to 3–year cladodes are high in water during winter and spring (85–90%), less in summer (75–85%), and the younger the cladode, the higher its water content. Cladodes as forage can solve the problem of livestock watering, but attention should be paid to their low dry matter content with regard to diet composition. To compensate for the low dry matter content, the ruminant consumes large quantities of cladodes, which may lead to diarrhoea. It is therefore recommended to associate a fibrous feedstuff, as well as appropriate supplements, in particular those rich in nitrogen.

Compared with conventional feedstuffs, *Opuntia* cladodes have a high ash content (Sawyer *et al.*, 2001). Depending on the species and cultivar, the ash content ranges from 100 to 250 g kg^{-1} DM, but often exceeds 200 g kg^{-1} DM. Ca – followed by K – is the most abundant mineral in the cladodes, but the availability of Ca to rumen microflora and the host animal is compromised by the high content of oxalates and the extremely high Ca–P ratio. Cultivated in northern Brazil, the cladodes of *Opuntia* cv. 'Gigante', *Nopalea* cv. 'Miuda' and *Opuntia* cv. 'IPA–20' contain 120–145 g kg^{-1} DM of ash, 29–42 g kg^{-1} DM of Ca and 3–4 g kg^{-1} DM of P (Batista *et al.*, 2003b). Data on trace minerals are scarce; nevertheless, the concentrations of iron, copper and manganese seem to be within the recommended range for ruminant diets (Abidi *et al.*, 2009b).

It is well documented that cladodes are low in CP. Under Tunisian conditions, cladodes of *O. ficus–indica* f. *inermis* contain 30–50 g kg^{-1} DM of CP. Most of total nitrogen (TN) is in soluble form (865 g kg^{-1}, Ben Salem *et al.*, 2002a). The older the cladode, the lower its CP content. Therefore, nitrogen supplements in cactus–containing diets are mandatory to ensure normal microbial activity in the rumen and to improve livestock performance. The literature suggests a range of options to solve the problem of the low N content of cactus cladodes:

- Inclusion of nitrogenous supplements (soybean meal, urea, *Atriplex nummularia* foliage etc.) in cactus–containing diets is currently the most widely adopted option and encouraging responses have been observed in sheep. Examples are reported in **Table 4**.
- Provision of chemical fertilizers (ammonite and superphosphate) increased CP content of cladodes from 45 to 105 g kg^{-1} DM (Gonzalez, 1989).
- Breeding successfully increased the CP content of cladodes (Felker *et al.*, 2006). Cladodes of the selected clone of spineless cactus (clone TAMUK accession 1270) reported by Peter Felker revealed higher (100 g kg^{-1} DM) than normal (30–50 g kg–1 DM) CP content.
- Solid fermentation is recommended as an alternative option for protein enrichment of cladodes (Araùjo *et al.*, 2005), although the technique is still at the laboratory stage of research. Cost–benefit analysis is required in order to enhance adoption of this technique by farmers.

Cactus cladodes are high in carbohydrates (approx. 600 g kg^{-1} DM), starch (approx. 75 g kg^{-1} DM) and β–carotene (approx. 6.5 mg kg^{-1} DM) (Ayadi *et al.*, 2009). According to Abidi *et al.* (2009a), mucilage is high in the cladodes of spineless (6–13 g kg^{-1} fresh material) and spiny (6–14 g kg^{-1} fresh material) cactus. Compared with winter, mucilage concentration increases at least twofold in summer. It reduces salivation in ruminants, thus avoiding a rapid decrease in rumen pH. This phenomenon was confirmed by Ben Salem *et al.* (1996), who reported rumen pH values of 6.3–6.8 in sheep fed on straw–based diets supplemented with increasing levels of spineless cactus cladodes. These values fit with the optimal pH (6.5–7) recommended for normal growth and activity of the microflora in the rumen. Other soluble carbohydrate–rich feedstuffs, such as molasses, cause acidosis in the ruminant, because they are low in or free of mucilage. As a succulent plant, cactus cladodes are low in fibre. In general, cell wall neutral detergent fibre (NDF) ranges between 180 and 300 g kg^{-1} DM, although the cladodes of a spiny cactus (*Opuntia imbricate*) contain 400 g kg–1 of NDF. Lignocellulose (acid detergent fibre – ADF, 120–200 g kg^{-1} DM) and lignin (sulphuric acid detergent lignin – ADL, 15–40 g kg^{-1} DM) are also low. Carotenes, titratable acidity and carbohydrates increase during development, while protein and fibre decrease. It is worth noting that cladodes are high in malic acid and the content of this acid oscillates due to a CAM–based diurnal rhythm. Several authors (Lila *et al.*, 2004; Mohammed *et al.*, 2004; Newbold *et al.*, 2005) conducted in vitro and in vivo studies to show that malic acid reduces methane emissions. Therefore, it is expected that the integration of cactus in livestock feeding could reduce methanogenesis, contributing to a decrease in greenhouse gas emissions. However, this hypothesis requires validation by scientists.

Anti–nutritive factors

Like many plants, cactus cladodes contain phytochemicals with no apparent detrimental effects on livestock. Negesse *et al.* (2009) determined the content of some anti–nutritive factors in mature and young cladodes of spineless cactus (*O. ficus–indica*) growing in Ethiopia and reported their total tannin content as 21 and 42 g equivalent tannic acid kg^{-1} DM, respectively. However, a very low content of these tannins (1 g equivalent tannic acid kg^{-1} DM) in the same species of cactus but growing in Tunisia was reported by Ben Salem *et al.* (2002a).

TABLE 4 Intake, *in vivo* digestibility, and growth rate of different animal species receiving cactus–containing diets.

Country	Animal	Period (days)	Diet composition (g DM day^{-1})	Water intake (litres day^{-1})	TDM intake (g W$^{-0.75}$)[h]	OMD (%)[h]	CPD (%)[h]	NDFD (%)[h]	Initial BW[h] (kg)	Growth rate (g day^{-1})	Ref.[i]
Ethiopia[a]	Lamb	97	508 teff straw+58 NSC	1.02	65.0	46	48	50	17.0	23	a1
	Lamb	97	273 teff straw+58 NSC+246 **cactus**	0.42	62.6	54	41	48	17.0	53	a1
Ethiopia	Lamb	90	685 pasture hay	1.22	70.0	59	57	49	20.0	11	a2
	Lamb	90	404 pasture hay+503 **cactus**	0.02	97.0	58	54	37	19.5	28	a2
	Lamb	90	218 pasture hay+508 **cactus**	0.01	77.0	61	49	30	19.0	0.0	a2
Tunisia[b]	Lamb	70	435 barley straw+178 barley+157 SBM	3.05	72.1	69	73	68	19.5	108	b1
	Lamb	70	262 barley straw+157 SBM+577 **cactus**	1.30	85.2	71	71	69	19.5	119	b1
Tunisia	Lamb	84	715 oat hay+300 concentrate	3.88	65.0	64	59	59	32.5	46	b2
	Lamb	84	544 oat hay+295 **cactus**+67 concentrate	2.47	68.9	65	59	66	32.5	39	b2
	Kid	84	454 oat hay+300 concentrate	3.20	74.9	65	63	59	19.3	46	b2
	Kid	84	488 oat hay+346 **cactus**+67 concentrate	1.38	94.5	67	64	59	19.3	24	b2
Brazil[b]	Lamb	35	400 tifton hay+280 ground corn+176 SBM+114 wheat bran+15 salt+15 limestone	4.90	96.5	73	74	57	26.6	255	c1
	Lamb	35	400 tifton hay+280 cactus+176 SBM+114 wheat bran+15 salt+15 limestone	2.30	102.1	83	87	77	27.9	231	c1
Brazil[c]	Buck	21	250 Cynodon hay+600 **cactus**	0.04	84.4	74	77	48	13.7		c2
	Buck	21	125 Cynodon hay+600 **cactus**+125 SBH	0.06	79.1	75	78	51	31.7		c2
	Buck	21	0 Cynodon hay+600 **cactus**+250 SBH	0.03	66.5	78	80	59	31.7		c2
Brazil[d]	Heifer		395 sugar cane+93 corn+479 WB		103.6		70	45			c3
	Heifer		390 sugar cane+92 corn+314 WB+163 **cactus**		107.4		76	47			c3
	Heifer		385 sugar cane+91 corn+156 WB+320 **cactus**		111.8		77	40			c3
	Heifers		381 sugar cane+92 corn+0 WB+469 **cactus**		103.4		80	37			c3
India[e]	Ram	45	752 Cenchrus hay+191 concentrate		73.9		49	46	29.8		d
	Ram	45	547 Cenchrus hay+243 **cactus**		61.2		31	45	31.7		d
	Ram	45	672 Cenchrus hay+237 **cactus**+48 GNC		74.4		54	45	31.8		d
South Africa[f]	Wether	63	660 ground lucerne hay+300 maize meal+40 molasses meal		90.6	73			33.9	118	e
	Wether	63	410 ground lucerne hay+240 dried **cactus**+300 maize meal+40 molasses meal+10 urea		89.2	76			33.9	116	e
	Wether	63	285 ground lucerne hay+360 dried **cactus**+300 maize meal+40 molasses meal+15 urea		88.3	78			33.9	96	e
Tunisia[f]	Lamb	60	482 **cactus**+190 straw	0.38	72.6	58	59	49	19.9	8	f
	Lamb	60	503 **cactus**+258 urea–treated straw	0.42	78.7	64	66	63	19.9	20	f
	Lamb	60	513 **cactus**+198 straw+121 atriplex	0.44	85.0	65	72	65	19.9	31	f
	Lamb	60	362 straw+393 concentrate	1.89	74.4	72	70	66	19.9	40	f

[a] NSC: Noug (Guizotia abyssinica) seed cake.

[b] SBM: soybean meal.

[c] SBH: soybean hulls.

[d] WB: Wheat bran. Values of dry matter intake (g kg^{-1} W0.75) were adapted from the data reported in the corresponding article.

[e] GNC: Groundnut cake.

[f] Values of dry matter intake (g kg^{-1} W0.75) were adapted from the data reported in the corresponding article.

[g] Atriplex nummularia. Values of dry matter intake (g kg–1 W0.75) were adapted from the data reported in the corresponding article.

[h] TDM: total dry matter. OMD: organic matter digestibility. CPD: crude protein digestibility. NDFD: total fibre (NDF) digestibility.

[i] a1: Gebremariam *et al.* (2006). a2: Tegegne *et al.* (2007). b1: Ben Salem *et al.* (2004). b2: Abidi *et al.* (2009). c1: Costa *et al.* (2012). c2 : Souza *et al.* (2009). c3: Monteiro *et al.* (2014). d: Misra *et al.* (2006). e: Einkamerer *et al.* (2009). f: Ben Salem *et al.* (2002b).

The total oxalate content varies between 60 and 120 g kg^{-1} DM. Abidi *et al.* (2009b) reported that cladodes of spiny cactus are higher in oxalates (110–118 g kg^{-1} DM) than spineless cactus (102–105 g kg^{-1} DM) growing in an arid area of Tunisia. It is good that these oxalates are insoluble, as they have no toxic effect. However, it is known that insoluble oxalates form complexes with Ca and Mg rendering them unavailable for rumen microflora and the host animal. According to Ben Salem *et al.* (2002a) and Abidi *et al.* (2009b), spiny and spineless cactus cladodes are low in saponins (2–5 g kg^{-1} DM), total phenols (10–34 g kg^{-1} DM), total tannins (1 g kg^{-1} DM) and condensed tannins (<1 g kg^{-1} DM). The authors are not aware of the presence of any other secondary compound in cactus cladodes with potentially negative effects on the nutritive value and animal performance and health.

Fermentation

Different *in vitro* techniques are used to evaluate the fermentation potential of the cladodes of different species and cultivars of cactus.

The gas production technique developed by Menke and Steingass (1988) and using calibrated glass syringes has been widely adopted in research laboratories in the last decade. The digestion of organic matter leads to the production of volatile fatty acids (VFA), ammonia and different gases, mainly dioxide carbon and methane. The technique is, therefore, based on the following hypothesis: the more gas is produced in the *in vitro* system, the more the substrate is digestible in the rumen. Equations have been developed to predict the digestibility and energy contents of a wide range of feedstuffs. Batista *et al.* (2003a) measured the gas production of three cultivars of spineless cactus growing in northern Brazil ('Gigante', 'Miuda' and 'IPA–20'). They reported high volumes of gas production from the 24–hour fermentation of these three cultivars: 'Gigante' was highest (210 ml g^{-1} DM), followed by 'Miuda' (202 ml g^{-1} DM) and 'IPA–20' (195 ml g^{-1} DM). In southern Tunisia, higher values of potential gas production were reported by Abidi *et al.* (2009b) for spineless (*O. ficus–indica* f. *inermis*) and spiny (*Opuntia amyclaea*) cactus cladodes harvested in winter (138 and 140 ml g^{-1} organic matter [OM], respectively) and summer (140 and 145 ml g^{-1} OM, respectively). High gas production in the early hours of incubation is a characteristic of soluble carbohydrate–rich feedstuffs, including cactus.

Single–flow continuous culture fermenters were used by Abidi *et al.* (2009b) to compare the fermentation traits of experimental diets composed of spineless or spiny cactus cladodes (17 g), *Atriplex nummularia* foliage (12 g) and wheat straw (24 g). Both diets (spineless/spiny cactus) exhibited similar pH, total VFA, total N flow, effluent bacteria and liquid and solid associated bacteria isolated from fermenter flask contents. However, the spiny cactus–containing diet showed higher acetate to propionate ratio ($P = 0.016$) and lower ammonia flow ($P = 0.007$).

The gas production technique was adopted by Negesse *et al.* (2009) to determine fermentation parameters and estimate the metabolizable energy (ME) content of some non–conventional feed resources, including mature cladodes (MC) and young cladodes (YC) of spineless cactus growing in Ethiopia. The ideal ME content is 10–13.6 MJ kg^{-1} DM, but MC and YC revealed an ME of 7.5 and 8.5 MJ kg^{-1} DM, respectively, and were not considered good sources of energy.

Intake

Considerable information on the response of different animal species to cactus–containing diets is available. Feeding trials usually evaluate spineless cactus cladodes (henceforth referred to as cactus) as an alternative fodder source for growing dairy and other ruminants. **Table 4** presents information generated by some studies. The more fresh cactus is consumed, the less water is drunk by the animal. The decrease in drinking water consumption by the various categories of sheep and other animal species (bucks, kids and heifers) is 40–98%, depending on the proportion of cactus in the diet. Gebremariam *et al.* (2006) reported a 59% decrease in drinking water in lambs receiving a diet composed of 43% fresh cactus. Furthermore, in a study conducted in Ethiopia, lambs stopped drinking water when there was access to a 55% fresh cactus–containing diet (Tegegne *et al.*, 2007). Cactus plantations are, therefore, a promising option for alleviating drinking water scarcity in dry areas and during drought periods.

Cactus is often used to supplement low–quality forage, including straw and pasture vegetation. Its impact on diet intake is improved when associated with a protein source. Total dry matter (TDM) intake in lamb receiving pasture hay and cactus was 26% higher than in lamb fed on pasture hay alone (Tegegne *et al.*, 2007). The replacement of energy sources, such as barley grain (Abidi *et al.*, 2009a) or ground corn (Costa *et al.*, 2012), by cactus in sheep diets increased TDM intake by 6% and 25%, respectively. Replacing barley in concentrate with cactus increased TDM intake by 26% in growing goat (Abidi *et al.*, 2009a).

Digestibility

Soluble carbohydrate–rich feeds like molasses and cactus improve diet palatability and enhance rumen fermentation, usually leading to an increase in TDM intake and/or diet digestibility. Depending on the diet composition, feeding cactus results in increased apparent organic matter (OM) digestibility of the diet or has no effect on this parameter. Studies conducted in Ethiopia (Gebremariam *et al.*, 2006; Tegegne *et al.*, 2007), Tunisia (Ben Salem *et al.*, 2004; Abidi *et al.*, 2009a) and Brazil (Costa *et al.*, 2012) showed an increase of the OM digestibility of the diet by 2 to 10 percentage units in cactus–receiving lambs and kids compared with cactus–free diets. This could be the result of improved rumen fermentation. The provision of cactus to Ethiopian lamb fed on teff straw or pasture hay resulted in a decrease in the apparent crude protein digestibility of the diet. Gebremariam *et al.* (2006) claims that the decreased CP apparent digestibility with increased cactus inclusion rate could be explained by the total tannin content of cactus. Indeed, tannins have great affinity with proteins, making them unavailable for rumen microflora and the host animal. The authors are not aware of any other study showing the effect of cactus tannins on ruminal digestion in ruminants; the interaction between cactus tannins and proteins has not been investigated in either in vivo or in vitro studies. Under Brazilian conditions, Costa *et al.* (2012) noted an increase of 13 percentage units in the CP digestibility of lamb's diet. Also in Brazil, Souza *et al.* (2009) reported high values of CP digestibility (77–80%) in bucks receiving Cynodon hay, cactus and soybean hulls. Ben Salem *et al.* (2002b), Gebremariam *et al.* (2006) and Misra *et al.* (2006) observed no effect of cactus on fibre (NDF) digestibility in the diet. Costa *et al.* (2012) report a positive impact of cactus on NDF digestibility – an increase of 20 percentage units in NDF digestibility with a cactus–containing diet, compared with the control (cactus–free) diet given to lamb. In brief, cactus supply has no negative effect on diet digestibility and may even improve it.

UTILIZATION

Cactus cladodes and waste fruits are a cost effective feed for ruminant animals. The benefits of using cactus as feed are well documented (Nefzaoui and Ben Salem, 2001; Ben Salem and Abidi, 2009).

Plantations of cactus for fodder production (harvested) or as forage (directly browsed by livestock or wildlife) have been developed in Sicily and North Africa since the mid–nineteenth century. Farmers wished to stabilize the fodder resource in arid and semi–arid zones, where feed shortages in summer and autumn are a quasi–permanent factor limiting livestock production (Le Houérou, 2002). These plantations are still used as:

- part of the common daily ration;
- supplementary feed in summer and autumn; and
- buffer feed reserve during drought periods lasting 1–3 years.

In contrast to other fodder and forage crops which need to be stored (e.g. hay or silage), cactus is a standing evergreen crop and can be used year–round. The natural and probably most efficient way of using cactus is to cut the cladodes and feed them without any processing. Moreover, cactus is rich in water and plays a crucial role in arid environments as a replacement for drinking water. Silage–making or drying is feasible, but entails additional costs in terms of handling, energy and labour.

The different uses are outlined below, with a focus on direct browsing, cut–and–carry, drying, silage and, finally, feed blocks and their potential for making use of low–quality fruits.

Direct browsing

Direct browsing of the stand occurs mainly in native plantations with both thorny and spineless cacti. It is currently practised in a small number of countries (e.g. Mexico), where the wild cactus populations are directly browsed by livestock. In Ethiopia, where cactus is sometimes invasive (e.g. in the Tigray region), it is also browsed directly. Camels and cattle are able to intensively browse spiny cactus (**Figures 6 and 7**). In human–made plantations, direct browsing is not recommended because it usually results in rapid damage to the stands. The most effective and low–cost option is grazing with an electric fence, where all the biomass in a row must be completely consumed before the livestock can access a new row; the greatest danger of direct grazing (i.e. loss and wastage because cladodes are only partially consumed) is thus avoided (Le Houérou, 2002).

Spines in wild populations may be burnt directly prior to grazing, as is practised in Texas. Maltsberger (1991) conducted an extensive investigation on the economics of burning spines using propane and on the supplementation of burnt cladodes to cattle. They found that 15 litres of propane were required for 14 cows per day, and that 8 work–hours were required to prepare feed for 200 cattle per day. Pluenneke (1990) showed that labour and fuel costs to burn spines are significantly reduced when the plantation is in rows. Nevertheless, there is still some wastage as cattle step on burnt portions of cactus; cut–and–carry is therefore preferred.

Cut–and–carry technique

Cut–and–carry is the most commonly used technique for cactus feeding. It prevents wastage and excessive grazing. Both spiny and spineless cactus cladodes can be harvested and transported to the barn, then chopped, mixed with other feeds and put in troughs. Spines must

Figure 6
Camel browsing thorny cactus in Ethiopia

Figure 7
Cattle browsing cactus, "fighting bull ranch" in San Luis Potosí, Mexico (Photo credit: Ali Nefzaoui)

Figure 8
Hand–cutting of spineless cactus cladodes in Tunisia (Photo credit: Ali Nefzaoui)

Figure 9
Hand–propelled cactus chopper in Tunisia

Figure 10
Hand–propelled Ethiopian cactus chopper (Photo credit: Ali Nefzaoui)

Figure 11
Cactus processing machines in Brazil

be burnt prior to chopping and feeding. Different types of choppers are available in the market, from simple small choppers to more sophisticated ones. In North Africa, cactus chopping is done manually with knives and the whole family helps, especially women and kids (**Figure 8**). In Tunisia and Ethiopia, transportable, low–cost choppers are made locally (**Figure 9 and 10**) and are propelled using human power. More sophisticated and motorized choppers are utilized in Brazil and Mexico (**Figure 11**). In addition to reducing wastage, slices of cactus are more convenient for incorporating in mixed diets.

Drying

Under certain circumstances, cactus cladodes are chopped into small slices then air–dried, for example, when the harvest period is short (pruning of cactus fruit plantations) or when the objective is to produce a commercial feed or mix the cladodes with other ingredients. In all cases, sun–drying is recommended to avoid using expensive fuels that will increase production costs. Once dried, cactus is ground to produce cactus meal – avoiding a too–fine meal that could transit too quickly in the gut. Sometimes, cladodes are dried to reduce their high water content (85–90%), on the basis that fresh cactus consumption leads to very wet faeces. However, the findings of De Waal *et al.* (2013) negate this assumption: they show that, even when animals are fed with dried cactus, faeces remain wet due to the presence of mucilage.

Cactus drying is mainly practised in Brazil and South Africa. Several studies (Zeeman, 2005; Einkamerer, 2008; Menezes, 2008) confirm that sun–dried and coarsely ground *Opuntia* cladodes can replace a large proportion of lucerne hay in the diet of young Dorper lambs. De Waal *et al.* (2013a) investigated the commercial potential of sun–dried cactus cladodes (*O. ficus–indica*) for feedlot diets for Dorper wether Lambs (**Table 5**). They showed that there are no significant differences in carcass characteristics, and suggested that carcass quality is not affected by the inclusion of sun–dried and coarsely ground cactus pear (*O. ficus–indica*) cladodes in diets or by the type of nitrogen source. On the other hand, the difference in average daily gain between the cactus–pear–based diets shows the importance of high–quality nitrogen sources for lambs. These results indicate good prospects for the commercialization of sun–dried *Opuntia* cladodes in balanced diets for ruminants.

Two forms of cactus processing: knife–chopped (KC) and fodder machine–sliced (FM), and two different feeding strategies: separate concentrate (SC) and total mixed ration (TMR), were investigated by Da Silva *et al.* (2010). They monitored the feeding behaviour of milking cows and concluded that cactus processing in a fodder machine is recommended to maximize the dry matter intake and avoid alterations in milk composition. The TMR feeding strategy is recommended to reduce selectivity in the cows, which leads to an imbalance between the diet offered and that consumed.

Silage

Under certain circumstances, it may be necessary to make silage from cactus cladodes: when the production is concentrated in a short period (pruning); or when wet agro–industrial by–products cannot be stored for a long time and must be valorized. To make high–quality silage, good acid lactic fermentation is necessary, requiring appropriate levels of moisture (30–40%) and sugar in a full anaerobic environment. Cactus cladodes contain sufficient carbohydrates for good lactic acid fermentation, but their high water content means that they need to be carefully mixed with other material (e.g. chopped straw or bran).

Abidi *et al.* (2013) conducted an experiment in Tunisia where the olive industry is well developed. They tested the ensiling potential of a mixture of chopped cladodes (350 kg), olive cake (by–product of olive oil mills, 400 kg) and wheat bran (250 kg). The mixture was ensiled for 75 days and then distributed with concentrate supplement (75% barley grain and 25% soybean meal) to lambs. Three diets were compared:

- Diet 1 (control: oat hay ad libitum and 400 g concentrate feed)
- Diet 2 (silage and 400 g concentrate feed)
- Diet 3 (50% diet 1 and silage)

The amounts of feed distributed were adjusted for iso–energetic and iso–nitrogenous diets. The silage

TABLE 5 Composition of diets (T0, T1 and T2) fed to young Dorper wether lambs (adapted from de Waal *et al.*, 2013a)

Feed ingredients (kg air–dried material)	**Diets**[a]	**(g kg^{-1})**	
	T0	**T1**	**T2**
Sun–dried and coarsely ground *Opuntia* cladodes	–	330	300
Coarsely ground lucerne hay	577	255	190
Yellow maize meal	358	340	275
Feed grade urea	10	20	–
Sunflower oilcake meal	–	–	180
Molasses meal (Enermol)	40	40	40
Feed lime	15	15	15
Average daily gain (ADG) in weight (g)	181a	125b	181a
Cost of diet head^{-1} day^{-1} (N$)	3.71a	2.73b	3.26b

[a] T0: conventional feedlot diet. T1 and T2: *Opuntia*–based diets with different nitrogen sources (T1 – non–protein nitrogen; T2 – natural protein).
Means followed by the same letter (a/b), within the same row, do not differ (P > 0.05) in the Tukey test.
N$ = Namibia dollar (1 N$ ≈ 0.072 US$).

obtained was of good quality with a pH of 4.5. The average daily weight gain of the lambs and the meat quality were also similar across the three diets.

Feed blocks

In many countries, and Tunisia in particular, large quantities of cactus fruits are not harvested because of their low quality or the labour costs. The over–ripened fruits attract the *Ceratitis capitate* fly, also called the "Mediterranean fruit fly" ("medfly" for short), which can cause extensive damage to a wide range of fruit crops. Therefore, farmers are encouraged to collect these fruits and incorporate them in feed blocks for livestock. Different formulas have been developed based on the replacement of molasses with cactus fruit. Chermiti (1998) investigated the potential of cactus fruit as a feed block ingredient and evaluated the voluntary intakes in heifers and ewes receiving an oat–vetch hay–based diet supplemented by two kinds of feed blocks (one containing cactus fruit, the other molasses). He concluded that the voluntary intakes by both animal species were identical for both types of feed block. Ben Salem *et al.* (2003) mixed processed cactus fruits (90 g kg^{-1} DM) with olive cake (367 g kg^{-1} DM), wheat bran (243 g kg^{-1} DM), quicklime (154 g kg^{-1} DM), urea (73 g kg^{-1} DM) and salt (73 g kg^{-1} DM) to make feed blocks. They supplemented the feed blocks with oak (*Quercus coccifera*, a tanniniferous shrub species) foliage to improve the nutritive value (total intake, organic matter and fibre digestibility of the diet, nitrogen retention) of the diet for goats. The administration of a small amount of polyethylene glycol in the feed blocks resulted in further significant improvements in the parameters, as a result of the deactivation of the oak tannins with the re–agent.

ANIMAL PERFORMANCE AND PRODUCT QUALITY

Productive performances

In many articles, authors conclude that supplementing low quality forage with fresh cactus increases the average daily gain (ADG) of growing ruminants. The response is even more positive when a nitrogen source is provided (**Table 5**). Replacing around 50% of teff straw with cactus increased the ADG of Ethiopian lamb from 23 to 53 g day^{-1} (Gebremariam *et al.*, 2006). Under Tunisian conditions, the substitution of barley grain with cactus increased the ADG of Barbarine lamb from 108 to 119 g day^{-1} (Ben Salem *et al.*, 2004). It should be mentioned that in both studies the cactus–based diet included protein supplements (noug seed cake and soybean meal, respectively). Any slight decrease in the growth rate of lamb on the cactus–containing diet was considered tolerable, taking into account the low production cost for smallholders and considering that cactus is available year round (Einkamerer *et al.*, 2009; Costa *et al.*, 2012). Although the association of cactus with soybean meal produced an ADG in Barbarine lamb of 119 g day^{-1}, Ben Salem *et al.* (2004) favoured a diet composed of locally available feed resources (i.e. cereal straw, cactus and *Atriplex nummularia* foliage) for two reasons: i) it is less expensive than a diet containing barley grains and soybean meal; ii) the shrubs bring additional benefits (e.g. soil fixation and fruit production).

To summarize, cactus can improve the nutritive value of poor–quality diets (e.g. straw–based diets) due to its high content of soluble carbohydrates. It may also increase weight gain in small ruminants and heifers fed on crop residues or poor–quality pastures, provided that a small amount of a nitrogen source is included in the diet.

Most studies on the effects of cactus feeding on milk production and quality have been carried out in Brazil. Cactus is highly valued in times of drought and water scarcity. Spiny cactus is fed to cattle in northern Mexico and the southwestern United States of America (Maltsberger, 1991). It is a cheap source of cattle forage and is frequently used by ranchers and dairymen in these areas. Spiny cactus is traditionally included in ruminants' diets, their thorns burnt from the standing prickly pear plants using a propane–fuelled flame. Since spineless cactus have become widely disseminated in recent decades, many farmers now use cactus in dairy cattle feeding. According to farmers in northern Brazil, Holstein cattle fed on a mixed diet of 60% chopped fresh cactus cladodes, 20% fibrous feedstuff (hay or straw) and 20% protein–rich concentrate produce around 20 litres day^{-1} of milk (H. Ben Salem, personal observation). Oliveira *et al.* (2007) studied the replacement value of cactus (0, 12, 25, 38 and 51%) for cracked corn and *Cynodon* hay on dairy cattle raised in northern Brazil. Based on their results, cactus can totally replace cracked corn and partially replace hay (around 40%) without any significant effect on milk production (20.3–21.8 kg day^{-1}).

Many experiments in northeast Brazil show that meal from dried cactus cladodes may replace corn in lamb feeding (Véras *et al.*, 2002). Four replacement levels of corn (0, 25, 50 and 75%) were tested and results show that there is no effect in the levels of replacement on the digestibility of dry matter, organic matter or fibre. Véras *et al.* (2005) also tested the effect of replacement levels (0, 33, 67 and 100%) on the performance of growing lambs in feedlots; they found that body weight gain and feed–gain ratio decreased, while intakes of NDF and ADF increased linearly with

Figure 12
Dairy cows in Pernambuco State, Brazil, feeding on processed cactus mixed with silage and concentrate feed (Photo credit: Djalma Santos)

corn replacement. The intakes of dry matter, crude protein, organic matter and total carbohydrates and carcass yield were not affected by the replacement of corn with forage cactus meal.

Product quality

Taking into consideration consumer preference and human health, some literature refers to the effect of cactus supply on meat quality. Abidi *et al.* (2009) conclude that the replacement of barley with cactus as energy supplements in the local goat kid and Barbarine lamb diet did not produce major changes on the intramuscular fatty acid composition of meat. However, vaccenic acid was found to be higher in the cactus–containing diet. This fatty acid – like conjugated fatty acids – has a positive impact on the cardiovascular system. While gross forage (oat hay) was used as basal diet in the research work reported by Abidi *et al.* (2009), Atti *et al.* (2006) analysed the meat quality of kids receiving cactus in concentrate–based diets supplemented with a small amount of oat hay. The authors report that cactus feeding resulted in increased proportions of linoleic, linolenic and conjugated linoleic acid. They also obtained a higher proportion of polyunsaturated fatty acids (PUFA) and higher PUFA to saturated fatty acids (SFA) ratio. The two studies confirm that cactus included in the diets of sheep and goats improves the quality of meat as per consumer preference: more PUFA and less SFA. Under northern Brazil conditions, Santos *et al.* (2011) evaluated the muscularity and adiposity of the carcass of Santa Ines lamb receiving cactus meal as a replacement of ground corn; there was no effect on hot carcass yield, biological yield (hot carcass weight to empty body weight ratio) or on the proportion of fat required for ensuring adequate carcass preservation.

Oliveira *et al.* (2007) conclude that cactus feeding did not affect milk production in dairy cattle receiving increasing levels of cactus. However, it did significantly change milk composition, in particular the profile of fatty acids. Indeed, cactus supply reduced the proportions of stearic and oleic acids, but did not affect the other long chain fatty acids, such as linoleic (C18:2) and linolenic (C18:3) acids.

FUTURE PERSPECTIVES AND RESEARCH NEEDS

Global warming, climate change, and increasing human and livestock population all require more efficient use of dryland systems. Adapted perennial crops with greater productivity per unit area are required to protect natural rangeland systems from degradation. Cactus fits well in this scenario, with productivity 60–75 times greater than natural rangelands. Small intensive cultivation of cactus can alleviate pressure on the natural resources of rangelands, reducing their degradation. At the same time, more animal products (e.g. meat and milk) produced by cactus–fed livestock can alleviate hunger, increasing food security and resilience of populations living in arid regions. There are numerous success stories from various countries and technologies are available to help other regions with similar environments. Policy–makers must be made aware of the benefits of cactus as a fodder as well as its environmental benefits; they should establish policies to increase the planted area accordingly. Research and development work is needed in this area and enhanced support from donors, policy–makers and science managers can help achieve increased cultivation of cactus in dry areas. It is also vital to increase collaboration among international research teams.

The information currently available on cactus for fodder production is adequate to implement successful systems in different areas. Further research is required to increase the knowledge of biotechnology, genotype × environment interactions, and locally adapted feeding systems utilizing cactus and local ingredients, and to enhance the efficiency of cactus use in different livestock production systems. Caution is necessary to avoid the introduction of invasive species. The use of spineless cactus for forage production needs to be encouraged. Insects and diseases are also a problem in localized areas; it is necessary to generate and promote varieties tolerant to diseases to deal with the problem. Therefore, conservation of genetic resources and promotion of multilateral cooperation is essential to address these challenges.

08

Nopalitos or vegetable cactus, production and utilization

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Nopalitos or vegetable cactus, production and utilization

INTRODUCTION

One of the great challenges of developing and underdeveloped countries is how to achieve food security without compromising the natural resource base, under continuous threat from the global trend of population increase and climatic change. Demographic growth also places additional pressure on water and land resources, with competition for first quality land and sources of clean drinking water, as these assets are continuously removed from agricultural production and dedicated to the needs of urban development. As a result, less land and water are available for agricultural production, leading to the dilemma: incorporation of grasslands and forests in agriculture versus undercut of development. The search for alternative crops and efficient agricultural technologies is clearly a reasonable approach.

Crops with built–in mechanisms conferring water efficiency, ability to grow in limiting soils and tolerance to cold and heat have been a beacon of agricultural science since the second half of the last century, when the effects of human population growth and poor resource planning policies become more evident. Cactus pear (*Opuntia ficus–indica*), a plant native to the semi–arid highlands of central Mexico and introduced to the rest of the world since the sixteenth century as a curiosity, receives increasing attention from governments, non–governmental organizations (NGOs) and private individuals. It comes up repeatedly as a serious alternative for the utilization of semi–arid lands affected by natural and induced desertification across the semi–arid tropics and subtropics.

Cactus pear is mostly known as a fruit crop and it is slowly achieving the status of formal crop in world statistics. Estimated data indicate that it is present on a commercial scale in over 20 countries, covering a planted area of around 150 000 ha (personal estimate). The cultivation and utilization of forage cactus is destined to follow suit, since the intake of proteins of animal origin continues to rise. Moreover, cultivation for forage is easier to adopt, both for commercial animal production and for pastoral production systems; cactus cultivation may ease the depletion of the natural grasslands.

The utilization of tender cladodes – known by Mexican consumers as *nopalitos* – as a vegetable originated and evolved in central Mexico. Their consumption is deeply rooted in the country's gastronomic culture as cactus pear is easy to cultivate and has high productivity. The trend is destined to increase, encouraged by recent discoveries of their functional properties (discussed in depth in this book). *Nopalitos* represent a unique example of ancient Mexican horticultural wisdom: by utilizing the vegetative structure, renewed by the continuous harvest, farmers exploit the physiological effects of pruning, securing valuable greens year round, in a region dominated by a climatic bimodal cycle of wet and dry seasons.

The introduction of vegetable *nopalitos* in other countries and cultures has not been easy, despite the plant's adaptability and high productivity in most locations. The presence of thorns – even the so called "spineless" cultivars present spines when young – the abundance of mucilage, and the lack of organoleptic appeal of cooked *nopalitos* have limited their adoption. Small orchards of *nopalitos* are found in the United States of America, mainly in California, Texas and Arizona; they produce limited quantities intended for local farmers' markets, aiming at consumers of Hispanic origin.

This chapter describes the domestication of cactus pear and presents varieties and production systems – from open–field crop to greenhouse production – as well as basic cooking techniques.

EARLY UTILIZATION AND DOMESTICATION

In the earliest stages of utilization of cactus pear, the organ of interest was the fruit; indeed, the consumption of ripe fruits has been documented through coprolites found in caves, demonstrating that the fruits were part of the diet of ancient Mexican tribes (Hoffmann, 1995). On the other hand, there is no record of the consumption of tender pads: due to their perishability, there are no remnants on archaeological sites. It may be speculated that early Mesoamericans following the gathering routes of cactus fruits, as the fruit became scarce, would turn to the succulent young cladodes as a source of water to quench their thirst. They were probably used as emergency foodstuff in times of fruit scarcity – a frequent situation in the harsh semi–arid climate predominant in central Mexico and exacerbated by the alternate bearing habit of the plant. They may have roasted the cladodes to eliminate the spines – essential to facilitate consumption.

Later on, an important part of the domestication process was the identification, nurturing and propagation of spineless plants, a mutant trait that limits the survival of the plant in its natural environment (Colunga Garcia *et al.*, 1986). All young cladodes, regardless of variety and species, present spines and glochids. Only mature cladodes may be spineless, allowing for easier manipulation. Modern vegetable *nopalito* varieties are all spineless and were originally obtained from family orchards.

The new demands of the modern market, less dependent on local production and seasonal availability, have led to increased interest in out–of–season production (ideally, year–round). Cultivated areas have, therefore, expanded to zones of mild winter or subtropical climate and, more recently, various forms of greenhouse. Given its original status of emergent crop suited to growers with limited resources and sites of low productivity, greenhouse production systems for *nopalitos* have gradually evolved from basic to more sophisticated. Three main types are in use in central and northern Mexico and are described later in the chapter.

VEGETABLE *NOPALITO* VARIETIES

In contrast with the wide range available for cactus pear production, the commercial varieties for cultivation as a vegetable are limited to 'Milpa Alta', 'Atlixco' and 'COPENA V1', described below.

'Milpa Alta' *Opuntia ficus–indica* (L.) Mill.

An indigenous cultivar, it probably originated and domesticated in the state of Hidalgo, Mexico (Reyes Agüero *et al.*, 2004). The commercial name 'Milpa Alta' refers to the region of the same name located in the outskirts of Mexico City where intensive production of *nopalitos* began. It has spread throughout Mexico, covering an estimated 7 500 ha. Its bright green, flat, thin, easy–to–peel cladodes and its tenderness are appreciated by merchants and consumers. It is planted in open–field plantations or under plastic covers, and may be rainfed or irrigated in dry areas. The plant is robust, erect, with oblong cladodes, highly productive but frost–sensitive. The fruit is medium large, with yellow–orange skin and pulp, not too juicy, with medium–sized seeds. It is well adapted to a semi–arid subtropical climate and to subtropical lowlands (Gallegos and Mondragón Jacobo, 2011). This variety is similar to the spineless cultivars of yellow–orange fruit present in other parts of the world: Italy, Morocco, Tunisia and South Africa (**Figure 1**).

'Atlixco' *O. ficus–indica* (L.) Mill.

This variety originated in the highlands of central Mexico, but was named 'Atlixco' after the town where its cultivation began. Nowadays, an estimated 800 ha are planted, mostly in the neigh-

Figure 1
Nopalito *varieties (clockwise: 'Milpa Alta'; 'Atlixco' or 'Negrito'; 'Blanco'; 'Valtierrilla')*

bouring states of Mexico City. The plant is vigorous, erect, with rhombic spineless cladodes of intense green colour and exceptional quality. The tender *nopalitos* are easy to clean, with an ovoidal shape and thicker than those of 'Milpa Alta'. The fruit are large (reaching > 180 g) with orange skin and yellow pulp; eating quality is acceptable but inferior to that of standard fruit cultivars. The mature cladodes are well accepted as forage. It is very productive under intensive cultivation, reaching 400 tonnes ha^{-1} $year^{-1}$ of fresh matter (Gallegos and Mondragón Jacobo, 2011), and is well adapted to field cultivation in the highlands under plastic tunnels (**Figure 1**).

'COPENA V1' *O. ficus–indica* (L.) Mill.

In terms of commercial stock available for vegetable production, 'Copena V1' is the only improved genotype, obtained by the late Dr Facundo Barrientos at the Postgraduate College in Chapingo, Mexico. The plant is vigorous, fast–growing and with erect habit growth; the cladodes are obovate, medium–sized, spineless. Although selected for vegetable production, its fruits are attractive: purple, large and sweet, of intermediate juiciness, and pulp with medium–sized seeds. While it is known that the breeder distributed planting material in several states, there is no accurate record of its acreage (**Figure 1**).

Other lesser known varieties useful for *nopalito* production in tropical semi–arid areas are:

- **'Valtierrilla'**, cultivated in a small area of the same name located in central Mexico and its surroundings; characterized by densely spined cladodes; preferred for its tender "baby" or "cambray" type *nopalitos*; sensitive to frost damage; performs well when brined.
- **'Blanco'** (*Nopalea cochellinifera*) (**Figure 1**), cultivated in Valtierrilla and in Michoacán and Tamaulipas states; sensitive to frost damage, but performs better than 'Milpa Alta' when brined – a feature that has sustained some cottage size industries. Note that some local types of O. robusta are also used for brining in San Luis Potosí (**Figure 1**).
- **'Spineless 1308'** (*Nopalea cochellinifera*), selected by P. Felker from accessions collected in the tropical region of Tamaulipas, Mexico, cultivated in the United States of America, planted in the coastal region of Texas and Tamaulipas.

AGRICULTURAL IMPORTANCE OF THE *NOPALITO* CROP

The cultivation of *nopalitos* reached the status of formal crop in Mexico in the 1980s, when official statistics reported only two main production zones, Milpa Alta and Tlalnepantla Morelos, both located near Mexico City and covering about 2 000 ha. Mexico City and its surrounding urban area still remain the largest market for all fresh produce, including nopalitos, reaching almost 21 million people in the last census (INEGI, 2010) (**Table 1**). By 1990, urbanization and demographics, combined with new research on the health benefits of *nopalito* consumption, led to an increase in planted area; by 2010, it had expanded from 5 269 to 12 201 ha. The planted area currently ranks 12th compared with other vegetable crops: an indication of its importance (SIAP, 2015). Nowadays, plantations of vegetable *nopalitos* are scattered throughout the central, west, north central and northeast parts of the country. A significant proportion of the production is destined for the national market (90%); however, the share for export to the United States of America has been increasing steadily during the last decade, facilitated by the bilateral North American Free Trade Agreement (NAFTA) and other similar treaties.

Per capita consumption of *nopalitos* in Mexico in 2013 reached 6.4 kg, with demand concentrated in the central and north central regions, where the fresh prod-

TABLE 1 Cultivated area of cactus plants in Mexico and product uses

Product	Planted area (ha)	Irrigated	Rainfed
Fruit	55 254	720	54 534
Fodder	16 266	42	16 266
Vegetable	12 039	3 204	8 835
Wild stocks*	3 000 000 (1.5% of the national territory)		

Source: SIAP (2015) and *Soberon et al. (2001).

uct is available all year round. A decade ago, *nopalito* consumption was highest at Easter; today, however, as more information becomes available about their functional properties, demand is increasing, and *nopalitos* have become a regular feature in supermarket vegetable sections.

In spite of the growing popularity of *nopalitos* in Mexico, consumption has not taken off in other countries. There is a lack of information on the modes of preparation and the beneficial effects attributed to its regular consumption, and the cooked product lacks appeal. Consumers are deterred by the spines and glochids on the cladodes and the release of mucilage after cooking. Despite the promotion of *nopalito* consumption in East and North Africa to utilize the naturalized stocks, there has been little impact, and likewise in India and Brazil.

As with other vegetables, *nopalitos* are subject to sanitary regulations and specific norms are available for *Opuntia* spp. and *Nopalea* spp. (NMX–FF–068–SC-FI–2006 for the national market; CODEX STAN 185^{-1} 993 for export). Both sets of norms relate to cladode colour, absence of deformations, pest and disease damage and absence of contaminants. In addition, there are official campaigns covering good agricultural practices focused on the importance of offering the consumer a product that is hygienic, safe and free of contaminants. Enforcement of these norms should help secure and increase the presence of *nopalitos* on international markets.

NOPALITO PRODUCTION SYSTEMS

Wild stocks

Nopalito gathering is still a traditional activity in the central and northern semi–arid regions of Mexico, which – in theory – cover 3 million ha (an overestimate, since it includes extensive areas containing only a few plants). *Nopalitos* are usually available at the end of winter or early spring, depending on the length and intensity of the frost season. The most common species collected wild are: *O. streptacantha*, *O. robusta*, *O. leucotricha* and *O. xoconoxtle*. The product is usually sold on local markets, and is characterized by variable quality, small volume and irregular availability. Gathering is slowly losing appeal as the density of wild stocks dwindle, making way for expansion of rangeland, and agricultural and urban development. Wild stocks are also prone to the compounded effects of natural disasters: severe frosts, drought and natural fires, most likely fuelled by climate change. Alternate bearing or cyclic growth also takes its toll on the volume of *nopalitos* and fruit collected from wild plants.

Family orchards

Family orchards are a common sight in semi–arid rural areas, characterized by the diversity of cactus pear species, the range of uses and the dominance of spineless types that can be fully utilized, providing tender cladodes, fruits and sometimes mature pads for domestic animals. Family orchards are found above all in the northern region. They functioned as gene reservoirs and as a breeding ground for local varieties, which in turn evolved into the commercial varieties that sustain the modern commercial market of cactus pears and *nopalitos* (Pimienta Barrios, 1990).

Traditional open–field production

This production system began in Milpa Alta – the oldest *nopalitos* growing region in Mexico, located in the suburbs of Mexico City – during the 1950s. It expanded to the neighbouring states of Morelos, Puebla and Hidalgo. The system relies on bushy plants (< 1.80 m), started from single cladodes planted in rows 0.80–1.50 m apart. The individual plants are planted 50–75 cm apart, resulting in planting densities of 10 000–40 000 plants ha^{-1} (**Figure 2**). The basal or mother cladodes are trained to two or three branches; they fill the row completely, but between the rows only partially so as to allow for transit between all rows. Harvest can begin just 2 months after planting, collecting excess cladodes once the primary branches are defined. Since it is open–field production, the system is highly dependent on soil moisture and air temperature. Tender *nopalitos* are very sensitive to frost damage, and even short episodes can damage the crown of the cladode, affecting the final shape, productivity and appearance of the cladode. Therefore, the harvest season is defined by the presence or absence of frosts; in other words, the length of the harvest season is determined by the duration of the frost–free period. In the highlands of Mexico, this period extends from mid–March to late October or November, depending on the specific local microclimate. The continuous emergence of new tender cladodes is also a response to timely harvest, because the continuous removal or harvest of tender cladodes stimulates the emission of new ones. On the contrary, if market conditions are inconvenient, stalling the harvest delays new sprouts.

Mini plastic tunnels

This system represents the earliest attempt to control the effects of frost on nopalito production. It was first adopted during the 1970–1980s, and is still in use in small family orchards across the country. There is a wide planting bed (120–150 cm), with 3–4 rows of cladodes;

row spacing is 30–40 cm, distance between plants 20–30 cm. The number of rows varies according to the width of the tunnel. With the above criteria, a 2–m long fraction of a bed can have 18–24 cladodes. The final planting density varies according to bed width and corridor separation, which in turn depends on the availability of labour and transport. In large operations, removal of harvested produce, application of fertilizer and manure, and spraying are performed with a tractor, and a blind bed between 2–3 planted beds is therefore necessary. Plastic tunnels are built with arched steel rods (3/8 caliber [9.5 mm]) fixed to the ground, covered by transparent polyethylene sheet (caliber 600 mils) and reinforced with polyethylene rope placed diagonally over the tunnel to secure the plastic against wind. The arches are usually < 2 m, designed to cover a single bed of *nopalitos*. Ventilation is passive, provided by manual lifting of the plastic cover during the hottest hours of the day.

This kind of structure provides protection from light frost (in the range of –1° C); its main function is to reduce cold winds and increase the temperature during the day (**Figure 2**).

There are numerous variations of planting layout, differing in bed width, cladode layout and height of the plastic cover. Diaz and Maya (2014) describe a system useful for tropical regions:

The beds should be oriented N–S to reduce wind force and maximize exposure to sunshine, the size of the beds will be 1.8 wide, and 45 m long, to optimize usage of plastic rolls, which usually come as 100 m long roll. The tunnel can be built using 3/8" corrugated steel rods, cut into pieces 4m long – enough to build a tunnel 1.4 m high –, shaped as arches of 1.8 m wide base. The arches will be inserted in pieces of white or clear colored plastic hose (1/2 in thick) that will protect the plastic from sunburn due to direct contact with the metal rods. The tip of each rod needs to be buried 30 cm deep to provide strength to the structure, then they are placed 2 m apart. The plastic sheet is placed on top and the edge buried firmly into the ground on the east side. It is recommended to use transparent plastic sheets 4m wide, and 600 mills caliber, with UV protection, special for greenhouses. The other edge is kept in place with some burlap bags filled with soil, so they can be easily removed to open the edge if temperature reaches more than 35 °C. Bury a short wooden stake on each end of the tunnel 1.2 m away from the edge of the bed; this stake will anchor seven strands of polyethylene rope. Then stretch them and tied them around on top of each arch, placing them evenly on top and both sides along the tunnel, to help the plastic keep the semi–cylindrical shape.

Low–tech greenhouses

Mexico, like many other subtropical countries, is experiencing a boom in protected agriculture; im-

Figure 2
Nopalito *production systems (clockwise: open field in Tlanepantla, Mor. Mexico; mini–tunnels; greenhouse; low–rise tunnel)*

ported and national materials for greenhouses are readily available for vegetable production. Market trends favouring out–of–season and year–round production result in increased product demand, benefiting farmers and consumers alike. Given the good response of nopal to irrigation, high temperatures and fertilizers, protected cultivation is the trend in both traditional and new cultivation areas. Several designs have been adapted to grow *nopalitos*, taking advantage of the rusticity of the plant. Greenhouses for *nopalito* production are usually simple, providing little frost protection but maintaining a beneficial temperature range (10–30° C). Attenuation of high temperatures is accomplished by means of manually operated windows. Since the nopal plant is self–standing, the metal elements in the structure are reduced to a minimum: 2 × 2 posts placed 2–3 m apart; arches (usually made of galvanized steel) welded on site and reinforced with galvanized steel poly latches; posts secured to the ground with concrete. Tunnel width varies from 6 to 9 m, depending on the means of the grower, and planting layouts vary to optimize the covered space (**Figure 2**).

Macrotunnels

These structures are designed to provide cover and protection against high radiation, excessive rain, hail and wind damage, thereby improving product quality. They were introduced in Mexico for high–value crops, such as vegetable seedlings, strawberries, raspberries, blueberries and peppers, but are being slowly adapted to *nopalito* cultivation in northern Mexico, especially in tropical areas with low frost risk. The typical macrotunnel does not have walls; it is built on 2–3 steel pipes secured in the ground, with steel arches and covered in UV–protected polyethylene. They are 4–5 m wide and 2–3 m high; they are relatively easy to build and of low cost compared with regular greenhouses. The planting layout is designed to optimize the protected space available and is similar to the wide bed system; irrigation is provided by dripping lines (**Figure 3**).

Hydroponic *nopalitos*

The most advanced system for growing *nopalitos* is in a hydroponic facility, for which there is an experimental model designed and promoted by the Regional Center for Arid and Semi–arid Zones (CREZAS) Postgraduate College. The system is based on a standard passive cooling plastic–covered greenhouse; it uses subirrigation and includes a ground cover on alleys to ensure maximum water saving, optimum usage of fertilizers and convenient weed control. Plants are established at high density and are kept bushy to reduce crowding and improve light interception by the nopal canopy (**Figure 4**).

Figure 3
Low–tech greenhouse for nopalito production, San Luis de la Paz, Gto. Mexico (clockwise: overall view; roof; foundation; wall)

PRODUCTION PRACTICE

Crop nutrition

Nopal is generally considered a rustic crop, able to survive in poor soils and dry areas. This is true; however, if the plant is exposed to good quality soils, abundant fertilization and irrigation, productivity is significantly boosted. The beneficial effects of the combination of manure and synthetic fertilizers for cactus pear under rainfed conditions are reported by Mondragón Jacobo and Pimienta Barrios (1990). Higher responses are achieved under irrigated conditions and using other organic sources, such as vermicompost, composted manure, solarized manure and mycorrhizal products.

The productivity of *nopalitos* or forage nopal can be expressed as kg of fresh cladodes per plant; it is a function of genotype, environment and crop management practices, including fertilization. Little is known about the nutrient requirements of nopal or the synergic and antagonistic interactions among nutrients for all different production systems. Nevertheless, Blanco Macías *et al.* (2006) report positive interaction between Mg–Ca, Mg–K and K–P, compared with significant and antagonistic interaction between Ca–N and Mg–N. The optimal concentration ranges for five essential nutrients to attain a target yield of 46.7 kg of fresh matter (considering only cladodes) are: N = 1.29 ± 0.47%, P = 0.35 ± 0.08%, K = 4.24 ± 0.88%, Ca = 4.96 ± 1.73%, Mg = 1.61 ± 0.27%.

Precise information on the nutrition of vegetable *nopalitos* is also reported by Magallanes Quintanar *et al.* (2004), Valdez Cepeda *et al.* (2009) and Blanco Macías *et al.* (2010), following several years of field experimentation. According to the curve threshold line technique, nutrient requirements depend on the quantity of nutrients available in the soil, expected yield and planting density. In order to obtain 95% of the optimal yield (56–60 kg plant^{-1}, assuming dry matter content of cactus

Figure 4
Nopalito *production under macro–tunnels (9.6 m wide × 4.3 m high);* nopalitos *planted in wide beds (1.40 m and 1.4 m alley); hydroponic unit for* nopalito/forage *production (CREZAS–CP, San Luis Potosí, Mexico)*

pear is about 5%), the plant needs to acquire 23.7 g N, 7.06 g P, 112.5 g K, 95.36 g Ca and 41.7 g Mg. For a planting density of 10 000 plants ha^{-1}, the soil must, therefore, provide 24 kg N, 71 kg P, 1124 kg K, 954 kg Ca and 417 kg Mg ha^{-1}, for a theoretical yield of 564 tonnes ha^{-1} of fresh matter or 28 tonnes ha^{-1} of dry matter. Valdez Cepeda *et al.* (2009) warns of the high response of nopal plants to nitrogen fertilization, and the possibility of accumulation at toxic levels, as nitrate concentration can build up in cladodes – potentially dangerous if used as forage or vegetable.

The addition of manure (mostly fresh or partially composted) is traditional in *nopalito* production, because the high response of the nopal plant is well known among Mexican growers – demonstrated by record rates of 800 tonnes ha^{-1} of fresh cow manure, recorded in *nopalito* orchards in Milpa Alta (Fernández *et al.*, 1990; Aguilar, 2007; Flores, 2013). Such high rates are justified, considering the long residual effect and the improvement of soil properties; however, they can also result in burning if applied during the hottest months of the year. Field experiments conducted by Zuñiga Tarango *et al.* (2009) demonstrate that 100 tonnes ha^{-1} of fresh manure is sufficient to obtain profitable yields of *nopalitos*.

Manure application is the subject of increasing attention, due to growing interest in organic products on the modern market and the continuous increase in prices of synthetic fertilizers. Both the direct experience of growers and the results of formal experimentation stress the value of fertilization and irrigation at adequate rates in order to attain high yields (Flores, 2013). The sources and rates applied depend on availability. The most common source is fresh cow manure obtained from dairies, followed by goat and chicken manure.

Due to rising transportation costs, there is growing interest in composts. In an evaluation for *nopalito* production in Milpa Alta, Mexico, Aguilar (2007) reports that similar yields (45–60 tonnes ha^{-1} year^{-1}) were obtained with 3.3 tonnes ha^{-1} of vermicomposted dairy manure instead of 800 tonnes ha^{-1} of fresh manure. In this study, the cost of the composted manure was just 22% of the usual rate of fresh manure. Given the perennial nature of the nopal plant, manure application may be repeated every 2–3 years based on the initial rate; whether to apply a single dose or two fractions depends on the local cost of manual labour.

Fertilization, irrigation and pruning are associated with the rapid emergence of new vegetative buds. Careful management is important to reduce frost damage, optimize rainfall and, most important, take advantage of specific market windows. The rainy season in central Mexico presents some variations, but basically follows a bimodal pattern, starting at the end of June, with a slight depression in August and rising again in September. Frost risk increases from the end of October to March – when demand for *nopalitos* is at its peak. Under these conditions, manure and fertilizers should be applied at the end of the rainy season and early in spring, if irrigation is available. In the case of fully rainfed operations, fertilizers and manure can be incorporated before the end of the rainy season. Fertilization in excess can cause cladode burning and rapid oxidation of *nopalitos*.

Crop irrigation

Drip irrigation is an efficient method in nopalito orchards. The advantages of drip irrigation include (Vázquez–Alvarado *et al.*, 2009):

- capacity to deliver soluble fertilizers;
- fertilizer savings of 30–50% (compared with furrow and spray irrigation);
- reduction of weed competition; and
- improvement of water and soil conservation.

Orona Castillo *et al.* (2003) provide specific data on water use, following a study of superficial and subsuperficial drip irrigation and three soil moisture levels – 30, 45 and 60% of daily evaporation (type A evaporation tank) – for several *Opuntia* species. They indicate a total yield of 100.4 tonnes ha^{-1} and 18.8 kg of *nopalitos* per m^3 of water. Total water use is 5 340 m^3 ha^{-1}, i.e. less than that required to produce corn, dry beans and forages (which need 5 500–18 000 m^3). Based on these data, the authors recommend for *O. ficus–indica* varieties: irrigation at 45% of daily evaporation; and annual application of 161, 60.7 and 914 kg ha^{-1} of N, P and K, respectively.

Flores (2013) – on the basis of data obtained for an orchard planted in furrows, using a drip irrigation system – estimates water consumption at 391.9 mm year^{-1}. Plants should be watered when the soil hydraulic tension reaches 35 cb, associated with a daily consumption of 1.1 mm, i.e. 2 321 m^3 ha^{-1} of water year^{-1}. Water productivity is estimated at 111 kg m^3 for *O. ficus–indica* plants fertilized with dairy manure and triple 17 solid fertilizer, i.e. significantly higher than the productivity of the control treatment (76 kg m^3). The recommended irrigation schedule is four waterings when the tensiometer reaches 35 and two when it reaches 70. Water needs also vary according to location: Nobel (1998) estimates 3.27 mm day^{-1} for California, while Fierro *et al.* (2003) recorded 1.65 mm day^{-1} in Milpa Alta, Mexico. Finally, to improve the efficiency of irrigation, it is necessary to consider the rainfall distribution and avoid excess watering, using a single dripping line for two consecutive rows.

Training

Training the nopal plant for *nopalito* production entails moulding it into a regular shape, avoiding branching towards the alley, and maintaining plant height < 1.8 m (in furrow or edge production systems) or below the fourth storey (for mini–tunnel plantations). Training eliminates excess cladodes produced on the second storey. *Nopalito* plants are usually allowed to retain 2–3 main branches, configured as "rabbit ears" or in a "fan"; the remainder are either harvested or discarded. In practice, training is combined with harvesting; however, when market demand stalls, the removal of mature cladodes is programmed on the basis of the expected date of market recovery.

Pruning waste disposal

A remarkable example of the utilization of pruning waste is the incorporation of fresh sliced cladodes in the field from where they were collected. For this operation the *nopalito* growers traditionally use machetes and knives. However, recently small specialized machines have been imported from Brazil, originally designed to prepare forage nopal, and similar machines of Mexican design are also available. This practice increases the moisture and organic matter levels in the soil and also suppresses weeds temporarily.

Pests and diseases

Most of the pests present in cactus fruit orchards are also found in *nopalito* orchards; however, their incidence and damage are limited due to the continuous pruning. The most serious pest in *nopalito* production is the cochineal insect; the most important Lepidopteran insect pests are the zebra worm (*Olycella nephelepsa*), the white worm (*Megastes cyclades*) and the cactus pad joint borer (*Metapleura potosi*). Similarly, cactus weevil (*Metamasius spinolae*), shot hole weevil (*Gerstaeckeria* spp.) and areole weevil (*Cylindrocopturus biradiatus*) are found. Earthworms (*Phyllophaga* sp.) are important in *nopalito* orchards planted in light volcanic soils. For detailed descriptions of these pests, refer to Chapter 11.

Harvesting *nopalitos*

Cladodes should be harvested 30–60 days after sprouting, when they weigh 80–120 g and are 15–20 cm long (Flores Valdez, 1995). Tender *nopalitos* present spines and glochids, and latex gloves and knives are, therefore, used during collection. The tender pads are carefully removed by inserting the knife between the joints of the cladodes – an operation requiring skill to maintain the product intact. They are deposited in baskets or plastic crates (**Figure 5**), and sorted according to market standards: small or baby, medium and large. Depending on the market destination, the grower may pack the *nopalitos* in cylindrical or rectangular bales, wrapped in brown paper or polyethylene sheets.

BASIC PREPARATION TECHNIQUES

Cleaning *nopalitos*

The most common method applied to *nopalitos* is still manual cleaning, using only a sharp knife and neoprene gloves. Other tools have been tried:

Figure 5
Standard polyethylene packaging of nopalitos *with 20–30 kg and the traditional cylindrical bales containing ≤ 300 kg or ≤ 4 500 cladodes*

razor–blade–type knives, hollowed and sharpened spoons, potato peelers etc., but always with less success. A laser machine was once proposed, but due to its high cost and low efficiency, it never passed the modelling phase. More recently, a cleaning machine based on rotatory knives and built from stainless steel has been introduced to clean large volumes for the preserved *nopalitos* industry. Developed by Mexican inventors, it is promoted by the brand Nopalli (http://www.agrocentro.org/#!services/c21r) and can be adjusted for different shapes and sizes of *nopalitos*. The machine can process ≤ 40 pads minute^{-1} with an estimated wastage of < 15%. The same manufacturer produces a second machine designed to slice clean *nopalitos* into different shapes: dices or strips (**Figure 6**).

The complete removal by hand of thorns and glochids takes skill and practice and a demonstration can be viewed in a public video (available at https://www.youtube.com/watch?v=XfekDxpqB–I).

On–the–spot cleaning of *nopalitos* offers the consumer proof of freshness. This initiative has been tried successfully in many Mexican supermarkets, where the freshly cleaned product is offered diced or filleted as the customer chooses.

Reducing the presence of mucilage

Mucilage is a common feature of all opuntias. Mucilage is released in response to wounding, and the quantity of mucilage released depends on the variety, as well as the cladode's age and stage of dehydration. Mucilage is also released when cooking, which normally involves boiling. Nevertheless, mucilage cannot be completely removed from *nopalitos* regardless of the cooking method adopted. Various practices have evolved to reduce or mask its presence in the final preparation:

- Addition of dry oregano leaves, bay leaves, chopped onion stems, tomatillo husks, sea salt grains, sodium bicarbonate, lemon juice, corn husk or garlic cloves, depending on the *nopalito* recipe used.
- Interrupting boiling to dip the *nopalitos* in cold or chilled water.
- Addition of a few copper or silver coins during boiling – although this particular method is the least advisable given the high risk of contamination.
- Scalding with common salt and oregano for 7 minutes (Pensaben *et al.*, 1995).

The most aggressive cooking methods have a greater negative effect on the vitamin and mineral content, reducing the functional properties and beneficial effects of *nopalito* consumption. The salt–oregano method (Pensaben *et al.*, 1995) reduces the presence of mucilage without affecting the green colour typical of the *nopalitos*.

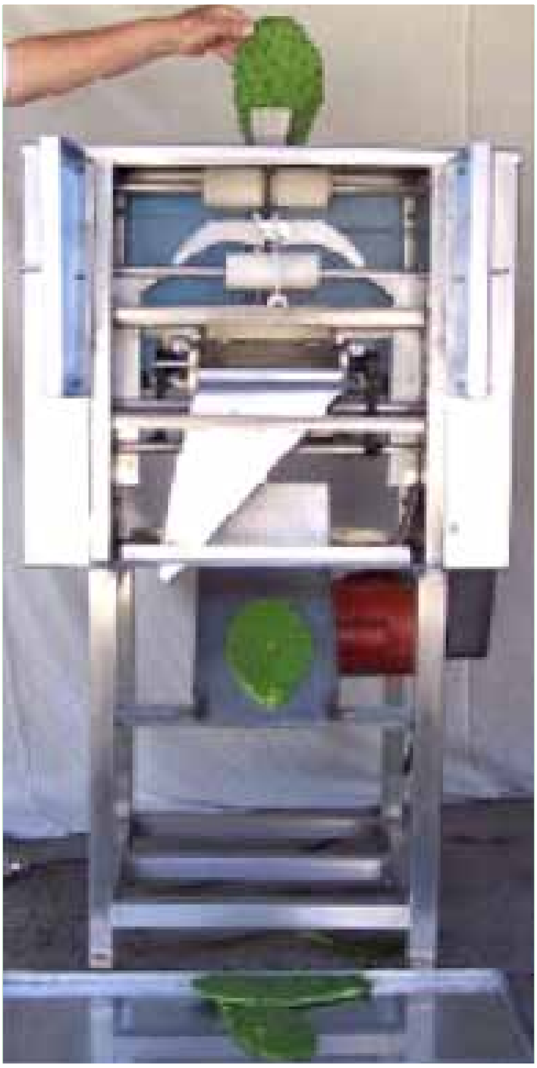

Figure 6
Cleaning and dicing nopalito machines, Mad Industrias, Monterrey N.L., Mexico

Scalding and brining are the standard treatments for large volumes of *nopalitos* used in the restaurant industry in Mexico and they led to the popularization of *nopalitos* in the 1990s.

Cladode acidity

Nopalitos are characterized by their acidity, which is due to the CAM photosynthetic pathway of *Opuntia* and can affect acceptance by new consumers. Acidity varies significantly (0.1–0.5% of titratable acidity), depending on the time of day. Acidity decreases during the day and increases at night, regardless of the time of harvest (Corrales García, 2010). The acidity of several varieties of *nopalitos* decreased during the day, in relation to the exposure to light – a typical response of CAM plants (Flores Hernández *et al.*, 2004). Even when detached from the plant, the variations are noticeable, since the cladode remains alive and photosynthetically active. Cantwell *et al.* (1992) report pH values of 0.94% in the morning, decreasing to 0.47% in the afternoon; Pimentel González (2013), therefore, recommends harvesting *nopalitos* 2 hours after sunrise. In any case, harvest is typically early in the morning when humidity is highest and the exposure of workers to glochids is reduced, making it the best time for work in the field.

Acidity seems to depend on the variety, according to Aguilar Sánchez *et al.* (2007) who studied 21 cultivars utilized as vegetable: 'Jalpa' and 'Morado Italiano' around 0.43%; 'Milpa Alta' 0.68%; 'Oreja de Elefante', a forage cultivar, 0.69%. The same study revealed that 'Jade' and 'Negrito' present low oxidation, another important trait for agro–industrial processing.

Acidity can be modified by the temperature during storage. Chilled storage (5 °C) maintains or slightly increases acidity, while storage at room temperature (20° C) decreases acidity. These fluctuations modify the flavour of *nopalitos*, and according to Corrales García *et al.* (2004), the time of processing and consumption are more important than the harvest time.

09

Cochineal breeding

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09

Cochineal breeding

INTRODUCTION

Cochineal (*Dactylopius* spp) is an American group of Hemipteran insects (Spodek *et al.*, 2014) thriving on *Opuntia* cactus plants. Cochineal is important to humankind for four reasons:

1. The insects are a source of carminic acid, a pigment (**Figure 1**) mostly extracted from *Dactylopius coccus*, used in food colouring, cosmetics, drugs, fabrics and many other products (Cañamares *et al.*, 2006; Chávez Moreno *et al.*, 2009).
2. Some *Dactylopius* species have been used for biological control against invasive cacti (Githure *et al.*, 1999; Volchansky *et al.*, 1999; De Felice, 2004).
3. *Dactylopius* spp. can become invasive to *Opuntia* species where they are non–native (Van Dam and May, 2012).
4. There is ongoing research into the antioxidant and antimicrobial properties of carminic acid, to understand its potential applications in immunology, wastewater treatment and solar cells (González *et al.*, 2009; García Gil *et al.*, 2007; Bae and Huh, 2006; El Moselhy *et al.*, 2011).

For a long time, there was controversy over the origin of cochineal (*D. coccus*), with some authors citing South America (Rodríguez and Niemeyer, 2000; Rodríguez *et al.*, 2001). However, research has now led to acceptance that it originates in North America, where its native ecological environment occurs and it has co–evolved with abiotic (**Table 1**) and biotic factors, mainly host plants (**Table 2**) and natural enemies (**Table 3**) (Griffith, 2004; Portillo, 2005; Novoa, 2006). Based on mtDNA data and climate niche modelling (Van Dam *et al.*, 2015), its origins were further specified to be in Mexico.

Cochineal has for centuries been one of the most important pigments and it is still used today (Serrano *et al.*, 2011, 2013). It was first used among the ancient cultures of America (Donkin, 1977; Piña, 1977), and when the Europeans arrived in America, its use and breeding spread. In the nineteenth century, the first artificial dyes were synthetized and the cochineal market declined and almost disappeared. Today, however, the use of natural pigment sources is again on the increase thanks to their health benefits, and cochineal

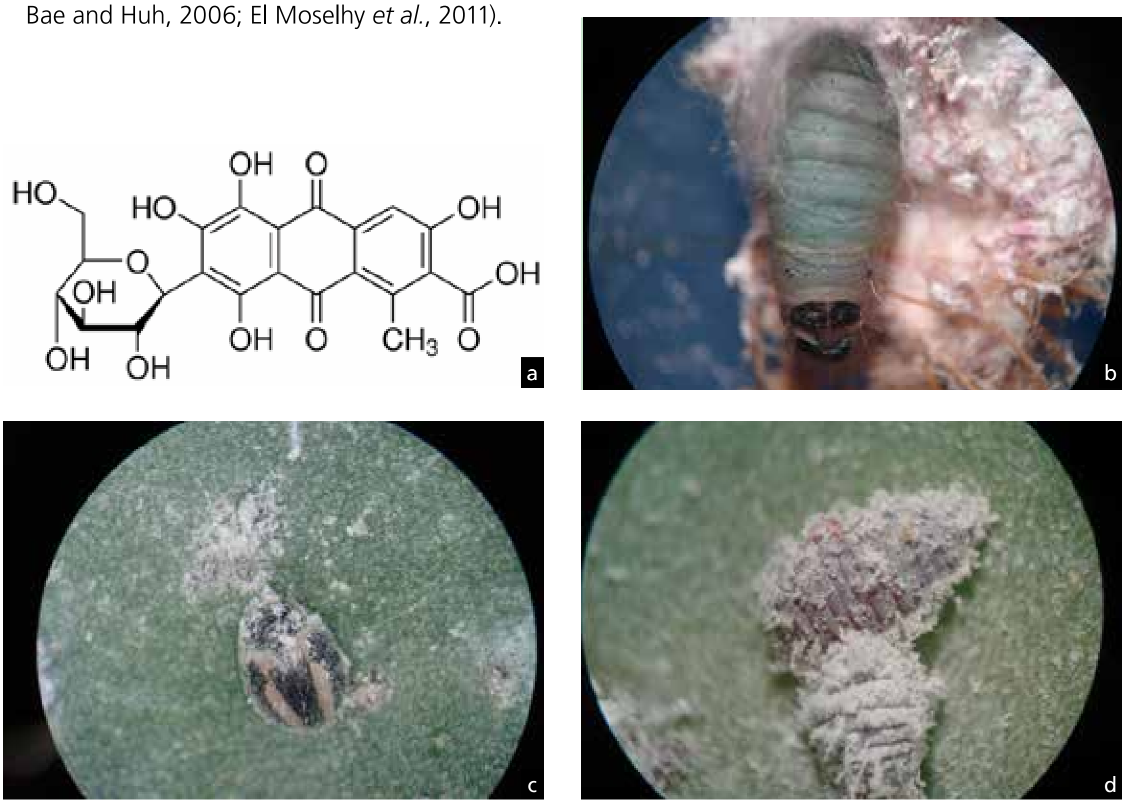

Figure 1
a) Carminic acid
b, c, d) Diversity of depredators

production is being re–established with a range of breeding technologies in many tropical and subtropical areas of the world.

This chapter describes the various methods for cochineal breeding and outlines harvest and post–harvest management practices, with a focus on both its biology and its ecology in native and non–native areas.

BIOLOGY

Dactylopius is the only genus of the Dactylopiidae family (Hemiptera: Coccoidea). All 11 species are parasitic of cactus plants (De Lotto, 1974; Spodek *et al.*, 2014) and present a disjunct distribution (Van Dam and May, 2012), native to:

- South America: *D. austrinus* De Lotto, *D. confertus* De Lotto, *D. zimmermanni* De Lotto, *D. salmianus* De Lotto and *D. ceylonicus* Green; or
- North America: *D. bassi* (Tozzetti), *D. coccus* Costa, *D. confusus* (Cockerell), *D. gracilipilus* Van Dam and May, *D. opuntiae* (Cockerell) and *D. tomentosus* Lamarck.

The species most used for commercial purposes – due to its high pigment content (> 20% of carminic acid) – is the domesticated species, *D. coccus* (fine cochineal). In ancient times, it was known as *nocheztli*, a Nahuatl word meaning "blood of cactus", in reference to the insect and the dye it produces (Wright, 1963). In 1758, it was called *Coccus cacti* by Linnaeus; in 1835, Costa classified it as Dactylopius coccus (Piña, 1977).

Sexual dimorphism

Dactylopius males have wings on their adult instar; they are smaller than females and highly mobile. Females are about 6.24 mm, wingless, stationary, oval–shaped and covered with a powder wax. Montiel (1995) states that since males undergo complete metamorphosis, their immature stages must be termed larvae. Since characteristics of dimorphism do not appear in the first immature stages, and it is the bodies of the female that are used to obtain the pigment, for the sake of convenience, all the immature stages are referred to as nymphs.

Life cycle

Females and males go through the egg stage (**Figure 2a**) and two immature stages. The biological cycle from egg to adult lasts 90–128 days, depending on temperature and other factors (Marín and Cisneros, 1977).

- **Nymph I.** The female in this immature stage has two substages: mobile and fixed. The first substage is also known as crawler (**Figure 2b**), characterized by movement and absence of white wax; in < 24 hours, it has to find a place in the cactus pear to insert its mouthpart. Once the nymph is fixed, it passes into the second substage, secreting large wax filaments over the body (**Figure 2c**); within days, the filaments disappear and make way for a powdery wax.
- **Nymph II**. After a first moult (**Figure 2d**), this immature stage (**Figure 2e**) is bright red and within hours starts to be covered with wax. Nymph I and II stages present no ostensible differences between males and females.
- **Adult female.** The female cochineal undergoes another moult (**Figure 2f**), synchronized with the adult males for copulation. During this stage, the female increases in size (**Figure 2g**). Each female usually produces 420 eggs, but about 10% of females show infertility (Vargas and Flores, 1986), which reduces the production of new crawlers.
- **Adult male.** The male cochineal begins to develop a cocoon (**Figure 2h**) to emerge as an adult

Figure 1
Two forms of coccidoculture:
e) under cover
f) in the open

male (**Figure 2i**). The male presents two pairs of wings, two tails, a non–functional mouthpart, and mobility to search for females for mating.

COCHINEAL BREEDING

Abiotic and biotic factors

Coccidoculture or cochineal breeding is an activity that can be carried out in many places in tropical and subtropical regions, but it is conditioned by both abiotic and biotic factors and it is, therefore, vital to understand which factors are present in a particular area. In the rainy season, it is recommended to carry out propagation of cochineal on isolated cladodes under protection. Indeed, in almost all of Mexico, coccidoculture takes this form because of:

- abiotic factors – unfavourable conditions in the open (**Table 1**); and
- biotic factors – essentially natural enemies (**Table 3**), with a wide diversity of depredators in Mexico (**Figures 1b, c and d**).

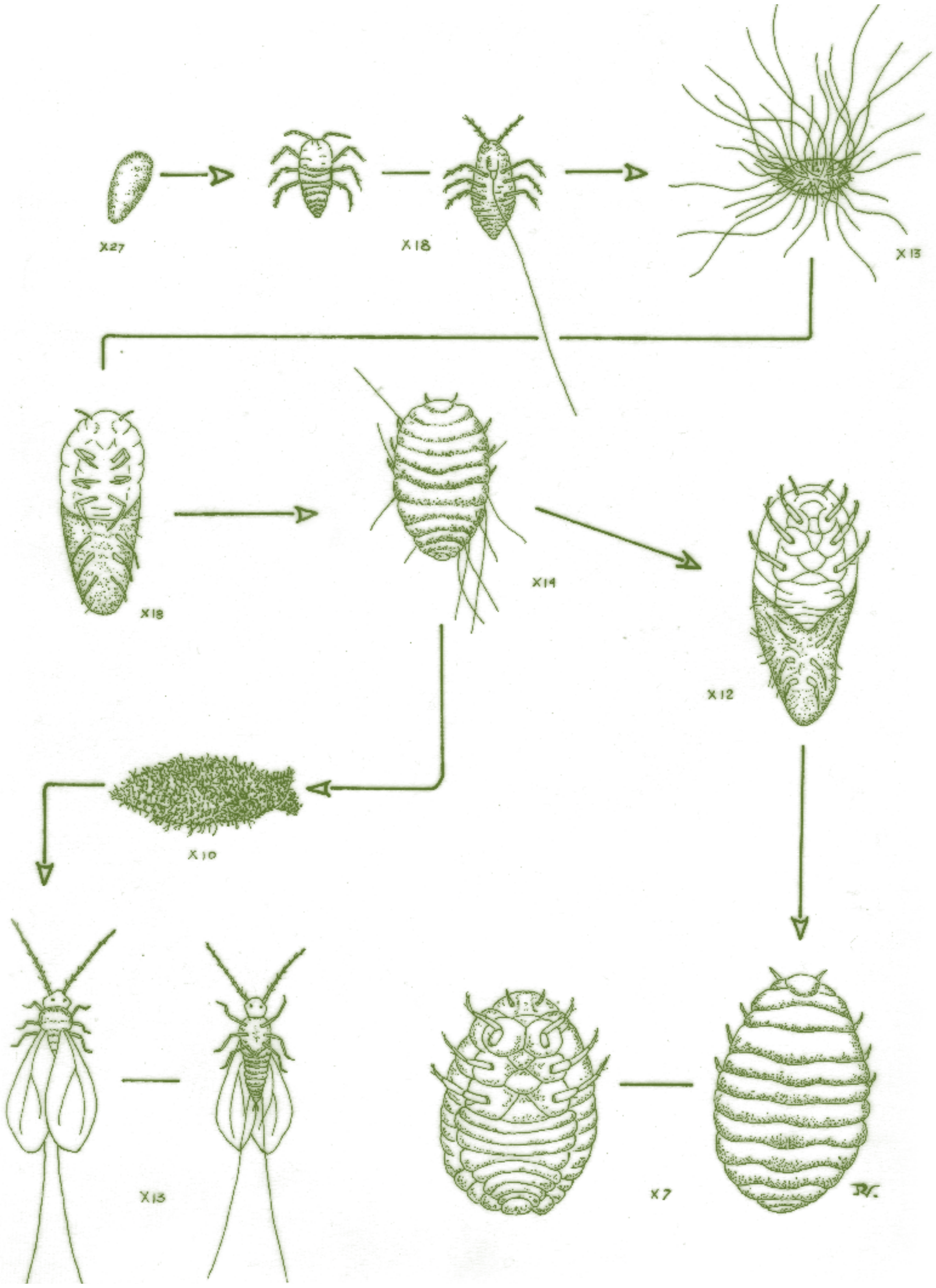

Figure 2:
a - i) The biological cycle from egg to adult

TABLE 1 Abiotic factors limiting cochineal breeding

Factor	Main effect	Source
Temperature	Altered length of biological cycle	Méndez, 1992
	Dehydration of nymphs	Flores, 1995
Rain	Elimination of 100% of cochineal population	Flores, 1995
	Suffocation of cochineal	Alzate and Ramírez, 1777
	Hindered fixation and development of nymphs	Flores, 1995
Wind	Limited fixation of cochineal	Aquino, 1992
	Increased dispersion and dragging of nymphs	Flores, 1995
Light	Movement of crawlers influenced	Flores, 1995
	Growth and development of cochineal enabled	Aquino, 1992
Hail	Cochineal thrown to the ground	Alzate and Ramírez, 1777
Frost	Elimination of > 50% of cochineal	Alzate and Ramírez, 1777

Cochineal breeding in Mexico has been reported on several *Opuntia* species (**Table 2**); the most important cultivars for commercial production are spineless 'Atlixco', 'Chicomostoc' and 'Milpa Alta', which all belong to *O. ficus–indica*.

TABLE 2 *Opuntia* species reported to host *Dactylopius coccus* in Mexico

Host species	Source
Opuntia amyclaea Tenore	Vigueras and Portillo, 2014
O. atropes Rose	Rodríguez and Portillo, 1989
O. cochenillifera (L.) Salm–Dyck[a]	Piña, 1981
O. crassa Haworth	Vigueras and Portillo, 2014
O. ficus–indica (L.) Miller	Piña, 1981
O. fuliginosa Griffiths	Portillo and Vigueras, 2003
O. incarnadilla Griffiths	Vigueras and Portillo, 2014
O. jaliscana Bravo	Portillo and Vigueras, 2014
O. megacantha Salm–Dyck	Piña, 1981
O. pilifera Weber	Portillo and Vigueras, 2003
O. sarca Griff. ex Scheinv.	Portillo and Vigueras, 2003
O. streptacantha Lem.	Piña, 1981
O. tomentosa Salm–Dyck	Piña, 1981
O. undulata Griffiths	Portillo and Vigueras, 2003

[a] This species belongs to the subgenus *Nopalea*.

TABLE 3 Predators of *Dactylopius coccus* Costa recorded in Mexico

Species	Order and family
Laetilia coccidivora Comstock	(Lepidoptera: Pyralidae)
Eosalpingogaster cochenillivora Guerin–Meneville	Diptera: Syrphidae
Sympherobius amiculus Fitch	Neuroptera: Hemerobidae
Hyperaspis trifurcata Schaeffer	Coleoptera: Coccinellidae
Chilocorus cacti Lineo	Coleoptera: Coccinellidae
Leucopis bellula	Diptera: Syrphidae

Source: Modified from Vigueras and Portillo (2014).

Cactus pear plantations for cochineal breeding

Commercial plantations of cactus pear always use spineless cultivars of *Opuntia ficus–indica* for cochineal breeding, whether in the open or under cover. Cultivars with yellow fruits are preferred, but white, red and purple cultivars may also be used. Plantations have an average of 20 000 plants ha^{-1}, but the number may vary depending on soil quality (good drainage), altitude (800–2 300 m asl), temperature (13–27° C) and water availability (Salas, 2016). Plants receive around 30 tonnes year^{-1} of manure (cow, goat or even chicken), and additional fertilization as required (N100–P50–K10).

Cochineal breeding methods

There are two forms for coccidoculture: under cover and in the open (**Figures 1e and f**). The choice of breeding method largely depends on the local climatic conditions. Structures for cochineal breeding under protection are traditionally made of wood, shade screens, palm leaves, plastic (transparent or black) and other materials (Santibáñez, 1990; Méndez, 2013); in recent years, however, intensive production has used large greenhouses (Escalante, 2013). The main methods are described below:

- **Microtunnel.** Structures (height approx. 1 m) are made of greenhouse polyethylene plastic or shade cloth (1 mm thick) (**Figure 3a**) to protect infested 2–3–year host plants or single planted 1–year cladodes (Vigueras and Portillo, 2014). This method is useful in regions where heavy rains are common or winter is cold (minimum 0–10° C).
- **Tapesco.** Shelters have a roof made from reeds, wood, logs, shade cloth, woven palm or plastic (Rodríguez and Portillo, 1989; Santibañez, 1990). These sheds are used to hang single mature cladodes for small cochineal breeding or to increase a particular cochineal colony while protecting it from undesirable factors.
- **Intensive production.** This system (proposed by the Campo Carmín enterprise) was implemented for the first time in 2002. Greenhouses are built using modules. They cover 1 356 m2 and have a minimum capacity of 432 000 hanged spineless cladodes (Escalante, 2013). This method is currently the most common in Mexico (**Figure 1e**).
- **Irrigation.** Single cladodes are established under hydroponic systems in Peru and Mexico, using formulations of macro– and micronutrients to promote growth of the host plants and cochineal (Vigueras *et al*., 1993). This method is common on the south coast of Peru (**Figure 1f**), where high–density plantations (around 9 000 or more plants ha^{-1}) with a fertigation system are infested in the open (Flores, 1995).

Infestation methods

Regardless of the cochineal breeding method selected, infestation is necessary in order to achieve harvest. Infestation methods require careful selection. Whether infesting whole plants or single mature cladodes (Llanderal and Campos, 1999), it is highly recommended to use different containers called "nests" to hold the adult females in oviposition period (OP). New infestation methods are frequently introduced on open–air commercial plantations to facilitate infestation and reduce labour:

- **Oaxacan.** Cylinders made of woven palm (length 10 cm, diameter 2 cm) carrying adult females in OP are held by the spines on the host plants for ≤ 20 days for infestation. Containers can be rotated to other plant areas for better results. In Bolivia, the same concept is applied using hollow cane sugar stems with a lot of small holes (Tukuypaj, 1993), and recently in Peru using plastic hose pieces.
- **Peruvian.** The adult females in OP are introduced in small tulle bags (10 × 10 cm), hung on the spines of the host plants until infestation is observed (Quispe, 1983).
- **Ricci.** A small triangular incision (sides 2 × 2 × 2 cm, depth 0.5 cm) is made in the centre of a cladode, which becomes dry and serves as a support for the adult females in OP to facilitate the infestation (Portillo *et al*., 1992).
- **Infested cladode.** Infested cladodes with adult females in OP are placed at the bottom or between two cladodes of the host plants to facilitate infestation (Tukuypaj, 1993).
- **Cotton fabric.** Small pieces of cotton fabric are placed on adult females in OP, allowing the crawlers to get on them; the pieces of fabric are then dropped on the host plants to be infested (Quispe, 1983).
- **Gravity.** As adult females start OP on hanging cladodes, the crawlers fall with the force of gravity on new ones collocated at the bottom and yet to be infested. This method is adopted in new greenhouses in Mexico used for intensive production of cochineal (Escalante, 2013). Gareca (1993) also describes a gravity–based system: a mesh tray with adult females in OP is placed at the top, and twice daily horizontal movements make the crawlers drop down to infest cladodes at the bottom.
- **Paper container.** The simplest method: any piece of discarded paper is used to make a small container (length 8 cm) with adult females in OP inside (Téllez, 1911); it is attached by spines to the host plants allowing the infestation (**Figure 3b**).

Harvesting

Harvest is a delicate process that involves separation of the female insects from the host plant when they are about to start oviposition, taking care to avoid injuring them. There are several methods for harvesting cochineal, depending on the breeding method (open or under cover) and host plant (spineless or spiny).

In the open

In the Andean region of Peru and Bolivia, there are many instruments made of sticks (length 0.60–1.50 m), with spoons, brushes or metal strips attached at the end to gather cochineal (**Figure 3c**). Spoons and brushes are used on spineless plants and metal strips on spiny ones. On the south coast of Peru and in Chile, cochineal is harvested from spineless plants using brushes without the stick. In Chile and South Africa, another method with pressurized air has been used to harvest cochineal from spiny cladodes (Brutsch and Zimmermann, 1993). In the Canary Islands, cochineal is harvested in November, 3 months after infestation, using a large spoon–like instrument called a "milana".

During harvest, the collected insects fall into bags made of cotton, and are later distributed on wood, metal or clay trays, taking care to avoid clumping that may crush the fresh insects.

Under cover

In Mexico, the cochineal harvest takes place about 3 months after infestation; however, it may be carried out at any time of year and using a wide range of instruments (reeds, metal spoons, brushes, sticks and plastic scrapers). Selection of the most suitable instrument depends on different factors: breeding method; extent of cultivation area; and cultivar characteristics (spineless, spiny or even pubescent plants). Where cochineal breeding is a recent activity, new techniques and instruments may need to be developed for harvesting (Vigueras and Portillo, 2014).

Post–harvest

Post–harvest activities involve the killing (in Mexico this step is known as "sacrifice") and drying of cochineal (Santibáñez, 1990), as well as its selection. There are several methods for killing cochineal:

- immersion in boiling water (Alzate and Ramírez, 1777);
- suffocation with steam;
- freezing in temperatures below 0 °C (experimental);
- suffocation with hexane;
- asphyxia in hermetic containers; and
- heating with hot air, inside ovens, on clay posts (Téllez, 1911) or by solar radiation (temperatures around 40°C).

To dry cochineal, solar dryers and stoves are used, as well as direct sunlight and in the shade; for shade–drying, the site must be completely dry. The selection process involves the separation of the males, immature cochineal, moults, wax and any other element that is not the adult female cochineal. Selection also takes size into account, as a bigger cochineal means more pigment; however, the end objective is to obtain cochineal with a high carminic acid content. Currently the preferred cochineal has the following characteristics:

- $>$ 22% carminic acid content;
- 14–mesh size ($>$ 1.295 cm); and
- $<$ 1% of impurities.

Cochineal meeting these specifications has an open market; otherwise there is virtually no demand and the price is low. The price of cochineal is directly influenced by the carminic acid percentage (1% = 1 US$), although the price may vary depending on the market.

ECOLOGY

Any organism is in balanced interaction with the factors prevailing in its native environment; however, if moved to a new range (non–native area), the equilibrium may be broken. This loss of equilibrium produces consequences, one of which is that it may become invasive. Biological control is the most common tool for reducing the effects of this phenomenon, controlling the alien invasive species until it becomes non–invasive and naturalized (Shine *et al.*, 2000).

Given their usefulness to humankind, species of *Opuntia* and *Dactylopius* that are of particular interest for commercial production, are frequently moved from their original distribution in the Neotropical and Nearctic regions, and they are now found in Afrotropical, Australasian, Palearctic and Oriental regions (Anderson, 2001; Bravo Hollis, 1978; Majure *et al.*, 2012b). These movements have led to the creation of new weed and plague problems, with *D. opuntiae* on *O. ficus–indica* plantations in Brazil, Spain and other countries of the Mediterranean Basin (Portillo, 2009; Vasconcelos *et al.*, 2009). Cochineal species may be considered invasive; fine or domesticated cochineal (*D. coccus*) has been declared an invasive agent in Ethiopia (Belay, 2015) (**Figure 3d**). Nevertheless, the species is considered a useful insect worldwide. Some species of *Dactylopius* have been and still are used as biological control agents of several *Opuntia* species that are considered invasive (**Table 4**). There is the risk that new issues will continue to arise among cochineals and *Opuntia* cultivars.

D. coccus shows adaptation and selectivity for particular *Opuntia* species or cultivars (Portillo *et al.*, 1992), and similar behaviour is reported for *D. opuntiae* (Volchan-

Figure 3
a) Microtunnels
b) Infestation method with paper container
c) Using instruments made of sticks to gather cochineal
d) Invasive cochineal species

TABLE 4 *Dactylopius* species used to control invasive *Opuntia* species

Cochineal species	*Opuntia* species	Country	Source
D. austrinus	*O. aurantiaca* Guilles ex Lindley	Australia 1970; South Africa 1979	Moran and Cabby (1979)
D. ceylonicus	*O. vulgaris* Miller	Sri Lanka 1863	Volchansky *et al.* (1999)
D. opuntiae	*O. ficus–indica*	South Africa 1938	Moran and Zimmermann (1984a)
D. opuntiae	*O. stricta* Haworth	Australia 1921	Hoffmann *et al.* (2002)
D. opuntiae	*O. ficus–indica*	Brazil 2001[a]	Batista *et al.* (2009)

[a] In Brazil the introduction of *D. opuntiae* was not for biological control; it has now become an invasive species, destroying thousands of hectares of cactus pear plantations.

sky *et al.*, 1999; Githure *et al.*, 1999). Cactus pear cultivars have been introduced to many countries outside Mexico and – from an ecological point of view – cactus pear is often a foreign biotic factor in a non–native area. Although it is sometimes considered invasive, it has now become a useful element, known and appreciated by the local inhabitants. It is utilized in many ways and ethnobotany relations have been established in many communities around the world. Nevertheless, the reality is that new biotic factors may arise and these must be faced; potential threats to cactus pear are wild cochineal (*D. opuntiae*), cactus moth (*Cactoblastis cactorum*) and black spot (*Pseudocercospora opuntiae*) (**Figure 3e**). Plant sanitary borders must be made stricter to counteract the new infestations of wild cochineal (*D. opuntiae*) that are constantly arising, most recently in Israel, Lebanon and Morocco. Wild cochineal is an insidious plague and highly aggressive to cactus pear, as was demonstrated in Brazil (**Figure 3f**). Continuing efforts are needed to manage *Dactylopius* invasions and find a threshold; to this end, the authors are currently gathering more information.

Figure 3
e) Black spot (Pseudocercospora opuntiae)
f) Wild cochineal

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Diseases of cactus pear

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Diseases of cactus pear

INTRODUCTION

Similar to other crops, cactus pear (*Opuntia ficus–indica* [L.] Mill.) suffers from several biotic and abiotic diseases; how important they are depends on the destined use of the crop.

There is a shortage of accurate information on the aetiology and epidemiology of the pathogens, and the scientific literature does not sufficiently cover the geographic distribution and worldwide economic impact of many cactus pear diseases. Nevertheless, it is certain that most of the infectious diseases are caused by fungi, while a very small number of bacteria, phytoplasmas and viruses are reported as pathogens.

Due to the dry climate of the regions where cactus pear is grown worldwide, these diseases become problematic only in certain periods when conditions become favourable. Nowadays, however, expansion of cactus pear cultivation, dense plantings and climate change, may contribute to a higher incidence and greater severity of diseases, as well as the possible emergence of new or unusual diseases. Early detection, precise identification and strict monitoring of the diseases in fields and on propagation material are essential to prevent their diffusion.

This chapter provides concise descriptions of the most common diseases affecting cactus pear and recommendations for their control.

FUNGAL DISEASES

Black spot

Causal agent: *Pseudocercospora opuntiae* Ayala–Escobar, Braun & Crous.
Host range: *Opuntia* spp., *Nopalea* spp.
Geographical distribution: Bolivia, Brazil, Mexico, Peru.
Symptoms and signs: The first symptoms are cuticle discoloration in the form of a circular spot; it becomes transparent and oily in appearance, and the brown central area increases in size. Later, the cladode tissue presents a light brown colour at the margins of the spot which changes to dark brown, presenting tissue collapse. The affected tissue turns black; conidiophores and conidia in the form of small grey protuberances can be seen (**Figure 1**). Finally the affected zone sinks through to the other side of the cladode. The injuries reach a diameter of 3–4 cm at the end of the infection. Different symptoms can appear simultaneously on the same cladode (Ochoa *et al.*, 2015b). Similar symptoms have been associated with anthracnose caused by *Colletotrichum gloeosporioides* (Penz.) Penz & Sacc. However, on the basis of pathogenicity tests, Quezada Salinas *et al.* (2006) affirmed that *C. gloeosporioides* is not the cause of black spot disease in cactus pear.

Disease management: Survey the cactus pear plantations after the rainy season to detect and eliminate the cladodes at the first sign of disease symptoms. Adopt preventive pruning to allow good ventilation. Apply copper–based fungicides just before the rainy season.

Cladode and fruit rot

Causal agent: *Lasiodiplodia theobromae* (Pat.) Giff. & Maubl. (teleomorph: *Botryosphaeria rhodina* Berk. & M.A. Curtis, Arx).
Syn.: *Botryodiplodia theobromae* (Pat.).
Host range: More than 500 hosts, including humans.
Geographical distribution: Brazil, Egypt, Italy, Mexico, South Africa, United States of America.
Symptoms and signs: Black roundish areas (15–50 mm diameter) appear on cladodes leaking a black gum exudate from the margin of the lesion. Pycnidia are often evident on the surface of the infected area. Probably, the same disease has been reported as gummosis canker on cladodes (**Figure 2**) in Linosa (Italy) and the causal agent attributed to *Botryosphaeria ribis* (syn. *Dothiorella ribis*) (Somma *et al.*, 1973).

Disease management: Avoid wounds, remove and destroy diseased specimens. Apply fungicides (tiabendazole and tiofanat–metil) proved effective for reducing disease incidence.

Alternaria dry rot

Causal agent: *Alternaria* spp.
Host range: Highly polyphagous.
Geographical distribution: Argentina, Italy, Brazil, Egypt, Mexico, South Africa.
Symptoms and signs: The first symptoms are circular chlorotic spots around the spines or wounds on the cladodes and fruits, which later become dark and necrotic (**Figure 3**). Penetration sites are generally the spines, but may also be wounds in the cuticle caused

Figure 1
Amaranthus cruentus

Figure 2
Gummosis canker (Linosa Island, Italy

by hailstones. In South Africa, different species of *Alternaria* were isolated from cladodes with dry rot symptoms (Swart and Kriel, 2002; Swart and Swart, 2002; Ammar *et al*., 2004; Souza *et al*., 2010). In Italy, *Alternaria alternata* causes golden spot (**Figure 4**) producing spots that are dark in the centre and golden yellow around the edges (Granata and Sidoti, 1997). The same disease is known as *mancha de oro or secamiento de la penca* in Mexico (Gutiérrez, 1992). A. *alternata* also causes a post–harvest fruit decay. The symptoms are a superficial dry rot of the peel, black in colour (**Figure 5**). Generally, the lesions with irregular margins are localized in the central part of the fruit and the decayed peel can be scraped off (Faedda *et al*., 2015b).

Disease management: Spray with a fungicide, such as copper, mancozeb and iprodione, for effective control of the disease, especially after hail. Apply hot water treatment for efficient control of post–harvest disease.

Armillaria root and stem rot

Causal agent: *Armillaria mellea* (Vahl) P. Kumm.
Host range: Highly polyphagous.
Geographical distribution: Italy, United States of America.

Symptoms and signs: Root and stem rot is caused by *Armillaria mellea*, a basidiomycetous fungus that colonizes the shoot and main roots of the plant and produces white mycelium and cordons of hyphae, called rhizomorphs, that spread from the infected tissues and contaminate neighbouring plants. Infected cactus pear plants suffer from a decline in tissue turgor and chlorosis resulting from phloem disorganization and altered water and mineral nutrition. The fruit growing on infected plants do not reach full ripeness and remain mummified on the cladode. Basal stem rot symptoms can be observed with the release of viscous exudate. Characteristic white mycelium fans of hyphae can be found beneath the surface of the lesions. The rotten portion of the stem has a bright red border which extends upwards above the soil line. The disease may affect the main roots (Raabe and Alcon, 1968; Magnano di San Lio and Tirrò, 1983).

Disease management: Since *Armillaria* often remains in the soil in residues from previous cultivations inevitably infecting new crops, it is recommended not to cultivate soil infected by this fungus for 2–3 years and to remove sources of inoculum (roots of previous cultures). Effective chemical control of the disease is not available yet.

Figure 3
Alternaria dry rot (Tunisia)

Figure 4
Golden spot (Italy)

Figure 5
Alternaria fruit rot (Italy)

Figure 6
Cottony rot (Peru)

Cottony rot

Causal agent: *Sclerotinia sclerotiorum* (Lib) de Bary.
Host range: Polyphagous.
Geographical distribution of disease: Chile, Mexico.
Symptoms and signs: The fungus causes a cottony rot in the cladodes (**Figure 6**). Infected cladodes initially become decoloured followed by a slight softening of the cuticle. They later turn dark, flake off and become covered with a white wool. Numerous black sclerotia soon appear from the decayed tissues (G. Granata, personal communication).

Disease management: Remove and destroy infected cladodes. It is of primary importance that the sclerotia are prevented from touching the soil where they may remain alive for many years.

Figure 7
Phytophthora foot rot (Italy)

Figure 8
Grey mould (Italy)

Rust

Causal agent: *Aecidium opuntiae* Magn.
Syn.: *Puccinia opuntiae* (Magnus) Arthur & Holw.
Host range: *Opuntia* spp., *Bouteloua simplex* Lag.
Geographical distribution: Bolivia, Italy, Peru.
Symptoms and signs: Known as "Roya" in South America, the disease is caused by *Puccinia opuntiae*, which produces yellow–orange pustules on the surface of cladodes or fruits. As the rust spot dries, a hole develops on the cladode. Similar symptomatology was described by Goidanich (1964) as rust scab and the causal agent attributed to *Phyllosticta opuntiae* Sacc. & Speg.

Disease management: Remove and bury the infected cladode.

Scaly rot

Causal agent: *Scytalidium lignicola* Pesante.
Host range: *Auricularia polytricha, Citrus paradisi, Mangifera indica, Manihot esculenta, Vanilla fragrans,* humans and animals.
Geographical distribution: Brazil.
Symptoms and signs: The disease is widespread on cactus forage (palma–forrageira) in the northeast region of Brazil. The symptoms begin with a dry rot that develops a scaly appearance at the base of the cladodes (Souza *et al.*, 2010). Plentiful yellowish gum exudates gush from the infected tissues. This polyphagous fungus is a pathogen causing skin, nail and hair infections in humans.

Disease management: To date, there has been no research to determine the optimum conditions for disease development. Remove infected plants to reduce the amount of inoculum infecting nearby plants.

Phytophthora foot rot

Causal agent: *Phytophthora nicotianae* Breda de Haan.
Host range: The pathogen infects plants from approximately 90 different families and different isolates have distinct host ranges.
Geographical distribution: Italy.
Symptoms and signs: *Phytophthora nicotianae* is the causal agent of foot rot in cactus pear in Italy (Cacciola and Magnano di San Lio, 1988). The most typical symptom of foot rot is gum exudate oozing from the lower stem. Diseased plants present water–soaked lesions with irregular brown margins on the basal stem surface and a soft rot of internal tissues that turn brown or reddish. Affected plants become chlorotic, growth slows, and cladodes wilt, causing the plant to fall over (**Figure 7**).

Disease management: Clay soils where water stagnates are prone to harbouring *Phytophthora*. For this reason, cultivate cactus pear in well–drained soil to prevent waterlogging.

Pythium crown and stem rot

Causal agent: *Pythium aphanidermatum* Edson (Fitzp.).
Host range: Widely polyphagous.
Geographical distribution: Mexico.
Symptoms and signs: The first symptoms are soft, dark brown lesions on the cladode at the soil line. The lesions gradually reach the upper part of the cladode and then extend upwards to the next cladode. Rotten cladodes are associated with root rots. The diseased plants finally collapse and large plants collapse more rapidly than small plants (Rodríguez Alvarado *et al.,* 2001).

Disease management: Avoid excessive water and maintain good soil drainage.

Fusarium root rot

Causal agent: *Fusarium oxysporum* f. sp. *opuntiarum* (Pettinari) W.L. Gordon.
Host range: *Echinocactus grusoni, Schlumbergera truncate.*
Geographical distribution: Brazil, Italy.

Figure 9
Penicillium fruit rot (Italy)

Figure 10
Macrophomina soft rot (Italy)

Symptoms and signs: Diseased plants present root rot with intense red discoloration of affected tissues. If root rot becomes severe, infected plants may develop other symptoms including stunting and wilting (Pettinari, 1951).
Disease management: Plant in well–drained soils and reduce soil compaction to make conditions less favourable to infection by *Fusarium* species.

Grey mould

Causal agent: *Botrytis cinerea* Pers. (teleomorph: *Botryotinia fuckeliana* [de Bary] Whetzel).
Host range: Highly *polyphagous*.
Geographical distribution: Italy.
Symptoms and signs: The pathogen penetrates through the wound that tends to occur when the fruit is detached from the cladodes. The infected area of the fruits is dark grey and usually circular; the internal tissues are decayed and soft (**Figure 8**). (G. Granata, personal communication).
Disease management: Avoid wounds during harvest and post–harvest processing.

Penicillium fruit rot

Causal agent: *Penicillium* spp.
Host range: Highly polyphagous.
Geographical distribution: Worldwide.
Symptoms and signs: *Penicillium* rot is regarded as a major post–harvest disease of cactus pear fruits in many production regions of the world. P*enicillium italicum* Wehmer and P. digitatum (Pers.) Sacc. are reported as major causal agents of this disease (Schirra *et al.*, 1999b). Other *Penicillium* species, including *P. citrinum* Thom, P. expansum Link (Scherm *et al.*, 2003; Oliveri *et al.*, 2007) and *P. polonicum* K.M. Zalessky (Faedda *et al.*, 2015a) are reported on cactus pear fruits in Italy (**Figure 9**). Physical injuries to the peel during harvesting and handling as well as cold storage predispose the fruits of the cactus pear to infection by this fungus. Infected tissues become brown–coloured, soft and watery. The lesions enlarge, a white mycelium emerges from the cracks of decayed peel and a blue–green spore mass appears on the surface of the peel along the lesions.
Disease management: Control the disease by careful picking and handling of fruits to reduce rind damage. In packing houses and storage facilities, sanitary practices may prevent sporulation of diseased fruits and reduce the amount of inoculum.

Macrophomina soft rot

Causal agent: *Macrophomina phaseolina* (Tassi) Goid.
Host range: Polyphagous with more than 500 plant hosts.
Geographical distribution: Italy.
Symptoms and signs: Symptoms begin with a brown soft rot originating at the proximal portion and extending to the entire fruit at post–harvest (Faedda *et al.*, 2015b). In the advanced stage, the infected area is covered by mycelial mass (**Figure 10**). Macrophomina has also been reported in Brazil and Mexico, causing charcoal rot on forage cactus pear (Oliveira *et al.*, 2003; Méndez Gallegos *et al.,* 2009).
Disease management: To date, there has been no research on the control of this disease.

Other fungi

Besides those discussed above, several other fungi have been found on cladodes and fruits of cactus pear plants. However, many of them are saprobes or secondary pathogens, often recovered from weakened plants, and their role as primary pathogens has not been clearly proved. The most commonly occurring fungi are outlined below.

- *Aspergillus niger* – found in Egypt associated with rotted cladodes and fruits (Ammar *et al.,* 2004).

- *Candida boidimi* – associated with soft rot of cladodes and fruits in Italy (Granata and Varvaro, 1990).
- *Capnodium* spp. and other fungi – cause sooty mould in Mexico (Méndez Gallegos *et al.*, 2009; Mondragón Jacobo *et al.*, 2012).
- *Cercospora* sp. – reported in Bolivia and Peru causing grey–coloured circular necrotic spots on cladodes (Granata and Sidoti, 2002).
- *Colletotrichum gloeosporioides* – found in Brazil, Korea and Mexico, causing anthracnose of cladodes. The symptoms consist of dark brown spots usually starting at the pad edges and then extending over the whole pad (Osada and Càrcamo, 1991; Kim *et al.*, 2000; Souza *et al.*, 2010).
- *Fusarium species* – found on cactus pear in many parts of the world, including Brazil, Egypt, South Africa and Mexico (Swart and Kriel, 2002; Ammar *et al.*, 2004; Swart, 2009; Souza *et al.*, 2010):
  - *Fusarium oxysporum, F. proliferatum and F. sporotrichoides* – associated with dry necrotic lesions of cladodes.
  - *F. solani* – reported as causal agent of top rot.
  - *F. lunatum* – reported as causal agent of circular spots of cladodes.
- *Cladosporium* sp. – associated with pad spot in Mississippi, United States of America (msucares.com).
- *Curvularia lunata* – reported in Brazil and Mexico causing symptoms of circular cladodes spot (Souza *et al.*, 2010; Flores Flores *et al.*, 2013).
- *Cylindrocarpon* sp. – found in South Africa associated with cladode necrosis (Swart and Swart, 2002).
- *Hendersonia opuntiae* – causes a disease known as "scorch" or "sunscald". The symptoms consist of spots at first distinctly zoned, later enlarging until entire cladodes turn a reddish brown. The centre of the diseased area is greyish brown and cracked (Horst, 2013).
- *Mycosphaerella* sp. – causes necrotic spots on cladodes in South America. This disease is known as mancha plateada in Mexico (Granata, 1995).
- *Phoma* sp. – found in Argentina, causing necrotic spots on cladodes (Granata, 1995).
- *Pleospora* sp. – causes necrotic spots on cladodes (Granata, 1995).
- *Pollaccia* sp. – reported to cause cladode rot on thornless cactus in the region of Alagoas (Northeast Brazil) (Franco and Ponte, 1980).
- *Rhizopus* sp. – found in Brazil and South Africa (Swart and Swart, 2002; Souza *et al.*, 2010).

BACTERIAL DISEASES

Black soft rot

Causal agent: *Erwinia carotovora* subsp. *Carotovora.*
Host range: Polyphagous.
Geographical distribution: Argentina, Italy.
Symptoms: In spring, the cladodes display water-soaked spots that become brown and coalesce (**Figure 11**). The external tissues become dry and frequently cracked; the internal tissues turn brown to almost black. These symptoms can also be observed on the fruits (Varvaro *et al.*, 1993; Saad *et al.*, 1998).
Disease management: Remove and destroy the infected segments. Spray immediately with copper compounds in high-risk situations, such as after a major wind or hail event.

Figure 11
Black soft rot (Italy)

Crown gall

Causal agent: *Rhizobium radiobacter* (previously known as *Agrobacterium tumefaciens*).

Host range: Highly polyphagous with more than 90 families of plants.

Geographical distribution: Mexico.

Symptoms: A tumorous overgrowth (gall) forms at the base of the stem. The gall colour ranges from brown to black and cracks at maturity. The tumour at the basal stem varies in size with a diameter of ≤ 15 cm (Gutiérrez, 1992).

Disease management: Do not plant susceptible varieties in soils known to be infested with this pathogen. Preventive treatment of cuttings with the non-pathogenic biocontrol organism *A. radiobacter* is a relatively inexpensive and effective means of managing the development of crown gall in commercial operations.

PHYTOPLASMA AND VIRUS DISEASES

One of the most serious diseases in cactus pear orchards reported in Mexico is commonly known as *engrosamiento de cladodios* (cladode enlargement) or *macho* (Pimienta Barrios, 1990). Typical symptoms of this disease – assumed to be caused by a phytoplasma – are severe stunting of cladodes, flowers and fruits. The disease also occurs in the United States of America (California), where it appeared in the mid-1980s, and in South Africa (Felker *et al*., 2010).

In Italy, symptoms of malformation, stunting and lack of flowers, fruits and spine production on cactus pear plants have been attributed to a phytoplasma strain belonging to ribosomal subgroup 16SrII-C (Figure 12) (Granata *et al*., 2006; Tessitori *et al*., 2006).

Bertaccini *et al*. (2007) identified two different phytoplasmas (16SrI-B and 16SrV-A) associated with cactus pear samples affected by cladode enlargement disease in California.

Symptoms of cladode malformation, bud proliferation, thickening and heart-shaping of cladodes, with arrested plant growth and yellowing of cladodes were observed in the Saint Martin Pyramids (northeastern State of Mexico) and associated with the 16SrII subgroup phytoplasma (Hernández Pérez *et al*., 2009a). Later, Fucikovsky Zak *et al*. (2011) reported symptoms of phytoplasmosis on cactus pear plants in the region of Nopaltepec (State of Mexico) associated with the 16SrI phytoplasma group (aster yellows strain, *Candidatus* phytoplasma asteris). More recently, in the same region, symptoms of distortion and thickening of the cladode, mosaic, yellowing, proliferation and deformation of fruits were observed on cactus pear plants, but the causal agent was attributed to the Mexican periwinkle virescence-16SrXIII phytoplasma (Suaste Dzul *et al*., 2012b).


Figure 12
Phytoplasma disease (Italy)

Felker *et al*. (2010) reported that in California cladode enlargement disease is caused by the tobacco bushy top virus, and it is possible that the symptoms observed in Mexico, South Africa and Italy are induced by this same virus. Similar results were obtained by Suaste Dzul *et al*. (2012a), who demonstrated the presence of a virus in samples of cactus pear from Nopaltepec showing thickening and mosaic syndrome of the cladodes. Therefore, the co-infection between the phytoplasma and the virus has been ascertained in this syndrome.

The phytoplasma and viral diseases of this crop are difficult to control due to the lack of scientific studies on cultivar susceptibility and insect vectors.

ABIOTIC DISORDERS

There is very limited scientific literature on non-infectious diseases of cactus pear. The most common abiotic disorders occasionally occurring in some cactus-pear-growing regions are reported below.

Frost injury

Frost damage due to temperatures < -5 °C may have a drastic effect upon the entire plant or affect only a small part of the plant tissue, reducing yield or only product quality. Susceptibility to cold varies depending on the age and physiological state of the plant and on the cultivar. Ripening fruits are the most susceptible to frost injuries, which consist of necrotic spots on the rind surface (Figure 13).

Hail injury

The degree of damage in cactus pear caused by hail depends on the duration and intensity of the storm, as well as on the stage of development of the plant. Hail injures result in wounds at the point of impact; even young cladodes and fruits can be perforated by the impact of hailstones (**Figure 14**). Since wounded tissues provide entry sites for bacteria and fungi into the plant, protective copper-based treatment soon after the event may prevent infection. Severely damaged cladodes and fruits should be pruned out as soon as possible.

Herbicide injury

Symptoms of herbicide toxicity vary according to the kind of herbicide applied, the concentration of the product and environmental factors (Figure 15).

Fruit splitting

Although the exact cause is unknown, fruit splitting occurs when plants take up water from rain or irrigation after a long dry period and the fruit expands, bursting the peel in a crack across the bottom (**Figure 16**).


13

Figure 13
Frost injury (Italy)


14

Figure 14
Hail injury (Italy)


15

Figure 15
Glyphosate injury (Italy)


16

Figure 16
Fruit splitting (Italy)

11

Insect pests of cactus pear

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Insect pests of cactus pear

INTRODUCTION

The Cactaceae family is a very distinct group of plants with peculiar characters of growth and habit and it has naturally evolved its own insect complex. Indeed, more than 160 insect species are harmful to cactus plants (Dodd, 1940; Mann, 1969; Zimmerman and Granata, 2002), and are largely, but not solely cactus enemies.

Cactus insects have adjusted to the general conditions of the regions in which their host plants grow. For example, most of the adult stages of beetle and lepidopteran insects are only active at night, and their immature development takes place in the internal tissues of the cladodes, branches and stems of the cactus plants; in fact, 75% of all cactus–feeding insects are internal feeders (Zimmermann and Granata, 2002). These insects have also adapted to the structure and habits of the cactus plants, and plant bugs and lepidopterans often lay their eggs on the spines of the plant's cladodes. No part of the cactus plant escapes from injury: insect species attack the roots, stems, cladodes and fruits (**Figure 1**).

Insect injury to cactus orchards affects the quantity and the quality of the harvest, as well as the duration of productive life. In general, insects feeding on the fruits pose a higher risk of crop loss than those feeding on the stems or cladodes. Insect density also plays an important role in defining the status of an insect pest.

INSECTS

This chapter presents the main groups of insects that feed on cactus plants worldwide, with a focus on identification, ecology and biology, as well as on pest management tactics.

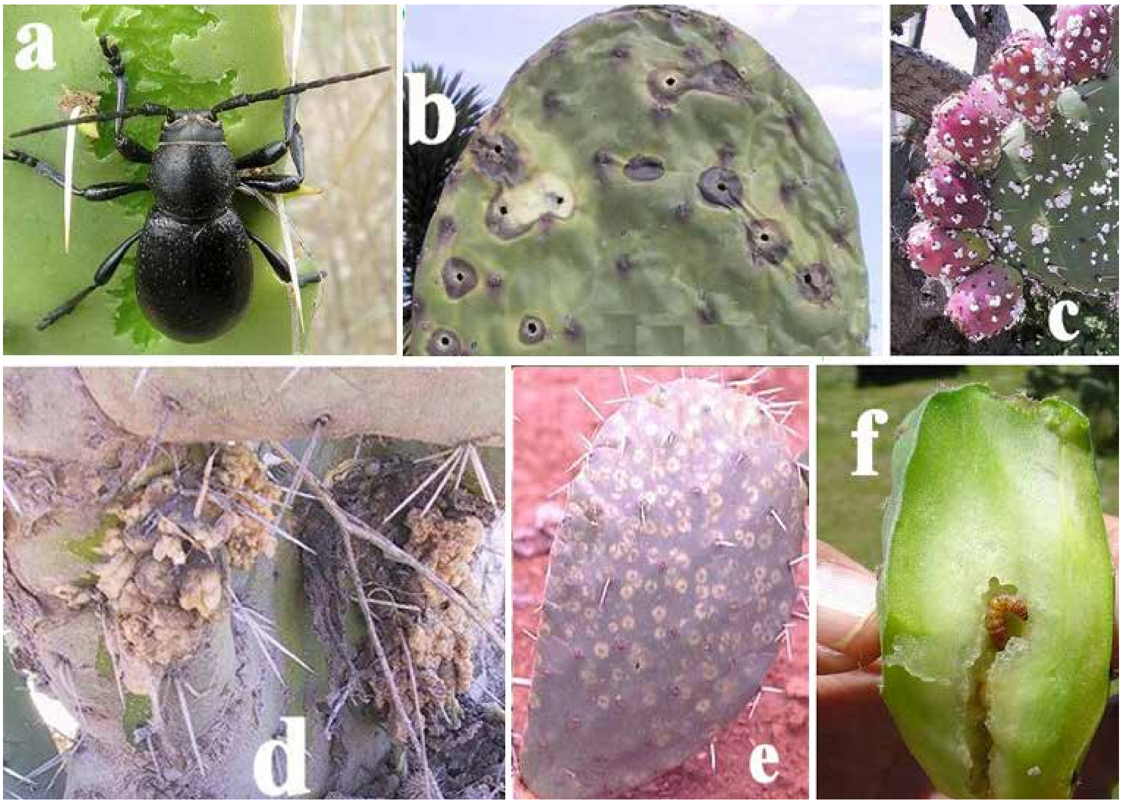

Figure 1
Insect damage to cactus plants: a) adult of Moneilema on tender cladode, b) shot hole symptoms, c) wild cochineal infestation on fruits, d) hard gum exudates on cactus main stem from Metamasius larvae, e) grey bug damage, and f) Metapleura larvae inside a cactus fruit.

Cottony cochineal insect *(Dactylopius opuntiae, Homoptera: Dactylopiidae)*

At present, the cottony cochineal (*Dactylopius opuntiae*) is perhaps considered the most important insect pest in cactus orchards worldwide. In Brazil, it has infested 100 000 ha of cactus cultivated for forage production, lowering productivity by 80% (Lobos *et al.*, 2013); in Mexico, it is the biotic factor that most limits cactus pear production (Mena Covarrubias, 2011); and in South Africa, it is one of the two most important pests limiting forage and fruit production (de Waal *et al.*, 2013b).

D. opuntiae is characterized by sexual reproduction and sexual dimorphism. The female has a four–stage life cycle (egg, first–instar larvae, second–instar larvae, adult), while the male has a six–stage life cycle (egg, first–instar larvae, second–instar larvae, prepupa, pupa, adult). The life cycle duration depends on many factors, but certain characteristics are common. The egg is oval and shiny red; hatching may occur inside the adult female; or the crawlers (first–instar larvae) may hatch within a few minutes of the eggs being laid (Flores Hernandez *et al.*, 2006). For females, the larvae stage lasts 18.1 days; this is followed by a pre–oviposition phase lasting 18.8 days; and finally the females spend 22 days in the oviposition stage. On average, one female lays 131 eggs (the range is 62–617) (Flores Hernandez *et al.*, 2006). The adult male looks like a small fly with two long tails. Males use flight to locate mates, and are short–lived. The cottony cochineal insect is easily recognizable: large woolly masses of white wax cover its body and, when crushed, the bright crimson colour of the body fluid runs out and contrasts with the cottony colour (**Figure 2**).

Successful colonization of new cactus plants depends on the female first–instar larvae, because they are the only ones with functional legs (**Figure 2b**). They also develop long waxy dorsal filaments, which are well developed by the time the crawlers are 2–3 days old. In preparation for dispersal, female crawlers climb to the top of the host plant cladodes and "take off" with the help of the wind (Mow *et al.*, 1982).

Cochineal insects live on the surface of the cactus plants, usually in aggregations or colonies composed of individuals in various stages of development, and settled at the base of the spines. All feeding damage is caused by the females and nymphs as they suck sap from the cladodes and fruits. Within a few weeks of establishment on a plant, yellow areas appear on the cladode (**Figure 2e**), which eventually drops off. Although new cladodes may grow, these will also drop off if the

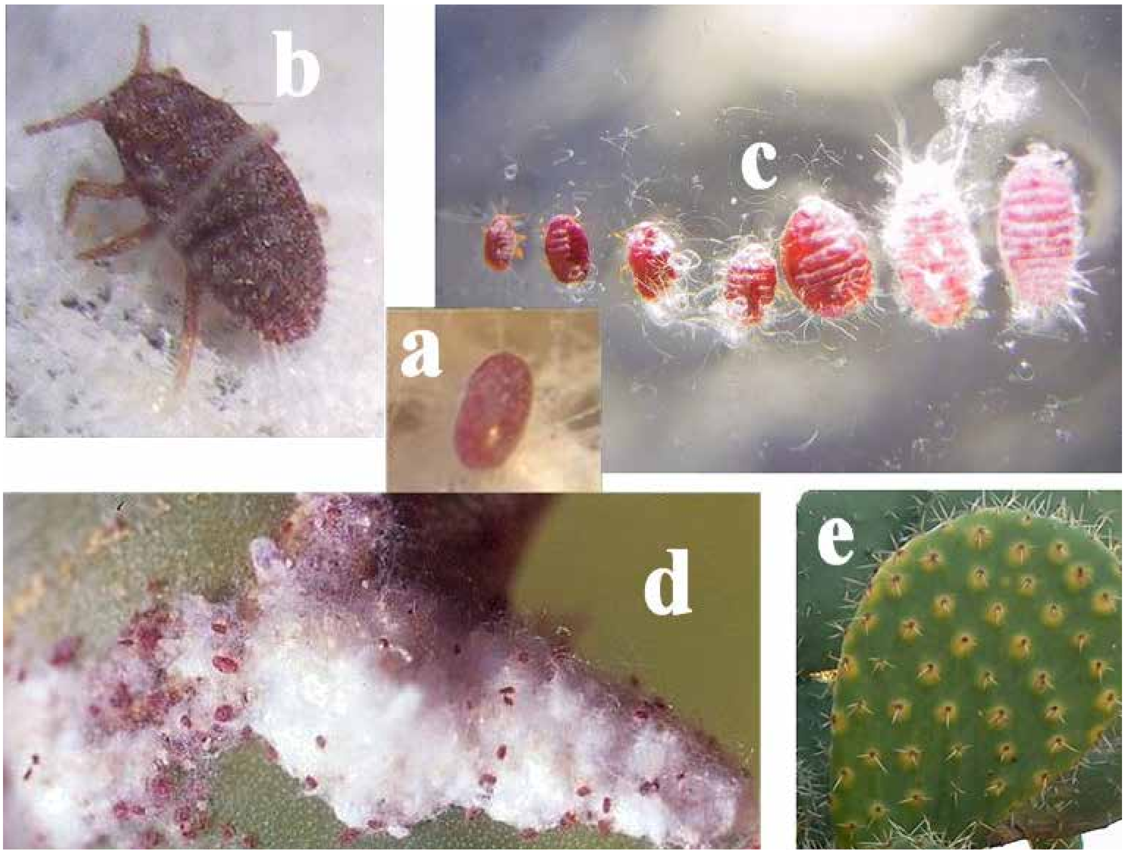

Figure 2
Wild cochineal, Dactylopius opuntiae life stages:
a) egg, b) crawler,
c) different stages of immature development,
d) colony of several adult females and some crawlers on them, and
e) feeding damage on a cladode.

cochineal remains on the plant. Depending on the severity of the infestation, the trunk may also die. Male cochineal insects never feed as adults.

For control, the first–instar larvae are the most susceptible and the easiest target.

Lepidopteran insect pests

The Pyralidae moth borers are the most important and abundant cactus insects; this family comprises about 50% more pest species than the cactus longhorn beetles, and 66% more species than the cactus weevils (Moran, 1980; Zimmermann and Granata, 2002). The cactus moth (*Cactoblastis cactorum*), the zebra cactus worm (*Olycella nephelepsa*), the cactus white worm (*Megastes cyclades*) and the cactus pad joint borer (*Metapleura potosi*) are four of the most important lepidopteran insect pests feeding on cactus plants. *Cactoblastis* poses the highest risk of damage since it is already present in South America and South Africa, and it threatens to invade commercial cactus pear production areas in the United States of America and Mexico (Zimmermann and Granata, 2002). These four lepidopteran insects are all internal feeders of cladodes; *Metapleura* also invades the fruits, boring from the cladode into the fruit, and leaving no trace of entry point (Mena Covarrubias, 2013).

The full–grown larvae of *Cactoblastis*, *Olycella* and *Metapleura* all have bright body coloration. *Cactoblastis* larvae are uniform bright orange, or orange–red with transversal rows of large black spots (**Figure 3l**); *Olycella* larvae are dark blue or blue–black with white transversal bands (**Figure 3i**); the dull red–orange–yellow larvae of *Metapleura* also have transversal rows of small black spots on a bright orange background (**Figure 3f**). *Megastes* larvae, on the other hand are creamy white in colour, with a light brown spot on each side of the segments (**Figure 3c**). *Cactoblastis* and *Olycella* females lay their eggs in chains called "eggsticks" attached to the spines of the cladodes. There are 35–150 eggs on a single *Cactoblastis* eggstick (Mann, 1969), and they are stacked one on another as if they were a part of the plant spines (**Figure 3k**); the *Olycella* eggsticks have only 1–8 eggs and are attached at right angles to the spine (**Figure 3h**), almost parallel to the cactus pear cladode. The *Megastes* female lays masses of 40–90 eggs on the surface of the cladodes, with the edges of the eggs overlapping like roof tiles (**Figure 3b**). *Metapleura* eggs are laid singly on the cracks, joints and surface of the cactus pads (**Figure 3e**). The adult stages of these four insects are moths with nocturnal activity (**Figure 3a, 3d, 3g, and 3j**).

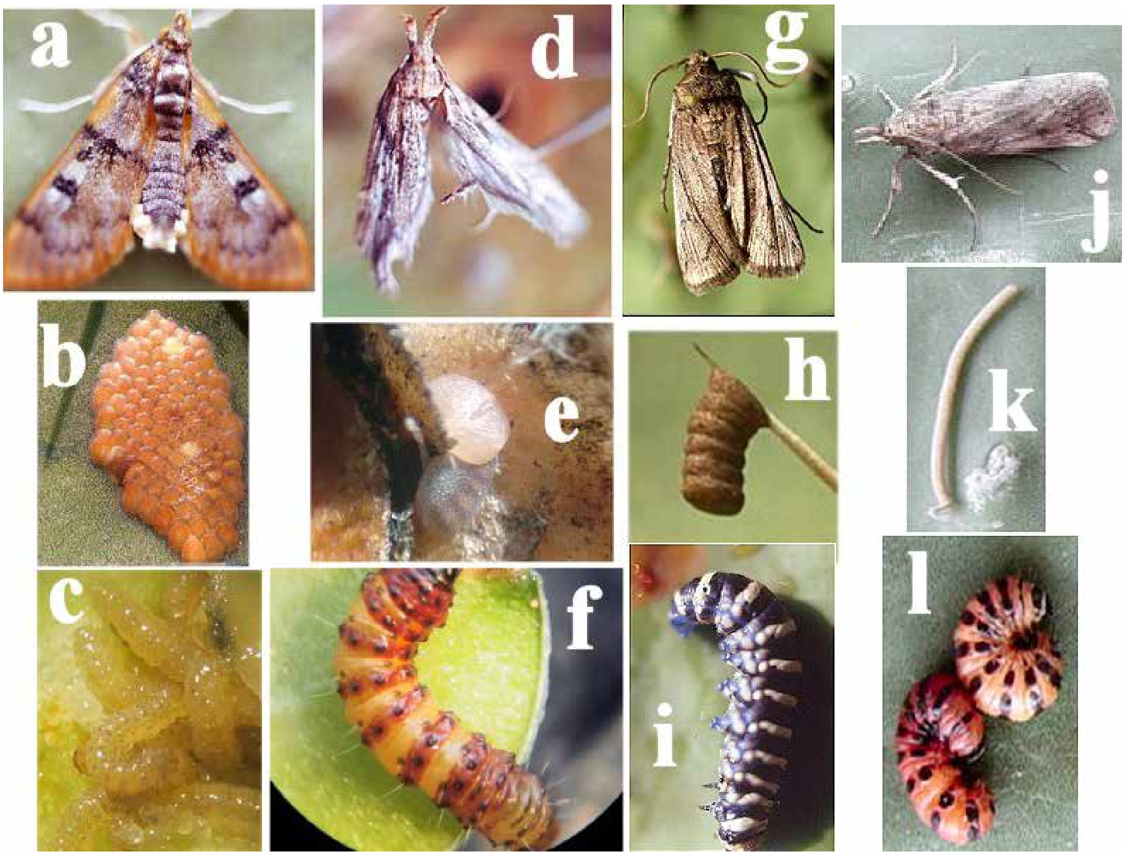

Figure 3
Lepidopteran insect pests and their life stages:
(a) Megastes cyclades adult,
(b) egg mass and
(c) larvae
(d) Metapleura potosi adult,
(e) eggs and
(f) larvae;
(g) Olycella nephelepsa adult,
(h) egg mass and
(i) larvae;
(j) Cactoblastis cactorum adult,
(k) egg mass and
(l) larvae.

Cactoblastis larvae can completely destroy a small–to–medium cactus plant in a single season: they consume all the cladode internal tissues and the larvae then leave the empty pad and move in groups to the neighbouring untouched ones. *Cactoblastis* may have two or three generations per year. *Megastes* larvae are not as mobile and destructive as *Cactoblastis*, but the galleries made by their larvae every year cause the collapse of the main branches and stems of the cactus plants. *Megastes* has only one generation per year, but it sometimes attacks the same plant for several consecutive years. *Metapleura* poses a high risk for growers selling fresh cactus fruit, because it is difficult to detect an infested fruit; the consumer only realizes when it is too late, with negative consequences for the consumer–farmer relationship. There can sometimes be as many as 15–20 larvae of *Metapleura* on the same cladode, inducing partial rotting or, if the damage is in the joints, the cladodes fall to the ground; however, in most cases, the damage is not significant. Finally, *Olycella* attacks young cactus orchards only in the first 3 years; damage is localized, and the single pests are found in excavations beneath tumour–like swellings in the cladodes.

The target of control for all these pests are the newly hatched larvae, but the window of opportunity varies from just one day (*Cactoblastis*) to a few days (other species). The eggsticks of Cactoblastis are the easiest target: they are easy to spot and they stay on the field for at least 3 weeks before hatching (Mann, 1969).

Cactus weevils (*Curculionidae*)

The cactus weevil (*Metamasius spinolae*), the "shot hole" weevil (*Gerstaeckeria* spp.) and the areole weevil (*Cylindrocopturus biradiatus*) are three of the most important curculionid insect pests for cactus plants. Metamasius poses the highest risk, since just a few larvae feeding on the base of the stem can knock out an entire plant; the other two genera feed mainly on the cladodes.

Weevils are easily identified in the adult stage by their long snout; in *Metamasius* it is 22–25 mm long, in *Gerstaeckeria* 0.5–0.6 cm and in *Cylindrocopturus* 3–3.5 mm. *Metamasius* is characterized by black elytra with two orange markings (**Figure 4a**); *Gerstaeckeria* commonly has a black–brown body with white scales (**Figure 4i**); *Cylindrocopturus* is a silvery colour with a yellow double cross marking in the middle of its body (**Figure 4e**). The larvae of these curculionid beetles are legless white worms with brown heads (**Figures 4c, 4g and 4j**).

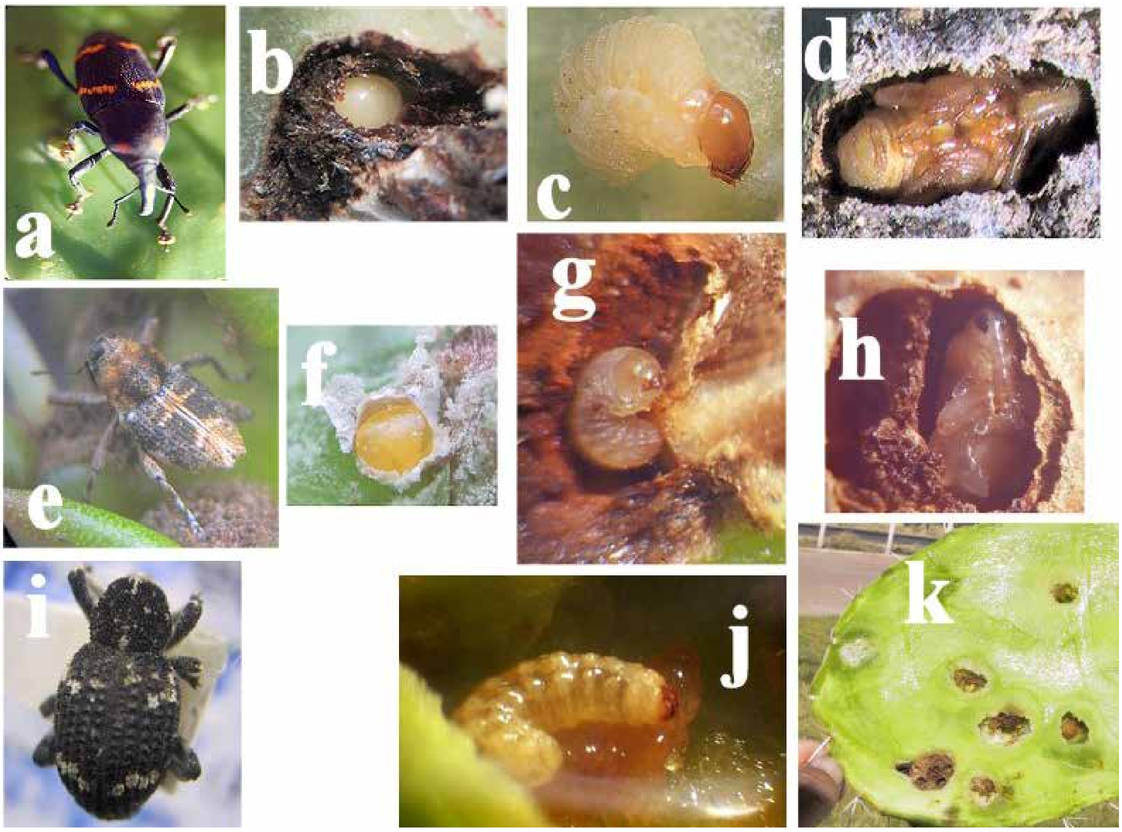

Figure 4
Cactus weevil insect pests and their life stages:
(a) Metamasius spinolae adult,
(b) egg
(c) larvae and
(d) pupae;
(e) Cylindrocopturus biradiatus adult,
(f) egg
(g) larvae and
(h) pupae;
(i) Gerstaeckeria spp adult,
(j) larvae,
(k) cladode internal damage by the larvae.

Metamasius and *Gerstaeckeria* are flightless weevils; the *Gerstaeckeria* adults are active only at night. The cactus weevil is potentially present year–round, but emergence peaks at the beginning of the rainy season; the shot hole and areole weevils are common from March to September. The female of the cactus weevils burrows into the cladode tissue, lays an egg and seals it with a mixture of food and regurgitated saliva. They have only one generation per year, but the adults have a long life span: *Metamasius* ≥ 1 year, *Gerstaeckeria* and *Cylindrocopturus* 4–5 months (Dodd, 1940; Mann, 1969; Mena Covarrubias, 2013).

Most of the damage to cactus plants is caused by the larvae as they feed on the internal tissues and set up conditions for rot, especially in the case of *Metamasius* and, to a lesser degree, *Gerstaeckeria*. *Metamasius* larvae are highly mobile, travelling from the stem to the lower part of the main branches, in order to obtain a better supply of food. It is common to find single cladodes, branches and whole plants lying fallen on the ground; scavenger insects greatly increase the rotting in affected areas (Dodd, 1940; Mann, 1969; Mena Covarrubias, 2012). Adults prefer to feed on young cladodes; *Gerstaeckeria* and *Cylindrocopturus* also use them for oviposition and larvae development, while *Metamasius* prefers stems and older cladodes for those activities.

The adult is the only stage that lives externally and for this reason is the main target of control. However, pruning could be an excellent option for controlling *Gerstaeckeria* and *Cylindrocopturus* larvae and pupae during the winter months.

Longhorn beetles (*Cerambycidae*)

This group is represented by the genus *Moneilema* (*M. variolaris* is one of the most common species in cactus orchards). They can inflict major harm and just two or three larvae in the base of a full size cactus pear may cause the whole plant to collapse. They also feed on the base of young plants and pose the same risk of damage as the *Metamasius* weevil. These cerambycids are robust, shining black beetles; the elytra and prothorax sometimes present irregular white marks. Their length is 15–25 mm (males are smaller than females), and the antennae are longer than half the insect body (**Figures 1a and 5a**). The larva is white and each segment is deeply creased along the body; it ranges in length from 15 to > 40 mm; the head is black (**Figures 5a and 5c**).

Moneilema are nocturnal, flightless insects; however, on cloudy days, these beetles are also active in the morning. The adults live for several months and are present from March to November. The eggs are laid singly and glued to the surface of ma-

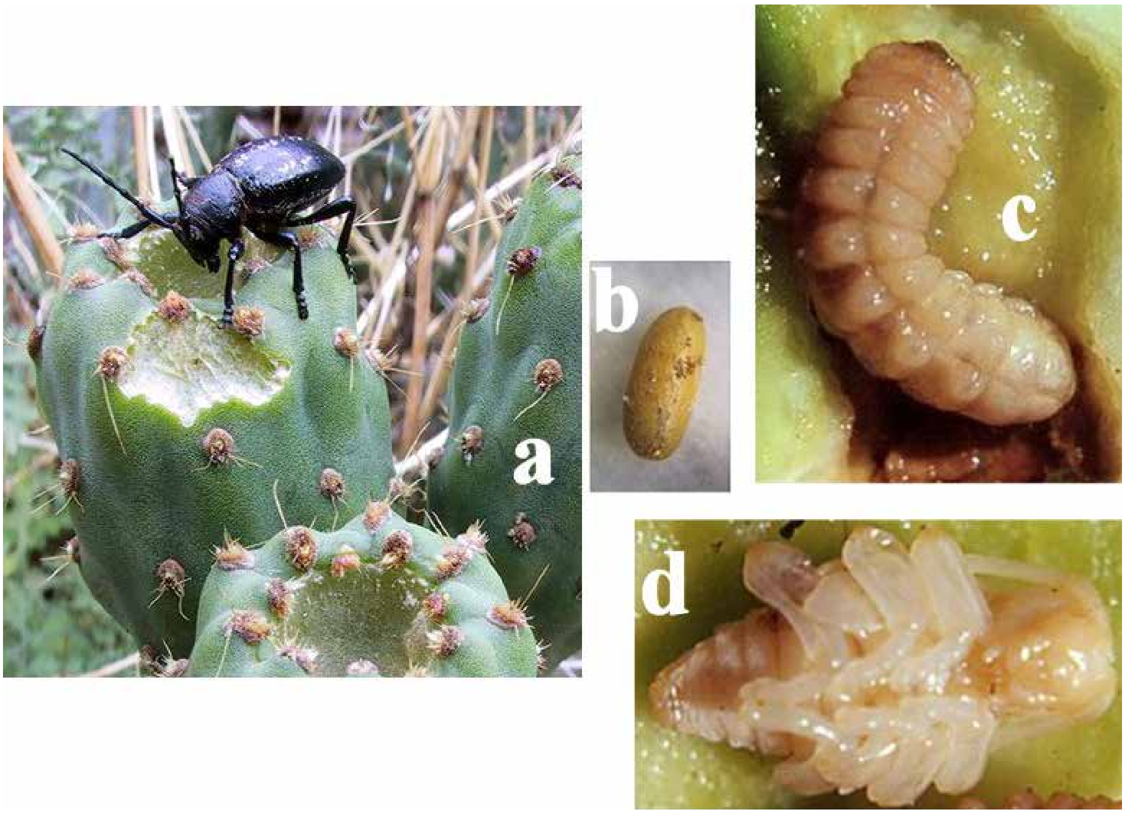

Figure 5
Moneilema life stages:
(a) adult,
(b) egg,
(c) larvae and
(d) pupae.

ture segments, in cracks, against the stem or just below ground level (Mann, 1969). There are one or two generations each year; in the case of two generations, spring emergence is much bigger than autumn emergence (Dodd, 1940; Mann, 1969).

The larvae infest the main stem and older joints of the cactus pear, constructing galleries filled with copious exudations that soon become blackened. Saprophytic insects are attracted to the feeding areas and help to make them spread. The larvae move considerably inside the cactus plants, usually in a downwards direction, ending in the basal stem of newly planted orchards. The adults, on the other hand, feed superficially by gnawing at the edges of the newly formed pads and occasionally the fruits (**Figures 1a and 5a**).

The adult stage is the target of control, because the larvae are difficult to locate and control inside the plants.

Plant–sucking bugs

There are very few cactus surface feeders with biting or chewing mouthparts – probably because of the absence of true leaves on the cactus plant (Dodd, 1940). The most common are stinky bugs, cochineal insects, thrips and scale insects. The coreid bugs of the genera *Chelinidea* and *Narnia* as well as the mirid red bug (*Hesperolabops*) are good examples of sucking bugs. These insects pose less risk of damage to the cactus plants compared with the lepidopterans, weevils, longhorn beetles or cochineal insect pests described above; very rarely will their feeding activities risk destruction of a cactus plant. The most common damage from the grower's point of view is the reduced quality of the cactus fruit. *Hesperolabops* has the greatest potential for causing this damage, because it reaches a wider population, feeds on both cladodes and fruits (*Narnia* also is a fruit feeder insect) and is harder to control.

The adult stage of the cactus grey bug, *Chelinidea tabulata* (Burmeister), has a brown–green body; the newly hatched first instars are black, becoming light green as they grow older; adults are 13–15 mm (**Figures 6a and 6c**). The cactus fruit bug, *Narnia femorata* Stål is coloured deep purple to black as an adult; it is slender and smaller than the cactus grey bug; the immature stages are dark grey with pale yellowing areas on the antenna, thorax and legs (**Figures 6d and 6f**). The adult stage of the cactus red bug (*Hesperolabops gelastops* Kirkaldi) has a red head and prothorax, while the rest of the body is smoky with a pale band on the edge of the thorax and abdomen (**Figure 6h**); it is a small bug, length 6–8 mm. The newly

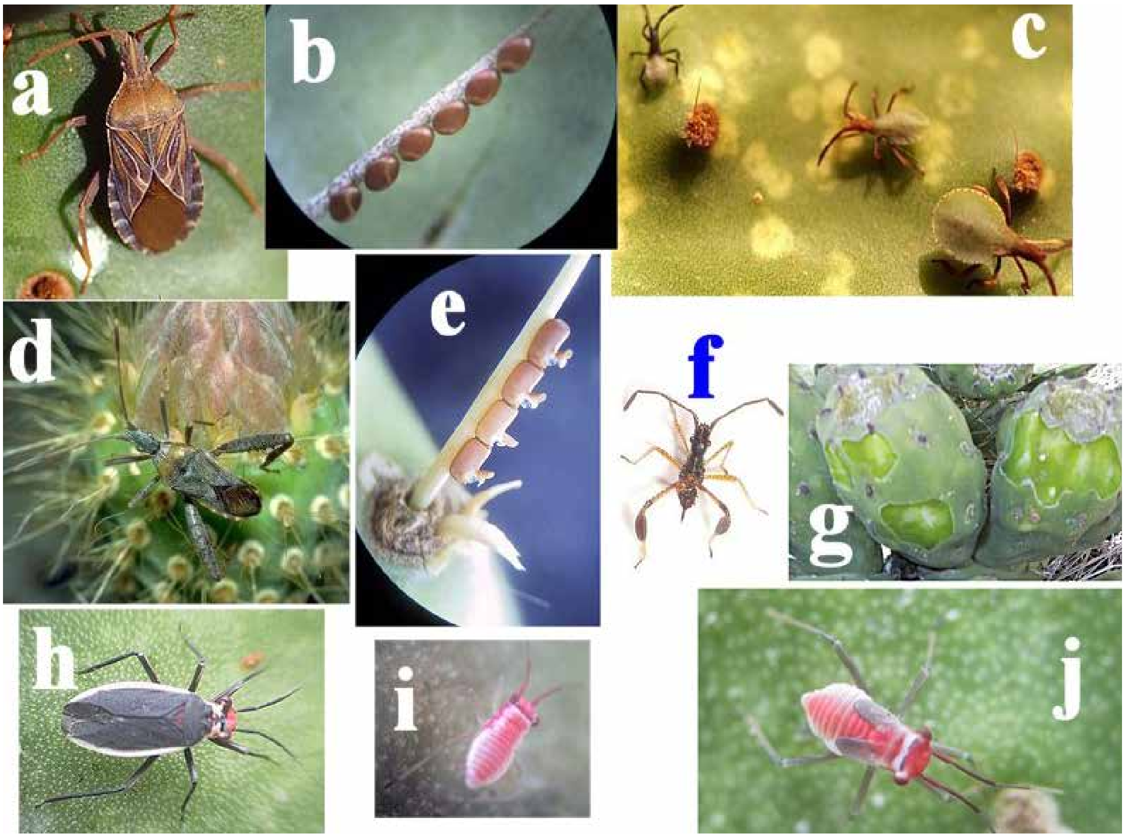

Figure 6
Cactus plant sucking bugs life stages:
(a) Chelinidea tabulata adult,
(b) eggs,
(c) and immature;
(d) Narnia femorata adult,
(e) eggs,
(f) immature,
(g) and damage to cactus fruits;
(h) Hesperolabops gelastops adult,
(i) first instar,
(j) and older instar.

hatched insects are completely red (**Figure 6i**) and they maintain the colour as they grow, as well as the pale band around their bodies; only the wing pads are grey (**Figure 6j**). Both *Chelinidea* and *Narnia* lay several eggs end to end along a cladode spine (**Figure 6**) (Mena Covarrubias, 2013). *Hesperolabops*, on the other hand, inserts its eggs under the epidermis layer of the cactus cladode, with the operculum close to the epidermis (Palomares Perez, 2011). Development periods for the egg and immature stages are, respectively: 21 and 56 days for *C. tabulata* (Brailovsky *et al.*, 1994); 13 and 67 days for *N. femorata* (Vessels *et al.*, 2013); and 269 and 36 days for *H. nigriceps* Reuter (Palomares Perez, 2011). Both the adults and the immature stages are gregarious to different degrees and they are present in the cactus orchard year–round; they move at the same time on the cactus plant, searching for the opposite part, as if they were trying to hide from the observer.

Adult and immature stages of the cactus plant–sucking bugs feed by puncturing the cladodes, joints and fruits; they leave a characteristic pale yellow circular area around each feeding puncture, so the affected areas have a spotted appearance (**Figure 1e**). Dense populations can cause cladodes to look yellow and sickly, especially in newly planted orchards. *Narnia* fruit damage produces a pulpy spongy area on each feeding site (**Figure 6g**); while the spot is less juicy and sweet, it is small and superficial, and the average person does not detect it. On the other hand, large populations of cactus red bug prevent the external tissue of the fruit from reaching its normal colour, and reduce the sugar content, which affects the price of the product. In addition, the cactus red bug is associated with "cacarizo", a disease that affects the 'Reyna' cultivar in the Mexican Highlands and covers the epidermal tissues of the cladodes with blisters (Palomares Perez, 2011), reducing drastically the productivity of the orchard.

The targets of control for the cactus–sucking bugs are both the adults and immature individuals, because they are all external feeders; newly hatched insects are more susceptible to control agents.

Other cactus insect pests

There are a small number of species of fly that feed on cactus plants. *Asphondylia* is the most important as it feeds on the cactus seeds, while *Mayetiola*, *Lonchaea* and *Dasiops* live in the cladodes and cause little damage (Mann, 1969). Fruit flies are occasionally reported as insect pests around the globe, particularly in the Mediterranean area (Zimmermann and Granata, 2002). Thrips are commonly found on cactus pear orchards, especially *Neohydatothrips opuntiae*; they damage the skin of tender cladodes and young fruits early in their development. Finally, scale insects – cactus scale (*Diaspis echinocacti*) and oyster scale (*Lepidosaphes* spp.) – feed externally on the cactus pads; their presence is limited to a small number of plants per orchard and they only become important if their natural enemies are destroyed with the use of broad spectrum insecticides.

INTEGRATED PEST MANAGEMENT FOR CACTUS INSECT PESTS

Integrated pest management (IPM) is a strategy for controlling insect pests using a full range of control tactics. In order to maximize the reduction of the pest population, a thorough knowledge is required of the ecology and biology of both the insect pest and its natural enemies. The key IPM management practices in cactus orchards are described below:

Pruning

Orchard maintenance includes yearly pruning, which can affect an insect pest population in three significant ways (Mena Covarrubias, 2011, 2012):

- A dense canopy offers abundant opportunities for insect survival during winter and also reduces the efficiency of spraying. To optimize the benefits of pruning, cladode overlapping must be kept to a minimum.
- Pruning provides an opportunity in winter to completely eliminate from an orchard and destroy the areole weevil, the shot hole weevil and the cactus cladode miner (*Marmara opuntiella* Busck), along with the infested first year cladodes. The efficiency of this practice is improved if several farmers carry it out at the same time. Neighbouring wild *Opuntia* should also be included in the campaign.
- To optimize the positive effects of pruning, never leave pruning waste on the orchard floor. The prunings are a potential refuge for the development and reproduction of cochineal insects, cactus weevils, longhorn beetles and cactus pad joint borers.

Targeting emergence

In order to control the newly hatched larvae of lepidopteran insect pests, it is essential to target them at emergence. Once the larvae are inside the cactus tissue, external control is no longer possible. It is, therefore, critical to monitor the adult stage (moths) and pinpoint population peaks. A pheromone has been developed to trap the cactus moth males (Heath *et al.*, 2006). The other moth species can be sampled using light traps in September–October (cactus white worm), April–June and September–November (cactus zebra worm) and year–round (cactus pad joint borer) (Mena Covarrubias, 2011, 2012). The adult stage of *Cactoblastis*, *Olycella* and *Melitara*, on the other hand, do not feed (Mann, 1969), and food traps cannot be adopted for trapping or monitoring.

Mass trapping

It is possible to carry out mass trappings of cactus weevils because the males release an aggregation pheromone for both females and males, especially if the traps are set on cactus cladodes (Tafoya, 2006). Cactus weevils, longhorn beetles and shot hole weevils are flightless beetles and can be controlled by hand picking, especially if the infested area is flagged and the activity is concentrated there. For longhorn beetles and shot hole weevils, control should be carried out at dawn and dusk because they are nocturnal insects; on the other hand, the adults leave a typical feeding footprint (**Figure 1a, 4m, 5a**), and by day it is possible to pinpoint which cactus plants were affected the previous night.

Biological control

Biological control is a fundamental element of insect pest management. In the case of cactus insect pests, biological control entails the conservation of the natural enemies present in the orchards, which in turn requires:

- identification of the beneficial insects;
- provision of alternative food sources for the adult stage, specifically pollen and nectar plants around the orchard; and
- no spraying of broad spectrum insecticides (Mena Covarrubias, 2014).

Biological control by augmentation can also be implemented using entomopathogenic fungi (e.g. *Beauveria bassiana*) to control insects such as the cactus white worm (Lozano Gutierrez and Espania Luna, 2008). The challenge is how to place the agent of control in contact with the target insect, because most cactus insect pests are internal feeders and spend most of their life cycle inside the cactus tissues.

Chemical control

Only a limited number of conventional insecticides are permitted for the chemical control of cactus plants However, organic insecticides – such as pyrethrum, diatomaceous earth, *Bacillus thuringiensis*, neem and insecticidal soaps – are available and can potentially increase the spectrum of chemical alternatives for insect control. Further research is required on spraying coverage and the impact speed of the droplet in order to optimize pest control on cactus plants.

12

Processing and utilization of fruit, cladodes and seeds

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12

Processing and utilization of fruit, cladodes and seeds

INTRODUCTION

A Sicilian writer once called cactus pear "a treasure under the thorns" because of its immense benefits, some of which were little known before today.
In many countries – Argentina, Chile, Peru, Bolivia, South Africa, Egypt, Turkey, Ethiopia, Eritrea and other countries in South America and the Mediterranean Basin – it is traditionally the cactus pear fruit that is eaten. In Mexico, on the other hand, in addition to the fruit, the tender cladodes (*nopalitos*) are consumed. However, both fruit and *nopalitos* are perishable and processing technologies are needed to increase their shelf–life. Moreover, both fruits and cladodes contain numerous bioactive compounds which must be preserved during processing if consumers are to reap the full benefits. Cactus pear is a multipurpose fruit and a wide range of products and by–products can be derived from it. The same applies for the cladodes. Sáenz *et al.* (eds, 2006, 2013) present numerous alternatives for processing fruits and cladodes. The recent advances in this field are presented in this chapter.

CHEMICAL COMPOSITION AND BIOACTIVE COMPOUNDS

Before any raw material is processed, it is essential to understand its chemical and phytochemical composition, as well as any technological characteristics regarding the industrial process. For cactus pear, information is required about the chemical composition of the fruits, seeds and cladodes. Furthermore, a thorough understanding is required of the bioactive compounds of these cactus parts, their activities and the relative health benefits.

There has been much research on the chemical composition of the edible parts of the fruit from plants grown in different parts of the world, including Egypt, Saudi Arabia, Mexico, Chile and Argentina. There is extensive information available regarding the composition and uses of seeds as a source of oil, fibre and protein, in particular the detailed analysis of Sáenz *et al.*, eds (2006). This chapter presents the latest information on the subject.

Within the genus *Opuntia*, the most cultivated species is *Opuntia ficus–indica*, characterized by sweet and juicy fruit and pulp of different colours: white–green, yellow, orange, red or purple. The proportion of pulp in the fruit varies and the peel is generally thin. Coloured ecotypes (**Figure 1**) have a dual application: production of natural colourants (betalains); and provision of health benefits thanks to their antioxidant properties (Butera *et al.*, 2002; Galati *et al.*, 2003a; Kuti, 2004; Tesoriere *et al.*, 2005a; Stinzing *et al.*, 2005; Azeredo, 2009; Fernández López *et al.*, 2010).

Other bioactive compounds present in the fruits are vitamin C, carotenoids and dietary fibre (Morales *et al.*, 2009; Sáenz *et al.*, 2009, 2012a). Cactus cladodes have a high content of water, dietary fibre and minerals (Pimienta Barrios, 1990; Sáenz *et al.*, eds, 2006). The seeds are rich in polyunsaturated essential fatty acids such as linoleic acid (Ennouri *et al.*, 2005; Özcan and Al Juhaimi, 2011).

There are minor variations in the chemical composition of coloured cactus pear fruits; major differences are related to the pigment content. **Table 1** summarizes the ranges of certain chemical compounds and technological characteristics,

Figure 1
Cactus pear fruits coloured ecotypes (Opuntia ficus–indica) (garden varieties, Antumapu Experimental Station, University of Chile, Santiago) (Photos: C. Sáenz and A.M. Fabry).

TABLE 1 Chemical and technological characteristics of cactus pear pulp from coloured fruits

Parameters	Green cactus pear	Purple cactus pear	Yellow–orange cactus pear
pH	5.3–7.1	5.9–6.2	6.2–6.3
Acidity (% citric acid)	0.01–0.18	0.03–0.04	0.55–0.57
Soluble solids (°Brix)	12–17	12.8–13.2	13.5–14.5
Vitamin C (mg 100 g^{-1})	4.6–41.0	20.0–31.5	24.1–28.0
β–carotene (mg 100 g^{-1})	0.53	–	0.85–2.28
Lutein (µg g^{-1})	26.0	0.15	0.04
Betacyanins (mg kg^{-1})	0.1–0.8	111.0–431.0	2.4–11.0
Betaxanthins (mg kg^{-1})	0.4–3.1	89.4–195.8	16.0–76.3

Source: Askar and El Samahy, 1981; Pimienta Barrios, 1990; Sawaya *et al.*, 1983; Sepúlveda and Sáenz, 1990; Sáenz and Sepúlveda, 2001a; Sáenz *et al.*, eds, 2006; Stintzing *et al.*, 2005; Hernández Perez *et al.*, 2009b; Morales *et al.*, 2009; El Gharras *et al.*, 2006; Coria Cayupan *et al.*, 2011; Sáenz and Fabry (unpublished data).

based on values reported by several authors. Red, purple and yellow–orange cactus pears contain betalains, while red and purple contain betacyanins and yellow–orange betaxanthins (Stintzing *et al.*, 2005; Sáenz *et al.*, 2012b).

The chemical composition may vary depending on different factors:

- origin of the plants (i.e. the climate where it is cultivated);
- agronomic factors, such as cultivation, fertilization and irrigation; or
- genetic differences (Muñoz de Chavez *et al.*, 1995; Ochoa, 2008).

Cactus pear is rich in calcium, although McConn and Nakata (2004) report that calcium bioavailability might nevertheless be low, because it is present as calcium oxalate, which is not absorbed. The high potassium content and low sodium content offer clear nutritional benefits for people with kidney problems and hypertension.

TECHNOLOGICAL CHARACTERISTICS

Fruit

Besides the chemical composition and bioactive compounds, there are other characteristics to consider during processing. In general, cactus pear fruits have a high pH (5.3–7.1) and are therefore classified as low acid foods (pH ≥ 4.5); an exception is *O. xoconostle*, which has higher acidity (pH > 3.5) (Mayorga *et al.*, 1990). It is well known that heat treatment temperatures depend on the pH (Casp and Abril, 1999). For this reason, when non–acidic foods are pasteurized or canned, unless the pH is reduced (by citric acid addition, for example), a higher temperature is needed to reduce the microbial counts to a safe level compared with the treatment of acidic foods (pH ≤ 4.5). Such high temperatures (generally > 121° C) can negatively influence traits such as taste, colour and aroma. The pH and high soluble solids content of the pulp favour the growth of microorganisms (Sáenz and Sepúlveda, 1999; Sáenz, 2000); it is, therefore, important to control heat treatments in preservation processes.

From a sensory point of view, the green fruit in some countries (e.g. Chile) has a better texture, taste (sweeter) and flavour than purple and orange ecotypes, which tend to be floury. Nevertheless, purple, red and orange fruits have great potential for processing, because the betalains contained in the colour ecotypes are more stable than the chlorophylls, with regard to both pH and heat (Merin *et al.*, 1987; Montefiori, 1990; Castellar *et al.*, 2003; Sáenz and Sepúlveda, 2001a; Sáenz *et al.*, 2012b).

Cladodes

The presence of mucilage and pectin in the cladodes influences the viscosity of some products, such as powder preparations mixed with water or juice before consumption. Both compounds are part of dietary fibre and are hydrocolloids, known for their ability to absorb and retain water. They can also be extracted and used as thickeners in foodstuffs (Sáenz *et al.*, 2003, 2004; Sepúlveda *et al.*, 2003a, 2007).

The chemical composition of *nopalitos* has been reported by Pimienta Barrios (1990) and Maki Díaz *et al.* (2015). As with other vegetables, there is a high content of water and fibre. Polyphenols are present and have antioxidant activity important in the diet; during preservation, however, they can cause browning due to oxidation (Rodríguez Felix, 2002). Furthermore, the acidity of *nopalitos* varies during the day – as a result of crassulacean acid metabolism (CAM) (Cantwell *et al.*, 1992) – and the optimal harvesting time must be chosen depending on the process to be applied.

Seeds

The seeds represent about 15% of the edible part of the fruit and they have a variable oil content (on average, 9.8 g 100 g^{-1} of seed) (Ramadan and Mörsel, 2003a).

Seed oil is rich in unsaturated fatty acids (Sepúlveda and Sáenz, 1988; Ennouri *et al.*, 2005; Ghazi *et al.*, 2013); it is, therefore, of interest to the pharmaceutical and cosmetic industries, for example, in Morocco and Tunisia. Given the low yield of oil from the seed, it is neither economical nor attractive as an edible oil. The presence of tocopherols, recognized as natural antioxidants, ranges from 3.9 to 50%. Matthäus and Özcan (2011) and Özcan and Al Juhaimi (2011) report that fibre and minerals are also important components in the seeds, with 12.5% crude fibre and high amounts of calcium, potassium and phosphorus, as well as other minerals. The relatively high protein content (approx. 6%) means that cactus pear seed is a source of protein for human consumption (Tlili *et al.*, 2011).

PROCESSING TECHNOLOGIES

A wide range of traditional preservation technologies can be applied to cactus pear fruit, cactus cladodes and seeds. Some technologies are described in Sáenz *et al.*, eds (2006) and some of the most innovative are described here.

Dehydrated products

Water activity (aw) is a measure of the "available water" in a food. Availability of water in plant tissues is variable, and a distinction is made between "free water" and "bound water". The proportions of free and bound water depend mainly on the food composition, as compounds such as hydrocolloids have higher water retention capacity. The mucilage present in *Opuntia* pads and fruits is an example of a hydrocolloid.

Microbial growth can be controlled by lowering a_w. The minimum aw for microbial growth is variable. According to Roos (2007), it is > 0.90 for bacteria, 0.87–0.90 for yeast, 0.80–0.87 for moulds and 0.60–0.65 for osmophilic yeasts.

The technologies used to decrease a_w to preserve food include dehydration, concentration and freeze–drying (drying under frozen conditions); the latter combines cold with decreasing a_w to control the growth of microorganisms.

Dehydrated cactus pear products

Dehydration is one of the oldest food preservation processes. It can be done naturally – solar drying – or with equipment, such as dehydration tunnels, rollers, dryers and spray dryers. Highly controlled processes have recently been developed to produce more homogeneous and better quality dried products.

With regard to cactus pear, there have been various studies about dehydrating thin layers of pulp to prepare chewable, natural products. They are known as “fruit sheets”, “fruit leather”, "fruit bars" or “fruit rolls” and differ in thickness and moisture content: sheets are thinner and low in moisture, while bars have a high moisture content (≤ 20%). The University of Chile developed a process whereby a blend of cactus pear pulp and quince or apple pulp is used to prepare fruit rolls. Coloured ecotypes are also used to make products with a pleasant flavour and texture and attractive appearance (Sepúlveda *et al.*, 2000, 2003b) (**Figure 3**). **Table 2** shows the characteristics of certain products. All treatments contain:

- 75% cactus pear pulp;
- 25% apple pulp;
- varying amounts of sucrose (T1 and T2 = 6% and T3 = 0% sucrose and 0.01% sucralose); and
- varying amounts of flaxseed (T1 = 0% and T2 and T3 = 1%).

The total dietary fibre content of the treatments is 14.1–43.9%; the purple ecotype has a high fibre content due to its high pulp content, and sucralose (instead of sugar) is added.

The flow chart in **Figure 2** shows the various steps involved in the production of cactus pear sheets and **Figure 3** shows the cactus pear and apple pulps, as well as an oven used for drying to make the sheets.

El Sahamy *et al.* (2007a) prepared orange–yellow cactus pear sheets; they tested different drying temperatures (60 and 70 °C) and a range of ratios of sucrose (0, 1, 2, 3, 4, 5 and 10%). The prepared pulps were spread to a thickness of 10 mm and dehydrated in an air convection oven for 44 hours. The preferred sheets were those prepared with 2 and 3% sucrose.

Dehydrated products do not usually contain additives; they are, therefore, “natural products”, accepted by consumers because they are considered safe.

This simple technology, to the best of the author’s knowledge, has not been used at commercial level. While there are companies offering apple, strawberry, cherry and apricot rolls, these products are not usually 100% natural and are typically made from pear puree concentrate and artificial flavourings and colourants.

TABLE 2 Dietary fibre and total phenolics compounds in coloured cactus pear rolls mixed with apple pulp and flaxseed

Parameter/Treatment	Rolls from yellow–orange cactus pear pulp		
	T1	T2	T3
Total dietary fibre (g 100 g^{-1})	14.1 a	24.3 b	38.8 c
Total phenolics (mg GAE kg^{-1})	1 445.3 a	1 365.0 a	1 640.1 b
	Rolls from purple cactus pear pulp		
	T1	T2	T3
Total dietary fibre (g 100 g^{-1})	20.2 a	28.9 b	43.9 c
Total phenolics (mg GAE kg^{-1})	1 404.7 a	1 438.0 b	1 846.0 b

[a] GAE = Gallic acid equivalent.
Means following different letters differ at $P < 0.05$.
Source: Sáenz *et al.*, unpublished data

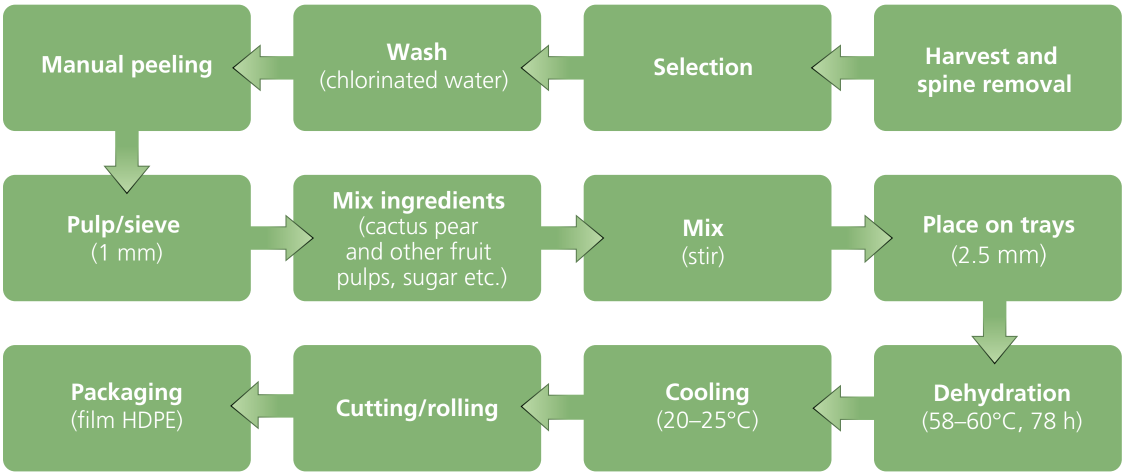

Figure 2
Preparation of cactus pear fruits rolls (adapted from Sáenz et al., eds)

Figure 3
Cactus pear and apple pulps; electric tray drier; rolls from coloured ecotype (Photos: C. Sáenz and A.M. Fabry)

The quality of such products could be easily improved by using coloured cactus pear pulp to prepare a more natural and healthier product.

Dehydrated cladode products

The dehydration options for cladodes are different from those for cactus pear fruits. The cladodes are not dehydrated for direct consumption, but are transformed into powders (Sáenz *et al.*, 2010) with a high content of dietary fibre. This powder can be used to make cookies (blended with wheat flour), puddings and – in some countries, in particular Mexico – breakfast cereals or tortillas. It can also be used in the production of food supplements (capsules, tablets etc.).

Rodríguez García *et al.* (2007) observed that during the development of young cladodes, insoluble fibre increases (from 29.87% in a 60–g cladode to 41.65% in a 200–g cladode), while soluble fibre decreases (from 25.22 to 14.91%, respectively). Ayadi *et al.* (2009) prepared powder using 2–3–year cactus pads; the total dietary fibre was 51.24%, of which 34.58% insoluble fibre and 12.98% soluble fibre.

This powder can make a nutritional contribution to several food products by increasing the daily dietary fibre intake. Inclusion of the powder in foods, however, implies certain technological challenges, as some aspects of taste and texture require improvement (Sáenz *et al.*, 2002b, c; Ayadi *et al.*, 2009). For example, heat treatments result in a herbaceous aroma and flavour, and the mucilage present in the cladodes produces texture defects (Sáenz *et al.*, 2012a). The research of Sáenz *et al.* (2012a) resulted in a purified natural dietary fibre with > 80 g 100 g^{-1} of total dietary fibre and 20–22 g 100 g^{-1} of soluble dietary fibre, one of the scarcest types of fibre present in vegetables. Purification results in an increase in total dietary fibre, a decrease in the green colour of the powder and a decrease in the total phenolic compounds, in particular when cladodes are washed at high temperatures. This purification process is promising and could result in more widespread use of cactus cladode powder as a food additive, especially in markets where consumers are not familiar with the herbaceous flavour of cactus cladodes and therefore are less accepting. Further research is required to obtain a powder rich in dietary fibre, low in flavour and colour and with high antioxidant capacity for use as an ingredient in new food formulas.

Figure 4
Coloured cactus pear toppings on a milk dessert

Cactus pear concentrates

The range of concentrated products derived from cactus pear includes syrups, jams and concentrated juices (Sáenz, 2000). Morales *et al.* (2009) developed dessert sauces (toppings) from coloured ecotypes with excellent results, preserving both their attractive colour and their functional compounds. Vacuum concentration was used on mixtures of cactus pear pulp with sugar (22.0–30.25%), fructose syrup (13.75–22.0%), glucose (11.0–19.25%), citric acid (0.14%) and modified starch (1.5%). These attractive products may be used in a range of different dishes (**Figure 4**). **Table 3** lists bioactive compounds present in two coloured toppings.

A wide variety of cactus–pear–based foods are manufactured (Sáenz *et al.*, eds, 2006). Companies use the Internet to advertise different ways of eating and enjoying cactus pear fruit products, offering concentrated products, such as jams, syrups and candies. The information available on-

TABLE 3 Bioactive compounds in coloured cactus pear toppings

Bioactive compound	Purple cactus pear topping	Yellow–orange cactus pear topping
Carotenoids (μg g^{-1})	0.186 ± 0.001	0.021 ± 0.001
Total phenolics (mg GAE $litre^{-1}$)[a]	350.50 ± 15.25	131.48 ± 5.72
Betalains	81.06 ± 1.83	63.80 ± 1.86
Betacyanins (BE mg kg^{-1})[b]	66.09 ± 1.03	0.92 ± 0.00
Betaxanthins (IE mg kg^{-1})[c]	14.97 ± 1.53	62.88 ± 1.86

[a] GAE: gallic acid equivalent; [b] BE: betanin equivalent; [c] IE: indicaxanthin equivalent (Morales *et al.*, 2009).

line suggests that these are mainly artisanal and small–scale companies. Cactus pear sweet gels

Research by the author's group at the University of Chile has recently led to the development of cactus pear sweet gels using the pulp of different coloured ecotypes to exploit the attractive pigments (Sáenz and Fabry, unpublished data). These products – obtained evaporating the pulp and adding gelling agents such as pectin – have proved very popular with small farmers in arid zones of Chile, where there are shortages not only of water, but of electric power. These sweet gels are made with available technologies, enabling small farmers to add value to their cactus pear production. The flow chart in **Figure 5** shows the different stages in the production of sweet gels from cactus pear.

These cactus pear sweet gels are made with:

- seedless cactus pear pulp (1 000 g);
- sugar (760 g)
- pectin (52 g) – another gelling agent (e.g. carboxymethyl cellulose – CMC) could be tried, or a mixture of fruit pulps rich in pectin (e.g. quince); and
- citric acid (16 g) – or substituted with lemon juice.

Figure 6 shows cactus pear sweet gels made by small farmers in the village of Codpa (Arica and Parinacota, Chile) in a workshop led by our group. The village is located in Camarones, in the middle

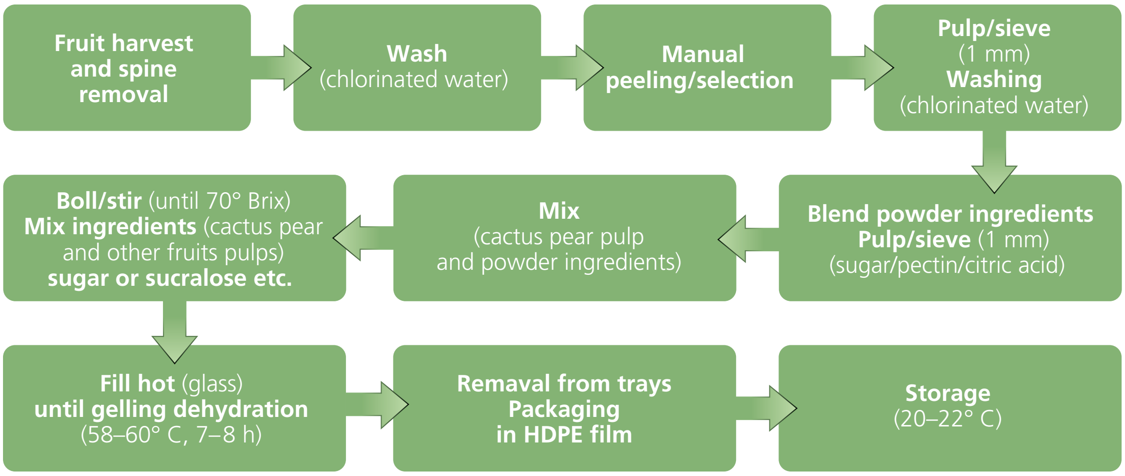

Figure 5
Preparation of cactus pear sweet gels

Figure 6
Cactus pear coloured sweets made in a workshop in the north of Chile (Photos: C. Sáenz and A.M. Fabry)

of the Tarapacá Desert in the north of Chile – an area with water and electric energy restrictions and where cactus pear grows as an alternative crop.

Recently, Sáenz and Fabry (unpublished data) developed cactus pear pulp gummy confections, mixing a fine screened pulp (2.5 litres) with unflavoured gelatin (0.45 kg), water (2 litres) and sugar (1.5 kg) (**Figure 7**).

The final product has a brilliant and attractive appearance (**Figure 8**) and a high sensory acceptance. The colour parameters of purple gummy confections are L = 5.6, a* 30.0, b* = 9.0, C* = 31.3 and hab = 16.6, corresponding to a dark purple colour. Despite the soluble solids content of 56.5° Brix, the product shows a high aw (0.92). For this reason, to ensure a good shelf–life, the use of preservatives (e.g. sodium benzoate and potassium sorbate) is recommended.

Nopal jams

The preparation of jams combines heat treatments with a decrease of aw (and sometimes also of pH to enable less severe thermal treatment). There are different jams and syrups on the market in several countries (Sáenz *et al.*, eds, 2006). One innovative product, for which technology was recently transferred to small farmers in the north of Chile, is cladode and lemon jam: nopal jam. To remove the excess mucilage affecting the texture, the cladodes are pre–treated with $Ca(OH)_2$. This pre–treatment may be avoided if the cladodes have a low mucilage content. The flow chart in **Figure 9** describes the steps involved in the preparation of nopal jam.

Figure 7
Preparation of cactus pear gummy confections

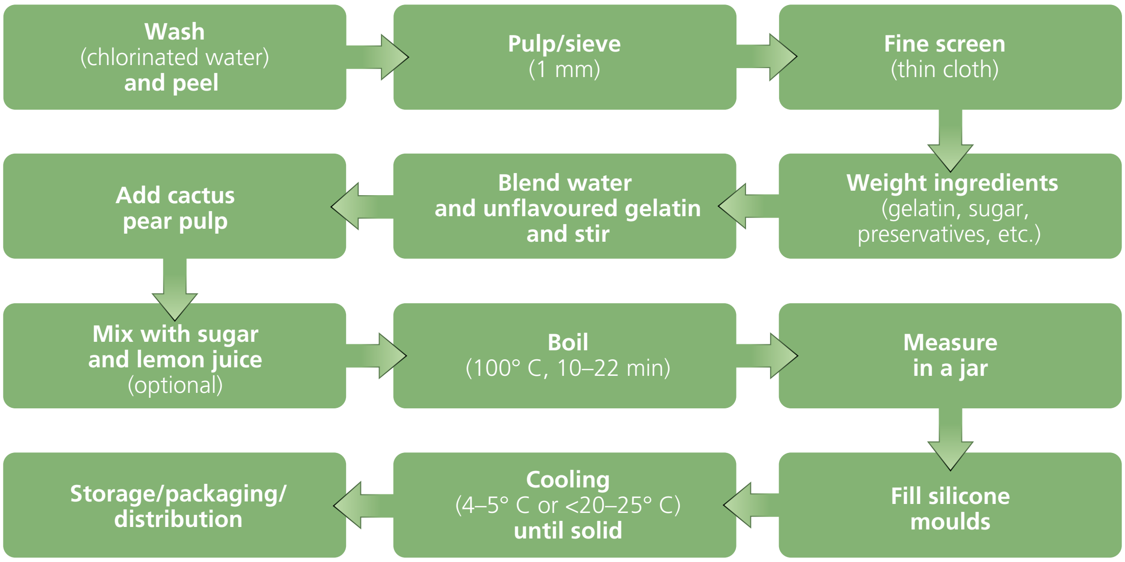

Figure 8
Gummy confections made from purple cactus pear, yellow–orange cactus pear and a mixture of both (Photo: C. Sáenz and A.M.Fabry)

Nopal jam represents a new alternative for processing cladodes. The jam can be eaten with crackers and baked goods, or served with meat and other dishes (**Figure 10**).

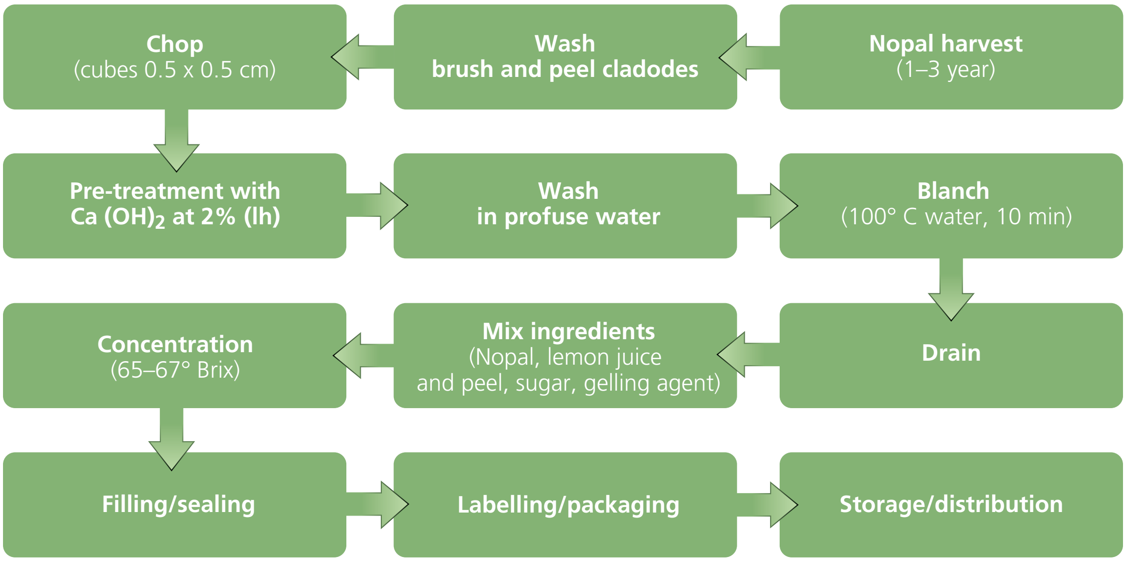

Figure 9
Preparation of nopal jam (cladode and lemon) (Modified from Sáenz et al., eds, 2006)

Figure 10
Cladode and lemon jam (Photos: C. Sáenz and A.M.Fabry)

Cactus pear juices

The pasteurization of cactus pear juice made with green fruit has produced unsatisfactory results, due to the unpleasant colour and aroma changes that occur during the process. On the other hand, purple cactus pear juice blended with other juices (e.g. pineapple) might represent an interesting alternative (Sáenz and Sepúlveda, 2001a). However, acidity is a potential issue: the addition of organic acid to increase acidity facilitates the heating process but can modify the taste, while consumers generally prefer cactus pear juices with the original acidity of the fruit, similar to that of the fresh fruit (Sáenz and Sepúlveda, 1999). El Samahy *et al.* (2007a) studied the production of pasteurized and sterilized cactus pear juices, adjusting the pH and adding preservatives in some treatments (sodium benzoate). Colour changes were observed at high temperatures, but microbiological stability was achieved in all the treatments. Baccouche *et al.* (2013) produced different formulations of a cactus pear beverage made with whey; it was pasteurized at 80° C for 20 minutes, and the physical stability was assessed after 40 days at 5° C. The authors observed an increase in sedimentation and turbidity (Nephelometric Turbidity Unit – NTU) during storage, and a decrease in colour, probably due to the Maillard reaction.

De Wit *et al.* (2014) made juices from eight cactus pear cultivars, with different fruit colours: one *O. robusta* cultivar ('Robusta', purple) and seven *O. ficus–indica* cultivars ('Berg' × 'Mexican', pink; 'Fusicaulis', green–white; 'Meyers', red; 'Algerian', red; 'Santa Rosa', orange; 'Skinners Court', green–white; 'Morado', white). The juices were pasteurized (60 °C for 10 minutes). The authors reported that the heat treatment had an unfavourable effect on the flavour of the juice and, for some of the cultivars (i.e. 'Santa Rosa'), pasteurization caused the cactus pear and melon taste of the fresh juice to turn bitter and astringent.

An example of a commercial product is a drink made from coloured cactus pear concentrate, water and natural flavouring. This product is available in the United States market, packaged in 1–litre Tetra Pak and sold for approximately US\$6 litre^{-1}.

Cladode juices and nectars

Rodríguez (1999) reported various formulations of a drink made from tender cladodes, which were blanched at 95° C, liquefied and filtered. For the best results, the liquid was diluted 30% with water, the pH was adjusted with citric acid (to reach pH 3.5) and aspartame was used as a sweetener (1 g 335 ml^{-1}). The product was pasteurized at 76° C for 15.2 minutes, with mild loss of heat–sensitive nutrients and other compounds.

Recent years have seen an increase in the supply of cladode juices and nectars, mainly sold in Mexico. The process for obtaining cactus pad juice is as follows:

- Remove spines from the cladodes.
- Cut into pieces.
- Grind using industrial or domestic equipment (blender).
- Add water to facilitate the process.
- Filter the liquid to separate the solids.

Cladode juice is produced by several companies in Mexico, and mixed juices are also made, combining cladodes with orange, pineapple, guava or celery; the juices are available in the domestic market and for export. Another product sold in the Mexican market is “nopal water", a drink made with cactus cladodes juice and sugar, usually produced on a small scale. Other products include cladode syrups, made from a base of sucrose syrup (55–75° Brix) with the addition of cladode juice. In Texas (United States of America), a company produces blackberry and blueberry syrups with added cactus mucilage.

Canned *nopalitos* (tender cladodes)

Canning and pasteurization technologies are widely adopted in the manufacture of various products made from *nopalitos*. In Mexico, for example, pickled or salted tender cladodes (*nopalitos*) have been available on the market for many years. (Corrales García and Flores Valdez, 2003). Detailed descriptions of the preparation of pickled *nopalitos* and *nopalitos* in brine, among others, are given in Sáenz *et al.*, eds (2006).

Frozen products

Freezing is widely adopted for food preservation. More than any other method, freezing allows the taste, texture, and nutritional and functional features to be preserved. Techniques, such as cold air tunnels (–40 °C) or spraying liquid nitrogen (–196° C), are widely used in the food industry to improve the quality of the final product. The faster the freezing, the smaller the ice crystals formed and the better the product quality achieved. Freezing combines the effects of low temperature (microorganisms cannot grow, chemical reactions are reduced, and cellular metabolic reactions are delayed) with a decrease in water activity (a_w) (Casp and Abril, 1999; Vieira, 1996; Delgado and Sun, 2000). However, experiments on cactus pear have not yet yielded good results (Sáenz *et al.*, eds, 2006). Several studies indicate that freezing technologies could achieve better results with cactus pear pulps, rather than whole, half or sliced fruits. Defrosting – regardless of the type of cut (whole, halves or slices) – presents some problems, with excessive mucilage drip after defrost, resulting in an unpleasant appearance. This happens even when individually quick frozen (IQF) technologies are adopted, involving freezing temperatures close to –40° C.

Ice creams made from coloured cactus pear pulps can be found in very few countries and may be an interesting alternative for the use of pulps or concentrates. El Samahy *et al.* (2009) studied ice cream made with the addition of concentrated red cactus pear pulp (30°Brix); a 5% addition of pulp was found to be the most acceptable. The author’s research group is currently conducting experiments with this attractive product.

OTHER TECHNOLOGIES

Fermentation

Fermentation is one of the oldest food preservation techniques and has been used with cactus pear to obtain various products. *O. streptacantha* (cactus pear ‘Cardona’) has been used to produce alcoholic beverages in Mexico since the pre–Hispanic period; the most traditional drink made with the juice of this species is *colonche* (Corrales García and Flores Valdez, 2003; Diaz, 2003).

Flores (1992) experimented with *O. streptacantha* and *O. robusta* to make a wine and a distilled alcohol. A wine of 11.6 °GL was obtained from juice concentrate (20 °Brix) using *O. streptacantha*; the distilled alcohol reached 56.2 °GL. The two species, *O. streptacantha* and *O. robusta*, produced alcohol with similar characteristics and a pleasant fruity aroma.

Another product with interesting potential is vinegar and some manufacturing experiences are worthy of note. Pérez *et al.* (1999) prepared vinegar from orange cactus pear using two types of substrate for acetic fermentation: must with previous alcoholic fermentation (13.5° GL) and cactus pear juice with added sugar (22° Brix). *Acetobacter pasteurianus* was used in the first case, *Acetobacter xylinum* in the second. Both vinegars obtained presented an intense yellow–amber colour, clean and bright, with a fresh and acetic acid smell.

Prieto *et al.* (2009) studied the development of balsamic–type vinegars from coloured cactus pear juices; the resulting products had an attractive colour, pleasant aroma and good sensory acceptability (**Figure 12**).

Membrane technologies

Membrane separation technologies have been increasingly used in the food industry in the last 25 years. Today their use is widespread and adopted for a range of purposes, including cold pasteurization, juice clarification and bioactive compound concentration (Cissé *et al.*, 2011; Rai *et al.*, 2006; Todisco *et al.*, 2002). Membrane technologies have advantages over other separation technologies (traditional filtration and concentration):

- Operation at low temperatures (15–35° C) – consequently affordable (low energy consumption) and degradation of heat–sensitive compounds is avoided.
- No use of chemicals (filter aids or enzymes) – unlike in filtration or traditional separation (Cassano *et al.*, 2010).

In membrane separation technologies, the membrane (ceramic or polymer) acts as a barrier: it allows only certain components in a mixture to pass and retains others. The flow of these substances is determined by various driving forces, including: pressure, concentration and electric potential. This selectivity means, for example, that it is possible to enrich a flow with one or more substances present in the feed. Two flows emerge from the feed: permeate (or filtrate) and retentate (or concentrate). The retentate contains substances that do not cross the membrane, while the permeate is rich in substances that pass through (Raventós, 2005). The selectivity depends on the size of the pores in the membrane and the chemical affinity between the membrane and the substances (Cheryan, 1998; Raventós, 2005).

Membrane technology processes used in the food industry include: microfiltration (MF), ultrafiltration (UF), nanofiltration (NF) and reverse osmosis (RO). RO is known for its effectiveness in desalinating seawater. Initial research on cactus pear juice focused on the application of MF and UF – the methods normally used in juice clarification. Cassano *et al.* (2007) experimented with cactus pear cv. 'Gialla' (yellow–orange) and combined membrane technologies with concentration by osmotic distillation (OD); they used low temperatures and preserved the organoleptic, nutritional and sensory characteristics of cactus pear juice. The concentration process (OD) resulted in 61° Brix and a good balance of betalains.

Cassano *et al.* (2010) later compared the performance of MF and UF in the physicochemical composition of yellow cactus pear juice. In both processes, the solids suspended in fresh juice were completely removed and a clarified juice obtained, and the betacyanins were retained. This retentate, rich in betalains, could be pasteurized and added to a juice concentrate to prepare, for example, pulpy juices, ice cream, jellies or infant formula (Cassano *et al.*, 2010).

Figure 12
Balsamic–type vinegars from coloured cactus pear juices (Photo: C. Sáenz)

The research group of the authors of this chapter recently used this technology to separate or concentrate betalains from purple cactus pear MF, UF and NF (Cancino, Robert and Sáenz, unpublished data). Thanks to the avoidance of high temperatures, there was no degradation of the pigments, and the betalain extracts obtained were free of mucilage and had a reduced content of low molecular sugars. **Table 4** shows the characteristics of purple cactus pear pulp: prediluted (P), ultrafiltered (UF) and nanofiltered (NF). The ultrafiltered and nanofiltered extracts were, as expected, fully clarified solutions (0 NTU), in comparison with the prediluted pulp (2 453 NTU), which contained mucilage. In the UF, the betacyanin content (247.9 mg BE litre^{-1}) was similar to that of P; however, in the NF, the betacyanin values (216.3 mg BE litre^{-1}) were lower than those in P and UF, taking into consideration that the pulp (feed) is diluted.

Cassano *et al.* (2010) obtained the highest betalain values with UF (32.8 mg BE litre^{-1}). The polyphenol content was concentrated in both membrane processes (UF and NF). Cassano *et al.* (2010) – applying UF to cactus pear cv. 'Gialla' and using other membranes and process conditions – reported lower values of total polyphenols (552.17 mg

TABLE 4 Physical and chemical characteristics of prediluted pulp, ultrafiltered and nanofiltered extract from purple cactus pear

Parameter	P	UF	NF
Total sugars (%)	13.2 ± 0.0 b	9.2 ± 0.3 c	17.5 ± 0.1 a
Turbidity (NTU)	2453 ± 64 a	0.00 ± 0.00 b	0.00 ± 0.00 b
Betacyanins (mg BE litre^{-1})	254.0 ± 0.2 a	247.9 ± 4.3 a	216.3 ± 7.0 b
Betaxanthins (mg IB litre^{-1})	85.4 ± 0.1 b	88.6 ± 1.2 a	79.1 ± 2.6 c
Total phenolics (mg GAE litre^{-1})	534.8 ± 4.4 b	659.7 ± 5.0 a	673.5 ± 13.5 a
Colour			
L	12.5 ± 0.9 c	17.8 ± 0.1 b	19.3 ± 0.03 a
C*	48.0 ± 1.7 c	59.3 ± 0.1 b	62.4 ± 0.1 a
H_{ab}	25.9 ± 1.0 c	30.3 ± 0.1 b	31.4 ± 0.1 a

P = pulp; UF = ultrafiltered pulp; NF = nanofiltered pulp; BE = betanin equivalent; IE = indicaxanthin equivalent; GAE = gallic acid equivalent.
Different letters in rows: means statistical differences (Tukey $p < 0.05$).
Source: Cancino, Robert and Sáenz (unpublished data).

GAE litre^{-1}). The results obtained for the different extracts (P, UF and NF) are due to the membrane pore size, as well as the chemical affinity between the membrane and the interaction between the different compounds and the membrane.

These kinds of products open new possibilities for the production of colourants from cactus pear. However, further research is required to improve the pigment concentration and other properties of the extracts.

OTHER PRODUCTS

Cactus pear colourants

Natural colourants – in particular, red and purple – are highly appreciated by consumers since synthetic red colourants used as additives in food have been restricted by official regulations in the European Union and the United States of America because of the possible adverse effects on human health (Tsuda *et al.*, 2001). Therefore, there is a growing interest in new, natural red pigment sources and their potential application in foods.

Red and purple cactus pear ecotypes have a variable betalain content in both the pulp and peel (Odoux and Domínguez López, 1996; Sepúlveda *et al.*, 2003c). This pigment is commercially obtained from red beetroot and is widely used in the food industry. Its use in food is permitted by both US and EU legislation (Sáenz *et al.*, 2009). The red beet extract (rich in betalains) is used mainly to colour food, such as dairy products, confectionery, ice cream, desserts, beverages and sausages. However, it has some disadvantages: an earth–like flavour, imparted by geosmin and 3–*sec*–butyl–2 methoxypyrazine, and high nitrate levels. Red or purple cactus pears are, therefore, an interesting alternative as a source of betanin for the production of food colourants (Sáenz *et al.*, 2009; Castellar *et al.*, 2003) (**Figure 13**).

The use of a purple concentrate cactus pear juice as food colouring for dairy products (e.g. yogurt) was studied some years ago (Sáenz *et al.*, 2002d; Sepúlveda *et al.*, 2002, 2003c). Topics including pigment purification and stability, crucial for application in industry, are currently being addressed.

Castellar *et al.* (2008) obtained a betalain concentrate by fermentation (*Saccharomyces cerevisiae* var. Bayanus AWRI 796) of *O. stricta* juice. The final product had 9.65 g betanin litre^{-1}, pH 3.41, 5.2° Brix and a viscosity of 52.5 cP.

Other studies focused on dehydration of cactus pear pulp by spray–drying or freeze–drying to obtain colourant powders. Mosshammer *et al.* (2006) adopted lyophilization and spray–drying with maltodextrin as carrier (18–20 dextrose equivalent [DE]) to dehydrate *O. ficus–indica* cv. 'Gialla' juice; they reported high betalain retention (≤ 90%) for both kinds of powder. Similarly, various species of purple cactus pear *(O. stricta, O. streptacantha, O. lasiacantha*) were spray–dried, using maltodextrin as drying carrier (10, 20 DE). Diaz *et al.* (2006) observed that after 24 weeks at 25° C, the powder retained 86% of the original content of betanin. Obón *et al.* (2009) used glucose syrup (29 DE) and reported that after 1 month stored at room temperature, the colour powder retained 98%. Rodríguez Hernández *et al.* (2005) observed that

Figure 13
Purple cactus pear fruits and microparticles (Photos: C. Sáenz)

cactus pear powder, when reconstituted, presented a slightly different colour from the fresh juice.

Betalain stability is affected by several factors: pH, water activity, exposure to light, oxygen, enzyme activity and, above all, temperature (Azeredo, 2009; Herbach *et al.*, 2006; Castellar *et al.*, 2003). A technology – microencapsulation – is available to stabilize the pigments (Sáenz *et al.*, 2009, 2012b; Gandía Herrero *et al.*, 2010; Vergara *et al.*, 2014; Robert *et al.*, 2015).

Microencapsulation is a technique involving the introduction of bioactive compounds (solid, liquid or gaseous) into a polymeric matrix to protect them from the environment, interaction with other food components or controlled release (Yáñez Fernández *et al.*, 2002). Microencapsulation by spray–drying is the most widely used technique: it obtains a powder of low water activity, enabling easier transportation, handling and storage and ensuring microbiological quality (Hayashi, 1989).

Vergara *et al.* (2014) combined membrane technology (to separate betalains) and microencapsulation (to protect them), obtaining a healthy colourant that can be used in the food industry. Gomez (2013) studied the microparticle betalains stability in soft drinks, comparing microparticles from cactus pear pulp, and ultrafiltered and nanofiltered extracts; he concluded that the stability of betalains is affected both by their source (pulp or extract) and by the encapsulating agent used. Betalains from cactus pear pulp are more stable in soft drinks, probably thanks to the mucilage. Alfaro (2014) applied purple cactus pear pulp microparticles in yogurt, and reported that after 45 days' storage, 60% of betalains were retained.

There has been relatively little research to date on the encapsulation of betalains from cactus pear (*O. ficus–indica*) (Sáenz *et al.*, 2009; Vergara *et al.*, 2014; Pitalua *et al.*, 2010; Gandía Herrero *et al.*, 2010; Robert *et al.*, 2015; Otárola *et al.*, 2015). Further investigation is required.

Extruded products

Extrusion cooking is a high–temperature short–time (HTST) technology. While there has been little relative study in cactus pear and cladodes, this technology is widely applied in food processes, such as breakfast cereals, salty and sweet snacks, baby foods and snack foods. Food materials are plasticized and cooked, combining moisture, pressure, temperature and shear. The factors affecting product quality include extruder type, screw configuration, speed, temperature and feed rate, as well as the composition of the raw material and the type of food ingredients used (Singh *et al.*, 2007; El Samahy *et al.*, 2007b).

El Samahy *et al.* (2007b) studied cactus pear rice–based extruded products – an innovative option for production of a new value–added snack based on cactus pear pulp concentrates. In this study, orange–yellow and red cactus pear pulps were concentrated (40° Brix), added to rice flour and the blend put in a single–screw extruder. Different formulations (varying the ratio of rice flour and cactus pear pulp concentrate) were tested. Substitution levels of 5% and 10% of concentrated cactus pulps gave the best results for extruded products with good functional, nutritional and sensory characteristics. The poor sensory attributes of the formula without cactus pear pulp were significantly improved by adding cactus pear concentrates.

Sarkar *et al.* (2011) extruded cactus pear pulp (yellow variety) with rice flour. The authors tested different solids ratios (rice flour solids : puree solids – 6 : 1, 8 : 1 and 10 : 1). The blends were dried in a twin–screw extruder. The results revealed that some characteristics, such as porosity, decreased when the fruit solid level increased.

Cactus pear pulp has potential for the production of extruded products; further study is required to better understand the behaviour of cactus pulp in this process and to improve characteristics of the products obtained.

Hydrocolloids (mucilages) from cladodes

Hydrocolloids are polysaccharides with variable complexity, generally used in the food industry as additives to provide viscosity to, for example, beverages, puddings and salad dressings. They include cactus mucilage, a polysaccharide–type arabinogalactan present both in cactus pads and in cactus pear fruits (Sáenz *et al.*, 2004; Matsuhiro *et al.*, 2006). The mucilage has an important physiological role in the *Opuntia* species as it has a high water retention capacity (Nobel *et al.*, 1992). It can be extracted from the matrix (cladodes or fruit peel) with water, and precipitated with ethanol; or other techniques can be adopted, such as pressing (Sepúlveda *et al.*, 2007). In general, the extraction yields are low (≤ 2% fresh weight [FW]), but they nevertheless offer an interesting prospect, considering that the cladodes (pads) are usually pruning residues and are available throughout the year. Various extraction methods have been reported using different solvents to precipitate the mucilage, such as ethanol, isopropyl alcohol and acetone (Rodríguez González *et al.*, 2014; Cai *et al.*, 2008; Sepúlveda *et al.*, 2007; Yahia *et al.*, 2009; Medina Torres *et al.*, 2000). Some studies have researched the application of this hydrocolloid in fruit nectars to replace other thickeners normally used in the food industry (e.g. CMC) (Sepúlveda *et al.*, 2003a, 2004).

The mucilage has also been tested as an edible coating to protect fresh fruits. Del Valle *et al.* (2005) used mucilage as edible film to increase the shelf–life of strawberries stored at 5° C, reporting that the fruits maintained their texture and flavour and no deterioration occurred after 9 days of storage. This edible film could provide an alternative for the preservation of different fresh fruits, such as berries. However, application to different products is a challenge, because the respiratory rate of each type of fruit must be taken into account. Aquino *et al.* (2009) used a mucilage solution blended with different citric acid and sodium bisulphite concentrations to inhibit the browning of banana slices during the drying process. The authors reported that a combination of 500 ppm sodium bisulphite and citric acid (1%), following treatment in the mucilage solution (35 mPas), inhibited browning and made the banana slices shinier.

Recently, Medina Torres *et al.* (2013) and Otárola *et al.* (2015) reported that mucilage can be used as an encapsulating agent for bioactive compounds, gallic acid and betalains; this points to new opportunities in the industrial sector. Sáenz *et al.* (2009) also reported this behaviour in a study of the encapsulation of betalains from purple cactus pear fruits.

Lira Ortiz *et al.* (2014) extracted low methoxyl pectins from *O. albicarpa* Scheinvar skin, and discovered its potential for use in the food industry as a thickening and gelling agent – the latter when calcium ions were added. The authors obtained a yield of 98 g kg^{-1} of dry matter.

Seed oil

Cactus pear fruits contain variable amounts of seeds, but they are usually present in a high proportion (10–15 g 100 g^{-1}). In most cactus pear fruit processes, the seeds are separated from the pulp, resulting in large quantities of discarded seeds that become an environmental waste problem. For this reason, in recent decades, researchers in different countries have studied the seed composition and sought different possible uses for the seeds.

Sawaya *et al.* (1983) studied the seed composition and its potential utilization in animal feed. They reported 16.6% protein content, 17.2% fat, 49.6% fibre and 3.0% ash. The mineral content is high in sodium (67.6 mg 100 g^{-1}), potassium (163.0 mg 100 g^{-1}) and phosphorus (152.0 mg 100 g^{-1}).

Cactus pear seed oil is edible; it could be another nutritive and functional product of potential interest to the food industry, but perhaps not for direct consumption (as indicated below). The oil is usually extracted in research using organic solvent (4.4–14.10%) (Sawaya and Khan, 1982; Sepúlveda and Sáenz, 1988; Ennouri *et al.*, 2005; Becerril, 1997; Tlili *et al.*, 2011; Ouerghemmi *et al.*, 2013; Chougui *et al.*, 2013), depending on factors such as growing conditions, variety and fruit maturity (Özcan and Al Juhaimi, 2011). Use of a cold press to obtain the seed oil was only reported by Gharby *et al.* (2015) from Morocco, with a yield of 6–7%. This type of extraction is more environmentally friendly as it avoids the use of organic solvents.

Yields of edible oils are 6–17%, which, in terms of waste stream, compares reasonably with other commonly used seed oils. The production of cactus pear seed oil as edible oil is only viable with integrated processing, using all parts of the plant (Sáenz *et al.*, eds, 2006).

Cactus pear seed oil is rich in unsaturated fatty acids and has a high linoleic acid content (57.7–73.4%) and low linolenic content. **Table 5** shows the percentages of the main seed oil fatty acids.

The oil has a high unsaturated fatty acid content, as well as other healthy compounds, such as sterols, tocopherols, vitamin E, β–carotene and vitamin K (Ramadan and Mörsel, 2003a; Kouba *et al.*, 2015). Phenolic compounds were reported by Tlili *et al.* (2011) and Chougui *et al.* (2013): respectively, 61 mg GAE 100 g^{-1} and 268 mg 100 g^{-1}, expressed as rutin equivalent. The researchers in Mexico and Taiwan reported higher figures (Cardador Martínez *et al.*, 2011). Further research is required before definitive conclusions can be drawn.

These and other physical and chemical properties, including refractive index, iodine index and saponification number, highlight the similarity between cactus

TABLE 5 Fatty acid content (%) in cactus pear seed oil (*Opuntia ficus–indica*) from different countries

Fatty acid	Countries						
	Morocco [a]	Turkey [b]	South Africa [a]	Tunisia [a,c,g]	Germany [d]	Chile [e]	Algeria [f]
Palmitic (C16 : 0)	11.9	10.6–12.8	13.7	12.2–12.7	23.1	16.2	13.1
Stearic (C18 : 0)	3.4	3.3–5.4	3.38	3.2–3.9	2.67	3.3	3.5
Oleic (C18 : 1w9)	21.3	13–23.5	15.7	16.4–22.3	24.1	19.9	16.3
Vaccenic (C18 : 1n–7)	–	5.1–6.3	–	4.8	–	–	5.3
Linoleic (C18 : 2w6)	60.8	49.3–62.1	64.38	53.5–60.6	32.3	57.7	61.8

[a] Gharby *et al.* (2015); [b] Mattháus and Özcan (2011); [c] Tlili *et al.* (2011); [d] Ramadan and Mörsel (2003a); [e] Sepúlveda and Sáenz (1988); [f] Chougui *et al.* (2013); [g] Ouerghemmi *et al.*, 2013.

pear seed oil and other edible vegetable oils, such as corn oil or grape seed oil. Oil extraction yields are low compared with other common edible seed oils; cactus pear seed oil could nevertheless be used in the food industry as a fat replacer in special confectionery products. However, pharmaceutical and cosmetics uses offer more and better alternatives. In this context, cactus pear seeds also contribute with essential oils, a group of compounds used mainly in the pharmaceutical field. Ouerghemmi *et al.* (2013) reported that essential oils comprise, among others, terpenes, esters and aldehydes, and the yield for cactus pear seeds is close to 4%.

In recent years, other applications have emerged, in particular for cosmetics; this industry has exploited the oil's characteristics (polyunsaturated fatty acid content, tocopherols, sterols, phenolics) and in countries such as Morocco a promising industry has emerged. There are several cooperatives and private companies that extract this oil for cosmetic purposes, and at least 20 producers of cactus oil exist (Abderrahman Ait Hamou, ANADEC, Morocco, personal communication). The industry extracts the oil by cold press – an environmentally friendly process that avoids the use of solvents (Berraaouan *et al.*, 2015; Gharby *et al.*, 2015). Before the oil is extracted by cold press, the seeds must be separated using a special machine (**Figure 14**).

CONCLUSION

There are a vast array of alternatives for processing the fruits, cladodes and seeds from *Opuntia* plants. In general, the technologies used are available to many small–scale agro–industries that could take advantage of this new raw material to diversify their production. When, on the other hand, the aim is the creation of new agro–industries for cactus pear processing, investment is required and must come from governments, NGOs or other sources. In some countries, a cooperative model could be promoted. The immense variety of cactus pear products and by–products can bring huge benefits to many people, in particular those living in arid and semi–arid zones of the world.

Figure 14
(a) Seed separator

13

Nutritional properties and medicinal derivatives of fruits and cladodes

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13

Nutritional properties and medicinal derivatives of fruits and cladodes

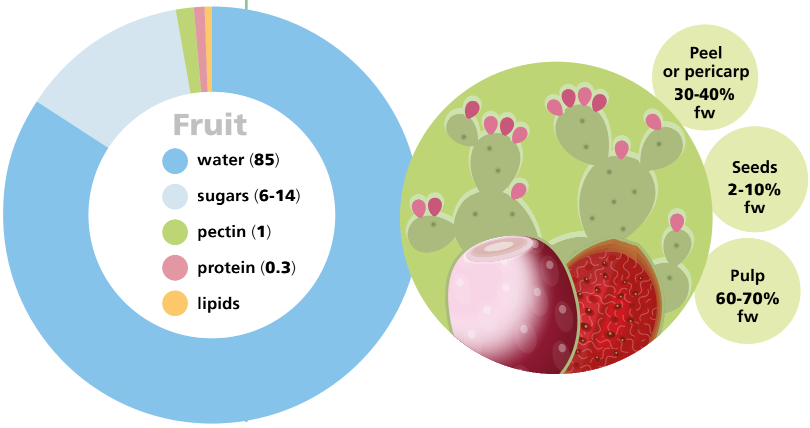
INTRODUCTION

Scientific investigation has confirmed that fruits and cladodes of cacti may be efficiently used as a source of nutrients and phytochemicals (e.g. sugars, mucilage, fibres, vitamins and pigments) of nutritional and functional importance. Cactus products show promising functional characteristics due to their health–promoting properties. This chapter presents a detailed description of the major active components of the different cactus species studied worldwide.

Since ancient times, cactus plants have been used to cure diseases and heal wounds. Cacti are traditionally used as natural medicines in several countries for the treatment of many diseases. Moreover, cladodes and cactus pear fruits are still used today in folk medicine as therapeutic agents. Remarkable progress has been made in recent decades to characterize plant constituents and explain the role of natural molecules in relation to disease prevention. In this context, there are strong recommendations to incorporate fruit and vegetables in the diet. Several manufactured products are currently available on the global market that exploit the medicinal properties of cactus plants; there is increasing interest in the industrial use of cactus products as nutraceuticals.

Cactus plants are multipurpose crops: not only do they provide food and feed, they contain bioactive phytochemicals. Fruits and cladodes already provide energy and nutrients for both humans and livestock. However, cactus plants are also rich sources of health–promoting substances that can be used as natural medicines to prevent and cure serious diseases. These beneficial properties of cactus, already known to ancient civilizations, are now generating interest among the scientific community. The scientific literature concerning the medicinal properties of cactus is in constant expansion, with new discoveries reported about the plant constituents responsible for such activities.

Figure 1
Cactus pear chemical composition (% in fresh matter) and fruit constitution as a percentage of fruit weight, fw (El Kossori et al., 1998; Duru and Turker, 2005)



NUTRITIONAL ASPECTS

The nutrient composition of fruits and cladodes depends on many factors: species, cultivar or variety; environmental factors, such as the climatic and edaphic conditions; crop management, including fertilization and post–harvest treatment; and maturity status.

Fruits

Many cactus species produce edible fruits. Currently, most of the cactus fruits in the global market belong to the *Opuntia ficus–indica* species and the fruits are known as "cactus pear". The typical cactus pear fruit is an oval–shaped berry with an average weight of 100–200 g. The juicy pulp constitutes 60–70% of the total fruit weight and contains numerous small hard seeds, varying from 100 to > 400 per fruit. **Figure 1** shows the fruit composition. Cactus pear is a non–climacteric fruit, it has a low respiration rate (Cantwell, 1995) and low ethylene production. Hence, the nutrient concentrations remain in the fruit without significant changes throughout storage; however, weight and firmness may change. Furthermore, the fruit's pH, acidity and total soluble solids do not vary during post–harvest storage; although some changes in vitamin C content have been reported, depending on the storage conditions (Coria Cayupán *et al.*, 2009).

The chemical and nutritional composition of cactus pears has been extensively studied (El Kossori *et al.*, 1998; Butera *et al.*, 2002; Feugang *et al.*, 2006). Sugars, fibre, mucilage and pectins are the major fruit constituents; proteins, amino acids, vitamins and minerals are the minor components (Tesoriere *et al.*, 2005b). Secondary metabolites with antioxidant properties have been described

(Kuti, 2004; Yahia and Mondragón, 2011; Coria Cayupán *et al.*, 2011). Cactus pear is characterized by high sugar content (12–17%) and low acidity (0.03–0.12%) with pH values between 5 and 7. Furthermore, total soluble solid content varies from 11.6 to 15.3° Brix, increasing with fruit maturity (Yahia and Mondragón, 2011). The relative ratio of glucose and fructose varies among different species and within fruit tissues: 53% glucose and 47% fructose of total sugar content (Kuti and Galloway, 1994). The fruit pulp is also rich in minerals, such as calcium (59 mg 100 g^{-1}) and magnesium (98.4 mg 100 g^{-1}) (Stintzing *et al.*, 2001). Fruit peel and pulp constituents contain mucilage in the dietary fibre; it is a hydrocolloid and has a high capacity to absorb water. The total amino acid content (257.24 mg 100 g^{-1}) is higher than the average of other fruits; the principal amino acids are proline, taurine and serine. Significant amounts of ascorbic acid are present in *Opuntia ficus–indica*, ranging from 180 to 300 mg kg^{-1} of fresh fruit (Piga, 2004).

Tocopherols, the fat–soluble vitamin E, are found in the lipid fraction of both the cactus fruit seed and pulp. The vitamin E homologues isoforms γ– and δ–tocopherols are the main components in seed and pulp oils, respectively, constituting up to 80% of the total vitamin E content (Ramadan and Morsel, 2003a). Lipids are distributed in the fruit peel, pulp and seeds. The fruit peel contains appreciable amounts of polyunsaturated fatty acids, in particular linoleic acid. It also contains other fat–soluble compounds, such as sterols, beta–carotene and vitamin K1; the main sterol is β–sitosterol (Ramadan and Mörsel, 2003b). Peel polysaccharides and pectins have been characterized by Habibi *et al.* (2004).

Seed and seed oil

Cactus pear contains many hard–coated seeds that represent 10–15% of the pulp weight. The fruits contain a large number of seeds although their oil content is relatively low. Oil content is 7–15% of the whole seed weight. Essential fatty acids (mainly linoleic acid) form a significant percentage of the unsaturated fatty acids of seed oil extract. Unsaturated fatty acids account for about 80% of all fatty acids (Ennouri *et al.*, 2005). The linoleic acid content varies between 61.4 and 68.9%. The α–linolenic acid concentration in all cultivars is < 1%. The oleic acid content varies between 12.4 and 16.5%. Therefore, although the seed oil content is relatively low, its fatty acid composition indicates that it has potential for use in the health and cosmetic industries (Labuschagne and Hugo, 2010). Seed oil destined for cosmetics sells at a very high price as organic oil for use in the production of anti–ageing and anti–wrinkle products. New applications are currently under development by the cosmetics industry. The seed endosperm is composed of arabinan–rich polysaccharides, while the major seed–coat component is D–xylan (Habibi *et al.*, 2002). Xylan has been used as an adhesive, a thickener and as an additive in plastics; it is of growing interest to the food industry due to its potential for packaging films and coating food; it also acts as an emulsifier and protein foam stabilizer during heating. Nowadays, it may play an important role in the development of new biomedical products for novel drug delivery systems, especially for controlled drug release.

Cladodes

Cladodes are modified flattened stems with a characteristic ovoid or elongated shape; they are able to exert a photosynthetic function. Young tender cladodes, called nopalitos, are consumed as fresh vegetables; they are used as an ingredient in a wide range of dishes, including sauces, salads, soups, snacks, pickles, beverages, confectionery and desserts (Saenz *et al.*, 2002a). The major components of cladodes are carbohydrate–containing polymers, comprising a mixture of mucilage and pectin. The chemical composition of fresh young cladodes is reported by Saenz *et al.* (2002a):

- moisture 91% (weight of water [w_w])
- total carbohydrates 4.5%
- protein 1.5% (w_x in dry basis [DB])
- fat 0.2% (w_w DB)
- ash 1.3% (w_w DB), of which 90% calcium

Guevara Figueroa *et al.* (2010) analysed the cladode proximate composition of wild *Opuntia* spp. (**Figure 2**). In addition, 100 g of cladodes contain 11 mg vitamin C and 30 µg of carotenoids.

The mucilage is a polysaccharide; it can be found in specialized storage cells or free within cells or intracellular spaces of the chlorenchymatic and parenchymatic tissue of the cladodes. The dried mucilage comprises on average: 5.6% moisture; 7.3% protein; 37.3% ash; 1.14% nitrogen; 9.86% calcium; 1.55% potassium (Sepúlveda *et al.*, 2007). Based on its chemical composition, the mucilage is considered a polymer (similar to pectin), composed of arabinose, galactose, xylose and rhamnose as neutral sugars, and of a small amount of galacturonic acid (Medina Torres *et al.*, 2000; Madjdoub *et al.*, 2001). Besides the direct consumption of tender shoots, mature cladodes are ground to make flour and other products. Nopal flour is a rich source of dietary fibre reaching up to 43% DB (Saenz *et al.*, 2002a); it can be used to fortify food recipes containing flours from other sources.

BIOACTIVE PHYTOCHEMICALS IN CACTUS PLANT

Cactus plants are also important sources of bioactive substances and excellent candidates for nutraceutical and functional food preparation. The fruits, cladodes, seeds and flowers all have a high content of chemical constituents, adding value to cactus products.

Fruits

Cactus pear fruits present high antioxidant activity, ascribed to the presence of vitamin C, flavonoids and betalains (Galati *et al.*, 2003a; Kuti, 2004). Antioxidant activity in the fruit is twice that of pear, apple, tomato, banana and white grapes, and is similar to that of red grapes and grapefruit (Butera *et al.*, 2002).

Betalains are nitrogen–containing pigments and can be classified as red betacyanins (e.g. betanin) and yellow betaxanthins (e.g. indicaxanthin). Betacyanins are ammonium conjugates of betalamic acid with cyclo–DOPA; betaxanthins are conjugates of betalamic acid with amino acids or amines. Betalains are the main pigments responsible for the ripe fruit colours and, therefore, they are a major factor in consumer acceptance. The concentration of pigments depends on several factors, in particular fruit ripening status (Coria Cayupán *et al.*, 2011). Stintzing *et al.* (2005) characterized the betalain composition of cactus pear fruit. These pigments do not only provide colour: their antioxidant properties are greater than those of ascorbic acid (Butera *et al.*, 2002; Stintzing *et al.*, 2005). In contrast with anthocyanins (another group of natural red pigments), betalains are stable in a wider pH range and are thus more appropriate for use as food colourants in low–acid products (Stintzing *et al.*, 2001). Due to their wide structural variety, and hence colour diversity, betalains constitute a very promising source of natural colourants to be used as functional colourants. Compared with red beets, cactus pear not only offers a wider range of colours, it also has technological advantages: absence of geosmin (an undesirable earth–like flavour); low nitrate levels; and lack of soil microbial contamination.

The presence of phenolics was also detected in cactus fruit pulp. Kuti (1992) reported an antioxidative effect due to the major flavonoids found in cactus fruits (e.g. quercetin, kaempferol and isorhamnetin derivatives). Flavonol derivatives detected in *Opuntia* spp. were reviewed by Stintzing and Carle (2005). The peel has a higher phenolic content than the pulp (Stintzing *et al.*, 2005). Consequently, from a functional point of view, it is advantageous to process both peel and pulp. Lee *et al.* (2002a) found that cactus flavonoids are also effective in protecting plasmid DNA against the damage induced by hydroxyl radicals.

Cladodes

Other functional components, such as chlorophyll derivatives, amino acids and flavonoids, are found in cactus pads (**Figure 3**). Guevara Figueroa *et al.* (2010) analysed cladodes of commercial and

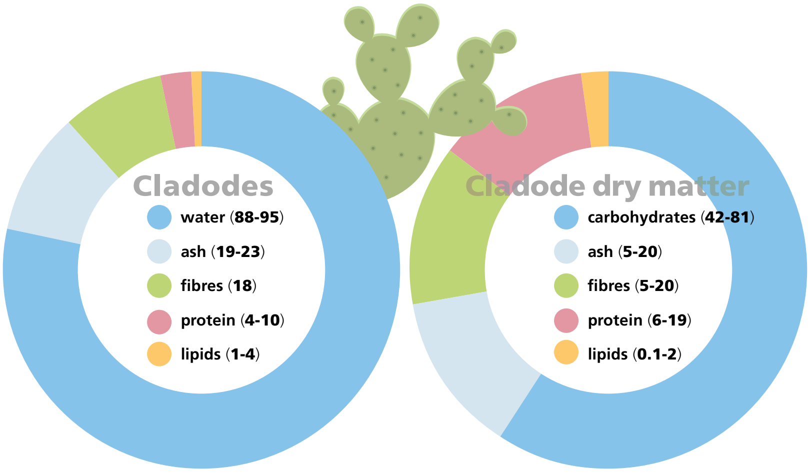


Figure 2
Cladode proximal composition, % (Stintzing and Carle, 2005; Guevara Figueroa et al. 2010)

Figure 3
Main phytochemicals in cactus fruits and cladodes

wild *Opuntia* spp. from Mexico and evaluated the polyphenolic and flavonoid profiles of both fresh and processed nopal products. The presence of five major flavonoids (isoquercitrin, isorhamnetin–3–O–glucoside, nicotiflorin, rutin and narcissin) was observed in all varieties and nicotiflorin was predominant.

Flowers

Cactus flowers accumulate betalains as well as colourless phenolic compounds (Ahmed *et al.*, 2005). The chemical composition of *O. ficus–indica* and *O. stricta* flowers extracted at four–flowering stage was studied by Ammar *et al.* (2012). The antiradical, antibacterial and antifungal activities in ethanol, as well as hexane extracts of flower, were also analysed. Phenolic content varies markedly with flowering stage, and these active constituents are at their peak during post–flowering stage. De Léo *et al.* (2010) reported the chemical profile of methanol extract of *O. ficus–indica* flowers. The volatile fraction of three *Opuntia* species obtained from aqueous distillation was characterized and assayed as antifungal agents (Bergaoui *et al.*, 2007).

MEDICINAL PROPERTIES

Cactus plants were used by ancient civilizations to cure diseases and heal wounds for thousands of years. The origins and history of cactus as medicine are, therefore, closely linked to the ancient Mesoamerican civilizations. For over 12 000 years, fresh cactus has been consumed by the natives for its nutritional qualities and healing properties. Cactus cladodes, fruits, seeds and flowers have been used as folk medicines in several countries for centuries.

There are numerous reports indicating that a diet rich in fruit and vegetables is linked to lower incidence of coronary heart disease and some types of cancer; this suggests that this kind of diet has positive effects on health (Bazzano *et al.*, 2002). These beneficial effects are associated, not only with the nutrient and vitamin content of foods, but with the action of certain bioactive components. Phytochemicals with antioxidant properties promote good health by protecting against the oxidative damage induced by reactive oxygen species (Prakash and Gupta, 2009).

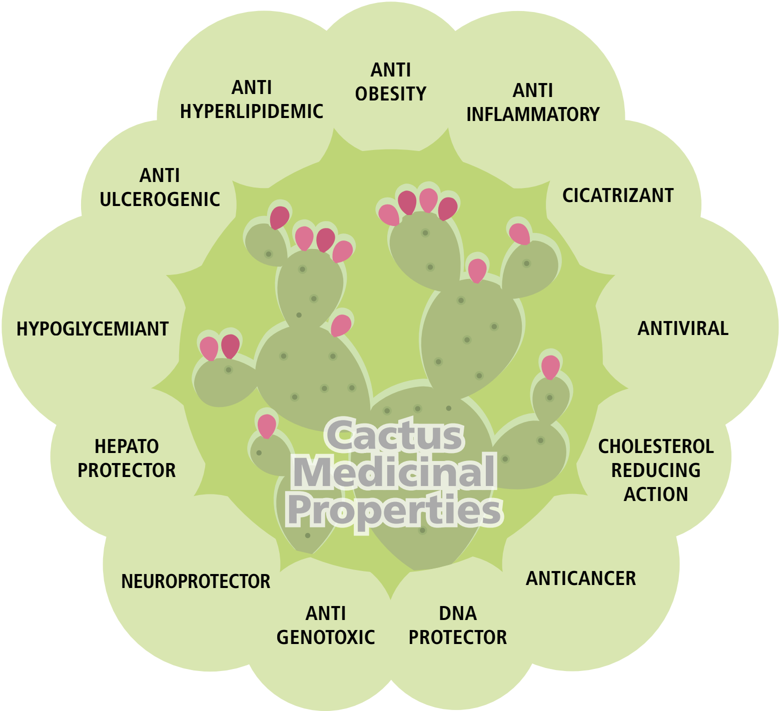
Several studies demonstrate that both cactus fruits and cladodes have high levels of important nutrients, minerals and vitamins, as well as antioxidants. The cactus plant appears to be an excellent source of phytochemicals of nutraceutical importance (El Mostafa *et al.*, 2014). The cactus plant can be fully exploited since its bioactive components can be extracted from its various parts: flowers, fruit, cladodes, roots and seeds (Nazareno, 2014). **Figure 4** summarizes the most relevant medicinal properties ascribed to cactus products.

Fruits

Diet supplementation with cactus pear fruits in a healthy human decreases oxidative stress, by improving the overall antioxidant status. The effect of cactus betalains on oxidative stress in humans was studied by Tesoriere *et al.* (2003, 2004, 2005a), who reported that fruit ingestion produced a decrease in oxidative stress markers, inhibited LDL oxidation and increased resistance to oxidative haemolysis red blood cells in *ex vivo* experiments. Budinsky *et al.* (2001) showed that regular consumption of *O. robusta* reduces oxidation–mediated damage.

Zou *et al.* (2005) studied the ability of cactus pear fruit extract to suppress carcinogenesis in cultured human cancer cell lines *in vitro* and an animal model *in vivo*. The results showed that the cactus extract inhibited the growth *in vitro* of ovarian, bladder and cervical cancer cells and suppressed tumour growth in the animal inoculated with ovarian cancer cells. The antiproliferative effects of betanin on human chronic myeloid leukaemia cell line–K562 were reported by Sreekanth *et al.* (2007). *O. humifusa* fruit extracts were assayed

Figure 4
Medicinal properties of cactus



against breast cancer and glioblastoma human cell lines (Hahm *et al.*, 2010). Emerging studies indicate remarkable anticancer activities displayed by cactus pear extracts. The chemopreventive and anticancer activities of crude extracts from plants belonging to the Cactaceae family, as well as their main active constituents are well reviewed by Harlev *et al.* (2013).

Studies *in vitro* of the interaction between purified betalains and hypochlorous acid and human myeloperoxidase revealed the anti–inflammatory action of these fruit pigments (Allegra *et al.*, 2005). Recently, remarkable anti–inflammatory effects of indicaxanthin were reported in an animal model (Allegra *et al.*, 2014). The anti–ulcerogenic and antigastritis effects of cactus fruits were studied in rats by Lee *et al.* (2001) and Galati *et al.* (2003a). Hepatoprotection of *O. ficus–indica* fruit juice and extract was demonstrated in rats (Galati *et al.*, 2005; Alimi *et al.*, 2012). Kim *et al.* (2006) demonstrated the neuroprotective action of *O. ficus–indica* fruit extracts against neuronal oxidative injuries induced by excitoxins in mice cortical cells. They also reported *in vivo* experiments where methanolic fruit extracts reduced neuronal damage produced by global ischemia in gerbils by 36% and ascribed these effects to bioflavonoid antioxidant action. Wolfram *et al.* (2002) reported that the ingestion of 250g day^{-1} of *O. robusta* fruits produced an anti–hyperlipidemic effect and cholesterol–reducing action in non–diabetic hyperlipidemic humans; there are also reports of the effects on glucose metabolism. The hypocholesterolemic action can be partially explained by the fibre (pectin) content of fruits. Although the hypoglycaemic mechanism is still unclear, investigations indicate that this is because fruits seem to promote – in both diabetics and non–diabetics – a faster and better glucose entry into the cell, and the enhancement of cellular sensitivity to insulin is suspected. Platelet function improvement due to regular consumption of cactus pear (250 g day^{-1}) in healthy volunteers and in patients with mild familial heterozygous hypercholesterolemia was described by Wolfram *et al.* (2003). Fruit ingestion induces beneficial actions on the cardiovascular system by decreasing platelet activity and improving haemostatic balance.

Cladodes

When *O. ficus–indica* cladodes were fed to hypercholesterolemic rats, a marked decrease in cholesterol and triglycerides levels was found in plasma samples. An anti–hyperlipidemic effect and cholesterol reduction were observed in guinea pigs, rats and mice (Galati *et al.*, 2003b; Oh and Lim, 2006). Experiments in diabetes mellitus non–insulin–dependent patients confirmed the hypoglycemic effects of *Opuntia streptacantha* cladodes. Moreover, consumption of young cladodes reduces obesity and blood glucose. The anti–obesity factor, hypoglycemic action and antidiabetic effects were all observed in rats and humans (Bwititi *et al.*, 2000; Frati Munari *et al.*, 2004; Yang *et al.*, 2008).

Galati *et al.* (2001) proposed that *O. ficus–indica* cladodes stimulate a protective response in the gastric mucosa, preventing the development of ethanol–induced ulcers (preventive treatment) and promoting a faster recovery (curative treatment). The cytoprotective effect of *O. ficus–indica* cladodes is ascribed to the physicochemical properties of the mucilage (Galati *et al.*, 2001). *O. ficus–indica* cladodes produce cytoprotection by increasing mucus secretion in the gastric mucosa of rats affected by ethanol–induced ulcers (Galati *et al.*, 2002). Cactus cladode administration is recommended for both preventive and curative treatment of gastric ulcer (Lee *et al.*, 2002a). *Opuntia ficus–indica* plant extract can alleviate alcohol hangover symptoms in humans (Wiese *et al.*, 2004).

Furthermore, the protective effect of *Opuntia ficus–indica* cladode juice against Ni–induced toxicity is reported by Hfaiedh *et al.* (2008). Experimental exposure to Ni was found to generate reactive oxygen species (ROS), leading to increased lipid peroxidation, loss of membrane integrity and alterations of the cellular antioxidant system. There is indication that cladode juice can prevent oxidative stress and decrease the related parameters in rats; in addition, regular ingestion of cladode juice can counteract the peroxidative effects of nickel. Similar protective effects against oxidative damage induced by various toxics are also reported by Ncibi *et al.* (2008) and Zourgui *et al.* (2008). The neuroprotective action against neuronal oxidative injuries of *O. ficus–indica* flavonoids extracts has also been assessed; they were found to be effective in cultured mouse cortical cells and against global ischemia in gerbils (Kim *et al.*, 2006).

Cladode extracts might have a hepatoprotective effect against aflatoxicosis in mice; they probably act by promoting the antioxidant defence systems (Brahmi *et al.*, 2011). Experiments concerning the antiviral action of cactus extracts have been conducted. A cladode extract from *Opuntia streptacantha* was reported to exhibit antiviral properties towards DNA viruses, such as herpes, and ribonucleic acid (RNA) viruses, such as influenza type A and human immunodeficiency virus HIV^{-1}. The active principle was located in the outer non–cuticular tissue and ascribed to a protein with unknown mechanisms of action (Ahmad *et al.*, 1996). Replication of both DNA and RNA viruses was inhibited. An International Patent[1] claims that nopal cactus has an effect against herpes simplex and influenza A viruses. Chlorophyll derivatives are proposed as the active compounds.

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[1] *International Patent (1993): Skinner and Ezra (GB, Israel). Nopal cactus effect on herpes simplex and influenza A viruses.*

TABLE 1 Medicinal properties of cactus products

Cactus species, parts and activities	Studied system and reference
Antiviral action	
O. streptacantha cladode extract	Intracellular virus replication inhibition and extracellular virus inactivation (Ahmad *et al.*, 1996)
Opuntia sp. cladodes	Guinea pigs (Fernández *et al.*, 1994)
Anti–hyperlipidemic effect and cholesterol level reduction	
O. robusta fruits	Non–diabetic hyperlipidemic humans (Wolfram *et al.*, 2002)
O. ficus–indica cladode	Rats (Galati *et al.*, 2003b)
O. ficus–indica seeds and seed oil	Rats (Ennouri *et al.*, 2006a, b, 2007)
O. ficus–indica var. saboten	Mice (Oh and Lim, 2006)
Anti–obesity factor	
Opuntia sp. cladode	Humans (Frati Munari *et al.*, 2004)
O. megacantha	Diabetic rats (Bwititi *et al.*, 2000)
O. lindheimeri	Diabetic pigs (Laurenz *et al.*, 2003)
Hypoglycemic and antidiabetic effects	
O. ficus–indica, *O. lindheimeri* and *O. robusta* fruits	Diabetic rats (Enigbocan *et al.*, 1996)
O. streptacantha	Humans (Meckes Lozyoa, 1986)
O. monacantha cladode extract	Diabetic rats (Yang *et al.*, 2008)
O. ficus–indica seeds and seed oil	Rats (Ennouri *et al.*, 2006a, b)
O. streptacantha	Humans (Frati Munari *et al.*, 1992)
O. filiginosa fruit extract	Rats (Trejo González *et al.*, 1996)
Anti–inflammatory actions	
O. humifusa extracts *O. ficus–indica* indicaxanthin	Nitric oxide–producing macrophage cells (Cho *et al.*, 2006); rat pleurisy (Allegraet*et al.*, 2014)
Healing properties	
O. ficus–indica cladodes	Human (Hegwood, 1990)
Neuroprotection	
O. ficus–indica var. Saboten extract	Primary cultured cortical cells (Dok Go *et al.*, 2003)
O. ficus–indica fruit extracts	In vitro studies in cultured mouse cortical cells e in vivo studies in gerbils (Kim *et al.*, 2006)
Antiulcerogenic effects and antigastritis	
O. ficus–indica cladodes	Rats (Galati *et al.*, 2001, 2002)
O. ficus–indica fruit juice	Rats (Galati *et al.*, 2003a)
O. ficus–indica var. Saboten stems	Rats (Lee *et al.*, 2002a)
O. ficus–indica fruit	Rats (Lee *et al.*, 2001)
Decreasing effect on the oxidative stress in humans	
O. ficus–indica fruits	Humans (Tesorieri *et al.*, 2004); in vitro human LDL (Tesorieri *et al.*, 2003) ex vivo human cells (Tesorieri *et al.*, 2005b)
O. robusta fruits	Humans (Budinsky *et al.*, 2001)
Alcohol hangover symptoms alleviation	
O. ficus–indica plant extract	Humans (Wiese *et al.*, 2004)
Protection upon nickel–induced toxicity	
O. ficus–indica cladode extract	Rats (Hfaiedh *et al.*, 2008)
Protection against oxidative damage induced by zearalenone	
O. ficus–indica cladode	Mice (Zourgui *et al.*, 2008)

(continued)

Cactus species, parts and activities	Studied system and reference
Diuretic effect	
O. ficus–indica cladodes, flowers and non–commerciable fruits	Rats (Galati *et al.*, 2002)
DNA damage reduction	
O. ficus–indica fruit extract	Human peripheral lymphocytes (Siriwardhana *et al.*, 2006)
Cancer preventive properties	
O. ficus–indica fruits aqueous extracts	Ovarian and cervical epithelial cells, as well as ovarian, cervical, and bladder cancer cells (Zou *et al.*, 2005), ovarian cancer cells (Feugang *et al.*, 2010); leukaemia cell lines (Sreekanth *et al.*, 2007)
O. humifusa fruit extracts	Breast cancer and glioblastoma human cell lines (Hahm *et al.*, 2010; Harlev *et al.*, 2013)
Opuntia spp. fruit juice	Prostate, colon, mammary and hepatic cancer cells (Chavez Santoscoy *et al.*, 2009)
Hylocereus spp. extracts	In vitro antiproliferative action (Kim *et al.*, 2011; Wu *et al.*; Jayakumar and Kanthimathi, 2011)
O. humifusa cactus fruit powder	Decreased number of papillomas and epidermal hyperplasia in mice (Lee *et al.*, 2012)
Liver protection	
O. ficus–indica fruit juice and extract	Liver (Galati *et al.*, 2005; Alimi *et al.*, 2012; Brahmi *et al.*, 2011; Ncibi *et al.* 2008)
Anticlastogenic capacity	
Cactus fruit juice	Mice (Madrigal Santillán *et al.*, 2013)
Bone density increase	
O. humifusa freeze–dried cladode	Rats (Kang *et al.*, 2012)
Insulin sensitivity improvement	
O. humifusa freeze–dried cladode	Rats (Kang *et al.*, 2013)

PERSPECTIVES

Cacti can be considered an important source of bioactive substances and excellent candidates for nutraceutical and functional food preparation. Scientific data reveal a high content of some chemical constituents in fruits, cladodes, seeds and flowers, which can add value to cactus products. Additionally, some constituents show promising characteristics as health–promoting substances. Several manufactured products are currently available in the nutraceutical market benefiting from the medicinal properties of cactus plants. Fruits are processed to prepare confectionery, syrups, spreads, jams and jellies. Fruit juice can be used to cure hangovers. Natural cactus pear juice is promoted as a healthy thirst quencher rich in vitamin C, flavonoids and antioxidants, and as an anti–ageing and anti–inflammatory agent. It is also considered to promote optimal cellular health and detoxify the body.

There is scope to further exploit the functional properties of cactus products in the food, cosmetic and pharmaceutical industries, but more scientific research is required in these fields. Although the progress made to date is significant, much remains to be explored. Cactus cladodes have health–promoting properties and they are dehydrated or powdered to prepare nopal pills and capsules. Seed oil, on the other hand, is used in cosmetics. The global growing demand for nutraceuticals and healthy products is accompanied by the development of natural products for the treatment and prevention of human diseases.

More study of cactus species is required to find new active compounds and their pharmaceutical and industrial applications. Moreover, antioxidant formulations must be tested in the search for possible synergistic effects between components. Market demand should be stimulated by publicizing these cactus properties. Although the beneficial properties of cactus have been known since ancient times, only recently have they been scientifically proven.

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Cactus ecosystem goods and services

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Cactus ecosystem goods and services

INTRODUCTION

The Cactaceae family includes about 1 600 species native to America but disseminated worldwide. *Opuntia* is the most widely known genus in this family and *O. ficus–indica* (L.) Mill. is cultivated in more than 20 countries (Nefzaoui *et al.*, 2014). Cacti are cultivated on 2.6 million ha across the world, and mostly used for forage or fodder: in Tunisia (600 000 ha), Mexico (230 000 ha) and Algeria (150 000 ha) (Nefzaoui and Ben Salem, 2006); in South Africa (525 000 ha) and Ethiopia (355 000 ha) (Reveles Hernández *et al.*, 2010); in Brazil (> 600 000 ha) (Torres Sales, 2010); and in southern Morocco (90 000 ha) (Anegay and Boutoba, 2010). In Argentina, the cultivated area of cactus is estimated at 10 000 ha for forage and fruit production, with syrup as a secondary product (Dubeux *et al.*, 2013); the area cultivated with *Opuntia* solely for fruit production was 2 000 ha in 2003 (Ochoa, 2006).

Cold winter temperatures are the principal limitation to cactus cultivation in parts of Argentina and northern Mexico (Borrego Escalante *et al.*, 1990), the Mediterranean Basin (Le Houérou, 1996a), the arid highland steppes of western Asia (Le Houérou, 1996b) and the southwestern United States of America (Parish and Felker, 1997). Under a range of climatic conditions, the thermal limit for frost–sensitive species such as *O. ficus–indica* is indicated by a mean daily minimum temperature in the coldest month of 1.5–2.0 °C (Le Houérou, 1995). Cactus and other drought–tolerant and water–efficient fodder shrubs can survive with as little as 50 mm rainfall in a given year, but with neither growth nor production. Mean annual rainfall of 100–150 mm is the minimum requirement for the successful establishment of rainfed cactus plantations (Le Houérou, 1994), provided soils are sandy and deep (Le Houérou, 1996a). Plantations of drought–tolerant and water–efficient fodder shrubs, especially *Opuntia* species, have been established as buffer feed reserves as a strategy to mitigate the effects of drought in animal production systems in various arid and semi–arid areas of the world (Le Houérou, 1991). Cacti have good water–use efficiency, thanks to the crassulacean acid metabolism (CAM) photosynthetic pathway (Han and Felker, 1997; Nobel, 1991, 1994); for this reason, they are especially suited for forage production in arid land.

Opuntia spp. can withstand prolonged drought, high temperatures, and wind and water erosion. This ability, plus the wide range of economic uses, makes them ideal for agricultural development in areas affected by the world's two biggest environmental problems: desertification and climate change (Nefzaoui and El Mourid, 2008).

"Humble", "aggressive", "gold green", "green jewel", "fruit of the poor", "fruit of thorns and delights", "priceless treasure", "treasure under the thorns", "dromedary of the vegetal world", "plant of the future" and "monstrous tree" are just some of the many epithets used to describe the plant and fruit of cactus pear (*Opuntia* spp.). They reflect what "tuna" means to those who work or live with a plant appreciated and loved by many, but feared and hated by others. In any case, this "humble" plant continues quietly but firmly, to earn a leading place in programmes aimed at the agricultural development of arid and semi–arid areas in many countries.

Cacti, endemic to America, were incorporated into many Native American cultures. For example, the nopal (*Opuntia* spp.) is one of the most important resources in arid and semi–arid areas of Mexico, where it has influenced culture, history and traditions. In the social, economic and religious life of the Aztecs, the plant played a very important role and the symbol of Great Tenochtitlan (now Mexico City) was an eagle on a cactus devouring a snake. This symbol is now incorporated in the Mexican national emblem. Opuntia is also linked with feelings of national unity in Mexico and is frequently associated with the Virgin of Guadalupe and the Indian Saint Juan Diego.

Tuna is now part of the natural environment, and has been integrated into the culture of many countries where it is well adapted to zones characterized by drought, erratic rainfall and poor soils exposed to erosion. It is naturalized in the landscape as part of the local flora, as can be seen in postcards and tourist advertisements in Italy, Spain, Morocco, Israel, Kenya, Yemen and Saudi Arabia. Notably, Lorenzo Bernini (1598–1680) included the cactus in the Fountain of the Four Rivers in Piazza Navona in Rome where the Río de la Plata is represented.

The controversy over whether it is a helpful or harmful plant depends on the species, where, when and how it is grown, and to whom it applies. There are contradictory assessments, true in one case and not in another, based on experiences under different ecological, economic and social conditions. Different situations evolve depending on the individual reality. For example, in Australia and South Africa, biological control was used to stop its expansion and even exterminate it in certain areas. In Ethiopia and Eritrea, on the other hand, where the climate is suitable and no natural enemies exist, nopal effectively invaded thousands of hectares after it was introduced > 150 years ago. In any case, while it may affect local plant genetic resources, the current reality is that after so many years, people have an economic dependency on cactus food and products, regardless of whether the introduction of nopal was a curse or a blessing. Its potential for adaptability and rapid expansion in wilderness areas or in areas previously disturbed by human intervention is another matter requiring examination. Cactus pear is more than useful: it is a vital plant that has been called "a crop that saves lives of humans and animals", especially in times of severe drought (Arias Jimenez, 2013b).

There are numerous reasons behind the diffusion of *Opuntia* spp. around the world, particularly of *O. ficus–indica*, including:

- simple cultivation practices required to grow the crop;
- rapid establishment soon after introduction in a new area;
- easy multiplication practices that favour rapid diffusion and exchange of material among users;
- ability to grow in very harsh conditions characterized by high temperature, lack of water and poor soil;
- generation of income from the sale of much–valued and appreciated fruits;
- use of stems in the human diet and as forage for livestock;
- useful deployment of plants for fencing farms;
- nutritional value of juicy fruits;
- long shelf–life of fruit; and
- production of a wide range of industrial derivatives from fruit.

These and other factors have contributed to such a wide distribution, from the regions of origin in Latin America to remote areas, spanning continents, cultures and traditions.

Main objective of this chapter

Despite its ecological, economic and social importance, *Opuntia* (cactus pear) continues to receive limited scientific, political and media attention. Well–maintained cactus plantations generate positive externalities and environmental goods and services: they can play a major role, not only in terms of biodiversity enhancement and carbon sequestration, but with regard to landscape and nature conservation, mitigation of soil erosion, water protection and cultural heritage. However, these public services do not have a market price, are difficult to disaggregate, are highly interrelated in complex dynamic ways and are difficult to measure. The strong links between cactus pear production and the provision of diverse ecosystem goods and services, especially in marginal areas, need to be considered and integrated into a standard evaluation framework for environmental impacts of agricultural production. **The main objective of this chapter is to highlight the benefits generated from cactus pear.**

RANGELAND IMPROVEMENT

Rangeland improvement using spineless cactus has been practised since the early 1930–1940s, principally in North Africa. Le Houérou (2002) reported that fodder plantations were systematically developed, especially in Tunisia, following the research conducted by Griffiths and collaborators in Texas, United States of America. Griffiths was invited by the Government of Tunisia in 1932 and his 30 years' experience with the use of cactus as fodder has since been applied in central Tunisia to mitigate the effects of drought on livestock. The development of cactus for fodder was strongly supported by the Government. Conditional land allotments were authorized in central Tunisia on condition that the contracting beneficiaries planted 10% of the allocated land with spineless cactus. This was to serve as an emergency standing fodder crop reserve, which would stand as a buffer in times of fodder shortages. This was a strategic move as the country faced 3 years of severe droughts from 1946–1948, during which livestock were decimated by 70–75%. Livestock losses were lower for those who had cactus plantations (Le Houérou, 2002).

The plantation of cactus is applicable in many settings, particularly where the environment is too limited or challenging for traditional agricultural crops or where the land is in need of rehabilitation. Cactus is recommended wherever soils are too shallow, too stony, too steep or too sandy, or when the climate is too dry for practical farming. As a result, they have a key role in rehabilitation strategies to improve rangeland, shrubland, bushland or poor farming areas. For rehabilitation, the planting density is 1 000–2 000 single or double pads per ha, with a spacing of 5–7 m between rows and 1–2 m within rows. Fertilization, pruning and pest/disease treatment are not generally applied, but they can be in order to improve productivity. Occasionally, if the first year is too dry, supplemental irrigation is applied during establishment. Plantations are exploitable after 3–4 years and fully grown after 7–10 years; they can remain productive for > 50 years when managed well. Since *Opuntia* can survive with minimal management, it is recommended in rehabilitation programmes.

Intensive management is not a prerequisite for cactus survival, but a plantation can reach high productivity levels if appropriation practices are applied. The productivity of rangelands planted with cactus can be increased by a factor of 1 to 10 when rangelands are very degraded and by 1 to 5 when rangelands are in good condition (Le Houérou *et al.*, 1991). Nefzaoui and El Mourid (2009) compared the productivity of rangelands in central Tunisia when they were rehabilitated with cactus (*Opuntia ficus–indica*) and fast–growing shrubs (*Acacia cyanophylla*). Rehabilitation with cactus (*O. ficus–indica*) yielded higher productivity rates than rehabilitation with fast–growing shrubs (*A. cyanophylla*) (**Table 1**).

Few plant species are able to increase land productivity at the high rate mentioned above, particularly in the case of marginal lands. Cacti can – because of their rain–use efficiency (RUE). Indeed, degraded Mediterranean rangelands have a RUE of 1–3 kg DM ha^{-1} year^{-1} mm^{-1}, rangelands in good condition exhibit a RUE of 4–6, and degraded rangelands may have a RUE as low as 0.1–0.5 (Le Houérou, 1984). In contrast, rangelands rehabilitated with *Opuntia ficus–indica* exhibit a RUE of 10–20 kg of above–ground DM ha^{-1} year^{-1} mm^{-1} in arid areas with annual rainfall of 200–400 mm.

ALLEVIATION OF SOIL EROSION

Land degradation occurs in all continents and affects the livelihoods of millions of people, including a large proportion of the poor in the drylands (Nefzaoui *et al.*, 2014). Dry zones with annual moisture deficits of > 50% cover approximately 40% of the earth's land surface. More than 70% of all dry areas suffer from desertification, currently accounting for 36 million km^2 (Winckler, 2002). Water and soil are the most precious renewable natural resources. Drought avoidance and coping strategies are imperative: for example, choose drought–tolerant crops, maintain low plant densities, and apply water conservation and water harvesting. However, only a small fraction of rainfall becomes usable soil moisture: 1–10% of the rain that falls in the drylands ends up in the tissue of natural vegetation and crops of economic significance (El Beltagy, 1999). Water erosion is accelerated by tillage on slopes and gully margins. Soil productivity is rapidly declining.

Soils of arid and semi–arid zones are very susceptible to water erosion (Cornelis, 2006), mostly due to the scarce vegetation cover, low organic matter content and poor resistance to erosion forces. The magnitude of water erosion also depends on texture, water content, evaporation, percolation and leaching. These soil characteristics are not favourable to the resistance of soil to water erosion (D'Odorico and Porporato, 2006). In arid and semi–arid areas, soils with little or no vegetation cover are exposed to torrential precipitation events, characterized by short duration and high intensity, and are prone to physical and chemical processes that change the surface layer conditions, such as surface sealing and crusting. When the surface is dry, a hard layer is formed (crust). Crusting soils are typical of dry areas, where soil degradation is induced by diminishing infiltration rates and increasing runoff and erosion rates (Ries and Hirt, 2008). Arid and semi–arid areas are fragile environments where vegetation cover is scarce and soil erosion processes occur rapidly and severely after rainfall events. However, even under such conditions, native vegetation has a very important role in the regulation of surface hydrological processes (Vásquez Méndez *et al.*, 2011).

Erosion control is another important use of cactus pear (*Opuntia* spp.), as it grows quickly and has small roots that regrow each year from the main root during times of rain. In dry periods, the small roots die, add-

TABLE 1 Productivity (forage units per hectare) of natural and improved rangelands in Tunisia (Nefzaoui and El Mourid, 2009)

Rangeland type	Productivity (forage unit per hectare)[a]
Natural rangeland in Dhahar Tataouine, Tunisia (100 mm rainfall)	35–100
Private rangeland improved by cactus crop in Ouled Farhane, Tunisia (250 mm rainfall)	00–1 000
Cooperative rangeland improved through *Acacia cyanophylla*, Guettis, Tunisia (200 mm rainfall)	400–500

[a] One forage unit is equivalent to 1 kg barley grain metabolizable energy.

ing organic matter to the soil. With an increased organic matter content, it is easier for the soil to absorb rainwater. *Opuntia* spp. are utilized in programmes to prevent soil erosion and combat desertification; they are very adaptable, growing in severely degraded soil which is inadequate for other crops, and are ideal for responding to increases in atmospheric carbon dioxide (CO_2) levels. *Opuntia* is also important as cover in arid and semi–arid areas, because it can survive and spread under conditions of scarce and erratic rainfall and high temperatures (Reynolds and Arias, 2001).

Tests involving the planting of cactus for water harvesting strips, contour ridges, gully check structures and biological control of rills and small gullies have had good results. Contour ridges consist of parallel stone ridges built 5–10 m apart to stop runoff water (and the soil it carries) from damaging downstream areas. Each ridge collects runoff from the area immediately upstream/uphill, which is channelled to a small plantation of fodder shrubs or cactus. With a combination of well–designed ridges and cactus, farmers can meet a large proportion of their fodder requirements. In North Africa, particularly Tunisia, cactus is successfully associated with water–harvesting structures. Planted according to contour lines, cactus hedges play a major role in erosion control (**Figure 1**). Soil physical properties and organic matter content are considerably improved under these hedges and in the immediate adjacent areas, with an improvement in organic matter and nitrogen compared with non–treated fields. There have been reports of rates of 40–200% increase in organic matter and nitrogen. Topsoil structural stability is enhanced, sensitivity to surface crusting, runoff and erosion are reduced, and permeability and water storage capability are increased. Marginal lands have been rehabilitated at low cost in Tunisia and Algeria by contour planting of cacti (Nefzaoui *et al.*, 2011).

Figure 1
Management in Tunisia for the protection of watershed

In a comparison of different cultivation systems, such as downhill planting, contour planting, reduced weeding, and intercropping with contour hedges, it was found that soil losses (0.13–0.26 tonnes ha^{-1} year^{-1}) are lowest with contour hedges. Cactus planting in contour hedges may help retain ≤ 100 tonnes of soil ha^{-1} year^{-1}. Experiments conducted in Brazil and Tunisia show clearly that planting cactus in an agroforestry system is more efficient for soil and water conservation than conventional land use (**Table 2**) (Margolis *et al.*, 1985).

The eruption of massive dust storms in the Sahara can move 66–220 million tonnes of fine sediment each year. Wind erosion is a major cause of soil degradation on agricultural land in arid and semi–arid areas throughout the world. Wind damages soil by removing the lighter, more fertile and less

TABLE 2 Comparison of soil loss (tonnes ha^{-1} year^{-1}) under different crops in semi–arid northeast Brazil (Margolis *et al.*, 1985)

Crop type	Soil preparation phase	Cultivation phase	Harvest until next growing season	Total soil losses	C factor
Bare soil	7.19	8.2	13.71	29.1	1
Cotton	2.42	1.77	6.72	10.91	0.392
Maize	1.51	0.68	3.75	5.94	0.199
Maize + beans	1.36	0.55	2.02	3.93	0.119
Opuntia ficus–indica	0.48	0.02	1.48	1.98	0.072
Perennial grass	0	0.02	0.01	0.03	0.001

dense soil components, such as organic matter, clay and silt. Reduced soil productivity is not the only agricultural impact of wind erosion. Blowing sediment cuts and abrades plants, reduces seedling survival and growth, lowers crop yields, and can increase susceptibility to diseases and the spread of plant pathogens (Northcutt, 2001). In arid lands subject to wind erosion, cactus planted alone as a biological barrier or together with physical barriers is an easy, cheap and efficient way to prevent and control topsoil loss, and it facilitates the accumulation of wind–borne deposits.

The somewhat scattered results obtained to date are testimony to the lack of research in this domain. Development actions are mainly based on assumptions and observations gathered by practitioners (Nefzaoui and El Mourid, 2010).

Many Cactaceae species live in arid environments and are extremely drought–tolerant. One survival technique of *O. microdasys* (Lehm.) Pfeiff., which originates in the Chihuahua Desert, lies in its unique and efficient fog collection system, attributed to the integration of its multilevel surface structures (Ju *et al.*, 2012; Bai *et al.*, 2015). This system comprises well–distributed clusters of conical spines and trichomes on the cactus stem; each spine contains three integrated parts, each with a different role in fog collection depending on their surface structural features. The gradient of Laplace pressure, the gradient of surface–free energy and multifunction integration provide efficient fog collection. There is also evidence that some cactus species can harvest dew on their stems and spines (Malik *et al.*, 2015).

Opuntia can tolerate drought in open spaces by increasing and moving chloroplasts and avoiding drastic decreases in their osmotic potential (Delgado Sánchez *et al.*, 2013). *O. ellisiana* Griffiths is a CAM plant, and its conversion efficiency of water to dry matter is several times greater than either C3 or C4 plants. A significant quantity of water (17 mm = 170 000 kg ha^{-1}) can be stored in this cactus and used for animal drinking water (Han and Felker, 1997). Cactus can take advantage of the lightest rainfall, because its roots are close to the soil surface. The water is quickly collected by the roots and stored in thick, expandable stems. The fleshy stems of the barrel cactus (*Ferocactus wislizen*i Britton & Rose) are pleated like an accordion and they shrink as moisture is used up. The green stems produce the plant's food, but they lose less water than leaves do, thanks to their sunken pores and a waxy coating on the surface of the stem. The pores close during the day and open at night and, therefore, only release a small amount of moisture. The price paid by cactus for these water–saving adaptations is slow growth (Zemon, 2015).

There is an urgent need to enhance ongoing research activities with a sound research initiative to investigate all possible benefits and the efficiency of new technologies using cacti as a keystone species to help control desertification and adapt to global warming (Nefzaoui and El Mourid, 2010).

BIOLOGICAL FENCING/VEGETATIVE BARRIERS

Cactus pear can be grown as hedges and fences by planting them around 30 cm apart. Within several years, the plants grow together to form a wall of spiny pads protruding at all angles. Plantings can also be established for erosion control in deforested areas. In time, cacti such as *O. ficus–indica* may grow into freely branching plants 3–6 m high (University of California Cooperative Extension, 1989). The use of various species of cactus for fencing has great benefits which reach well beyond the savings made by not having to use expensive resources such as iron. Once created, a living fence provides fruit and excellent security for crops and homes, while providing home or habitat for wild fauna species. Deer and its main predators can jump over it or crawl through natural tunnels. Also, if given reasonable amounts of water, cactus can grow quickly and – since most farms and homes have water – a fence can be established in as little as 1 year. The closer pads are planted, the quicker the fence fills in, but a difficult pruning job later becomes necessary. Once established, a cactus border provides security, beautiful flowers (bees and other insects are attracted to them) and fruit. Each variety should be sampled for ease of handling and flavour, as some are too seedy. A spiny variety of standard cactus pear *Opuntia* makes a good fence; and spineless varieties will not keep humans away if the lack of spines can be seen from a distance. The bluish *O. violacea* Engelm var. *santa–rita* (Griffiths & Hare) L. D. Benson makes an excellent fence – the fruit is beet red, packed with seeds and has almost no edible pulp; it also has thick spines clustered on the fruit. To make a fence, cut the thickest pads from a plant, allow the scar to heal for about a week and then plant the pads at a 1.3 m spacing. However, if there is little time available, place the pads flat on the ground on the same day and leave for a year or two; they form a cup–shape and retain rainwater. If this latter method is adopted, very thick or woody pads are best (White Dove Farm, 2015).

Thorny cacti *O. ficus–indica* var. *amyclaea* (Ten.) A. Berger and var. *elongata* Shelle are often used as defensive hedges for the protection of gardens, orchards and olive groves throughout North Africa and in parts of Italy and Spain. These hedges demarcate boundaries while helping to control erosion. However, in regions where winters are temperate to mild (mean daily minimum temperature in January > 3° C), the fruits of *Opuntia* hedges may host the fruit fly, *Ceratitis capitata* L. Fruit–bearing cacti may, therefore, need to be treated against fruit fly or eliminated from other fruit crop areas. In the case of fodder cacti, however, if harvested every 2–3 years, they do not produce fruit and cannot, therefore, host fruit fly. Not only do these hedges have a very efficient defensive role (particularly when established in double rows), they also play an important part in landscape organization and the local socio–economy, defining land rights and land ownership in countries or regions where no land registry exists. Cactus hedges are often planted as testimony of land ownership, because in some countries, tradition dictates that tribal land may become the property of whoever among the rightful users has established a permanent crop on it. This is a strong motivation for planting cactus hedges (and olive groves) on communal lands, and explains their popularity in countries such as Tunisia. Cactus hedges also play a major role in erosion control and land–slope partitioning, particularly when established along contours. Soil physical properties and organic matter content are considerably improved under hedges and in the immediately adjacent areas (Monjauze and Le Houérou, 1965b). The aggregates in the topsoil become more stable and less sensitive to surface crusting, runoff and erosion; permeability and water storage capacity increase. Moreover, hedges are a physical obstacle to runoff: they help accumulate temporary local runoff and silting and prevent regressive erosion. Some badlands, developed in outcrops of shale and stony/rocky slopes, have been rehabilitated at low cost in Tunisia and Algeria with contour planting of cacti. In arid lands subject to wind erosion, cactus hedges are an easy, cheap and efficient way to prevent and control topsoil loss and aid accumulation of wind–borne deposits (Le Houérou, 1996a).

The costs of establishing a fence depends on the material used. A metallic fence (four strands of barbed wire) costs about US$1 m^{-1}, i.e. US$150 ha^{-1} in Tunisia for plantations of about 10 ha. A fence made of a double row of spiny cactus costs less than US$60 ha^{-1}, but needs to be established for at least 2 years before it begins to function (Le Houérou, 1989).

CARBON SEQUESTRATION POTENTIAL

Over the last four decades, it has become evident that rising atmospheric CO_2 from fossil fuel consumption is causing increased climate variability. This leads to important issues associated with global warming and modified continental patterns of precipitation that are already having significant effects on species distribution and function in the plant biosphere (Walther *et al.*, 2002; Root *et al.*, 2003). Research has focused on evaluating the potential of biological CO_2 sequestration for various types of plants. In comparison with C_3 and C_4 plants, CAM plants (agaves and cacti) can use water much more efficiently with regard to CO_2 uptake and productivity (Nobel, 2009). Biomass generation per unit of water is on an average 5–10 times greater than in C_4 and C_3 plants (**Table 3**). The potential of CAM systems to accumulate high biomass depends on their capacity to partition more carbohydrates to growth than to nocturnal acid metabolism (Borland and Dodd, 2002).

The role of cactus plantations in the carbon cycle is extremely important. They help complete the cycle of life by recycling building block nutrients to the plants and carbon (CO_2) to the atmosphere (Doran, 2002). This is important in the soil decomposition process and is often mediated by organisms in the soil. Various experiments in different regions have been carried out to quantify the carbon sequestration potential of *Opuntia*. Measurements of gas exchange in *O. ficus–indica* began in the early 1980s, when Nobel and Hartsock (1983) measured CO_2 uptake on single cladodes, using portable infrared gas analysers with cuvettes adapted to fit cladode morphology. At optimal temperature and intercepted radiation, instantaneous values of net CO_2 uptake of 1–year cladodes may reach 18 mmol m^{-2} s^{-1}, with a total daily CO_2 uptake of 680 mmol m^{-2} (Nobel and Bobich, 2002). In a similar study – evaluating the effects of seasonal variations in temperature, irradiation and soil moisture content on the photosynthetic rates of *O. ficus–indica* – the total daily net CO_2 uptake was 393 mmol m^{-2} averaged over five measurement dates, and annual CO_2 uptake was 144 mol m^{-2} (Pimienta Barrios *et al.*, 2000).

Opuntia has greater water–use efficiency than C_4 or C_3 plants due to the CAM photosynthetic pathway, which is more efficient in converting water and CO_2 to plant dry matter (Nobel, 1991, 1994; Han and Felker, 1997; Nobel, 2009). As stated by Nobel (2009), the consequences of nocturnal gas exchange depend on temperature. Temperatures are lower at night, which reduces the internal water vapour concentrations in CAM plants, and results in better water–use efficiency. This is the key reason for which CAM species are the most suited plants for arid and semi–arid habitats. The importance of nocturnal opening and diurnal closure of stomata in CAM species for water conservation has long been recognized (Black and Osmond, 2003). In addition to the advantages of being a CAM species, *Opuntia* plants are also known for their ability to regenerate and grow easily. They act as carbon sinks and can be grown on a large scale in areas where precipitation is inadequate or unreliable. They can grow where evaporation is so great that rainfall is ineffective for crop growth (Osmond *et al.*, 2008). C_3 and C_4 plants suffer irreparable damage once they lose 30% of their water content, while many cacti can survive an 80–90% loss of their hydrated water content and still survive. This is due to the ability of CAM plants to store large quantities of water; to shift water around among cells and keep crucial metabolism active; and to tolerate extreme cellular dehydration (Nobel, 2009). These abilities, in turn, stem from the cactus characteristics: extra thickness of the cuticles providing an efficient barrier for water loss; presence of mucilage; and daytime stomatal closing. In addition, cacti are characterized by asynchronous development of various plant organs, so that even under the worst conditions, some part of the plant remains unaffected. It is well known that cacti grow in the desert where temperatures are extremely high. Many authors (e.g. Nobel, 2009) report that many agaves and cacti can tolerate high temperatures of 60–70° C.

This aspect is covered in detail by Nobel (2009). In view of the specific phenological, physiological and structural adaptations of cacti described above, they may be considered well positioned to cope with future global climate change. Opuntia ficus–indica, for example, can generate a carbon sequestration of 20 tonnes of dry matter (equivalent to 30 tonnes of CO_2) per ha and per year under suboptimal growing conditions similar to those in the arid regions of North Africa.

One *Opuntia* species is known to occupy open and abandoned farmland and to invade open scrubland and forest. This occurs especially in the unpredictable but frequently wet habitats of central eastern Australia that have non–effective rainfall for the growth of agricultural crops (Leeper, 1960; Osmond *et al.*, 1979). The plant has succeeded in its adopted habitat for multiple reasons: in part, because it is a CAM plant with exceptional water–conserving potential; in part, because its extraordinarily low root–to–shoot ratio, dominated by above–ground cladode biomass, can focus on photosynthetic activity; but most of all, because it is characterized by extraordinary vegetative and sexual reproductive activities.

Increased atmospheric CO_2 stimulates further growth and carbon sequestration of *O. ficus–indica* (Gomez Casanovas *et al.*, 2007). Drennan and Nobel (2000) reported that doubling atmospheric CO_2 stimulated the total CO_2 uptake by an average of 31% for six large cacti, and stimulated growth and biomass by 33%. These responses were unexpected because elevated CO_2 was not expected to stimulate CO_2 assimilation in the presence of closed stomata in the light; further, it was expected that CO_2 assimilation in the dark by phosphoenolpyruvate carboxylase would be saturated at internal CO_2. However, these responses are in good agreement with what is now known of the diffusion limitations of CO_2 fixation in all growth states of CAM species (Rascher *et al.*, 2001; Nelson *et al.*, 2005; Griffiths *et al.*, 2007). Wang and Nobel (1996) found that the growth of *O. ficus–indica* in elevated CO_2 for 3 months showed little evidence for downregulation of photosynthesis commonly found in herbaceous plants. Herbaceous plants usually experience sink limitations and feedback effects of sugar on CO_2 assimilation and gene expression. However, in *O. ficus–indica*, higher CO_2 assimilation (source capacity) was found with greater sucrose transport in the phloem and stronger sink strength. Drennan and Nobel (2000) concluded that high–biomass CAM communities offer potential as a low–input system for atmospheric CO_2 sequestration in arid habitats. Although more research is needed, long–lived CAM plants in arid ecosystems may present effective regional carbon sequestration systems on time scales of decades to centuries.

Limited data are available on cladode net CO_2 uptake according to cladode age. Liguori *et al.* (2013a) used an open gas exchange chamber to measure whole plant or single organ net CO_2 uptake in cactus pear, particularly to understand the response of the whole plant to environmental stress. Unlike with single cladode measurements, after 60 days of drought the whole plant maintained the same level of net CO_2 uptake, although there was substantial water loss in the parenchyma of the most photosynthetically active cladodes. Future research on individual cladode CO_2 uptake is required to understand the best pruning practices needed to increase CO_2 uptake, particularly for cultivated fields of *O. ficus–indica*.

ALLEY CROPPING

Expansion of cereal cropping into rangelands, combined with not allowing lands to go fallow, is one of the major reasons for declining soil fertility and wind erosion. One way of combating degradation resulting from cereal monocropping is the introduction of adapted forage legumes, shrubs/fodder trees and cactus in the cropping system (Nefzaoui *et al.*, 2011). Alley cropping is an agroforestry practice where perennial crops are grown simultaneously with an arable crop. Shrubs, trees or cactus are grown in wide rows and the crop is grown in the interspace. Alley cropping is a form of hedgerow intercropping. Leguminous and fast–growing tree/shrub species are preferred because of their soil–improving attributes, i.e. their capacity to recycle nutrients, suppress weeds and control erosion on sloping land. This technology enables the farmer to continue cultivating the land while the trees/shrubs planted in intermittent rows help maintain the quality of the soil. Cactus can function in this system as a windbreak, resulting in improved grass/cereal yields.

The wide alleys allow animals to graze biomass strata or cereal stubble during summer; cactus pads can be harvested, chopped and given directly to grazing animals as an energy supplement to low–quality stubbles (Nefzaoui *et al.*, 2011).

Although cacti are well known as the best plants for reforestation of arid and semi–arid areas because of their resistance to scarce and erratic rainfall and high temperatures, alley–cropping systems in Tunisia are a largely new phenomenon. When properly managed, alley cropping can provide income at different time intervals for different markets in a sustainable, conservation–orientated manner. Alley designs can also optimize the space available between trees, adding protection and diversity to agricultural fields.

The practice of planting only shrubs is not widely adopted for various reasons, including the technical design of the plantation, mismanagement, and competition for land often dedicated to cereal crops. Some of these disadvantages can be overcome by **alley cropping**, which:

- improves soil;
- increases crop yield;
- reduces weeds; and
- improves animal performance.

Properly managed alley cropping allows diversification and the farmer can benefit from several markets. It also promotes sustainability in both crop and livestock production. The benefits of cactus–barley alley cropping were evaluated in Tunisia (Alary *et al.*, 2007; Shideed *et al.*, 2007). Compared with barley alone, the total biomass (straw plus grain) of barley cultivated between rows of spineless cactus increased from 4.24 to 6.65 tonnes ha^{-1}, while the grain yield increased from 0.82 to 2.32 tonnes ha^{-1} (**Table 3, Figure 2**). These figures are the result of the micro–environment created by alley cropping with cactus, which creates a beneficial "windbreak", reducing water loss and increasing soil moisture. The barley crop stimulated an increase in the number of cactus cladodes and fruits, while the cactus increased the amount of root material contributing to the soil organic matter.

Figure 2
Alley cropping using Opuntia ficus–indica and barley crop

BIODIVERSITY CONSERVATION

The intensification of agricultural practices in a context of climate change is cause for concern, as it dramatically alters soil characteristics and affects the local flora and fauna communities (Ouled Belgacem and Louhaichi, 2013). These disturbances affect biodiversity, the most important factor affecting the stability of ecosystems and agro–ecosystems (Fontaine *et al.*, 2011). Stopping or reversing the decline in biodiversity is a major challenge for the maintenance of biodiversity and wider ecosystem services.

TABLE 3 Total biomass changes and barley crop yields (tonnes ha^{-1}) in Sidi Bouzid (Tunisia)[a] (Alary *et al.*, 2007)

Treatment	Natural rangeland	Barley crop (alone)	Cactus crop (alone)	Alley cropping (cactus + barley)
Above–ground biomass (tonnes ha^{-1})	0.51	0.53	1.87	7.11
Underground biomass (tonnes ha^{-1})	0.33	0.11	1.8	1.98
Barley grain yield (tonnes ha^{-1})	1.51	0.82		2.32
Barley grain + straw + weeds (tonnes ha^{-1})	1.36	4.24		6.65

[a] Average rainfall in Sidi Bouzid is 250 mm year^{-1}. All treatments were without fertilizers.

Cactus pears are prominent in many arid and semi–arid habitats. They have an important role in the ecology and are important for the fauna and flora sharing their habitat. Padilla and Pugnaire (2006) report that some plants benefit from closely associated neighbours, a phenomenon known as facilitation. Cacti often act as "nurse plants" in hot climates: their shade, and sometimes nutrients associated with their presence, help seedlings of other species to become established, which they might otherwise not be able to do in hot or poor soil. Cacti can be an attractive source of shelter for wildlife and their shade is very important for animals, as well as for other plant species. Cactus species provide significant nesting sites for birds, rodents and other animals. Birds perch on their branches to examine their surroundings. Bird droppings often contain seeds of other plants and the shade of the cacti can provide a microclimate that promotes other plant life.

Cacti provide fruits and flowers for a range of animals – many species of bird, bat and insect, including bees. Cacti survive in the natural environment without artificial watering and they produce most of their flowers and fruits during the dry season, when very few other resources are available for wildlife; moreover, their flowers attract butterflies and other pollinating insects. Some *Opuntia* species produce juicy fruit in summer, appreciated by many birds. The succulent fruits containing many seeds are particularly attractive to passerine birds; for this reason, it is not uncommon to find plants developing to maturity in rocky outcrops, on wooden fence posts or along wire fence lines. Prickly pear cactus offer good escape cover for birds. For instance, the cactus wren (*Campylorhynchus brunneicapillus* Lafresnaye) is native in the southwestern United States of America and southwards to central Mexico. It is found in deserts and arid foothills characterized by cactus, mesquite, yucca and other types of desert scrub. It nests in cactus plants – sometimes in a hole in a saguaro and or where it is protected by the prickly leaves of a cholla or yucca. Building the nest in cactus provides some protection for the young, but the wrens also use these nests throughout the year to roost. They eat mainly insects, occasionally seeds or fruits, but they rarely drink water, getting moisture from their food.

Hundreds of species of ants use cacti for food and – together with other insects – are important cactus pollinators. While other predators find the spines daunting, ants forage along cactus stems, capturing small fauna and feeding from extra–floral nectaries, which provide a sugar mixture often high in amino acid content. Furthermore, ants and other insects feed on cactus seeds and play a role in seed dispersal. Cacti provide a habitat for many different types of insects. The bee assassin, *Apiomerus crassipes* Fabricius, lies in wait in cactus flowers and preys upon its bee or ant victims by injecting a paralyzing enzyme with its hypodermic–like beak. The cochineal insect, *Dactylopius coccus* Costa, is a cryptic species (a taxon that uses anatomy or behaviour to elude predators) and the females spend their entire lives in colonies on the stems of prickly pear. This insect species is noted for the secretion of carminic acid, used by the ancient Aztecs to produce a crimson dye. Hundreds of butterfly, moth and skipper species are known pollinators of Cactaceae (Hogan, 2015). The flowers contain large amounts of nectar and the fruits are rich in water.

Cacti are also important for many desert animals. Nectar–feeding bats, *Leptonycteris curasoae curasoae* Mill. and *Glossophaga longirostris elongata* Petit and Pors, are valuable for the pollination of many important plants in Curacao, and they depend on columnar cacti for their survival. Their diet consists mainly of cactus nectar, pollen and fruits when available. Larger mammals, such as white–tailed deer (*Odocoileus virginianus* Zimmerman), actually consume the pads of prickly pears, despite the formidable spiny armour (Ramawat, 2010). The cactus pads are filled with water, used by several animals including prikichi (brown–throated parakeet, *Aratinga pertinax* L.) and the white–tailed deer. Coyotes (*Canis latrans* Say) feed in a semi–desert grass shrub habitat and consume a variety of foodstuffs throughout the year. Many cactus species in the Sonoran Desert bear fruit during summer – an important food source in drier months. Coyotes feed on cactus fruits when they are ripe, as shown by the analysis of scats collected in autumn (Short, 1979). In Arizona, packrats, also known as the American rat, live primarily in the desert beneath fallen cactus and debris piles. They burrow under a cactus (usually cactus pear), killing the roots and causing the cactus to collapse over them. This creates a prickly armoured home relatively safe from mammal and bird predators. Some species use the base of a prickly cactus pear as the site for their home, utilizing cactus spines for protection from predators.

Unfortunately, the habitat provided by cactus is not always beneficial or agreeable to humans. As a result, during the summer months many ranchers burn cactus to eliminate them from their fields. While cacti are often considered invasive weeds in much of the southern United States of America, the presence of many *Opuntia* species was actually documented by the first settlers to the area. Also in Mexico, the plant is often regarded as a weed, but it is an important food source in Mexican culture. Cactus pads have recently become a health trend and they are sold as a vegetable in many supermarkets in the United States of America. It is hoped that its use as a food will highlight the importance of the plant; however, many have yet to realize its ecological importance for biodiversity.

CONCLUSION AND RECOMMENDATIONS

Human societies derive many essential goods and services from natural ecosystems. This chapter focuses on the importance of cactus pear and its significant role in the livelihood of farmers. The goods and services provided by cactus pear include: soil and water erosion control; regulation of climate through carbon sequestration; biodiversity conservation; habitat for wildlife; pharmaceutical and industrial benefits – in addition to their aesthetic beauty as evergreen plants. Despite their ecological, economic and social importance, cacti receive limited scientific and media attention and there is insufficient focus on their conservation merits. This is largely due to limited knowledge and a narrow vision focusing on cacti for forage and fruit production. A major shift in the role of cactus and its production is required, towards a much broader concept of ecosystem goods and services. A **holistic approach** is needed, with a balance among environmental conservation, farming system production and socio–economic development. It would be of great benefit to promote the ecological, economic and social benefits of cacti and strengthen the technical capacity of human resources dedicated to these species. In addition to the analysis of current trends in research, it is vital to present new discoveries and plans for future research in all areas concerning cacti. Public policies and credit are essential in order to increase cultivation of this important plant in the arid and semi–arid regions of the world.

15

Global invasions of cacti (*Opuntia* sp.): control, management and conflicts of interest

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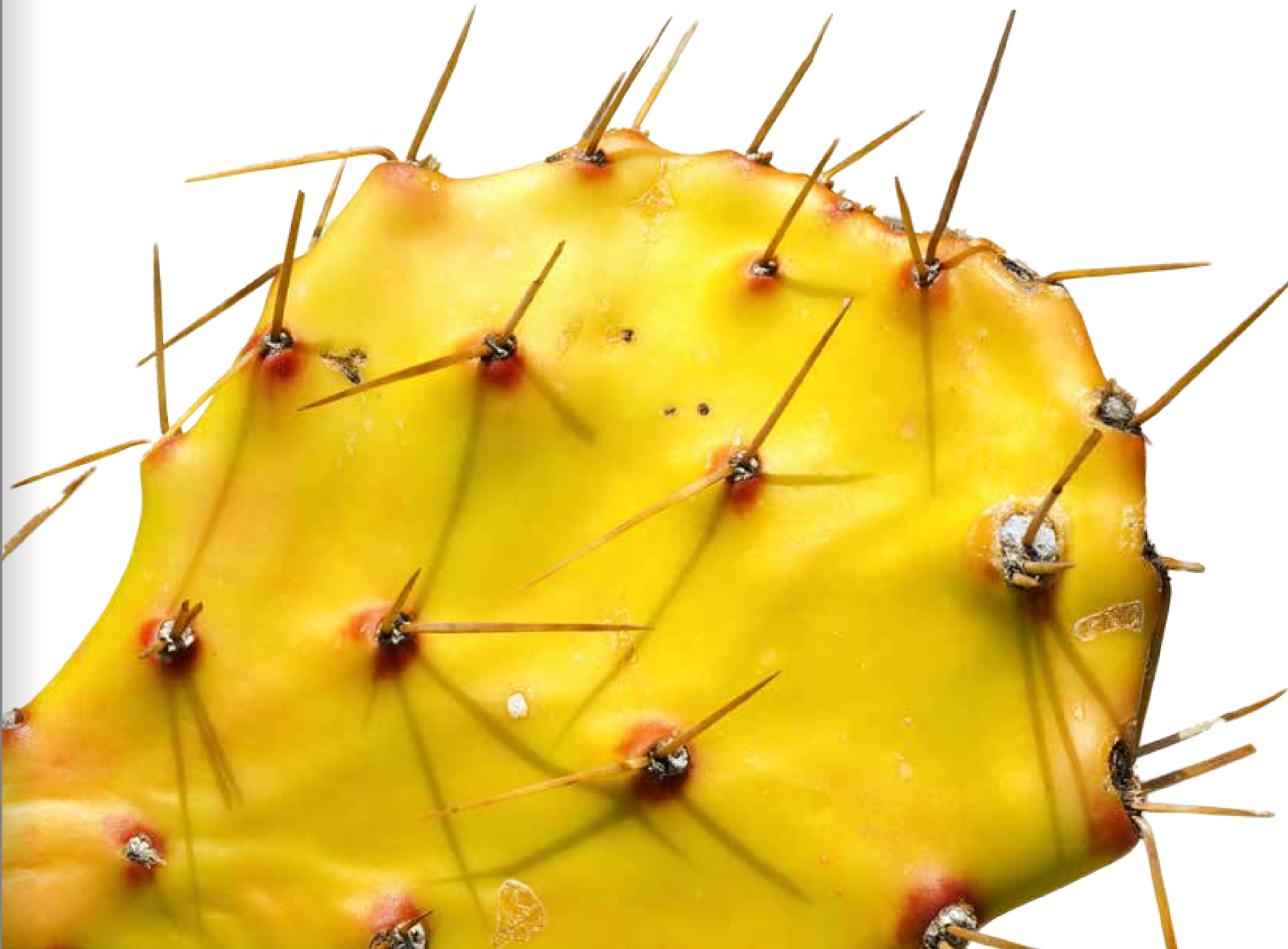

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Global invasions of cacti (*Opuntia* sp.): control, management and conflicts of interest

INTRODUCTION

The value of cactus pear, *Opuntia ficus–indica* (L.) Mill., is indisputable (Barbera *et al.*, eds, 1995; Mondragón Jacobo and Pérez González, 2001; Nobel, ed., 2002; Sáenz *et al.*, eds, 2006) and there have been considerable efforts to introduce this emerging crop to several developing countries with some success (De Waal *et al.*, 2015). The value of cactus pear as a source of fodder has almost surpassed its value as a fruit crop. Nevertheless, several countries – including developing countries in sub–Saharan Africa – have yet to seriously adopt this new crop plant, for example, Botswana, Namibia, Angola, Zimbabwe, Mozambique, the United Republic of Tanzania and Zambia. Cactus pear remains an underutilized, emerging crop with many potential uses. Other recently commercialized cultivated cacti are also gaining in popularity, for example: *Nopalea cochenillifera* (L.) S–D, *O. undulata* Griffiths (Brazil) (Cordeiro dos Santos and Gonzaga de Albuquerque, 2001), *O. monacantha* Haw. (Kaufmann, 2001), *Hylocereus undatus* (Haworth) Britt. & Rose and *Cereus hildmannianus* KSch (= *C. peruvianus*) (Israel) (Nerd *et al.*, 2002). Unfortunately, commercially valuable cactus species (including *O. ficus–indica* and *O. monacantha*) have become invasive in several countries (Novoa *et al.*, 2016), resulting in well–publicized attempts to manage and control them (Kaufmann, 2001; Zimmermann and Moran, 1982).

Over the past 50 years, there has been an increase in the number of invasive species, particularly within the subfamily Opuntioideae, but several new emerging invaders from the Cactoideae and Pereskioideae subfamilies have also become invasive, bringing the total number of reported invasive species to about 57 (Novoa *et al.*, 2016). The number of invasive species in South Africa increased from 13 (all *Opuntiae*) in 1947 to 35 in 2014, including at least eight Cactoideae species. Some invasive *Opuntia* species have required drastic control measures e.g. chemical control, usually followed by biological control when conventional control methods proved unsuccessful (Pettey, 1948; Annecke and Moran, 1978; Moran and Annecke, 1979; Zimmermann and Moran, 1982). The spiny form of *O. ficus–indica*, known as prickly pear, and two newly recorded *Opuntia* invaders, namely *O. robusta* Pf and *O. engelmannii* S–D, are currently being considered, mainly as a source of fodder, partly in order to reduce infestation, but mostly to derive benefits from a large untapped resource (Felker, 1995). In the past there have been conflicts of interest based on true or false perceptions of cactus/prickly pear as invasive or beneficial, resulting in delays in the implementation of biological control programmes. In view of the increased importance of commercially cultivated *Opuntiae*, permission for the release of the relevant biological control agents would not have been granted today, with direct consequences for future projects on biological control of new emerging species in both subfamilies.

This chapter provides a historical overview of cactus invaders in the three subfamilies Opuntioideae, Cactoideae and Pereskioideae – according to the taxonomy of Anderson (2001) and Hunt (2006) – and the control of these invaders, focusing on new approaches to overcome the increasing problem of conflicts of interest. Cactus densifiers, which have become weeds within their native ranges in the Americas, are not included in these discussions.

CACTI AS A PROBLEM

Despite the limited information available, an attempt has been made to identify all the major invasive cactus species, the extent of invasion, their origins, utilization and management (if any). This information is summarized in **Tables 2 and 3**. The perceptions of cultivated and invasive *Opuntiae*, and how these relate to the management of problematic species and the acceptance of cactus pear as a new emerging crop, are also presented. Solutions are then proposed for achieving acceptable management options.

Within the Opuntioideae subfamily, the genera *Cylindropuntia* and *Opuntia* contain most of the invaders outside the Americas; they are confined mainly to Australia and sub–Saharan Africa (**Table 1**).

Within the Opuntioideae, the genus *Opuntia* counts by far the most invaders; they are detailed in **Table 2**. At least 37 countries have actually reported invasive *Opuntiae*, but small invasions are emerging in many more countries, e.g. numerous islands and developing countries in Africa. **Table 3** lists the invasive cacti in the Cactoideae and Pereskioidea subfamilies; compared with Opuntioideae, there are fewer, but the numbers of reported invasive species have nevertheless steadily increased in the past decade. Only eight Cactoideae species were recorded in 1984 (Moran and Zimmermann, 1984b), compared with 18 in 2015. New serious invasions can be expected from this group.

TABLE 1 Invasive cacti by genera in three subfamilies and in countries where serious invasions have been recorded

Genera in Opuntioideae	Countries where invasive	Total no. species in genus	No. invasive species
Austrocylindropuntia	Australia, Kenya, Namibia, South Africa, Spain, Italy, France	11	2
Corynopuntia	Australia	14	1
Cylindropuntia	Australia, Botswana, Israel, Kenya, Namibia, Spain, Zimbabwe	33	8
Opuntia	Angola, Algeria, Australia, Austria, Canary Islands, China, Croatia, Czech Republic, Eritrea, Ethiopia, France, Germany, Ghana, India, Kenya, Madagascar, Mauritius, Morocco, Namibia, New Zealand, Pacific Islands, Portugal, Reunion, Saudi Arabia, Somalia, Spain, Sri Lanka, South Africa, Swaziland, Switzerland, United Republic of Tanzania, Tunisia, Uganda, Yemen, Zimbabwe	181	27
Tephrocactus	Australia, South Africa	6	1
Genera in Cactoideae	**Countries where invasive**	**Total no. species in genus**	**No. invasive species**
Acanthocereus	Australia	6	1
Cereus	Australia, South Africa, Namibia	34	3
Harrisia	Australia, South Africa, Namibia	20	4
Hylocereus	Australia, China, New Zealand, Portugal, Pacific Islands, Spain, South Africa	18	4
Echinopsis	Australia, South Africa	128	3
Myrtillocactus	South Africa	4	1
Peniocereus	South Africa	18	1
Selinicereus	Pacific Islands	28	1
Genera in Pereskioideae	**Countries where invasive**	**Total no. species in genus**	**No. invasive species**
Pereskia	Australia, South Africa	17	1
TOTALS		**518**	**58**

TABLE 2 Major alien Opuntioideae invaders: origin, countries of invasion, utilization, status and management

Species and origin	Countries where introduced and invasive	Utilization	Status as invader	Management	Key references
Genus: *Austrocylindropuntia*					
A. cylindrica (Lam.) Backeb. Ecuador, Peru	Australia	Not utilized	Emerging invader	Chemical control	Chinnock, 2015
	South Africa	Popular garden ornamental			
A. subulata (Muehlenpf.) Peru, Bolivia	Australia Kenya Namibia South Africa Spain	Widely utilized as a living fence	Serious in Kenya Emerging invader in other countries	Chemical control	Chinnock 2015 Walters *et al.*, 2011
Genus: *Opuntia*					
O. aurantiaca Lindl. Argentina, Uruguay	Australia	Not utilized	Serious invader	Fairly good biocontrol	Hosking *et al.*, 1988 Zimmermann and Moran, 1982
	South Africa	Not utilized	Serious invader	Fairly good biocontrol	
	Zimbabwe	Not utilized	Status unknown	None	

(continued)

Species and origin	**Countries where introduced and invasive**	**Utilization**	**Status as invader**	**Management**	**Key references**
O. cordobensis Speg. *(= O. ficus–indica)* Argentina	Hawaii	Not utilized	Insignificant	Good biocontrol	
O. elatior P. Miller Columbia, Venezuela, Panama	Australia Indonesia Kenya	Utilized as a living fence in Kenya	Only problematic in Kenya with increasing populations	Good biocontrol except in Kenya where it is still a weed	Rao *et al*., 1971 Hosking *et al*., 1988
O. elata Link & Otto ex S–D Argentina, Uruguay	Australia	Not utilized	Becoming increasingly invasive in South Africa	Some biocontrol	Walters *et al*., 2011
	South Africa			No control	
O. engelmannii S–D ex Eng. (six varieties recognized) USA, Mexico	Australia Caribbean Indies Ethiopia? South Africa (Varieties *engelmannii* and *lindheimeria* are invasive	Not utilized in countries invaded Utilized in Mexico and Texas as stock feed	Serious invader in some countries	Inadequate biocontrol in South Africa Management in other countries unknown *C. cactorum* having an impact in Caribbean	Moran and Zimmermann, 1984b Winston *et al*., eds, 2014
O. ficus–indica (L.) Mill. (spiny prickly pear variety) Mexico	Hawaii South Africa Australia Ethiopia Eritrea Saudi Arabia Yemen	Extensively utilized in South Africa, Ethiopia, Eritrea Yemen	Perceptions on weediness varies Conflicts of interest prevail	Biocontrol effective in South Africa, Hawaii and Australia only Serious weed in other countries where limited control is done	Zimmermann *et al*., 2009 Haile *et al*., 2002
O. humifusa (Raf.) Raf. Eastern USA	Australia South Africa	Not utilized	Serious invader in South Africa	Biocontrol successful in South Africa	Majure *et al*., 2012b,c Walters *et al*., 2011
O. leucotricha (DC) Mexico	Australia South Africa	Not utilized	Serious invader in South Africa	Biocontrol successful in South Africa	Majure *et al*.., 2012b,c Walters *et al*., 2011
O. microdasys (Lehm.) Pf Mexico	Australia South Africa	Utilized as ornamental only	Becoming increasingly invasive	No control	Smith *et al*., 2011
O. monacantha (Wild.) Haw. Argentina, Uruguay Brazil	Australia India Kenya Sri Lanka Mauritius Madagascar South Africa	Intensively utilized in Madagascar only	Low status after successful biocontrol	Successful biocontrol everywhere	Zimmermann *et al*., 2009
O. robusta Wndl (spiny varieties)	Australia	Utilized as fodder in South Africa	Seriously invasive	Biocontrol partially successful	De Kock and Aucamp, 1970 Walters *et al*., 2011
	South Africa		Spiny form becoming invasive		
O. salmiana (Haw.) Haw. (including *stricta* and *dillenii* subspecies) Mexico, USA, Caribbean	Australia Angola Ghana Kenya Ethiopia Madagascar Namibia India Sri Lanka Saudi Arabia South Africa Yemen	Fruit is consumed fresh by some but is mainly utilized for confectioneries, juice and colourant Cladodes not utilized	Very serious invader in many countries	Biocontrol effective where implemented Other control measures uneconomical	Moran and Zimmermann, 1984b Mann, 1969 Julien and Griffiths, eds, 1998 Zimmermann *et al*., 2009

(continued)

Species and origin	Countries where introduced and invasive	Utilization	Status as invader	Management	Key references
O. streptacantha Lem. Mexico	Australia	Not utilized	Small remnant populations left	Good biocontrol	Mann, 1970
O. tomentos Salm–Dyck Mexico	Australia South Africa	Not utilized	Small remnant populations left	Good biocontrol	Mann, 1970
Genus: *Corynopuntia*					
Corynopuntia sp.	Western Australia	Unknown origin	Emerging weed	Chemical control	Chinnock, 2015
Genus: *Cylindropuntia*					
C. fulgida (Engelm.) F.M. Knuth var. *fulgida* USA, Mexico	South Africa Zimbabwe	Living fences	Serious invader	Good biocontrol	Paterson *et al.*, 2011
C. fulgida var. *mamillata* USA	Australia South Africa Namibia	Popular ornamental	Serious invader	Good biocontrol	Paterson et *al.*, 2011
C. imbricata (Haw.) F.M. Knuth USA, Mexico	Australia Botswana South Africa Zimbabwe Namibia	Not utilized	Serious invader	Moderately good biocontrol	Zimmermann *et al.*, 2009
C. pallida (Rose) F.M. Knuth (= C. *rosea*) Mexico	Australia South Africa	Introduced as ornamental	Serious invader	Chemical control Biocontrol under investigation	Walters *et al.*, 2011 Laguna *et al.*, 2013
	Namibia Spain	Not utilized			
C. kleiniae (DC) Southern USA, northern Mexico	Australia	Not utilized	Emerging invader	Biocontrol	Chinnock, 2015
C. leptocaulis (DC) F.M. Knuth Southern USA, northern Mexico	Australia South Africa	Not utilized	Limited invasions	Good biocontrol	Zimmermann *et al.*, 2009
C. prolifera (Eng.) F.M. Knuth Southern USA, Baja California	Australia	Not utilized	Emerging invader	Unknown	Chinnock, 2015
C. spinosior (Eng.) F.M. Knuth Southern USA	Australia South Africa	Not utilized	Serious invader in Australia only	Chemical control Biocontrol under investigation	Chinnock, 2015
C. tunicata (Leh.) F.M. Knuth Southern USA, northern Mexico	Australia South Africa ?	Not utilized	Emerging invader	Chemical control	Chinnock, 2015
Genus: *Tephrocactus*					
C. articulatus (Pf) Bkbg Argentina	South Africa Namibia	Popular garden ornamental	Emerging invader	Chemical control	Walters *et al.*, 2011

Figure 1
Opuntia engelmannii invasion in South Africa: origin USA

According to Moran and Zimmermann (1984b), 46 cactus weeds were recorded globally in 1983 – amounting to 42 if the latest taxonomic classifications of Hunt (2006) and Anderson (2001) are adopted. In 2014, 57 of the approximate 1 922 recognized cactus species were recorded as invasive (Novoa *et al*., 2014). The figure now stands at 58, but it remains a gross underestimate as only a small number of developing countries have an inventory of invasive cacti. South Africa and Australia are the invasion hotspots with, respectively, 35 and 27 species recorded as invasive (Novoa *et al.*, 2014). Between 1947 and 2014, 24 cactus invaders were listed in South Africa (Pettey, 1948; Anon., 2014). Even the established invaders have drastically expanded their range and are now invasive in many more countries, with serious invasions reported from China, Italy, Spain, Portugal, Saudi Arabia, Ethiopia, Yemen and France (Novoa *et al.*, 2014). Many notorious cactus invaders are cultivated or have been naturalized in Madagascar, but are not yet recognized as invasive (Kull *et al.*, 2012). In 2010, a brief survey of invasive cacti in Namibia revealed 25 species seriously invading, but with no incentives to manage them or prevent new invasions (Zimmermann, 2010). Only two introduced cactus species have been recorded for Angola (Figueiredo and Smith, 2008). In general, cactus invader lists are grossly underestimated on account of poor herbarium specimens and inadequate surveys. It is difficult to prepare good herbarium specimens of succulents; in addition, many samples, including type specimens, become lost due to decay or poor processing (Anderson, 2001; Chinnock, 2015).

Nowadays aggressive cactus invaders are commonplace in private and public rockeries as far afield as Greece, Turkey and Croatia. Easy access to known cactus weeds in nurseries (**Figure 1**) and on the Internet (Humair *et al.*, 2015) will inevitably increase the establishment of, and subsequent invasion by, such weeds. Fortunately, cactus weeds tend to have a long lag period before they are recognized as invaders; this provides opportunities for early detection and rapid response initiatives. An exponential increase in cactus invasions can be expected.

TABLE 3 Major alien Cactoideae and Pereskioideae invaders: origin, countries of invasion, utilization, status and management

Genera, species, origin	Countries where introduced and invasive	Utilization	Status as invader	Management	Key references
Subfamily: Cactoideae					
Genus: *Acanthocereus*					
A. tetragonus (L.) Hmlk Central America	Australia	Ornamental	Not serious and localized	None	Mann, 1970
Genus: *Cereus*					
C. jamacaru (DC) South America	South Africa Namibia	Ornamental	Serious	Biocontrol reasonably effective but slow	Paterson *et al.*, 2011
C. hildemanianus Schum (= *C. uruguayanus*)	South Africa	Ornamental	Not serious	None	Walters *et al.*, 2011
C. hexagonus (L.) Mill. Northern South America	Australia	Ornamental	Not serious	None	Hosking *et al.*, 1988

TABLE 3 (continued) Major alien Cactoideae and Pereskioideae invaders: origin, countries of invasion, utilization, status and management

Genera, species, origin	Countries where introduced and invasive	Utilization	Status as invader	Management	Key references
Genus: *Echinopsis*					
E. oxygona (Link.) Zucc. ex Pf Northwest Argentina	Australia	Ornamental	Not serious	None	Novoa *et al.*, 2014
E. chamaecereus FrdH & Glae	Australia	Ornamental	Not serious		Novoa *et al.*, 2014
E. schickendantzii Weber (*E. spachiana*) Northwest Argentina	South Africa	Ornamental	Serious	Limited chemical control	Walters *et al.*, 2011
Genus: *Harrisia*					
H. balansae (K. Scum) Tayl. & Zappi Argentina	South Africa	Ornamental and hedges	Not serious and very localized	Rapid response programme aimed at eradication	Walters *et al.*, 2011
H. martinii (Lab.) Britt. Argentina	Australia South Africa	Ornamental	Not serious after good biocontrol	Biocontrol with *Hypogeococcus festerianus*	Klein, 1999
H. pomanensis (Web.) Britt. & Rose Chaco of South America	Australia South Africa	Ornamental	Very localized	Rapid response programme in South Africa aimed at eradication	Novoa *et al.*, 2014
Genus: *Hylocereus*					
H. undatus (Haw.) Britt. & Rose Central America	South Africa	Commercial cultivations for fruit	Not serious and localized	None	Walters *et al.*, 2011
H. polyrhizus (Web.) Britt. & Rose	Pacific Islands	Ornamental	Unknown status	None	Novoa *et al.*, 2014
H. costaricensis (Web.) Britt. & Rose	Pacific Islands	Ornamental	Emerging weed	None	Novoa *et al.*, 2014
H. triangularis (L.) Britt. & Rose	Spain	Ornamental	Emerging weed	None	Novoa *et al.*, 2014
Genus: *Myrtillocactus*					
M. geometrizans (Pf) Cons Central America	South Africa	Ornamental	Not serious and very localized	None	Walters *et al.*, 2011
Genus: *Peniocereus*					
P. serpentinus (Lag. & Rodr.) Tayl Mexico	Australia South Africa	Ornamental	Not serious	None	Walters *et al.*, 2011
Genus: *Selenicereus*					
S. macdonaldiae (Hk) Britt. & Rose Honduras	Australia	Ornamental	Not serious	None	Randall, 2002
Subfamily: Pereskioideae					
Genus: *Pereskia*					
P. aculeata Mill.	South Africa Australia	Hedge and fruit was used for confectioneries	Serious in South Africa Localized in Australia	First attempt at biocontrol using two insects Chemical control	Paterson *et al.*, 2011

MANAGEMENT OF INVASIVE OPUNTIOIDEAE SPECIES

Wide–ranging options exist for the **management and control** of invasive Opuntioideae:

- prevention (pre–border control);
- early detection and rapid response;
- risk analysis;
- chemical, biological and mechanical control; and
- utilization.

Control is often hampered by conflicts of interest: a cactus weed may be perceived by some as beneficial, but by others as problematic and necessitating control. This can become the biggest stumbling block in the search for solutions, particularly among Opuntiae and the Hylocereeae and Cereeae tribes.

Figure 2
Opuntia stricta iinvasion in Saudi Arabia: Origin USA

Biological control

The first reports of a deliberately planned and successful biological control project on cactus date back to 1913 when the cochineal, *Dactylopius ceylonicus* (Green), was introduced from India to control *O. monacantha* in South Africa (Lounsbury, 1915; Zimmermann *et al.*, 2009). This success was repeated in Reunion, Mauritius and Australia and it encouraged scientists in Australia to embark on one of history's largest and most dramatic projects of biocontrol of weeds, namely, the successful biocontrol of *O. stricta* (Haw.) Haw. in Queensland and New South Wales in the 1920s and 1930s (Dodd, 1940; Mann, 1970; Zimmermann *et al.*, 2009). Since then, biocontrol has been deployed against 28 other cactus invaders, involving ≥ 22 successfully established cactus–feeding insects and mites (Zimmermann *et al.*, 2009). Almost 42% of these projects have been completely successful; another 18% have achieved substantial control (Zimmermann *et al.*, 2009; Klein, 2011; Hosking, 2012; Winston *et al.*, eds, 2014). Most recently, *Cylindropuntia fulgida* var. fulgida (Eng.) Knuth and *C. fulgida* var. *mamillata* (**Figure 2**) were successfully controlled in South Africa (Paterson *et al.*, 2011).

Table 4 lists the most important cactus invaders that have been subjected to biocontrol. The list does not include species that have become invasive in their native habitats, and it does not include biological control agents that have neither established nor had an impact on their cactus host[1].

TABLE 4 Invasive alien cactus invaders: countries of introduction and outcome of deliberately introduced natural enemies for biological control

Cactus invader	Country where biocontrol was introduced	Utilization	Status as invader
Subfamily: Opuntioideae			
Genus: *Opuntia*			
O. aurantiaca Lindl. (Argentina, Uruguay)	Australia	*Cactoblastis cactorum* (Berg)	Moderate variable
	South Africa		Moderate
	Australia	*Zophodia tapiacola* (Dyar)	Moderate
	Australia	*Dactylopius austrinus* De Lotto	Considerable
	South Africa		Considerable
O. elata Link & Otto ex S–D	Australia	*Dactylopius ceylonicus* (Greeen)	Trivial
O. elatior Mill. (Central America)	Indonesia	*Dactylopius opuntiae* (Cockerell) "*ficus–indica*" biotype	Extensive
	Kenya		?
	India		Extensive

[1] *For a more detailed update of the biological control of cactus invaders, consult Winston et al., eds (2014) or www.ibiocontrol.org/catalog*

(continued)

Cactus invader	Country where biocontrol was introduced	Utilization	Status as invader
O. engelmannii S–D ex Eng. 3 varieties (USA)	South Africa Australia	*Dactylopius opuntiae* (Cockerell) *"ficus–indica"* biotype	Moderate to trivial depending on the variety
	Kenya		Unknown
O. ficus–indica (L.) Mill. (spiny) (Mexico)	Australia	*Dactylopius opuntiae* (Cockerell) *"ficus–indica"* biotype	Moderate
	South Africa		Considerable
	Hawaii		Considerable
	Australia	*Cactoblastis cactorum*	Considerable
	South Africa		Considerable
	Hawaii		Considerable
	Mauritius		Considerable
	South Africa	*Metamasius spinolae* (Gyllenhall)	Considerable (localized)
	Hawaii	*Archlagocheirus funestus* (Thomson)	Considerable
	South Africa		Trivial
O. humifusa (Raf.) Raf. (USA)	South Africa	*Dactylopius opuntiae* (Cockerell) *"stricta"* biotype	Extensive
		Cactoblastis cactorum (Berg)	**Trivial**
O. leucotricha (DC.) (Mexico)	South Africa	*Dactylopius opuntiae* (Cockerell) *"ficus–indica"* biotype	Moderate
		Cactoblastis cactorum (Berg)	**Trivial**
O. monacantha Haw. (South America)	Australia	*Dactylopius ceylonicus* (Green)	Extensive
	India		Extensive
	Kenya		Moderate
	Sri Lanka		Extensive
	Madagascar		Extensive
	Mauritius		Extensive
	Tanzania		Moderate
	South Africa		Extensive
	Ascension Island ?		Moderate
	Mauritius	*Cactoblastis cactorum* (Berg)	Considerable
	South Africa		Trivial
O. robusta (spiny) (USA)	Australia	*Dactylopius opuntiae* (Cockerell) *"ficus–indica"* biotype	Considerable
	South Africa		Moderate
	Australia	*Cactoblastis cactorum* (Berg)	Considerable
	South Africa		Considerable
O. salmiana (Parm.) ex Pf (Argentina)	South Africa	*Cactoblastis cactorum* (Berg)	Trivial
O. stricta[b] (Haw.) Haw. (two varieties) (USA, Mexico)	Australia	*Dactylopius opuntiae* (Cockerell) *"stricta"* biotype	Initially extensive
	India		Extensive
	Kenya		Extensive
	India		Extensive
	Namibia		Moderate
	Saudi Arabia		Probably extensive
	Sri Lanka		Considerable

(continued)

Cactus invader	Country where biocontrol was introduced	Utilization	Status as invader
O. stricta[b] (Haw.) Haw. (two varieties) (USA, Mexico)	Australia	*Cactoblastis cactorum* (Berg)	Extensive
	Kenya		Trivial
	Namibia		Moderate
	New Caledonia		Considerable
	South Africa		Moderate
	Australia	*Moneilema blapsides* Newman	Trivial
O. streptacantha Lem. (Mexico)	Australia	*Dactylopius opuntiae* (Cockerell) "*ficus–indica*" biotype	Considerable
		Cactoblastis cactorum (Berg)	Moderate on young plants
		Archlagocheirus funestus (Thomson)	Trivial
		Moneilema blapsides Newman	Trivial
		Lagocheirus funestus Thomson	Trivial
O. tomentosa S–D. (Mexico)	Australia	*Dactylopius opuntiae* (Cockerell) "*ficus–indica*" biotype	Moderate
	South Africa		Considerable
	Australia	*Cactoblastis cactorum* (Berg)	Trivial
O. tuna[a] (L.) Mill. (Caribbean)	Mauritius	*Dactylopius opuntiae* (Cockerell) "*ficus–indica*" biotype	Initially moderate
		Cactoblastis cactorum (Berg)	Extensive
Genus: *Cylindropuntia*			
C. fulgida (Eng.) Knuth var. *fulgida* (Sonora, Mexico, USA)	South Africa	*Dactylopius tomentosus* (Lamarck) "*cholla*" biotype	Extensive
	Zimbabwe		Extensive
C. fulgida (Eng.) Knuth var. *mamillata* (USA)	Australia	*Dactylopius tomentosus* (Lamarck) "*cholla*" biotype	Good progress
	Namibia		Extensive
	South Africa		Extensive
	Zimbabwe		Extensive
C. imbricata (Haw.) Knuth (Mexico, USA)	Australia	*Dactylopius tomentosus* (Lamarck) "*imbricate*" biotype	Extensive
	Namibia		Considerable
	Botswana		Considerable
	South Africa		Considerable
	South Africa	*Cactoblastis cactorum* (Berg)	Trivial
C. leptocaulis (DC) Knuth (USA)	Australia	*Dactylopius tomentosus* (Lamarck) "*imbricate*" biotype	Considerable
	South Africa		Extensive
C. kleiniei (DC) Knuth (Mexico, USA)	Australia	*Dactylopius tomentosus* (Lamarck) "*imbricate*" biotype	Considerable
C. rosea (DC) Bkbg (Mexico)	Australia	*Dactylopius tomentosus* (Lamarck) "*imbricate*" biotype	Trivial
Subfamily: Cactoideae			
Genus: *Acanthocereus*			
A. *tetragonus* (L.) Hmlk (Argentina)	Australia	*Hypogeococcus festerianus* (Lizer & Trellis)	Moderate
Genus: *Cereus*			
C. jamacaru (DC) (Argentina, Brazil)	South Africa	*Nealcidion cereicola* (Fisher)	Considerable where established
		Hypogeococcus festerianus (Lizer & Trellis)	Considerable

(continued)

Cactus invader	Country where biocontrol was introduced	Utilization	Status as invader
Genus: *Harrisia*			
H. balansae (KSch) Taylor & Zappi (Argentina)	South Africa	*Hypogeococcus festerianus* (Lizer & Trellis)	Considerable
H. martinii (Lab.) Britt. (Argentina)	Australia	*Hypogeococcus festerianus* (Lizer & Trellis)	Considerable
	South Africa		Considerable
	South Africa	*Nealcidion cereicola* (Fisher)	Trivial to moderate
H. pomanensis (Web) Britt. & Rose (Argentina)	South Africa	*Hypogeococcus festerianus* (Lizer & Trellis)	Considerable
H. regelii (Wngt) Borg (Argentina)	Australia	*Hypogeococcus festerianus* (Lizer & Trellis)	Considerable
H. tortuosa (Otto & Dietr.) Britt. & Rose	Australia	*Hypogeococcus festerianus* (Lizer & Trellis)	Considerable
Subfamily: Pereskioideae			
Genus: *Pereskia*			
P. aculeata Mill. (Argentina, Brazil)	South Africa	*Phenrica guerini* Bechyne	Trivial

[a] *O. tuna* is no longer recognized as a species (Hunt et al., 2006).

[b] *O. dillenii* is now regarded as a spiny form of *O. stricta* and is sometimes cited as a subspecies.

Biological control of cactus weeds has generally been easier than of taxa in other plant families. This is due to the absence of native cactaceous species outside the Americas, with the exception of *Rhipsalis baccifera* (Mill.) Stearn, which arrived in South Africa, Madagascar and Sri Lanka probably with migrating birds (Rebman and Pinkava, 2001). This set of circumstances has permitted the safe use of phytophagous insects and mites that are less host–specific. However, as cactus pear (*O. ficus–indica*) is becoming increasingly important worldwide, the choice of biocontrol agents for new cactus weeds is increasingly restricted, particularly in the case of opuntias, as the safety of this new world crop cannot be allowed to be compromised. It is increasingly difficult to find natural enemies outside the Dactylopiidae that are sufficiently host–specific to be considered for biocontrol of *Opuntia* invaders.

More recently, the successful biological control of cactus invaders may be attributed to new association effects (Hokkanen and Pimentel, 1989). This applies primarily to cochineal insects and entails the use of biocontrol agents that do not have a recent history of intensive interaction in evolutionary time with their host. The objective is to take advantage of the lack of evolved commensalism common to many predator–prey systems. Two cochineal biotypes (=genotypes) have recently been identified and evaluated: *Dactylopius opuntiae* (Cockerell) ("*stricta*" biotype) and D. *tomentosa* (Lamarck) ("*cholla*" biotype) (Githure *et al.*, 1999; Volchansky *et al.*, 1999; Mathenge *et al.*, 2009; Jones *et al.*, 2014). They provide excellent control of *O. stricta* var. *stricta* and *C. fulgida* var. *fulgida* and *C. fulgida* var. *mamillata* resp., not only in South Africa but also in Australia, Kenya and Saudi Arabia (Paterson *et al.*, 2011). Further research is focusing on finding new cochineal biotypes for *O. engelmannii*, *O. elata* S–D, *C. pallida* (Rose) Knuth and *C. spinosior* (Eng.) Knuth. The existence of host–adapted biotypes within the mealybug species, *Hypogeococcus festerianus* Granara de Willink, to control invaders in the genera, *Harrisia* and *Cereus*, should not be ruled out. The prospects of biological control of new invaders from the Cactoideae are generally good.

The risks of biological control are minimal. There are no known cases of unpredicted non–target effects of cactus biological control agents. Cactophagous arthropods are known to be host–specific to Cactaceae species; as the family is endemic to the Americas, it is very unlikely that an unpredicted host–switch to another plant family will occur outside its native range. The cactus moth, *Cactoblastis cactorum* (Berg), and the cochineal, *D. opuntiae*, were known to have many hosts within the genus *Opuntia*; it was predicted that both insects would establish on cactus pear and invasive *Opuntiae*. The use of these two insects for biological control was based on calculated risks, given the seriousness of cactus invasions at that time. On the other hand, the deliberate introduction of the cactus moth to some Caribbean islands in 1957 was most unfortunate and ill–conceived (Zimmermann *et al.*, 2001). It was introduced to control the indigenous *O. triacantha* (Willd.) Sw and it was known that the moth would also develop on most other species in the genus *Opuntia* in the West Indies. In time, the moth spread to the American mainland through the nursery trade (Pemberton, 1995), via weather events or by multiple introductions directly from South America (Marsico *et al.*, 2011). It is now threatening native *Opuntia* species in the United States of America and Mexico.

The cochineal, *D. opuntiae*, widely used as a biological control agent outside its native range (United States of America and Mexico), may have been carried as a contaminant on vegetative plant material to several countries, including the Mediterranean region. It has also been introduced inadvertently, mistaking it for the carmine cochineal, *D. coccus.* In addition, since it is wind dispersed, there is also a remote chance that it reached cactus pear plantations through air currents, especially where plantations are close to invasive *Opuntia* populations infested with the insect. This can only occur where *D. opuntiae* is used for biocontrol, for example, in South Africa, India, Sri Lanka, Kenya, Indonesia, Australia, Hawaii and Mauritius. It is vital to ensure that only contaminant–free vegetative material is used for new cactus pear plantings.

Chemical and mechanical control

Mechanical control is seldom a viable option for dealing with cactus invasions, because vegetative reproduction is possible from small fragments that remain after physical clearing. Chemical control is recommended where small and new invasions are to be confined, controlled or even eradicated, but it is seldom viable when large and extended populations need to be controlled. Several chemical campaigns in the history of cactus control have failed owing to the costs involved and the rapid recovery of populations: chemical control is never–ending (Dodd, 1940; Annecke and Moran, 1978; Moran and Annecke, 1979).

The thick protective wax layers and the crassulacean acid metabolism (CAM) photosynthetic pathway (closed stomata during daytime) in most cacti severely restrict the uptake of foliar applied herbicides, unless effective wetting additives are used. Most cactus invaders, however, lend themselves to stem injection treatments with systemic herbicides due to their succulent nature. The advantages are rapid translocation to all parts of the plant, minimal damage to non–target species and low costs. Access to the stems in certain thicket–forming and spiny cacti is a potential problem when using the stem injection method (Grobler, 2005).

Prevention

Research is underway to prevent the introduction and establishment of new cactus invaders. Initiatives include strict pre–and post–border control, risk assessments before species are introduced, and identification and regulation of the potential pathways of introduction (Novoa *et al.*, 2015). Legislation can play an important role in preventing the establishment of new invaders or in controlling invasive cacti. This may include the compilation of lists of prohibitive species and of species with prescriptive control measures. In South Africa, 34 cactus species are listed in several categories of invasive alien plants in terms of the National Environment Management Authority (NEMA) regulations, which make control mandatory (Anon., 2014).

An analysis of the 57 cactus invaders on a global scale shows that species in some genera are more likely to become invasive than species in others. In the genus *Opuntia* alone, 26 species (of a total of 181) are already invasive somewhere in the world. Similarly, in the genus *Harrisia*, five species (of a total of 20) are now invasive. It might, therefore, be justifiable for a particular country to declare an entire genus as unwanted. This approach is already applied in South Africa, where it is prohibited to introduce all new species in the genera *Cylindropuntia*, *Harrisia* and *Opuntia* (Anon., 2014), while those species that are already naturalized (except for the commercially valuable species) are subject to compulsory control (Anon., 2014). With the exception of spineless *O. ficus–indica*, all species in the genera *Opuntia*, *Austrocylindropuntia* and *Cylindropuntia* are declared "weeds of national significance" in Australia (the genus *Corynopuntia* may be added to the list) (Chinnock, 2015). It is highly unlikely that permits will be granted for the introduction of any species in these genera. Other countries may have to consider similar legislation.

There are more than 800 species in the ornamental cactus trade, including 25 known invaders (Novoa *et al.*, 2016). At least 266 of these species are introduced to other countries primarily as seeds. Screening such large numbers of introduced species for prohibited or potentially invasive species is a challenge, especially when they are imported as seeds (Humair *et al.*, 2015), and New Zealand is the only country that screens all incoming postage for seeds. However, a general rule of the thumb is that species with large and heavy seeds are more likely to be invasive than species with small seeds (Novoa *et al.*, 2016) (exceptions are the genera *Echinopsis*, *Cereus* and *Harrisia*). The best option for prohibiting the introduction of harmful species may be a risk assessments at genus level, carried out in consultation with importers and the horticultural cactus trade. One recommendation exists that all genera containing invasive species should be prohibited. For now, South Africa has only prohibited imports of species not already in the country in the genera *Opuntia*, *Cylindropuntia* and *Harrisia* (Anon., 2014). Most cactus species in the ornamental trade belong to genera with no recorded invasive species. To date, no invasive species have been reported in the large genus *Mamillaria*; this very popular group of ornamentals could thus be excluded from regulation.

Other characteristics that can be useful in risk assessments are reproduction strategies and vectors of dispersal.

UTILIZATION AND CONFLICTS OF INTEREST

A culture of utilization of cactus species (mainly *Opuntiae*) has developed over thousands of years, mainly in Mexico and some countries of Central and South America. Over the past 400 years, when a plant has been introduced to another country, the culture of utilization has not always transferred with it. In countries where prickly pear (spiny *O. ficus–indica*) has become invasive, there has been a clear shift from "useful" during establishment to "troublesome" in the subsequent expansion phase until it is eventually perceived as a national disaster. More recently, however, there has been a significant revival in the multiple uses of cactus pear (spineless *O. ficus–indica*), and these can also be applied to prickly pear. There is a wide range of literature on these uses, including many recipes and by–products of "tuna" (fruit) and *nopalitos* (tender cladodes used as a green vegetable) and medicinal applications (De Waal *et al.*, 2015; Sáenz *et al.*, eds, 2006). Use of the vegetative parts of *O. ficus–indica*, *O. robusta* and more recently *N. cochenillifera* as a source of fodder is increasingly practised; in some countries, such as Brazil, it has developed into a substantial industry (Mondragón Jacobo and Pérez González, 2001; Dubeux *et al.*, 2015a). *Opuntia ficus–indica* is also the principal host for the production of the carmine cochineal, *D. coccus* (Costa), which is a major industry in Peru (Flores Flores and Tekelenburg, 1995). There have been considerable efforts to apply these many uses to invasive populations of prickly pear, in an attempt to reverse the status of the invader and turn it into an asset. Utilization alone is not sufficient, however, to curtail the densification and spread of prickly pear in Eritrea, Yemen and Ethiopia, where many thousands of hectares are invaded and expanding.

There is much to be learned from countries where cacti in all three subfamilies have been widely utilized by ancient civilizations for thousands of years, such as Mexico (Hoffmann, 1995; Anderson, 2001). In Mexico, well–known aggressive invaders, for example, *Cyl. imbricata* (Haw) Knuth and *O. engelmannii*, are widely utilized for forage (Benson, 1982; Nobel, 1994).

There were many years of debate and negotiations before it was decided to embark on a biological control programme against prickly pear (*O. ficus–indica*) to halt further invasions in South Africa (Annecke and Moran, 1978). Two natural enemies, the cactus moth (*C. cactorum*) and the cochineal (*D. opuntiae*), were released in 1933 and 1938, respectively. Following successful biocontrol (Pettey, 1948), an effort was made to utilize the small infestations remaining in order to further reduce its status as an invader (Brutsch and Zimmermann, 1993, 1995). Today these remaining infestations are well used, mainly as a source of fruit; control is no longer needed, except in particular situations, such as in conservation areas (Beinart, 2003). In contrast, Ethiopia (Tigray province) and Eritrea have not implemented biocontrol and are unlikely to do so in the future; consequently, dense infestations of > 300 000 ha in Ethiopia alone persist (Behailu and Tegegne, 1997; Haile *et al.*, 2002). Local farmers have become very dependent on prickly pear as there is little natural vegetation left. They are reluctant to destroy even part of the cultivation through biological control, because they fear losing the resource on which they have become dependent. Despite an effort by FAO to promote new uses and to improve the utilization of fruit and fodder, there is no evidence of reduction of the infestations (Portillo, personal communication). In other countries with large invasions, such as Saudi Arabia and Yemen, active utilization programmes have yet to begin and prickly pear populations continue to increase.

Madagascar is a special case: it was not prickly pear (*O. ficus–indica*), rather *O. monacantha* (Raketa), that invaded large parts of south Madagascar. The cactus was intensively utilized – mainly as a source of fodder and fruit – until the local population became fully dependent on it (Middleton, 1999; Kaufmann, 2001). Nevertheless, some locals saw the cactus as a problem (Kaufmann, 2001). Similar large–scale invasions occurred in India, Australia, Mauritius, Sri Lanka and South Africa, but the weed was not actually utilized, except for a brief period in India when it was used to rear the carmine cochineal, *D. coccus* (Zimmermann *et al.*, 2009; Winston *et al.*, eds, 2014). The introduction of the cochineal, *D. ceylonicus*, to Madagascar in 1924 (apparently mistakenly identified as *D. coccus*, with the intention of starting a cochineal industry) resulted in the destruction of practically all cactus populations within 4 years (Middleton, 1999). This led to severe starvation among the local population. According to Middleton (1999), the rehabilitation of the pastures following the demise of the cactus was too slow to be able to support the same level of pastoralism, resulting in the death of thousands of cattle. The conflicts of interest between pastoralists, local communities, authorities and politicians are well documented by Middleton (1999) and Kaufmann (2001, 2004). It seems that the Malagasy people learned to live with this transformer species, involving intense utilization of this foreign new resource (Kull *et al.*, 2012, 2014), in part because they had no other choice. The *O. ficus–indica* invasions in Tigray (Ethiopia) offer parallels.

In South Africa, on the other hand, conflict raged for years over whether to start a biological control programme against *O. ficus–indica* (Beinart, 2003). A project was finally launched in 1932 and biological control reduced infestations by about 80%, leaving enough plants to be widely utilized by the rural population (Annecke and Moran, 1978). The pastoralists were never as dependent on prickly pear as in Madagascar, and the resulting deficiencies were partly made up for by cultivated spineless cactus pear and spineless *O. robusta* – a project initiated by the South African Government to compensate for the loss of cactus fodder and fruit (Beinart, 2003). The resistance to biological control of prickly pear invasions in some countries is understandable; this resistance is exacerbated when the population's dependency on the plant increases, as in Ethiopia, Eritrea and Yemen.

More recently, severe invasions of *O. stricta, O. dillenii* (Ker–Gawler) Haw. (= *O. stricta* var. *dillenii*), *O. elatior* Mill. and *O. engelmannii* are emerging at an alarming rate in Madagascar, Ethiopia, Yemen, Somalia, Angola, Namibia and Kenya. Since most effective biocontrol agents are not species–specific, and due to conflicts of interest (past or present) in some of these countries, there is little chance of implementing biological control on these species. Risk–benefit analysis will eventually show that biological control can be considered part of a management plan, even if it may entail slight damage to cultivated species. Most cactus invasions are already beyond the stage where chemical control can be implemented. In time, the option of biological control will become more compelling until it might eventually become part of a broader integrated management programme.

The "*ficus*" biotype of the cochineal, *D. opuntiae*, has become a pest on cultivated cactus pear, not only where biocontrol was deliberately implemented, but in other countries, such as Brazil, Morocco, Spain, Egypt and Lebanon, where the cochineal was accidentally introduced. Another level of conflict of interest may develop as some countries contemplate the introduction of cochineal predators from Mexico for the biological control of cochineal in cactus pear cultivations. These predators are not host–specific and may control all *Dactylopius* species and biotypes, including those that are vital for the control of several invasive cacti. This may severely reduce the efficacy of biological control. For this reason, South Africa has a moratorium on the importation and release of any predator that may negatively impact on natural enemies of cochineal. Unfortunately, any releases of predators in North Africa will eventually migrate southwards to countries that depend on cochineal for the biological control of invasive cacti.

CONCLUSIONS

Cactus pear is a multipurpose dryland crop destined to become more important as global warming and desertification increase. It offers great potential for developing countries in arid regions. At the same time, however, these countries face the escalating problem of invading cacti. Innovative utilization of these cacti, mainly from the genus *Opuntia*, may be one way to partly alleviate the threat. A more feasible option is to prevent the introduction and establishment of new invaders in the first place. Research is required to find innovative and integrated methods to manage these invasions. It is recommended that research focus on utilizing the large biomasses of many invasive species. In some cases, it may be possible to find new species–specific biocontrol agents, including new cochineal biotypes, which would solve some of the problems (Zimmermann *et al.*, 2009). Invasive experts in South Africa and elsewhere have undertaken valuable research to predict new invaders, particularly from within the succulent nursery trade. Conflict of interest has until now been confined to *Opuntiae*, but new emerging crops in the *Cereus* and *Hylocereus* genera (Nerd *et al.*, 2002), both of which contain invasive species, could cause new conflicts to arise. Natural enemies (e.g. *H. festerianus*) that have been released for the control of invasive *Harrisia* and *Cereus* species in Australia and South Africa are known to have the potential to cause damage to several species in the Cereeae and Trichocereeae tribes (McFadyen, 1979; McFadyen and Tomley, 1981).

Compared with 20 years ago, there are many new invaders in the Cactoideae subfamily, mostly originating from the nursery trade. This trend is likely to continue. Many new cactus invaders lie in waiting, ready to move into the exponential phase of invasion. In Madagascar alone, of 52 cactus species that are cultivated or have become naturalized, only two are currently regarded as invasive (Kull *et al.*, 2012, 2014). Of the remaining 50 species, 24 have been recorded as invasive in other countries (**Tables 2 and 3**), including some of the worst cactus weeds known: *O. aurantiaca*, *O. stricta*, *O. dillenii*, *C. leptocaulis*, *C. tunicata* and *Harrisia* spp.

With the exception of the insect enemies associated with the genus *Harrisia* (McFadyen, 1979) in South America, the cactophagous insects associated with the Cactoideae subfamily have not yet been surveyed extensively, unlike those associated with the genera of the Opuntioideae (Mann, 1969). There are good prospects for finding effective and host–specific natural enemies, should biological control become necessary.

Figure 3
Opuntia ficus–indica invasion in South Africa: Origin Mexico

Figure 4
Opuntia robusta invasions in Australia: origin Mexico

Figure 5
Opuntia humifusa invasion before biological control in South Africa: origin USA.

Figure 6
Opuntia humifusa after biological control in South Africa. Helmuth Zimmermann

Figure 7
Opuntia stricta invasions in Ethiopia

Figure 8
Opuntia aurantiaca invasions in South Africa and Australia: origin Argentina

Figure 9
Excellent biological control of Opuntia stricta in South Africa, Kenya, Saudi Arabia and Australia using a host–specific cochineal, Dactylopius opuntiae "stricta" biotype.

Figure10
Opuntia stricta invasion in the Tsavo National Park, Kenya, before biological control., 2012) (photo A. Witt)

Figure11
The same locality after successful biological control using a host–specific biotype of Dactylopius opuntiae (2015) (Photo A. Witt)

16

Biogas production

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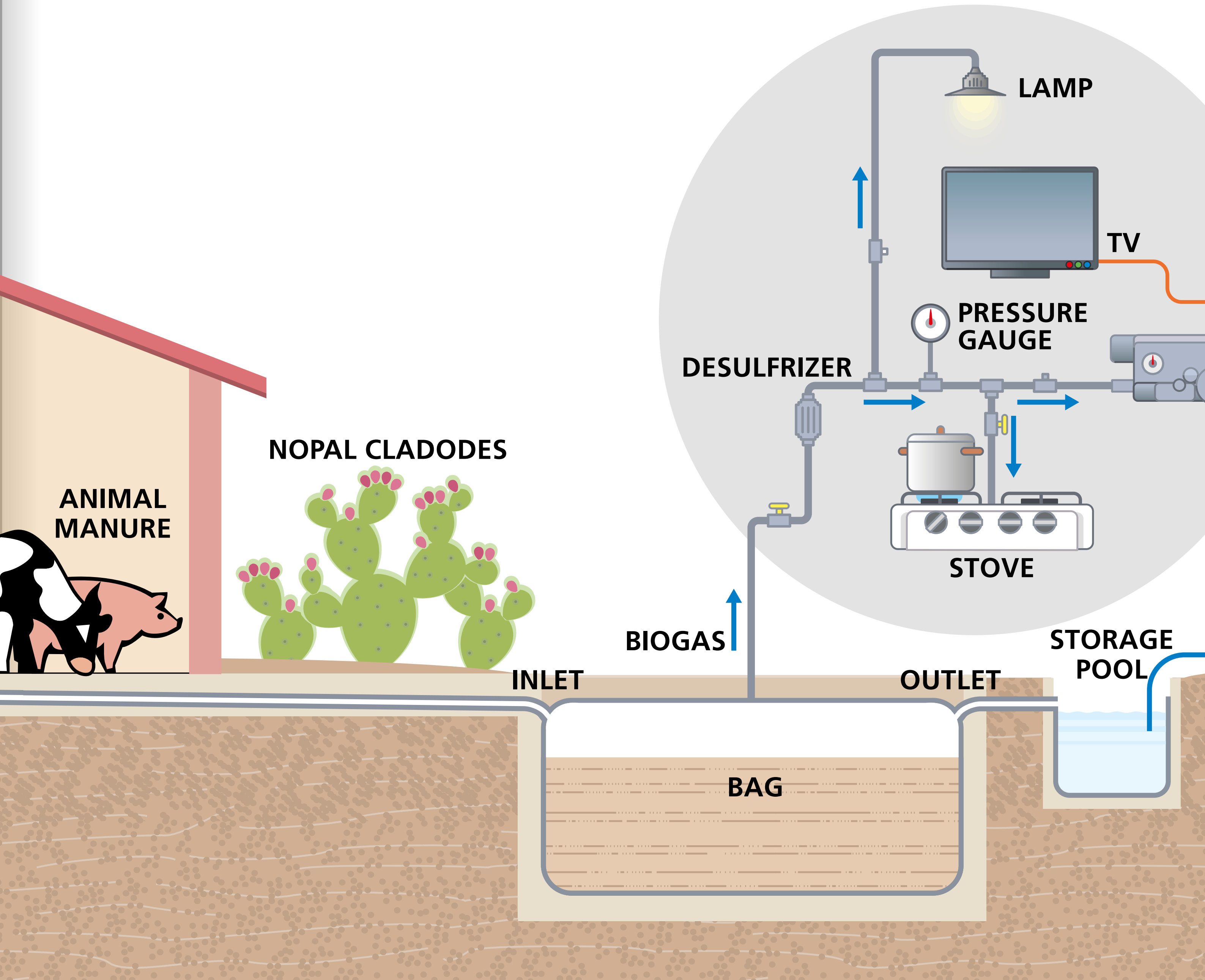


16

Biogas production

INTRODUCTION

Non–conventional renewable energy (NCRE) is increasingly prominent, providing an inexhaustible energy source compatible with human and environmental sustainability. The various forms of NCRE include wind, solar, small hydro, tidal, geothermal and biomass. Biomass uses biological, chemical and physical processes to generate liquid or gaseous biofuels, such as biodiesel, bioethanol and biogas.

Biogas is a viable and essential form of energy in agricultural and rural areas, obtained from the processing of organic waste through anaerobic digestion. In addition to biogas (comprising mainly methane and carbon dioxide, plus other trace gases), the process also produces a stabilized organic waste, digestate (also known as biol or biofertilizer), which can be used as a soil conditioner or biofertilizer (Varnero, 1991, 2001).

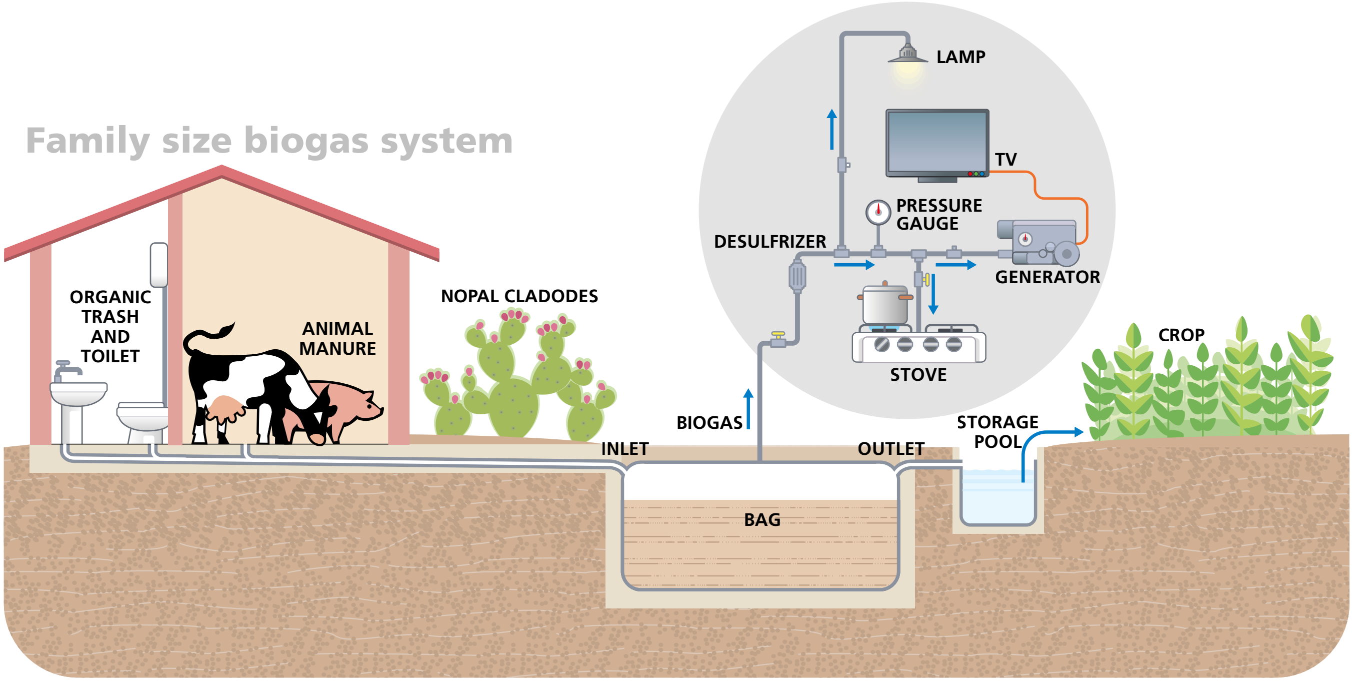
The biodegradation rate of organic residues is related to the microbial activity in the anaerobic system. This activity depends on the type of raw material, the pH of the medium, the total level of solids, the temperature of the process and other parameters that determine the digestion period for the production of biogas and biofertilizer.

USING CACTUS WASTE IN BIOGAS PRODUCTION

Dry climate areas have reduced availability of organic waste – an obvious disadvantage for biogas production. This obstacle can be overcome by developing energy crops well adapted to arid areas. In this context, opuntias – among them, *Opuntia ficus–indica* (L.) Mill. – characterized by crassulacean acid metabolism (CAM), are recommended as an alternative energy source as they have a high potential for biomass production (García de Cortázar and Nobel, 1992; García de Cortázar and Varnero, 1995). Farmers can thus reduce their electricity and gas bills (liquefied petroleum gas, LPG) by producing their own energy, while improving the quality and conditions of the soil by applying the digestate to the fields.

In the Faculty of Agricultural Sciences of the University of Chile, experiments with *Opuntia ficus–indica* (Uribe *et al.*, 1992; Varnero *et al.*, 1992; Varnero and López, 1996; Varnero and García de Cortázar, 1998) indicate that the cladodes are not a good methanogenic material. The quality of the starting material in the digesters, particularly when batch–loaded (Hilbert, 2009), is vital for the process. It is, therefore, necessary to include

Figure 1
Family size biogas system



a particular material derived from another digester and enriched with methanogenic bacteria, or to incorporate a percentage of animal manure. Such adjustments advance the starting time of the methanogenic phase in the digester and increase the production of biogas. Moreover, the pH of the pulp is very low, and this too affects the production of biogas; for this reason it is preferable to mix with other raw materials, mostly animal manure.

The fermentation efficiency of mixtures containing different proportions of cladodes and animal manure showed that it is crucial to maintain the pH of the mixture close to $pH = 6$ in order to obtain biogas with a methane content of > 60%. The composition of the biogas produced by methanogenic fermentation is closely related to the pH of the raw materials biodigested. At $pH < 5.5$, biogas is predominantly carbon dioxide, with reduced combustibility and energy content; conversely, with a neutral or basic pH, the biogas is methane–enriched. It is, therefore, important to increase the proportion of animal manure in the mixture and use cladodes older than 1 year. The particle size of the chopped material has no significant influence on the efficiency of the fermentation process (Varnero and López, 1996; Varnero and García de Cortázar, 1998).

During the anaerobic digestion of animal manure, the addition of cactus cladodes promotes the methanogenic fermentation, provided that the pH of the mixtures of these raw materials remains within a neutral or slightly acidic range. Furthermore, adding an appropriate percentage of cladodes to the animal manure helps the fermentation process start earlier (Uribe *et al.*, 1992; Varnero *et al.*, 1992): the energy and carbon content of the cladodes favours the development of acidogenic bacteria, which generate the substrate required by methanobacteria, thereby accelerating the methanogenic process and reducing the time required for this activity (Varnero and García de Cortázar, 2013).

OPUNTIA SPP. PLANTATIONS FOR BIOGAS PRODUCTION

Opuntias can grow successfully in areas with a range of climates and soils; therefore formal plantations can be established to optimize biomass production. Its economic evaluation is still pending.

Studies have shown that 1 ha of *Opuntia* over 5 years old can produce up to 100 tonnes of fresh cladodes per year in areas with little rainfall (≤ 300 mm) (García de Cortázar and Nobel, 1992). In some semi–arid parts of Mexico, cladodes are traditionally collected from wild cactus plants as a source of forage; regular pruning boosts yield and improves fruit or *nopalitos* quality.

Pruning can yield approximately 10 tonnes of dry matter (DM) ha^{-1} $year^{-1}$, and the prunings can be used for biogas, compost or animal feed (García de Cortázar and Varnero, 1995). Pruning can also provide the raw material to feed digesters, combined with animal manure. Mature cladodes (1 year old) can be cut, chopped and fed directly into the digesters. It is important to use them as soon as they have been chopped, in order to reduce biodegradation and improve the efficiency of biogas and biofertilizer production. If the capacity of the digester is not sufficient for immediate use, the cladodes can be stored in a shaded, cool, dry place for several days (Varnero and García de Cortázar, 2013).

As the plantation matures, the growth of the cladodes slows, because the net photosynthetic

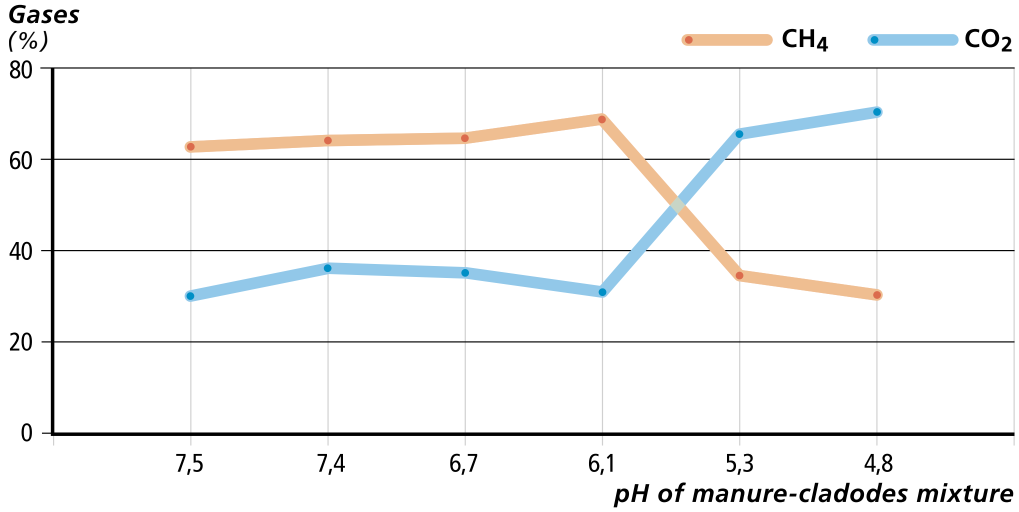


Figure 2
Biogas composition as a function of pH of manure–cladode mixture (Varnero and Arellano, 1991)

rate decreases due to the shading effect of the upper cladodes (Acevedo and Doussoulin, 1984). The dry matter content is not affected, however, as growth continues throughout the year. In Chile, the maximum commercial fresh fruit yield is estimated at 16 tonnes ha^{-1} for plants 16–20 years old under good management. This begins to decline between 21 and 35 years of age, reaching 8 tonnes ha^{-1} (Acevedo and Doussoulin, 1984; Pimienta Barrios, 1990). During the January–April harvest season, yield is 5–16 tonnes ha^{-1}, while and in June–September, it is just 0.5 tonnes ha^{-1} (Sudzuki *et al.*, 1993).

Tohá (1999) indicates that 3 kg of dried cladodes produce 1 m^3 of biogas, which is equivalent to an output of 10 kWh. Moreover, Baeza (1995) indicates that the calorific value of biogas from cactus is 7 058 kcal m^{-3} (range of 6 800–7 200 kcal m^{-3}) and the biogas potential of *Opuntia* is equivalent to 0.360 m3 kg^{-1} DM.

- **Scenario 1: low production.** With a yield of 10 tonnes DM ha^{-1} year^{-1}, the potential biogas production is equivalent to 9.86 m^3 biogas day^{-1} (27.40 kg DM day^{-1}, with a potential estimated 0.36 m^3 biogas kg^{-1} (27.40 × 0.360 = 9.86 m^3 biogas day^{-1}).
- **Scenario 2: intermediate conditions.** Pruning waste production of 18 tonnes ha^{-1} year^{-1} generates 17.75 m^3 biogas day^{-1} and 49.3 kg DM day^{-1}.
- **Scenario 3: optimum production.** A commercial plantation with irrigation and fertilization can produce ≤ 30–40 tonnes DM ha^{-1} (García de Cortázar and Nobel, 1992; Franck, 2006). Production of 30 tonnes year^{-1} is equivalent to 82.2 kg day^{-1}, which can be used as raw material for biogas production with a potential of 29 m3 day^{-1} (82.2 × 0.360 = 29 m^3 biogas day^{-1}), or 10 885 m^3 ha^{-1} year^{-1} biogas – comparable to 6.4 tonnes of oil (Varnero, 1991).

There is a significant difference in biogas production between the best and worst scenario as a result of the constraints involved.

Based on the family biogas system for small operations illustrated in **Figure 1**, organic waste can be collected by connecting the bathroom to the digester, and/or by accumulating kitchen waste. Furthermore, if there are animals (e.g. one cow and two pigs), they too provide organic matter (**Table 2**). This would give a biogas potential of 1.05 m^3, leaving a further 2.6 m^3 to achieve the 3.61 m^3 needed. In order to determine the minimum cactus plantation area required to supply enough raw materials to achieve this amount, it should be considered that a maximum of 3 kg of cactus is necessary to produce 1 m^3 of biogas. The digester must, therefore, be provided with 7.1 kg day^{-1}; this is obtained in an area of 0.28 ha, assuming an availability of 10 tonnes of cladodes ha^{-1} year^{-1}, equivalent to 27.47 kg ha^{-1} day^{-1}.

Practical example

TABLE 1 Average consumption of biogas energy in a family of 5 people

	Average biogas consumption	Cactus biogas consumption
	Calorific value 5 000 kcal m^{-3}	Calorific value 7 058 kcal m^{-3} (75% of CH_4)
Kitchen (5 hours)	0.30 m^3 h^{-1} × 5 h = 1.50 m^3 day^{-1}	0.21 m^3 h^1 × 5 h = 1.05 m3 day^1
3 lamps (3 hours)	0.15 m^3 h^1 × 3 h × 3 = 1.35 m^3 day^{-1}	0.11 m^3 h^1 × 3 h × 3 = 0.99 m^3 day^1
Cooling medium	2.20 m^3 h^1 × 1 = 2.20 m^3 day^1	1.57 m^3 h^{-1} × 1 = 1.57 m^3 day^{-1}
Total	**5.05 m^3 day^{-1}**	**3.61 m^3 day^{-1}**

Source: Baeza, 1995.

TABLE 2 Summary of the calculations

	Quantity (units)	kg unit^{-1}	kg	Potential biogas (m^3 biogas kg^{-1})	Biogas (m^3)
Kitchen waste	5	0.56	2.8	0.092	0.26
Human faeces	5	0.13	0.65	0.092	0.06
Cow manure	1	10	10	0.04	0.40
Pig manure	2	2.8	5.6	0.06	0.336
				subtotal	**1.053**
Cladodes	0.28	27.47[a]	7.7	0.3	2.60
		total	**26.64**		**3.62**

[a] 10 tonnes ha^{-1} year^{-1} (364 days).

On the basis of the biogas production described above, 0.45 m^3 of gas is obtained per m^3 of digester; the minimum size of the digester is, therefore, 8 m^3. In addition, a daily load of 26.24 kg must be incorporated, combined with sufficient water for a solid concentration of 7%: equivalent of 221 litres (also equivalent to the digester's volume, divided by 35 days, i.e. the time required to degrade organic matter). When loading the digester with 221 litres, the same amount of biofertilizer is produced, which can be used for irrigation, fertilization and organic matter input (5.20 g N kg^{-1}, 3.90 g P kg^{-1}, 3.60 g K kg^{-1} and 561 g Mo kg^{-1} DM).

BIODIGESTERS DESIGN AND OPERATION

The biodigester must have certain characteristics:

- Airtight – to prevent both output of undesirable gas and intake of unwanted air.
- Thermally insulated – to avoid major temperature changes.
- Fitted with safety valve.
- Easily accessible – for loading and unloading of the system with raw material, removal of digester scum and maintenance of the digester (Varnero, 1991, 2001).

There is extensive information available in various countries, including India, China and Germany, on the design of biodigesters (García de Cortázar and Varnero, 1995). While most production and use of biogas is obtained from family biodigesters (**Figure 1**), community digesters may also be feasible in some situations, in particular when large amounts of raw material and technological expertise are available.

There are two types of digester: continuous and batch (discontinuous).

- **Continuous.** Material loading is frequent (daily or weekly), each load replacing approximately 5–15% of the total volume. The solids concentration is low (6–8% of the volume), and once the digestion process starts, the biogas production rate is relatively constant (this is mainly dependent on temperature). Continuous digesters are best suited to situations where there is a constant production of material for biodigestion, i.e. if cladodes are collected throughout the year. They are also suited to small properties where household waste can be added as a raw material – for example, incorporating faeces produced by the farm animals or through a connection between the bathroom and digester (Varnero and García de Cortázar, 2006; FAO, 2011). Three models of continuous digester are available:
  - Taiwan type, made of plastic sleeves (polyethylene) (**Figure 4a**);
  - Indian type (**Figure 3a**) – gasometer included in the digester in the form of a floating bell; and
  - Chinese type (**Figure 3b**) – closed, with gas accumulation at the top, while the Indian digester.
- **Batch.** Discontinuous digesters (**Figure 3c**) comprise a sealed battery of tanks or deposits, with a gas outlet connected to a floating gasometer, where the biogas is stored. With multiple digesters, one is always loading or unloading while the others are in biogas production. Feeding or charging the digester with the raw material, which has a higher concentration of solids (40–60%), is done only once, since there is no recharging during the fermentation process. The stabilized organic material is discharged once the biogas production is complete. Biogas production has an initial waiting period, during which fermentative hydrolysis, organic acid formation and methane formation take place. Most of the biogas production then occurs, be-

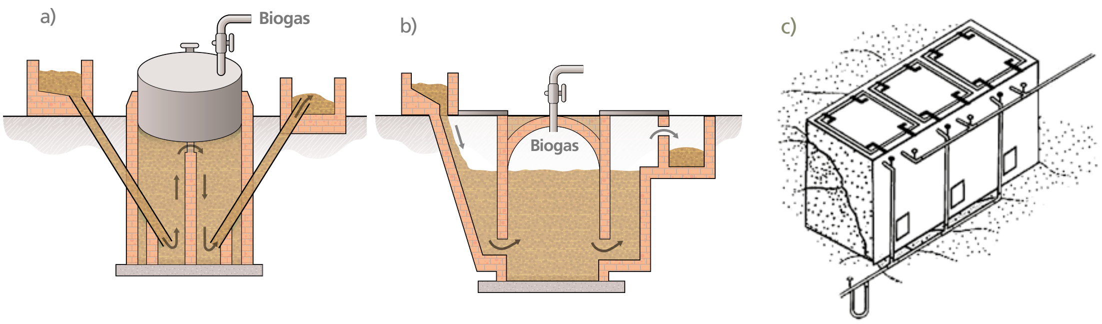


Figure 3
a) Indian digester;
b) Chinese digester;
c) Batch digester

fore slowing down and eventually decreasing to almost zero, as the batch–loaded materials run out. The total duration of the process depends on the temperature. The discontinuous system is suited to certain situations, for example, when: raw materials exhibit handling problems in continuous systems; materials are difficult to digest by methanogenic fermentation; or raw materials are available intermittently. Raw material from the cladode harvest is available once or twice a year (Varnero and García de Cortázar, 2006; FAO, 2011).

Under optimal conditions and for the same volume of dry matter, the two types of digester produce the same amount of biogas. Therefore, the choice should be based on the frequency of waste production (in this case, cladodes) and the availability of water.

For small and medium–sized producers, a wide range of materials may be used for constructing a biogas digester. The most economical continuous types are made from low–cost polyethylene tube (or EPDM, PVC, HDPE) as shown in **Figure 4a**. Known as the Taiwan type, it is widespread in Asia and some Latin American countries. The material costs for this type are US$7 m^{-3}. The Indian or Chinese models can be made with different materials (**Figures 4b–f**).

ECONOMIC ASPECTS

The initial cost of biogas production in rural households is around US$50 per biodigester (Bui Xuan An *et al.*, 1999). This cost is recovered within 9–18 months through savings in fuel costs. In rural areas where the main fuel is wood, the use of biogas reduces ecosystem damage (less deforestation and contamination) and leads to time savings of up to 5 hours a day per household – time which can be used for other more productive tasks (Rutamu, 1999). To calculate the economics of using biogas, it is assumed that one pound (0.45 kg) equals 1 m^3 of biogas; therefore a theoretical calculus of 3.61 m^3 day^{-1} would correspond to 3.61 pounds (1.63 kg) of gas daily, with a value of approximately US$2.98 day^{-1}, or US$1 078 $year^{-1}$.

The residue obtained from digestion processes (**Figure 5b**) has a high nutrient content; it is, therefore, a valuable fertilizer and allows to save on the expense of commercial fertilizers. According to Varnero (1991), 1 tonne of biofertilizer is equivalent to 40 kg of urea, 50 kg of potassium nitrate and 94 kg of triple superphosphate. International fertilizer prices vary from US$255 to US$380 $tonne^{-1}$ (Indexmundi, 2015). Assuming an average price of US$0.32 kg^{-1} of fertilizer, each tonne of biofertilizer saves US$58.8 on fertilizers

Figure 4
Different materials used for the construction of biodigesters:
a) plastic sleeves;
b) brick;
c) concrete;
d) recycled plastic drums;
e) recycled metal drums;
f) prefabricated

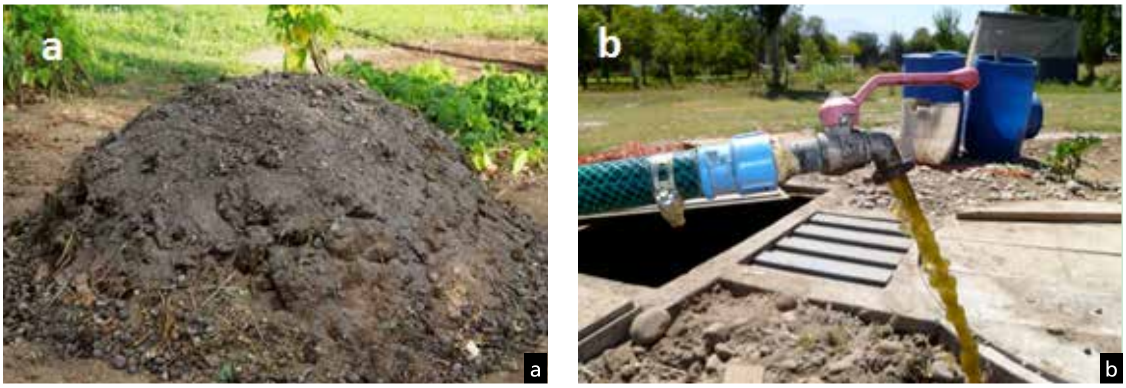


Figure 5
a) Solid digestate;
b) biofertilizer (biol or liquid digestate)

costs; this saving is in addition to the important contribution in terms of microorganisms and organic material, as well as the possibility of obtaining solid materials when emptying the digester (**Figure 5a**).

OTHER BIOENERGY USES

Cactus cladodes have other bioenergy uses, such as biodiesel or ethanol production. With an annual production of 40 tonnes ha^{-1} in crops grown specifically for energy use or 10 tonnes ha^{-1} in pruning waste from fruit plantations, energy can be obtained through direct burning. The cladodes are harvested, sun–dried and crushed, then used in direct burning or cogeneration mix coal–fired; the calorific value is 3 850–4 200 kcal kg^{-1}.

The technology for ethanol production is more complex than that for biogas production; it therefore adapts better to a larger scale, given the high investment costs, and produces concentrations of > 98% ethanol. At fermentation, specific yeast is required to maximize the alcohol production. The ethanol concentration at fermentation is 8–12% (García de Cortázar and Varnero, 1995), attainable only by distillation to achieve the required concentration of ethanol as fuel.

Estimates indicate that cactus mucilage can be used to produce small amounts of ethanol: about 20 ml kg^{-1} of mucilage. On the other hand, 8.6 litres were produced from 100 kg of dried cladodes, and 24.7 litres from 100 kg of dried fruits, and so it is not considered competitive compared with production from fermented fruits. With a density of 635–5 000 plants ha^{-1}, if only the cladodes are used (Retamal *et al.*, 1987), an average of 300–3 000 litres of ethanol can be obtained from non–irrigated and irrigated plantations, respectively.

17

Marketing and communication constraints and strategies

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17

Marketing and communication constraints and strategies

INTRODUCTION

The aim of this chapter is to analyse agribusiness strategies applied to cactus pear and derived products and to examine business issues affecting their development. The records reviewed are from various sources, but are mainly of Mexican, Italian and Chilean origin. However, it should be noted that the product information is scarce, and moreover, it is not up to date, as indicated by Inglese *et al.* (2002a). Consequently, Chile is the main focus of this chapter, and the analysis is supplemented and discussed with literature associated with the major producer countries, Mexico and Italy.

According to the Foundation for Agrarian Innovation (FIA, 2010), many countries throughout the world produce cactus pear, and Mexico is the world's largest producer (currently close to 70 000 ha). Other important cactus–pear–producing countries are Italy, South Africa, Argentina, Chile, Bolivia, Peru, Colombia, United States of America, Morocco, Algeria, Libya, Tunisia, Egypt, Jordan, Pakistan, Israel, Greece, Spain and Portugal. However, in a significant number of these countries, especially in Africa, cactus pear fruits are considered a by–product, as the plant is mainly used for the conservation of degraded soils. There is potential for development of cactus pear through a wide range of applications, including:

- cultivation as forage complement, of which Brazil is the main producer (Callejas *et al.*, 2009);
- consumption as vegetable (cladodes) and fresh fruit;
- medicinal uses;
- industrialization for processed food (e.g. cladode flour, jams and juices);
- non–food industrialization (e.g. bioenergy and cosmetics); and
- carmine production.

Cactus pear also plays an important role in subsistence agriculture in many areas of the world. Whether cultivated on a small scale or in natural stands, cactus pear is a crucial source of food (fruits and its derivatives) for the rural poor, as well as fodder or forage for their livestock. This is the case, not only in North Africa and the Horn of Africa (Eritrea, Ethiopia), but in Mexico, the Near East and the Americas. While it is not possible to give an economic dimension to this phenomenon, northern Tigray (Ethiopia) conveys the importance of cactus pear: natural cactus pear stands give subsistence to an entire population in months or years of food scarcity.

In most producing countries, cactus pear has developed in arid and semi–arid zones (Inglese *et al.*, 1995b; Russell and Felker, 1987b). It is a marginal crop in the fruit market, but in Mexico it produces employment and income in areas where few other crops can be produced (Timpanaro *et al.*, 2015b). The crop is often located in areas of high "rurality", cultivated by small and micro–farmers; this makes it attractive from a strategic point of view and it should be seriously considered in public policy development actions.

Moreover, with regard to sales and marketing, the fresh fruit is marketed mainly in the domestic fresh market with small and isolated incursions into export markets. Italy, the second producer worldwide, is the leading exporter of cactus pear. In the Italian island of Sicily, numerous festivals take place around harvest time (October–November) in villages, including San Cono, Biancavilla, S. Margherita Belice and Roccapalumba (Sáenz *et al.*, eds, 2006).

PRODUCTION AND MARKETING BACKGROUND

Mexico is the largest producer, accounting for about 80% of world production of cactus pear, estimated at about 500 000 tonnes. Italy (12.2%) is the second largest producer, and South Africa (3.7%) ranks third. These three countries account for approximately 96% of world production. Average yields of cactus pear vary enormously: from 6.5 tonnes ha^{-1} (García *et al.*, 2003) in Mexico to 20 tonnes ha^{-1} in Italy and 25 tonnes ha^{-1} in the United States of America and Israel. In Chile, cactus pear is traditionally cultivated between Arica and Parinacota and the Bío–Bío regions; however, more recently it has also been grown between Atacama and Maule, mainly to meet domestic consumption demand. There is a strong concentration of the crop in the central zone of Chile. The area covered by cactus pear in Chile has declined to 800 ha and according to the Office of Agricultural Studies and Policies (ODEPA, 2015a) and Franck (2010), it is concentrated in regions close to large cities, such as Santiago, Viña del Mar and Valparaíso (**Table 1**), and in Atacama and Maule. Sicily accounts for over 96%

of the total Italian cactus pear harvest, with 8 300 ha producing about 87 000 tonnes annually (Timpanaro *et al*., 2015b).

The value addition and creation of derivatives for commercial purposes is minimal. Nevertheless, there has been some important research with the development of agro–industrial products from cactus pear (Sáenz *et al*., eds, 2006). On the other hand, a quite different dynamic is present in Italy with cultivation increasing over the past 20 years. Nevertheless, development is limited for various reasons, including limited supply, lack of coordination throughout the value chain supply and scarcity of resources to boost research, innovation and cultivation techniques (Timpanaro *et al*., 2015b). The average yield of a cactus pear plantation in Chile is around 10 tonnes ha^{-1}. However, with modern cultivation practices, yields could more than double.

The most popular cactus pear ecotype is a local selection with yellow–green flesh (CEZA, 2011). There are, however, other coloured *Opuntia ficus–indica* genotypes with purple, orange, yellow, red and white fruits (Aquino *et al*., 2012). These ecotypes are only produced at experimental level in Chile (Sáenz and Sepúlveda, 2001b). Marketing of cactus pear is atomized at producer level and oligopsonic/oligopolistic at wholesale level; this generates information asymmetries between producers and buyers and increases the market power of buyers, hindering the development of producers in Chile. In many cases, it means producers cannot sell directly or establish business contacts with other buyers. Consequently, producers wait for the same buyers to come every year, bringing their own workers for the harvest. A decade ago, the same situation existed in Italy (Inglese *et al*., 2002a): most of the crop was sold by the farmer in the field, with limited participation of the producer in the value chain. Nowadays, farmers' organizations are more sophisticated; farmers get higher incomes and make a greater impact in the market. One of the most efficient examples is Euroagrumi s.c.c., a consortium operating in Sicily and trading 1 500 tonnes year^{-1} of cactus pears to a value of €2.5 million.

Fruit production is from late July to late November in the Northern Hemisphere, plus a small winter production in Israel in January–March, mostly destined to the home market. Italy concentrates its production in October–November, with > 60% of the market concentrated in Sicily, 15–20% exported within Europe and a very small fraction exported to Canada (Timpanaro *et al*., 2015b). North Africa fails to reach the European markets in early summer (June–July), when no fruits are available in Italy and high temperatures during the summer harvest affect post–harvest management and exports. Mexico produces fruits from June to October, with very modest exports to the United States of America and Canada. In the Southern Hemisphere, Argentina and South Africa produce from January until March and only for local markets. Rarely do they adopt the Italian practice of *scozzolatura* (removal of the first flush of flowers and cladodes) to obtain a second, out–of–season harvest. Chile, on the other hand, produces two crops with no technical help, the second one in June–September. Overall, cactus fruit comes on the market seasonally; however, with better coordination among the producing countries and accurate post–harvest management, cactus fruit could be supplied to markets at almost any time during the year, as is the case with kiwi fruit.

In Chile, the main market for cactus pear is represented by wholesale traders (Lo Valledor and Mapocho Fair), who then sell to retailers. According to Mora *et al.* (2013), wholesalers account for about 60% of cactus fruit sales. Another important outlet, accounting for approximately 18% of produce, are informal shops located on street corners and at traffic lights. Finally, supermarkets account for a mere 2%. Prices have a slightly upwards trend generally. During the year, prices rise when smaller volumes reach the wholesale markets and vice versa. There is also a direct relationship between size and price. It should be noted that during winter (June–September in the Southern Hemisphere), a small quantity of cactus pear tends to reach prices well above the seasonal average (**Figure 1**).

Table 2 shows the unit value per kg of cactus pears for export by air – around US$1.9 in 2011. If export costs (approximately US$0.6 kg^{-1}) are subtracted (free on board, FOB), the unit value is around US$1.3 kg^{-1} (based on the September 2015 exchange rate of 685.6 Chilean pesos = US$1). While this is an attractive figure, it is difficult to bring together large volumes of export quality cactus pears, since only a very small fraction reaches this quality. In contrast, the domestic market pays an equivalent of about US$0.6 kg^{-1}, i.e. almost half the export price.

TABLE 1 Chile: Producer number and cactus pear area

Region/Variety	Number	Total (ha)
Atacama Region		
'Chilena'	2	5.18
Total	**2**	**5.18**
Coquimbo Region		
'Blanca'	1	14.09
'Chilena'	7	69.01
No information	2	2.57
'Til–Til'	1	3.91
Total	**11**	**89.58**
Valparaíso Region		
'Blanca'	3	1.73
'Chilena'	58	65.75
No information	6	6.32
'Til–Til'	2	8.72
Total	**69**	**82.52**
Metropolitana Region		
'Chilena'	22	228.11
'Nopal De Castilla'	4	29.30
No information	6	20.60
'Til–Til'	50	306.22
'Undulatta Griffiths'	1	2.84
Total		**587.07**
L.B. O'Higgins Region		
'Chilena'	1	0.20
No information	1	7.00
'Til–Til'	1	18.00
Total	**3**	**25.20**
Maule Region		
'Chilena'	1	5.00
'Til–Til'	1	5.00
Total	**2**	**10.00**
Total country		**799.55**

Source: ODEPA–CIREN, 2015a, b, c; ODEPA–CIREN, 2014, 2013.

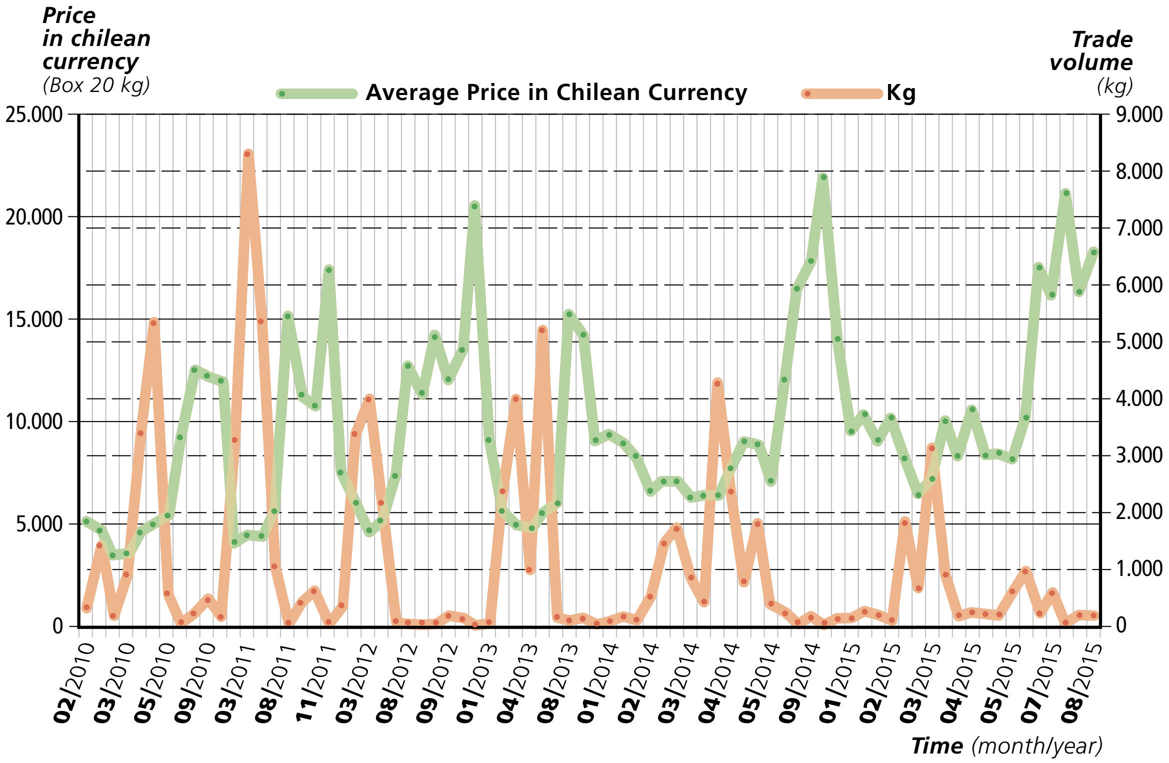

Figure 1
Price and trade of cactus pear (high quality) in principal wholesale markets, Chile
Source: ODEPA (2015b).

TABLE 2 Fresh cactus pear exports by air from Chile

Year	FOB	Volume (kg)	FOB/US$	Country for export and transport type
2002	53 795	23 641	2.3	Canada, USA
2003	37 829	18 766	2.0	Japan, USA
2004	24 252	12 423	2.0	Saudi Arabia, USA
2005	29 497	17 152	1.7	Canada, USA
2006	54 626	17 168	3.2	Saudi Arabia, USA rest
2007	75 963	20 172	3.8	Spain, USA rest
2008	42 173	12 138	3.5	Spain, UK, USA rest
2009	28 779	11 201	2.6	Spain, USA rest
2010	0	0	–	
2011	21 738	11 362	1.9	USA
2012	0	0	–	
2013	0	0	–	
2014	0	0	–	

Source: ODEPA (2015b).

PERCEIVED QUALITY IN CACTUS PEARS: FROM INTRINSIC TO EXTRINSIC ATTRIBUTES

According to Olson and Jacoby (1972), quality attributes may be described as: either extrinsic – related to the product (e.g. price, colour, labelling and packaging); or intrinsic – tied to the physical attributes of the product (e.g. nutrient composition and flavour). As Grunert *et al.* (1996) asserts, quality is a multidimensional phenomenon, described by a set of attributes that are subjectively perceived by consumers before (quality expectation) and after (quality experience) the purchase. Credence attributes, however, increasingly influence consumer preferences in response to rising concerns about safety, health, convenience, locality, ethical factors and the environmental. (Migliore *et al.*, 2012, 2015a; Bernués *et al.*, 2003).

The marketing of cactus pears in Chile and the main producing countries has focused on the fresh fruit, highlighting its essentially intrinsic characteristics. Chile has seen the commercial development of containers, labels, brands or denominations of origin, but none have succeeded as formal commercial agents. In Italy, two protected designation of origin (PDO) labels are active:

- "Ficodindia dell'Etna" refers to production in the area of the Etna volcano, where the white flesh 'Trunzara Bianca' is the most important Italian cultivar, because of its firm flesh and early ripening time in summer (July–August).
- "Ficodindia di San Cono" refers to the most important cactus pear cultivation area in Italy where the three main cultivars grow ('Gialla', 'Rossa' and 'Bianca').

According to FIA (2010), the agro–industrial potential of countries such as Mexico and Italy has enabled the development of a variety of alternatives for the agrifood sector, for example, flour, tortillas, jams, supplements, confectionery, snacks, frozen products and juice. In Italy, however, the sector is limited to some liqueurs and – on a very small scale – jams, while the interest in and commerce of by–products for nutraceutical and medicinal uses is undergoing rapid expansion. Sáenz *et al.*, eds (2006) point out that there are a significant number of products that can be obtained from the various parts of the plant, and even more by exploiting the coloured fruit ecotypes. The fruit can be used to prepare a large number of products, including jams, liqueurs and vinegars, sauces, juice concentrates and canned products. Cladode powders, on the other hand, can be used as functional foods and colouring ingredients, while other encapsulated bioactive compounds act as colouring agents (Sáenz *et al.*, 2009). More specifically, many functional ingredients are characterized by their potential beneficial effects on health, thanks to the fibre, hydrocolloids (mucilage), pigments (betalains and carotenoid), minerals (calcium, potassium) and vitamins (e.g. vitamin C), which are present in the fruit and the cladodes (Piga, 2004; CEZA, 2011).

Most consumers of fresh cactus pear fruit focus on the intrinsic attributes, because there has been practically no development of the extrinsic attributes. Intrinsic signals are related to the physical aspects of a product, such as colour, size, texture, shape and appearance (Mora *et al.*, 2011; Sulé *et al.*, 2002).

Extrinsic signals are related to the product, but are not part of its essence, for example: brand, packaging, seal of quality, price, PDO, shop, sales force and production information. Migliore *et al.* (2015a) report that important attributes of credibility for the Italian market are environmental sustainability, healthiness and Italian origin.

VALUE ATTRIBUTES AND CONSUMER PREFERENCES

In Chile, there are 17 ecotypes of the genus *Opuntia*, probably introduced from Mexico by the Spaniards; the green variety (*Opuntia ficus–indica*) is the most commercialized at present (Sudzuki *et al.*, 1993). In this context, a study of cactus pear preferences developed by our group (Matamala *et al.*, 2015) focused on the study of six ecotypes of different colours, and evaluated intrinsic attributes, such as weight, number of seeds, peel thickness, internal and external colour, and sweetness. According to Mokoboki *et al.* (2009), a weight of around 120 g is a positive attribute on the market. The thickness of the shell and the seeds also have commercial impact (FIA, 2010). Green fruits are preferred by the Chilean population, while yellow cactus pear is the most consumed worldwide and red is the most attractive to first–time consumers (Migliore *et al.*, 2015a).

Matamala *et al.* (2015) identify three preliminary market segments: i) traditional, regular consumption of cactus pear; ii) sporadic, occasional consumption; and iii) skeptical about the characteristics of the product. Esparza (2015), on the other hand, identifies three consumer market segments: i) "practical" (48.8% of the surveyed population); ii) "essential" (18.5%); and iii) "healthy" (13.5%). In general, price was the most important attribute, followed by place of origin and lastly, by the colour of the flesh. There also exists a potential market segment attracted to the purchase of minimally processed cactus pear.

Migliore *et al.* (2015a, b) report similar findings in the Italian market. Inglese *et al.* (1995b) indicate that the challenge for researchers is related to reduced fruit size and the high number of seeds, together with poor promotion and issues of quality standardization. Moreover, there are other attributes related on an emotional level: moods and emotions are factors that constitute the motivational bases of the purchasing process. With regard to cactus pear, Chironi and Ingrassia (2015) report three consumer profiles. The first analyses cactus pear, not only for the qualitative and sensory elements, but also in relation to new hedonistic needs. The second associates the image of the fruit with the territory. The third allows consumers to develop secondary needs, increasing the chances of overcoming the limitations related to this fruit.

PROPOSED COMMERCIAL DEVELOPMENT STRATEGY FOR FRESH CACTUS PEAR AND ITS PRODUCTS

Callejas *et al.* (2009) provide guidelines for a better product in terms of aspects, quality, added value and competitive price.

Price

This variable depends a lot on doing things the right way; however, in a competitive value chain, cactus pear prices are potentially attractive. Increasing competitiveness through improved performance quality (based on a yield of around 12 tonnes ha^{-1}, i.e. 600 boxes – 20% more than current production in a plantation in central Chile) would result in an estimated average price of 6 000 Chilean pesos (US$8.75) per box premium (lowest wholesale price offer is projected). This would generate an income of 3.6 million Chilean pesos (US$5 251) ha^{-1}.

The Italian experience indicates that fruit of the best size (classified as A or AA) may reach prices of €1.5–3.0 at farm level, while smaller sizes show a sharp decrease in price, down to 30–40% for class B fruits and even less for class C fruits. Therefore, only with proper crop management is it possible to reach the best results in the market, by cultivating class A size cactus pear fruits, totally without glochids and defects, harvested at the appropriate ripening stage and with an adequate proportion (55–65%) of flesh (Inglese *et al.*, 2002a).

Product

Quality as perceived by consumers depends mainly on the intrinsic attributes of the fruit. Certain aspects require improvement to achieve, for example, uniform size, thin epidermis and fewer seeds. For fresh cactus pear fruit in Chile, the preference is for green and yellow cultivars. Yellow (Inglese *et al.*, 2002a) and red cactus pears (Migliore *el al.*, 2015a) are the most appreciated in the Italian market. Moreover, there is a growing market space for minimally processed cactus pears, particularly in public catering and in the refrigerated section of supermarkets. Research is required to explore the market potential of other cactus pear derivatives, such as jams, flour, juices, concentrates and functional products. Finally, for a quality product preferred by consumers, innovation of the primary activities in the value chain is required: it is necessary to improve cultivation techniques, with particular attention to organic practices (Timpanaro *et al.*, 2015b; Migliore *et al.*, 2015a).

Promotion and advertising

In general, the cactus pear is a product known and consumed by a specific part of the market. A communications strategy must, therefore, present the intrinsic attributes – functional ingredients with beneficial effects on health, such as fibre, pigments (betalains and carotenoids), minerals (calcium, potassium) and vitamins (e.g. vitamin C) – and make them known to a wider public. Communication actions associated with public policy are essential and are recommended for cactus pear and its derived products.

CONCLUSIONS

Cactus pear producers throughout the world face similar challenges with regard to improving the value chain. The main issues are outlined below:

- Irrigation systems are required at production level, as cactus pear grows in places characterized by water shortages.
- Fruit quality must be improved, with particular attention to the intrinsic attributes associated with homogeneity.
- Marketing strategies are needed. As cactus pear producers are generally small and lack the resources to access modern technologies, it is recommended that they develop associations to improve organization, optimize resources and deal with the significant asymmetries and failures inherent in markets.
- More up–to–date information needs to be made available, especially with regard to markets, costs, prices and quality. Major producing countries could develop a joint project for the generation of a database with standardized information and economic and business updates.
- The social role played by cactus pear in its production areas must be recognized. Public policies should be implemented to help associations improve productive and economic results and to generate innovation throughout the value chain, in both primary and secondary activities. The aim is to improve the level of competitiveness and welfare of the people living in those territories.

- Market research is required to understand the potential interest in products prepared from cactus pear and cladodes. Many interesting attributes could be well received in the market. Quality assurance systems must be installed for processed products, as they are essential tools for dealers selling such products.
- Development of the **intrinsic attributes** of cactus pear is at the centre of any marketing strategy:
  - Improve current systems of production (productivity and quality).
  - Carry out economic and technical feasibility studies to assess the production and trade potential of both domestic and international markets.
  - Explore consumer receptivity for new products developed by research centres (mainly agro–industrial), bring them to prototype stage and continue testing and market validation.
  - Communicate the intrinsic attributes that create value but which the average consumer is not aware of.
  - Explore new commercialization channels, such as speciality shops, catering businesses, pharmaceutical companies and the Internet.
  - Continue research to decrease the number of seeds.
  - Develop minimally processed cactus pears.
  - Elaborate and communicate credence attributes with labelling of food safety, quality, nutritional and environmental aspects.
- Development of the **extrinsic attributes** (packaging and labelling) is also essential for added value.

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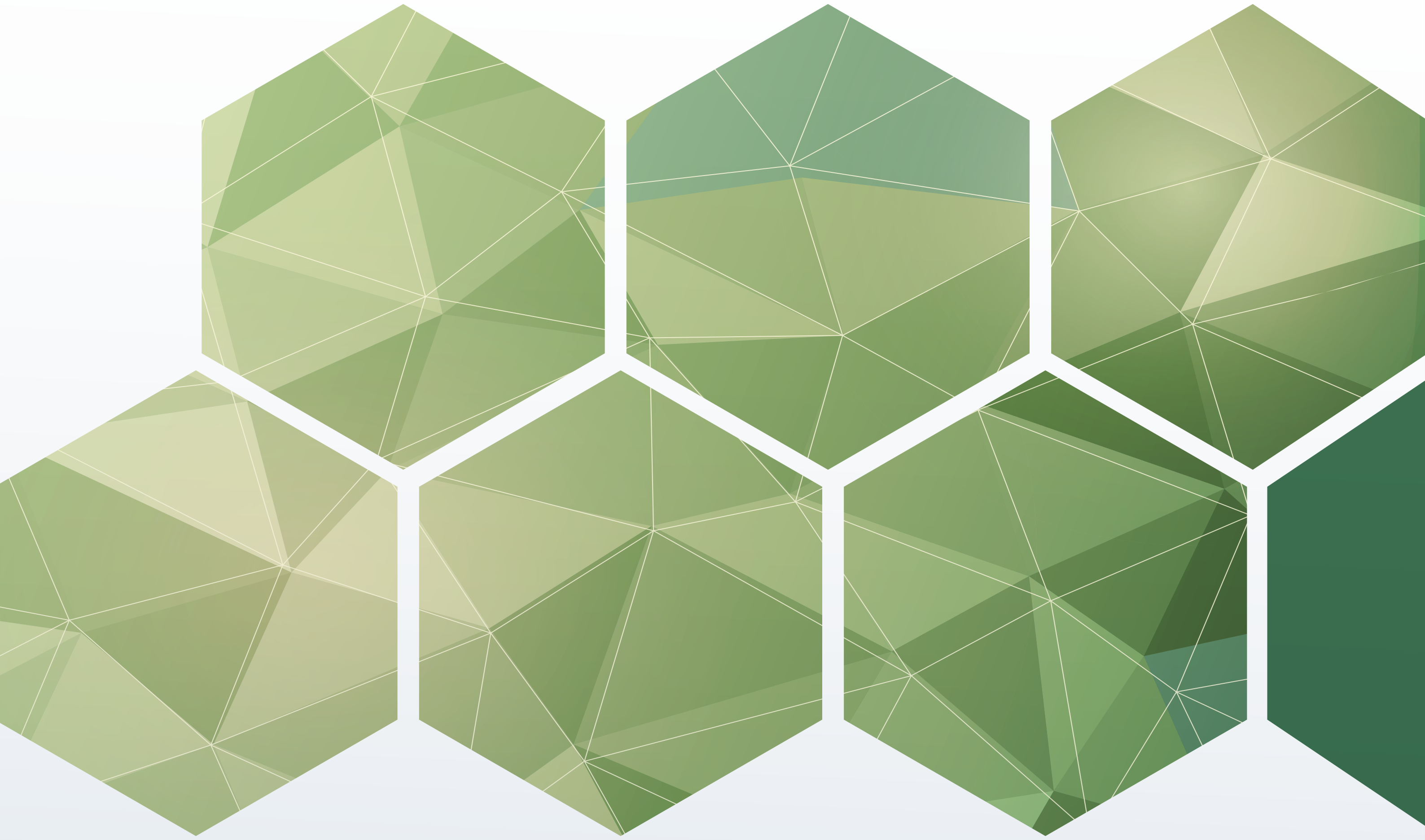

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