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Achieving sustainable cultivation of tropical fruits

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Contents

Series list xiii
Foreword xviii
Acknowledgements xix
Introduction xx

Part 1 Citrus fruits

1 Mapping and exploiting the citrus genome 3
Patrick Ollitrault, CIRAD, France

1 Introduction 3
2 Characteristics of the citrus gene pool 5
3 Forty years of molecular markers development to study and exploit the citrus genome 9
4 Citrus genetic mapping 12
5 Recent development of genomic resources 20
6 Linking phenotypic and molecular variability and MAS 24
7 Future trends and conclusion 26
8 Where to look for further information 27
9 References 28

2 Harvesting citrus: challenges and perspectives in an automated world 43
Marcos David Ferreira, Embrapa Instrumentação, Brazil

1 Introduction 43
2 Manual harvesting 44
3 Harvesting aids 47
4 Mechanical harvesting 52
5 Robotic harvesting 56
6 Precision agriculture to estimate citrus yield 57
7 Future trends 58
8 Conclusion 58

9 Where to look for further information 59
10 References 60

3 Advances in postharvest handling of citrus fruit 65
John Golding and John Archer, New South Wales Department of Primary Industries and University of Newcastle, Australia

1 Introduction 65
2 Background 67
3 Nutritional content 68
4 Fruit physiology 69
5 Degreening 69
6 Physiological storage disorders 70
7 Chilling injury 71
8 Preharvest factors affecting chilling injury 72
9 Postharvest management to reduce chilling injury symptoms 73
10 Postharvest decay 74
11 Fungicides 74
12 Alternative decay control treatments 75
13 Sanitisers 76
14 Food safety 77
15 Market access 78
16 Consumer and retail trends driving changes in citrus production and postharvest 80
17 Conclusions 86
18 Future trends 88
19 Acknowledgements 89
20 References 89

4 Advances in understanding the ecology of citrus insect pests 91
Robert W. Jones, Universidad Autónoma de Querétaro, Mexico; Pablo Liedo, Departamento de Entomología, El Colegio de la Frontera Sur, Mexico; and Santiago Vergara-Pineda, Universidad Autónoma de Querétaro, Mexico

1 Introduction 91
2 Important pests of citrus 92
3 New tools in citrus pest research 98
4 Case study: understanding the ecology of *Diaphorina citri*, vector of citrus greening disease (huanglongbing) 101
5 Case study: fruit fly management and the sterile insect technique (SIT) 104
6 Future trends and conclusion 107

7 Where to look for further information 108
8 References 109

5 Advances in integrated pest management (IPM) in citrus cultivation 117
Lukasz Stelinski, University of Florida, USA

1 Introduction 117
2 Integrated pest management (IPM) in Florida citrus: historical perspective 118
3 The arrival of HLB 120
4 Root weevil complex 123
5 Response to HLB 123
6 Current management practices in the HLB era 125
7 Conclusion and future trends 130
8 Where to look for further information 133
9 References 133

6 Lime breeding: a way forward 139
Muhammad Usman, University of Agriculture, Pakistan; Muhammad Mumtaz Khan and Rashid Al-Yahyai, Sultan Qaboos University, Oman; and Bilquees Fatima, University of Agriculture, Pakistan

1 Introduction 139
2 Lime varieties 140
3 Economic importance and distribution of limes 145
4 Reasons for low productivity 148
5 Germplasm collections, biodiversity and conservation 148
6 Breeding systems 152
7 Molecular approaches in crop improvement 161
8 Future trends and conclusion 169
9 Where to look for further information 169
10 References 171

7 Advances in mandarin breeding 183
José Cuenca, Luis Navarro and Pablo Aleza, Instituto Valenciano de Investigaciones Agrarias (IVIA), Spain

1 Introduction 183
2 Conventional mandarin breeding programs 185
3 Genetic, genomic, and biotechnological tools for mandarin breeding 188
4 Case study: Achieving sustainability using triploid mandarin cultivars resistant to Alternaria Brown Spot disease 193
5 Conclusions 197
6 Where to look for further information 198
7 References 198

Part 2 Other tropical fruits

8 Advances in avocado propagation for the sustainable supply of planting materials 215
Jayeni Hiti-Bandaralage, Alice Hayward, Chris O'Brien, Madeleine Gleeson, William Nak and Neena Mitter, The University of Queensland, Australia

1 Introduction 215
2 Avocado cultivation 216
3 The problem of clonal avocado propagation 217
4 Tissue culture for plant propagation 219
5 Tissue culture as a sustainable alternative for avocado propagation 220
6 Advances in micropropagation of avocado 221
7 Meristem culture for the future of sustainable avocado propagation 225
8 Micrografting for complete field-ready disease-free planting material 228
9 Conclusion 230
10 Where to look for further information 231
11 References 231

9 Advances in cultivation of avocado 239
Gary S. Bender, University of California Cooperative Extension, USA

1 Introduction 239
2 Advances in soil management 241
3 Advances in fertility management 244
4 Advances in irrigation management 248
5 Advances in cultivars and rootstocks 250
6 High-density production 252
7 Root rot management 254
8 Pest management 255
9 Conclusion and future trends 256
10 Where to look for further information 256
11 References 256

10 Ecological intensification of banana production systems 261
Charles Staver, Bioversity International, France

1 Introduction 261
2 Types of banana production systems 263
3 Measuring the potential for improvement in banana production systems 266
4 Using yield gap analysis 266
5 Assessing gaps in resource efficiency 270
6 Assessing the ecological intensification gap 272

7 Using life cycle assessment (LCA) and other certification-based measurements to assess performance 275
8 Identifying priorities for improving banana production systems 281
9 Ecological intensification as a basis for improving banana production systems 281
10 Improvement options: planting material selection, planting date, replanting frequency and desuckering 286
11 Improvement options: mat density and associated crops 295
12 Improvement options: banana cropping systems with trees 301
13 Improvement options: nutrient cycling/balance and soil health 304
14 Improvement options: addressing climate and weather variability in banana production 308
15 Conclusion and future trends 310
16 Where to find further information 312
17 References 313

11 Advances in breeding of coconut 323
L. Perera, Coconut Research Institute, Sri Lanka; R. Manimekalai, Sugarcane Breeding Institute, India; and S. Sudarsono, Bogor Agricultural University, Indonesia

1 Introduction 323
2 Coconut cultivation and uses 324
3 Origin and botany 326
4 Genetic resources 330
5 Conventional breeding techniques: mass selection and hybridization 331
6 Molecular breeding techniques 334
7 Conclusion 336
8 Acknowledgements 337
9 References 337

12 Advances in cultivation of coconut 345
M. A. Foale, Quang Thien Nguyen and Steve W. Adkins, The University of Queensland, Australia

1 Introduction 345
2 Improving potential yield of the coconut 348
3 Protecting the coconut from biohazards 350
4 Mass production of elite genotypes 350
5 The challenge of affordable SE 351
6 Molecular aspects for SE in coconut 359
7 Management from nursery to productive plantation 360
8 Harvesting 364
9 Products and processing 365

10 Conclusion and future trends 368
11 Where to look for further information 369
12 References 369

13 Advances in guava breeding 377
Pankaj Kumar and K. Usha, Division of Fruits and Horticultural Technology – Indian Agricultural Research Institute, India; and Bhupinder Singh, Centre for Environment Science and Climate Resilient Agriculture (CESCRA), India

1 Introduction 377
2 Floral biology 379
3 Breeding objectives 381
4 Methods of guava improvement 383
5 Biotechnological techniques 394
6 Conclusion and future trends 401
7 References 402

14 Advances in guava cultivation 411
Noosheen Zahid and Mehdi Maqbool, University of Poonch, Pakistan; and Ajit Singh and Asgar Ali, University of Nottingham Malaysia Campus, Malaysia

1 Introduction 411
2 Crop climatic requirements and distribution 412
3 Composition, nutritional value and uses 414
4 Propagation methods 415
5 Planting and cultivation techniques 419
6 Irrigation and fertilization 422
7 Pests and diseases 423
8 Harvesting and postharvest operations 426
9 Conclusion and future trends 427
10 References 427

15 Crop improvement in jackfruit 435
S. Shyamalamma and S. Priyanka, University of Agricultural Sciences, India; and G. S. K. Swamy and P. M. Sampath, University of Horticultural Sciences, India

1 Introduction 435
2 Origin, distribution and uses 436
3 Biology 439
4 Nutritional composition 440
5 Breeding and examples of improved varieties 441
6 Conclusion 454

7 Where to look for further information 454
8 References 455

16 Achieving sustainable cultivation of litchi 457
Xuming Huang, South China Agricultural University, China

1 Introduction 457
2 Extension of the production season 459
3 Improving cultivar quality and yield 461
4 Improving tree management 461
5 Conclusion and future trends 467
6 Acknowledgement 467
7 References 467

17 Advances in breeding of mangoes 471
Sunday O. S. Akinyemi, National Horticultural Research Institute, Nigeria

1 Introduction 471
2 Conventional breeding methods 472
3 Molecular methods in breeding 474
4 In vitro techniques 475
5 The use of molecular markers 478
6 Genetic engineering of mango 480
7 Conclusion 481
8 References 481

18 Advances in mango cultivation 489
Víctor Galán Saúco, Instituto Canario de Investigaciones Agrarias, Spain

1 Introduction 489
2 Genetic considerations 490
3 Physiological aspects 493
4 Cultivation techniques 497
5 Conclusion 510
6 Where to look for further information 512
7 References 512

19 Advances in breeding of papaya 519
Sunil Kumar Sharma, Indian Agricultural Research Institute, India

1 Introduction 519
2 Origin and distribution 520
3 Breeding methods 522
4 Breeding for particular traits: identification of plant sex at seedling stage 524
5 Breeding for disease resistance: papaya ringspot virus (PRSV) 527

6 Breeding for disease resistance: black spot and bacterial dieback disease 533
7 Case studies: breeding programmes in India and Malaysia 534
8 Conclusion and future trends 537
9 Where to look for further information 538
10 References 539

20 Advances in papaya cultivation 547
Parmeshwar Lal Saran, ICAR – Directorate of Medicinal and Aromatic Plants Research, India; and Ravish Choudhary, Indian Agricultural Research Institute, India

1 Introduction 547
2 Plant morphology 548
3 Floral morphology, biology and pollination 550
4 Genetics and plant breeding 551
5 Climate and cultivation requirements 555
6 Papaya propagation 557
7 Raised bed sowing 558
8 Fertilization 559
9 Pests and diseases affecting papaya 560
10 Ripening and harvesting 563
11 Conclusion and future trends 563
12 Where to look for further information 564
13 References 564

21 Advances in breeding and cultivation of pomegranate 569
Ibrahim Kahramanoglu, Serhat Usanmaz and Turgut Alas, European University of Lefke, Cyprus

1 Introduction 569
2 Advances in pomegranate breeding 571
3 Advances in propagation methods 573
4 Advances in planting systems, training and pruning 576
5 Advances in irrigation and fertilization 578
6 Advances in pest and disease management 581
7 Advances in fruit thinning 584
8 Advances in physiological disorder management 584
9 Advances in postharvest handling 585
10 Conclusion and future trends 588
11 Where to look for further information 588
12 References 589

Index 597

Foreword

Practically all tropical crops are grown in developing countries The exquisite taste, nutritional value and, in many cases, the nutraceutical properties of these fruits make them highly attractive to consumers. In recent years, these fruit crops have gained importance due to growing consumption all over the world, particularly in developed countries with high purchasing power. According to FAOSTAT data, tropical fruit crop production has grown by 35% in the last 10 years. A striking example is avocado which has been called '*green gold*' because of its high economic and nutritional value, with production growing by a spectacular 52% over the last 10 years.

In parallel to the increase in the planted surface area, there is an increasing interest in more sustainable production of these fruit crops, including a growing demand for technical information on cropping, production and postharvest management. Edited by Prof. Elhadi Yahia, a well-known expert in this area, this book provides an up-to-date review of the state of the art in tropical and subtropical fruit production systems. It focuses on the most successful strategies to ensure long-term sustainability in cultivation of tropical woody species, including careful soil management and optimal soil nutrition both to minimize environmental impact and ensure the long-term economic viability of farming operations.

As well as a wide-ranging coverage of key aspects of citrus production, the book reviews advances in papaya growing and breeding and discusses the ecological issues in intensive banana production systems. It provides valuable information on avocado, its propagation and growing systems, including the use of rootstocks to improve resistance to *Phytophthora cinnamomi*, the devastating fungus causing root rot. It analyzes coconut growing systems and presents novel information on sustainable production of important crops which are barely mentioned in scientific literature, including litchi, pomegranate, guava and jackfruit. In these chapters, the reader will learn about crucial aspects of production, including irrigation management, the use of effective rootstocks, canopy management and planting density, and the use of biological control agents. Combining these strategies provides a sustainable approach to production which fully respects the environment.

This magnificent book will become a valuable reference for technicians, consultants, professors, students and growers who want to use the latest advances to optimize yield and quality of these fruit species, while ensuring long-term sustainability; an essential requirement in every modern agricultural system.

Dr. Javier Z. Castellanos
President of the Institute for Agricultural Innovation (INTAGRI), Mexico.
September 2019

Introduction

Tropical fruits have been cultivated for centuries. The Chinese have grown lychee/litchi for thousands of years while mango, for example, has been cultivated in India for more than 4000 years (Yahia et al., 2006). Carambolas have been popular in Malaysia for centuries and papaya was consumed throughout Latin America long before Columbus's arrival in 1492. While customers in many developed countries may just be discovering some tropical fruits, they have been staple foods for many ethnic cultures for generations.

It is not easy to clearly distinguish between most tropical and subtropical tree fruits but, with some exceptions, the growth of these trees is practically impossible below 10°C. Tropical trees require a climate with average mean temperatures higher than 10°C during the coldest month (Watson and Moncur, 1985). In addition, most tropical trees require humid environmental conditions. The tropics extend between the Tropic of Cancer and Tropic of Capricorn, at 23° north and south of the equator. However, in terms of actual cultivation, these boundaries are too rigid. Not only do they contain areas, especially at higher altitudes, that do not conform to the climatic characteristics generally assigned to the tropics, but also regions outside this belt have coastal areas or inland climates with similar climatic conditions to areas in the tropics. As a result, the region for tropical fruit cultivation has been extended to the 30th parallels (Nakasone and Paull, 1998). The most important feature characterizing the tropics is less a specific minimum or maximum temperature than steady warm temperatures throughout the year. Samson (1986) defined the tropical climate as having temperatures averaging 27°C. He emphasized the importance of stable temperatures, with the warmest month being only a few degrees higher than the coldest month and temperature differences between night and day being greater than those between winter and summer. He also highlighted a little variation in day length.

Subtropical fruit crops are commonly grown in climatic conditions between temperate and tropical. The subtropics have hotter summers and cooler winters than the tropics and the humidity is generally lower. The limit for the subtropics is those areas that are able to maintain an average temperature of 10°C for the coldest month (Nakasone and Paull, 1998). Subtropical fruits may be either deciduous or evergreen and are usually able to withstand a low temperature but not frost. Since differences in day length become greater with increased latitude, subtropical fruit plants are able to adapt to fluctuations in light during the day. Some subtropical fruit plants require chilling for flower bud differentiation, as in the case of grape, citrus, durian and jackfruit.

Tropical and, in particular, subtropical fruits, grow in all continents, but most of the best-known fruits are commercially produced in the tropical and subtropical regions of the Americas (such as avocado, banana, citrus, guava, mango, papaya and pineapple) and Asia (such as banana, lychee/litchi, mango, jackfruit, mangosteen and durian). Almost no tropical fruits and limited quantities of subtropical fruits are grown in Europe.

Key factors in the spread of many tropical fruits have been migration and trade. As an example, mango spread this way throughout Southeast Asia from its origin in the Indo-Burman region and then spread to Africa possibly via Arab traders (Galán Saúco, 1999; Yahia et al., 2006). Malaysian travelers introduced banana to Madagascar. Arab conquest brought the orange to the Mediterranean and southern Europe. In the Americas, evidence suggests exchanges between the cultures of Mexico and Peru dating as far back as 1000 B.C.E. (Purseglove, 1968), allowing tropical and subtropical fruits to disseminate in the region.

The arrival of Europeans in the Americas accelerated the exchange of plant species between the Old and New Worlds. The sixteenth-century monk Bartolomé de las Casas recorded that orange seeds were carried from the island of La Gomera (Canary Islands, Spain) to Haiti on Christopher Columbus's second voyage in 1493 (Amador de los Ríos, 1851–1855). Banana was carried to the Caribbean island of 'Santo Domingo' from the Canary Islands in 1516. In the sixteenth and seventeenth centuries, Portuguese trading routes linked Europe, Latin America, Africa and the Far East, including Brazil, Goa, Malacca, the Moluccas, Canton, Macao Japan and Formosa. Similarly, Spanish traders connected countries such as Mexico and the Philippines. Dutch, British and French traders were also important in spreading tropical and subtropical fruits around the world.

Several factors have influenced the distribution of tropical and subtropical fruits, such as crop adaptability to different climatic conditions, ease of propagation, sensory qualities and fruit postharvest life. For example, the taste of pineapple, the long-term viability of the plant's suckers as planting material and the rapidity with which it produces fruit have been factors in its distribution (Nagy and Shaw, 1980; Galán Saúco, 2001). Similar factors also helped in the distribution of other fruits such as banana, papaya, mango and guava. However, some true tropical trees, such as mangosteen, rambutan and durian, have strict climatic requirements and are difficult to propagate, meaning that they have been confined almost exclusively to their area of origin in Southeast Asia. The mangosteen is notable among tropical fruits and in that it has proven particularly intractable to most attempts to establish it outside of its area of origin via selection of cultivars capable of adapting to different environments. The species consists of a single genotype, which, in essence, means no genetic variation exists with which to breed or improve stock (Yaacob and Tindall, 1985).

Classifying tropical and subtropical fruits

Tropical and subtropical fruits not only include woody plants, such as mango or oranges, but also herbaceous crops such as banana and vines such as passion fruit. Most botanical families can lay claim to at least one species of tropical or subtropical fruit. Martin et al. (1987) listed some 137 families, with the best-known shown in Table 1. Tropical and subtropical fruits are botanically and morphologically diverse, including single fruits such as avocado or orange, drupes such as mango, pomes such as loquat, capsules such as durian, nutlets such as litchi and longan, to compound fruits such as the typical syncarpium of the pineapple, or a bunch of individual berries such as in the banana.

Table 1 Well-known tropical and subtropical fruits and their botanical families

Family	Common names of species
Anacardiaceae	Mango, Cashew
Annonaceae	Cherimoya, Guanábana, Custard apple
Bombacaceae	Durian
Bromeliaceae	Pineapple
Cactaceae	Pitaya
Caricaceae	Papaya
Ebenaceae	Caki
Guttifferae	Mangosteen
Lauraceae	Avocado
Malphigiaceae	Acerola
Meliaceae	Langsat or Lanson
Moraceae	Breadfruit, Jackfruit
Musaceae	Banana, Plantain
Myrtaceae	Guava
Oxalidaceae	Carambola
Palmaceae	Coconut, Date
Passifloraceae	Passion fruit, Granadilla
Proteaceae	Macadamia
Rosaceae	Loquat
Rutaceae	Orange, Grapefruit, Mandarin
Sapindaceae	Litchi/Lychee, Longan, Rambutan
Sapotaceae	Chicosapote, Lucuma
Solanaceae	Sweet pepino, Lulo, Tamarillo

Tropical and subtropical fruits are also very diverse in size, shape and other morphological and anatomical characteristics. Some of these fruits have large seeds, inedible skin or tough rind, which can contribute to a relatively high waste index (compared with temperate-zone fruits). For example, waste indexes in papaya, banana and pineapple are 25, 30 and 41%, respectively. Fruit weight can range from 5–7 gm in acerola to up to 20 kg in jackfruit. Tropical fruits can also be classified on the basis of their variation in texture as follows (G = green, R = ripe): 'hard' such as guava (G), mango (G), passion fruit (G) and pineapple, (G), 'semi-hard', such as banana (G), cherimoya (G), papaya (G) and 'soft' such as date, banana (R), guava (R) and lychee (R).

Uses and nutritional value

Most tropical and subtropical fruits are consumed fresh. Some fruits need further preparation such as breadfruit, which is cooked and plantain, which is commonly fried. Flour is also made from some tropical and subtropical fruits such as durian and banana. Other fruits are made into pickles, chutneys, jams, dips or spreads (Yahia et al., 2006). Commercial processed products include juices, sauces, ice cream and other desserts as well as confectionery and baby foods

Tropical and subtropical tree crops also have a range of non-food uses. On a commercial scale, tropical and subtropical fruits are used to make soaps, bath gels and shampoos. The fruit and flowers of some species, particularly oranges, are used to manufacture essential oils. There is an increasing interest in the potential use of leaves or flower extracts as biological products for the control of pests and diseases. Parts of plants have traditionally been used as animal feed such as banana leaves, dried dates and their pits, breadfruit leaves and mango seeds kernels. Pineapple and banana leaves are used for papermaking and cloth, while avocado wood is used for decorative carvings. Banana and date palm leaves have traditionally been used as roofing material, while the wood of breadfruit, citrus, guava, longan, mango, mangosteen and persimmons has been used for interior paneling.

While most tropical and subtropical fruits are characterized by relatively low caloric values, they are rich in carbohydrates, vitamins, minerals and phytochemicals, ensuring they play a very important role in human diet and nutrition (Yahia et al., 2011a). Bananas, plantains and breadfruit are widely used as a source of starch. Acerola fruit contains the highest known ascorbic acid (vitamin C) content among all fruits (1000–3300 mg/100 gm fresh weight). Other fruits, such as citrus, guava, lychee, papaya and passion fruit are good sources of ascorbic acid. Mango and papaya are good sources of vitamin A. Breadfruit and cherimoya contain relatively high amounts of niacin and thiamin. Guava contains fair amounts of niacin and iron. Most tropical fruits are good sources of minerals, especially potassium and iron. Banana is a good source of vitamin A, B and C, riboflavin and potassium. Papaya fruit has high quantities of vitamin C and A as well as potassium and calcium. Papaya also contains papain, an enzyme that promotes digestion. Pineapple is rich in vitamin C and carbohydrates and is a good source of calcium, phosphorus, iron, potassium and thiamine. Litchi/lychee, longan and durian are good sources of carbohydrates and vitamin C and durian has fair amounts of iron and niacin. Carambola is low in calories, rich in vitamin C and an adequate source of vitamin A. Macadamia nut is rich in protein, oil, iron, calcium, thiamine, riboflavin and niacin. Dates have a high nutritive value, being rich in carbohydrates and are a good source of vitamin A, potassium and iron. Coconut is high in phosphorus and iron. Tropical and subtropical fruits are also rich in pectin and fiber, which promote intestinal health. In common with other fruits, tropical and subtropical fruits are good sources of antioxidants (Martin et al., 1987; Yahia et al., 2011a). Many tropical and subtropical fruits, notably mango and papaya, are good sources of carotenoids. Traditionally, this has meant use of the fruit and other parts of the plant to treat a wide range of ailments, from cold, asthma and other lung conditions to intestinal disorders. Modern science has now linked the phytochemicals in many tropical and subtropical fruits to the prevention of a range of chronic diseases, resulting in their being marketed as 'superfruits' to western consumers (Yahia et al., 2018).

Tropical and subtropical fruit production

Production and trade figures assume a division of tropical and subtropical fruits into the following three main categories:

- Major fruits, such as banana and plantain, avocado, citrus, kiwi, mango, papaya and pineapple. These are cultivated in most tropical and subtropical countries and are well-known in local and export-import markets.
- Minor fruits, many such as abiu, atemoya, breadfruit, cactus pears, caimito (star apple), carambola (star fruit), cashew apple, cherimoya, custard apples, durian, guanabana (soursop), guava, jaboticaba, jackfruit, langsat, litchi, longan, macadamia, mabolo (velvet apple), mamey sapote, mangosteen, monstera (ceriman), papaya, passion fruit, pejibaye (peach palm), pitaya, pulusan, rambutan, sapodilla, soursop, sugar apple (annona), white sapote. and wax apple (wax jambu). Minor fruits are not so extensively cultivated and consumption and trade tend to be limited, both geographically and quantitatively. Most are commonly known only in very

specific regions. Many are of considerable economic importance in their respective regional markets such as durian and mangosteen.

- Wild fruits belonging to diverse botanical families such as jamun (Syzygium cumini L), among several others, which are not cultivated commercially.

As noted above, examples of truly tropical fruit tree crops include mangosteen, durian and rambutan. Some fruit crops, such as banana, avocado and citrus can be cultivated equally well in either the tropics or the subtropics. Tropical fruit plants are generally evergreen and are extremely sensitive to cold. They do well with few fluctuations in diurnal temperature or periods of daylight. They require a moist warm climate but are capable of withstanding dry weather in some cases for example, mango, banana, papaya and sapota.

Global aggregate production of major tropical fruits was estimated at 93.7 million tons in 2017 (Table 2). The sector saw 3% growth in 2015 and 2016, a slight decrease on the 4% average annual growth rate seen over the previous decade, which has been related to poorer weather conditions in 2015 and 2016 (Altendorf, 2019). About 98% of tropical fruit production is in developing countries. Around 50% of tropical fruit production is consumed fresh and the rest is consumed in different processed forms. There is a considerable gap between world per capita consumption (less than 60 kg per year) and estimated potential consumption (about 100–120 kg per year) (Jansen and Subramaniam, 2000) which suggests significant potential for growth.

The leading producer of major tropical fruits is India, accounting for an estimated 30% of total global production of major tropical fruits in 2017, due to its strong position in the production of fruits such as mango and papaya. India accounts for approximately 40% of total global mango and papaya production, which is predominantly destined for domestic market. Other significant producers of tropical fruits include China and Brazil, with most production also destined for the domestic market and Costa Rica and Mexico, which rank as the two biggest exporters of tropical fruits.

About 50 million tons of mango, mangosteen and guava were produced globally in 2017 (Table 2), an increase of 4% over 2016. It is estimated that mango accounts for approximately 75% of total production volume, guava for 15% and mangosteen for the remaining 10%. In 2017 approximately 75% of mango, mangosteen and guava production was in Asia, 15% in Africa and 10% in Latin America and the Caribbean. Production in India, the largest producer of these fruits, increased by an estimated 1 million tons in 2017. With an estimated output of 19.7 million tons in 2017, India accounted for approximately 40% of total global production.

Global pineapple production was approximately 27 million tons in 2017 (Table 2). Output in 2017 only increased fractionally because of weather-related crop damage in Costa Rica, the main producer of pineapple (accounting for

Table 2 Global cultivated area (1000 Ha) and production (1000 tons) of some tropical and subtropical fruits in 2017 (FAOSTAT, 2019)

Fruit	Area (1000 Ha)	Production (1000 Tons)	Major producing countries
Avocados	587.278	5,924.398	Brazil, Chile, Dominican Republic, Colombia, Kenya, Mexico, Peru, USA, Venezuela
Bananas	5,637.508	113,918.763	Angola, Brazil, China, Colombia, Ecuador, Guatemala, India, Indonesia, Mexico, Tanzania, The Philippines
Coconuts	12,303.924	60,773.435	Brazil, India, Indonesia, Papua New guinea, Mexico, Sri Lanka, Thailand, Tanzania, The Philippines, Vietnam
Figs	36.535	307.685	Algeria, Brazil, China, Egypt, Greece, India, Iran, Libya, Morocco, Spain, USA, Turkey
Grapes	6,931.353	74,276.583	Argentina, Brazil, Chile, China, France, India, Italy, South Africa, Spain, Turkey, USA
Grapefruits	348.212	9,063.143	China, India, Mexico, South Africa, Thailand, Turkey, USA, Vietnam
Kiwi fruit	247.793	4,038.872	China, Italy, New Zealand, Chile, USA
Lemons and limes	1,084.505	17,218.173	Argentina, Brazil, China, Colombia, Egypt, India, Iran, Italy, Mexico, South Africa, Spain, Sudan, Turkey, USA
Mangos, mangosteens and guava	5,681.310	50,649.147	Brazil, China, Egypt, India, Indonesia, Mexico, Pakistan, Thailand
Olives	10,804.517	20,872.788	Argentina, Algeria, Egypt, Greece, Italy, Libya, Morocco, Portugal, Spain, Turkey, USA
Oranges	3,862.449	73,313.089	Brazil, China, Egypt, India, Indonesia, Mexico, Pakistan, Spain, Turkey, USA
Papayas	440.629	13,016.281	Brazil, Colombia, Cuba, India, Indonesia, Mexico, Venezuela
Pineapples	1,098.705	27,402.956	Brazil, China, Colombia, Costa Rica, India, Indonesia, Mexico, The Philippines
Plantains	5,522.745	39,241.376	Cameron, Colombia, Cote d` Ivoire, Ghana, Myanmar, Nigeria, Peru, The Philippines, Uganda,

over 11% of global production). This marked a significant curtailment of global production growth compared to the average annual rate of 4% seen over the previous decade. The country's prolonged and intense 2016 rainy season, which lasted until December and the drought that followed in January and February of 2017, caused significant damage to production in the first half of 2017, resulting in an estimated 6% decline in output. Other major producers of pineapple include Brazil and the Philippines, with an estimated 11% and 10% share of production in 2017 respectively, followed by China, India and Thailand. Thailand is the world's leading producer and exporter of processed pineapple.

In global production terms, avocado remains one of the less important of the major tropical and subtropical fruits. Global production of avocado reached an estimated almost 6 million tons in 2017, representing a 2% increase from 2016. Avocado has seen very fast production growth over the last decade, primarily due to increases in harvested area among the major producers. Nearly half of all production takes place in Central America and the Caribbean, notably in Mexico, the Dominican Republic, Colombia, Peru and Chile. Production in Mexico alone accounted for more than one-third of the global output in 2017. Although adverse weather conditions in the country affected both the quantity and quality of the harvest in the first 9 months of the year, overall production increased by 6% from 2016, reaching a new peak of nearly 2 million tons. Production in the Dominican Republic, hitherto the world's second leading producer of avocado, experienced significant hurricane damage in October 2017 with an estimated 55% decline in output in 2017 compared with 2016. As a result, the share of the Dominican Republic in global production dropped to 5% in 2017. The peak harvest period in the Dominican Republic is between October and March, when approximately 80% of production is harvested, making the crop particularly vulnerable to hurricane damage. Production in Peru, meanwhile, registered a 22% increase over 2016, following a near equivalent increase in harvested area. This was stimulated by strong import demand from the European Union, the largest export destination. Consequently, Peru ranked as the second leading producer of avocado, with an estimated 10% volume share in 2017.

Global production of papaya reached an estimated 13.7 million tons in 2017, a 5% increase from 2016. Due to the crop's greater resilience to adverse weather conditions, papaya production in 2017 experienced significantly less disruption from adverse weather events compared to other tropical fruits, exceeding the average annual growth rate of 3% achieved over the past 10 years. In terms of regional distribution, an estimated 56% of global papaya production originated from Asia in 2017, 33% from Latin America and 11% from Africa. India, the largest papaya producer in the world, with an estimated 45% output share in 2017, achieved 7% production growth from 2016, largely due to increases in harvested area. Production in Brazil, the second largest producer in the world, increased by an estimated 6%, after recovering from a 4% drought-induced decline in production in 2016.

The trade in tropical and subtropical fruit

Many tropical and subtropical fruits are of great importance in the trade in fresh fruit, such as citrus, bananas, pineapples, mango, avocado and papaya. Several tropical and subtropical fruits are also very important in the trade in processed fruits and vegetables, such as citrus and pineapples. The main producers of subtropical and, in particular, tropical fruits are developing countries, while the main importers are developed countries in Europe as well as the United States, Canada, Japan and China.

While a small number of tropical and subtropical fruits, such as banana, pineapple and citrus, have a long history of international trade, other fruits such as mango and avocado have only started to develop significant export markets in the last few decades. Most tropical fruits were considered ‘exotic’ in developed countries until a few years ago, but many are now familiar products in supermarkets around the world such as guava, lychee/litchi, carambola, mangosteen, passion fruits and rambutan.

There are a number of reasons for the growth in export markets for tropical and subtropical fruits, including:

- Overall growth in world trade;
- Improved breeding, production, postharvest handling and processing systems in developed countries, resulting in a sufficient volume and quality of produce for export;
- Better international distribution and storage technologies and systems (such as improved cold chain technologies, or the use of modified ad controlled atmosphere technologies);
- The growing ethnic diversity of populations in developed countries, increasing interest in new foods;
- Growing consumer interest in the perceived nutraceutical properties and health benefits of tropical and subtropical fruits.

As with other products, the tropical and subtropical fruit trade benefitted from the World Trade Organization (WTO) agreement in Marrakesh on 15 April 1994 following the conclusion of the Uruguayan round of talks on the General Agreement on Tariffs and Trade (GATT). This agreement helped to reduce trade barriers and promote free trade.

Globally, banana, pineapple, mango and avocado are the four most significantly traded tropical fruits. Other fruits such as papaya are traded in much lower volumes but have shown significant export growth. Global trade in major tropical fruits was an estimated 6.6 million tons in 2017, following a small 1% contraction on the previous year (Altendorf, 2019). Adverse weather conditions in two leading exporting countries, Mexico (for avocado, mango and papaya) and Costa Rica (for pineapples) has been cited as the main cause of low production.

Global exports of mango, guava and mangosteen were an estimated 1.7 million tons in 2017 with mango accounting for 90% of these exports. Exports in 2017 represented a 9% increase from 2016, significantly higher than the 5% average annual growth registered between 2007 and 2016 (Altendorf, 2019). The expansion follows strong growth in demand in the main export destinations, namely the United States, which expanded its import share to 34% of global imports and the European Union, which held a 20% global share in 2017. The latest available figures indicate that per capita availability of mangoes reached 1.8 kg in the United States and 0.7 kg in the European Union in 2017, up from 1 kg and 0.4 kg in 2007, respectively. The leading exporter of these fruits is Mexico, presenting 24% of overall exports by volume in 2017, followed by Thailand (14%), Brazil (10%) and Peru (9%). Mexico primarily exports mangoes to the United States (approximately 80% of the country's entire shipments in 2017) and benefited strongly from a combination of favorable weather in the main production areas and higher import demand for the fruit in 2017, expanding overall shipments by 19%. Mango exports from Brazil are mainly destined for the European Union market, where the country maintains a strong position through its ability to produce mangoes perennially, including a number of varieties that are popular in European markets such as Tommy Atkins, Keitt and Kent. In 2017, mango exports from Brazil additionally benefited from growing demand in the United States. Thailand, which also ranks as one of the leading exporters of mangosteen, ships the bulk of its mango production to foreign markets, primarily to destinations within the confines of the Southeast Asian region. Peru exports mainly fresh mango and mangosteen, with approximately 40% of shipments going to the Netherlands, 30% to the United States and 10% to the United Kingdom in 2017.

Global exports of pineapple fell to an estimated 2.8 million tons in 2017, representing a 9% decline from 2016 (Altendorf, 2019). Costa Rica, which accounted for approximately 65% of global exports by volume, experienced an estimated 10% fall in exports from 2016 due to adverse weather conditions. The Philippines, the second largest exporter with an approximately 17% share in 2017, also experienced an estimated 9% decline in exports. Despite the supply shortages in Costa Rica, imports by the United States, the largest importer of pineapple globally, increased by an estimated 7% in 2017 from the previous year on the back of strong demand. Imports reached approximately 1.2 million tons in 2017, representing 40% of total global import volumes.

Global exports of avocado reached 1.6 million tons in 2017, representing a 3% increase from 2016, significantly slower than the 11% average annual growth rate seen over the previous decade. Mexico accounted for an estimated 58% of global avocado exports in 2017, with around 77% of shipments going to the United States of America. Exports in 2017 represented a 4% decline from 2016 due to poor weather, in contrast to the 15% annual average growth rate achieved between 2007 and 2016. Other significant exporters are Peru, Chile, South Africa, Israel and Kenya, which export primarily to the European Union and have benefited from significantly increased demand from customers in the European Union.

Global exports of papaya reached an estimated 350 000 tons in 2017, an annual increase of 5% from 2016 (Altendorf, 2019). This represented a healthy recovery from the estimated 6% decline in export volumes experienced in 2016, caused by weather-related supply shortages in Brazil and Guatemala. The largest importers of papaya in 2017 were the United States, with an estimated 57% volume share and the European Union, with an approximate 13% volume share. Mexico accounts for approximately half of all the global papaya exports, with shipments almost exclusively destined for the United States. Rapid growth in demand from the United States gave Mexican producers a strong incentive to improve production practices, resulting in a 6% improvement in average yields between 2010 and 2015, though overall papaya exports from Mexico declined slightly in 2017 (Altendorf, 2019). While the largest share of papaya production in Brazil is destined for the domestic market, the country ranks as the second largest exporter behind Mexico and has rapidly raised its export volumes in response to growing demand from the United States and the European Union. In terms of market potential, the latest available data indicate a per capita availability of 0.6 kg in the United States in 2017, up from 0.4 kg in 2005. Despite the European Union ranking as the second largest importer, consumer awareness of the fruit remains low, with per capita consumption of papaya remaining at a negligible 0.1 kg in 2017. This indicates the potential for future growth as well as the need for more promotion of the fruit and its nutritional benefits to customers, particularly in the European Union.

Key challenges facing tropical and sub-tropical fruit production and trade

As the discussion of production and trade in tropical and subtropical fruits shows, there is significant potential to develop export markets but production can be very vulnerable to weather fluctuations, a problem that is likely to be exacerbated by climate change. Other challenges include the availability of good-quality planting materials, the need to achieve more consistent yields and quality in cultivation, improving postharvest practices to maintain quality as well as threats from pests and diseases (also linked to the effects of climate change, which is allowing pests and diseases to spread into new areas).

Tropical and subtropical fruit species have been neglected areas of research, for example in the quality of germplasm collections and the application of modern biotechnological techniques (such as tissue culture techniques) in conservation and breeding. They therefore represent a wealth of as yet untapped potential for development.

Since the 1990s, there have been increased efforts to improve this situation. As an example, Bioversity International (formerly IPGRI) initiated research on conservation and use of tropical fruit tree species in Asia in 1993 in collaboration with national partners, subsequently followed by large regional projects funded by donor agencies to strengthen Bioversity's work in genetic resources management. The International Tropical Fruits Network (TFNet) was established in 2000 under the auspices of the Food and Agriculture Organization of the United Nations (FAO) and now plays a major role in promoting the health benefits of tropical fruits and facilitates cooperation among countries, the private sector and other stakeholders. Two species in particular, papaya and citrus, have recently been the focus of extensive research and have become the models for the application of biotechnology to other tropical fruit species. Most citrus research has been conducted on subtropical citrus species but is highly relevant to commercially important tropical citrus species.

A major focus of research is improving the postharvest handling of tropical and subtropical fruits. The tropics are characterized by warm, humid climatic conditions that promote spoilage of fruit (Yahia et al., 2011b). Most tropical fruits have a limited postharvest life or shelf life due to their high perishability, sensitivity to low (chilling) temperatures and vulnerability to attack by spoilage organisms and pests (Kader and Yahia, 2011). The main causes of postharvest losses for tropical and subtropical crops include:

- Mechanical damage due to mishandling along the supply chain;
- Loss of moisture which causes shriveling of fruit;
- Early senescence when stored in higher or lower than optimum temperatures;
- Sensitivity to chilling (lower than optimum) temperature;
- Spoilage due to attack by pathogens and pests.

While some fruits (such as grapefruit, mandarin, orange and pomegranate) have a relatively long shelf life others are highly perishable, such as avocado, guava, lychee/litchi, longan, rambutan, loquat and kiwifruit. This makes it critical to implement the correct postharvest practices for individual fruit species (Yahia, 2011; Yahia et al., 2011b).

While some are non-climacteric (such as citrus fruits and pineapples), most tropical fruits and several subtropical fruits are climacteric, that is, characterized by a marked and sudden rise in the respiratory rate just prior to full fruit ripening (Yahia, 2011). These characteristics are critical in establishing the best time to harvest fruit as well as appropriate postharvest treatments. For example, bananas (climacteric fruit) can be harvested when mature green and ripened later, while pineapple (non-climacteric fruit) should be harvested in a partially ripe state to attain good eating quality when ripe. As examples, maturity indices commonly used for banana, mangoes, papaya and pineapples are shown in Table 3.

Chilling injury (CI) is one of the main sources of deterioration and losses in all tropical and several subtropical fruits (Kader and Yahia, 2011). Sensitive fruits can be injured at temperatures from 0 to 18°C, depending on the type of fruit and the duration of exposure to the incorrect temperature. Some fruits are highly sensitive to CI, such as banana, breadfruit, cherimoya, jackfruit, mamey, mango, mangosteen, papaya, pineapple, rambutan and soursop. Others are moderately sensitive such as carambola, durian, guava, sugar apples and tamarillo. Subtropical fruits that are less sensitive to chilling include grapes and kiwifruit. Table 4 shows CI symptoms in banana, mango, papaya and pineapple.

Tropical and subtropical are also sensitive to several other physiological disorders (Kader and Yahia, 2011). For example, endogenous brown spot (EBS) of pineapples can be induced by holding the fruit at 8°C for one week followed

Table 3 Maturity indices of banana, mango, papaya and pineapple fruits

Fruit	Maturity indices
Banana	Fullness of finger (disappearance of angularity), days after flowering or fruit set
Mango	Fruit shape, internal color, formation of shoulder, external color change in some cultivars
Papaya	Surface color (6–33% yellow), soluble solids content (11.5% or higher)
Pineapple	Shell color: ‘color break’ to 25% yellow stage

Table 4 Chilling injury symptoms in banana, mango, papaya and pineapple fruits

Fruit	Minimum safe temperature (°C)	Chilling injury symptoms
Banana	13–15	Surface discoloration, dull color, failure to ripen, browning of flesh.
Mango	10–12	Grayish scald-like discoloration of skin, uneven ripening, poor flavor, increased decay
Papaya	10–12	Pitting, failure to ripen, off-flavor development, accelerated decay.
Pineapple	8–10	Uneven ripening, dull color, water-soaked flesh, off-flavor, increased acidity, loss in ascorbic acid content, wilting of crown leaves, endogenous brown spot.

by holding for another week at 20°C. EBS may also occur before harvest during cool and overcast periods. Exposure of pineapple fruit to high temperatures (35–38°C) for one day before or after transit reduces the development of EBS symptoms. Waxing pineapples also reduces the severity of EBS because of increased endogenous concentration of CO_2.

Diseases are the major cause of postharvest losses in tropical and subtropical fruits. The most important decay-causing organisms are *Colletotrichum gloeosprioides* (causing anthracnosis), *Diplodia natalensis* (causing stem end rot), *Ceratocystis paradoxa* (causing black rot in banana and pineapples) and *Penicillium* and *Fusarium* (causing brown rot on pineapple). Anthracnose is the major postharvest problem in tropical fruits and latent infection often occurs in green fruit before harvest. Preharvest treatments and methods of disease control are important. These include the use of healthy seedlings as well as proper field sanitation practices. Some pesticides are still allowed for applications before and after harvest to control decay, however other non-chemical treatments, such as postharvest heat treatments are effective and safer for consumers. For example, hot water treatments (48-55°C for 5-15 minutes) are commonly used for mango and papaya.

Many insects infect tropical and subtropical fruits (Yahia et al., 2011c). Some of these are restricted to certain regions, such as the Mediterranean fruit fly (*Ceratitis capitata*) which has spread from Africa to Australasia and the Americas, several *Anastrepha* species which are restricted to South, Central and parts of North America and the West Indies and the genus *Dacus* in Africa and Asia. This has led to strict quarantine measures to prevent such pests being accidentally introduced into new areas. Traditionally control of such pests has been via the use of fumigants such as methyl bromide but methyl bromide is now being restricted because of its environmental impact. This has led to the search for alternative methods of control.

Heat treatments are an effective, non-chemical method of treatments, widely used to treat mangoes, papaya and some other tropical fruits grown for export. Heat treatments maintains produce at a certain (high) temperature for a fixed period of time, using a hot water or steam vapor system. For example, a hot water treatment at 46.1°C for 65–90 minutes (depending on fruit weight) is commonly used for mango in several countries (Yahia et al., 2006, 2011c). For papaya a 2-stage heating process has been used to eradicate the Mediterranean fruit fly consisting of treatment at 42°C for 30 min, followed by 49°C for 20 min. Vapor heat treatments have also been developed. Irradiation at low doses (about 300 Grays) are also been used in some countries to disinfect fruits such as guava and mango (Yahia et al., 2011c).

Tropical and subtropical fruits should be pre-cooled as soon as possible after harvest and should be transported at ideal temperature. Several tropical and subtropical fruits, especially banana and mango, are transported by sea in modified (MA) and controlled (CA) atmospheres (Yahia, 1998; (Yahia et al., 2011b). Some tropical fruits, such as bananas, are artificially ripened after arrival to destination market and ethylene gas is commonly used for this process (Kader and Yahia, 2011). Ideal temperature for ripening is 20–24°C in high relative humidity (RH = 90 to 95%). Temperatures above 27°C accelerate softening and may cause tissue discoloration, excessive decay and off-flavors. Temperatures above 35°C inhibit ethylene production and action and consequently inhibit the process of ripening. Ripening is also impaired when fruits are exposed to chilling temperatures. Ethylene concentrations commonly used for fruit ripening are 10 to 100 ppm. Removal of ethylene, using different agents such as potassium permanganate, is used to delay ripening in different tropical and subtropical fruits (Yahia et al., 2011b). The application of waxes is a also very common practice in postharvest handling of some fruits such as citrus. Waxes modify the internal atmosphere of the fruit, reduce weight loss and improve surface appearance. However, the selection of a wax or coating is very crucial, because improper waxes or coatings may lead to development of off-flavors and surface pitting.

Conclusions

Cultivation, production and trade of tropical and subtropical fruits are gaining increased importance and interest globally. Important tropical and subtropical fruits in world trade include banana/plantain, citrus, grapes, pineapples, mango, papaya and avocado. However, many others such as jackfruit, lychee/litchi, durian, mangosteen, longan, cherimoya, among others, are growing in importance but are still not widely known among consumers in developed countries who constitute the key export markets, suggesting strong potential for the future.

This book reviews recent research on key tropical and subtropical fruits such as avocado, banana, citrus, coconut, guava, jackfruit, lychee, mango, papaya and pomegranate. Chapters cover topics such as advances in production systems, breeding, propagation, soil nutrition and management, irrigation, use of growth regulators, understanding insects pests and their control, harvesting and postharvest handling practices. The book should be of great interest and benefit to producers and traders, as well as researchers and students.

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Part 1

Citrus fruits

Chapter 1

Mapping and exploiting the citrus genome

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1 Introduction
2 Characteristics of the citrus gene pool
3 Forty years of molecular markers development to study and exploit the citrus genome
4 Citrus genetic mapping
5 Recent development of genomic resources
6 Linking phenotypic and molecular variability and MAS
7 Future trends and conclusion
8 Where to look for further information
9 References

1 Introduction

Citrus belongs to the Aurantioideae subfamily in the Rutaceae family. Most of the cultivated citrus species are part of the *Citrus* genus. According to traditional taxonomy, the *Citrus* genus included between 16 (Swingle and Reece, 1967) and 156 species (Tanaka, 1961). The phenotypical variability of citrus for morphological and agronomic traits is very large. Several sources of tolerance have been identified for abiotic stresses (Krueger and Navarro, 2007). Tolerance to salinity is present in Rangpur lime (*C. limonia* Osb.), Cleopatra mandarin and *C. macrophylla* Wester. The *Microcitrus* and *Eremocitrus* species and at lower level the Rangpur lime display tolerance to water deficit. Adaptation to iron chlorosis is found in Rough lemon (*C. jambhiri* Lush), Volkamer lemon (*Citrus limonia* Osbeck), *C. amblycarpa* (Hassk.) Ochse and *C. macrophylla*. The Satsuma mandarins, the Kumquats (*Fortunella* sp.) and *Poncirus trifoliata* (L.) Raf. are cold tolerant. Important variability is also observed for resistance/susceptibility to important pests and diseases. Sour orange, Volkamer lemon, *C. amblycarpa,* trifoliate oranges and certain pummelos and mandarins are tolerant to *Phytophthora* sp., while tolerances to the African cercosporiosis (fungal disease due to *Phaemularia angolensis* De Carvalho and O. Mendes

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P.M. Kirk) are found in pummelos, lemons and Satsuma and Beauty mandarins. The susceptibility to another fungal disease, *Alternaria alternata* of tangerine, is only found in a limited set of mandarins, principally Dancy and its hybrids including Orlando tangelo and Fortune mandarin. Resistance to the citrus tristeza virus (CTV) is highly variable. Immunity is found in trifoliate orange, partial resistance in some pummelos and kumquats and tolerance in different germplasm used as rootstocks such as *C. amblycarpa,* Cleopatra mandarin, Rangpur lime, Rough lemon and Volkamer lemons. Different levels of tolerance to citrus canker (bacteriosis due to *Phoma tracheiphila* (Petri) L. A. Kantsch. & Gikaschvili) are found in Kumquats, Yuzu, Satsuma and Dancy mandarins. *P. trifoliata* is a source of resistance to the nematode *Tylenchulus semipenetrans* Cobb. Recently true resistance to Huanglongbing (the most devastating citrus disease due to the bacteria Candidatus Liberibacter sps.) was described in *Microcitrus* and *Eremocitrus*. The variability for fruit morphology and quality traits is also huge and is closely linked with the evolution of cultivated citrus as we will discuss below.

The important variability for biotic and abiotic tolerance traits opens very broad prospects for the exploitation of citrus genetic resources for adaptation breeding, particularly at rootstock level (Cimen and Yesiloglu, 2016). The identifications of molecular markers linked to adaptation traits for abiotic stresses and to disease and pest resistances are now essential to drive efficiently multi-traits breeding projects. In the same way, it is essential to develop molecular markers for early selection of fruit traits. Indeed, due to the juvenile phase and size of evaluation plots, conventional breeding for quality is very costly and the numbers of hybrids to work with are very limited compared with annual crops.

The recent development of genomics in citrus and particularly the availability of reference genome sequences for sweet orange (Xu et al., 2013), clementine (Wu et al., 2014) and pummelo (Wang et al., 2017) and ongoing re-sequencing projects (Wu et al., 2018; Wang et al., 2017) pave the way for a more efficient exploitation of citrus genetic diversity in conventional breeding programmes. The present challenge is to associate genome polymorphisms with the diversity of useful traits. The most common genetic approaches are to perform quantitative trait loci (QTLs) analysis or genome-wide association studies (GWAS), both based on genetic linkage between genes implied in the phenotype diversity and genetic markers (i.e. close genomic position of the implied genes and genetic markers). QTL analysis is conducted on sexual recombining populations, while GWAS explore associations in more diverse germplasms. GWAS has the advantage of allowing identification of key genes that should be monomorphic in a single hybrid population and to bypass the necessity to create designed segregating progenies. It should therefore offer advantages in citrus-breeding programmes where breeding materials are even derived from several parental combinations. The uses of GWAS in fruit crops has increased in recent years (Farneti et al., 2017; Minamikawa et al., 2017; Iwata et al., 2016; Moriya et al., 2017). However, the genetic structure of the germplasm under investigation, and particularly the decay of linkage disequilibrium (LD) with genetic distance, are key elements in applying GWAS. These elements are strongly affected by the historical evolution of the gene pools being used.

The application of GWAS is also strongly dependent on the advance in genomics and genetic marker resources development. In recent years, with the development of next-generation sequencing (NGS) methods, new high-throughput genotyping methods have been developed combining NGS and reduced genome representation such as allelic capture sequencing (Holtz et al., 2016) and methods based on restriction site-associated DNA sequencing (RADseq (Miller et al., 2007); GBS (Elshire et al., 2011)). These make it possible to perform high-throughput phenotyping at the same time as SNP mining, while microarray genotyping can identify useful polymorphisms. High-throughput genotyping at affordable costs open the way to the analysis of large segregating progenies and marker-trait association studies (Baxter et al., 2011; Ipek et al., 2016; Montero-Pau et al., 2017) and further to genomic selection (GS).

This chapter reviews the recent developments in genetics and genomics to decipher the citrus genomes and optimize their exploitation. It starts with a reminder about important and distinctive characteristics that determine the citrus gene pool which define priorities for the international citrus research community and the challenge of marker-traits association in citrus. The recent developments of genetics and genomics resources and knowledge are then reviewed discussing studies of the links between molecular and phenotypic diversity and resulting concrete applications for marker-assisted selection (MAS) and perspectives for GS.

2 Characteristics of the citrus gene pool

2.1 The taxonomic position

While previously it was included in the Geraniales order (Swingle and Reece, 1967), taxonomists now agree that *Citrus* L. genus is part of the Sapindales Berchtold & J. Presl. order in the Rutaceae Jussieu family (Stevens, 2017; NCBI, 2017). The genus *Citrus* belongs to the subfamily Aurantioideae, which is divided into two sub-tribes (Swingle and Reece, 1967): the Clauseneae (five genera) and the Citreae (28 genera). The Clauseneae tribe is considered more primitive than the Citreae tribe and there is no sexual compatibility between the two tribes. Citreae are divided in three sub-tribes: Triphasiinae, Balsamocitrinae and Citrinae. Swingle and Reece (1967) recognized three groups in the Citrinae. One of them, the ‘true citrus’ group includes the *Citrus* genus and five other genera: *Clymenia*, *Eremocitrus*, *Fortunella*, *Microcitrus* and *Poncirus*. Maternal phylogenetic studies (Bayer et al., 2009) confirmed the monophyly of the 'true citrus group' and suggested including the neo-caledonian *Oxanthera* genus in the same group.

2.2 A large interspecific and intergeneric sexual compatibility

The different species of the other 'true citrus' genera display sexual compatibility with the *Citrus* species (Iwamasa et al., 1988). Particularly, many fertile hybrids have been produced between different *Citrus* species *and P. trifoliata* which is a key germplasm for citrus rootstock improvement. Hybrids between sweet orange, grapefruit, lemon, sour orange and mandarin and *P. trifoliata* are, respectively, called citrange, citrumelo, citremon, citradia and citrandarin. *Fortunella* species were also used as breeding parents during the twentieth century (mandarinquat, limequat) and the natural origin of Calamondin from intergeneric hybridization between *Fortunella* and *Citrus* was recently demonstrated from WGS data (Wu et al., 2018). Several hybrids have been created between *Citrus* and *Microcitrus* (e.g. 'Australian blood' lime). Hybrids between *Citrus* and *Eremocitrus glauca* were also obtained (eremorange and eremolemon, respectively, with sweet orange and lemon). The different 'true Citrus' genera present interesting traits for citrus breeding such as cold tolerance, dwarfing, disease and pest tolerances (including phytophthora, nematodes) and overall CTV immunity in *Poncirus*; cold tolerance and citrus canker (bacteriosis due to *Xanthomonas axonopodis*) resistance in *Fortunella*; high tolerance and resilience to water deficit and recently found (Ramadugu et al., 2016) resistance to citrus greening in *Microcitrus* and *Eremocitrus*. Therefore, the 'true citrus' group can be considered as the fundamental germplasm to improve citrus by sexual hybridization and needs to be integrated in the international efforts to map and exploit the citrus genome.

2.3 The reticulate evolution of the cultivated citrus and facultative apomixes resulted in a highly structured gene pool

Within the *Citrus* genus, the taxonomy remained confused and conflicted for a long time with two principal classifications that are still used today: the Tanaka system (Tanaka, 1954) which recognizes 156 species of *Citrus* while the Swingle and Reece classification (Swingle and Reece, 1967) is limited to 16 species. The reticulate evolution of the cultivated citrus combined with partial apomixis and vegetative propagation were the main sources of difficulties to establish *Citrus* classifications. Indeed many taxonomists considered interspecific hybrids, propagated true to ness by apomictic seeds, as new species (Lawrence, 1951). Recently, phylogenetic and phylogenomic studies revealed the origins and admixtures of modern cultivars and wild types and clarified the organization of the citrus gene pool.

Most recent molecular studies (Nicolosi et al., 2000; Garcia-Lor et al., 2013b; Ollitrault et al., 2012b; Barkley et al., 2006; Curk et al., 2015, 2016; Wu et al., 2018; Carbonell-Caballero et al., 2015) agree that the cultivated *Citrus* results from a reticulate evolution involving four ancestral species: *C. maxima* (the pummelos), *C. medica* (the citrons), *C. micrantha* (a wild papeda) and *C. reticulata* (very closely related with the mandarin horticultural group). The differentiation between these four sexually compatible ancestral taxa resulted from a founder effect in four geographic zones and initial allopatric evolution (Swingle and Reece, 1967; Scora, 1975; Webber, 1943; Wu et al., 2018). *C. reticulata* originated and initially diversified in Vietnam, Southern China and Japan; *C. maxima* evolved in Indonesia and the Malay Archipelago; *C. medica* originated in Northeastern India and the nearby region of Burma and China; and *C. micrantha* is native to the southern Philippines. Interestingly, while most actual pummelos, citrons and 'Small flowered papedas' appear, respectively, as pure representative of *C. maxima, C. medica* and *C. micrantha,* the recent phylogenomic studies (Wu et al., 2014, 2018; Oueslati et al., 2017; Curk et al., 2015) revealed that most of the cultivated mandarin where introgressed by *C. maxima*.

All other edible *Citrus* secondary species such as *C. sinensis* (sweet oranges), *C. aurantium* (sour oranges), *C. paradisi* (grapefruits), *C. aurantiifolia* ('Mexican lime' type) and *C. limon* (lemons), for the most important horticultural groups, resulted from admixture of these ancestral taxa (Curk et al., 2015, 2016; Oueslati et al., 2017; Wu et al., 2018; Ahmed et al., 2019). The *C. reticulata/C. maxima* admixture gene pool is particularly important from a horticultural point of view as it includes mandarins, pummelos, sweet and sour oranges, grapefruits and recent hybrids such as tangelos (mandarin × grapefruit), tangors (mandarin × sweet oranges) and orangelo (orange × grapefruits). In many cases, the interspecific hybrids resulting from the reticulate evolution were polyembryonic and the facultative apomixes greatly limited further sexual recombinations resulting in mosaics of large genome fragments from different species including frequent interspecific heterozygosity (Wu et al., 2014, 2018; Oueslati et al., 2017).

Another consequence of this reticulate evolution coupled with apomixes, and resulting limited interspecific recombination, is the very high structuration of the genetic diversity of the gene pool when considering the *Citrus* genus globally. An important part of the actual phenotypic diversity of edible citrus should be related to the interspecific differentiation during the allopatric evolution of the ancestral taxa. As a result, the organization of phenotypic polymorphisms is closely associated with the pattern of genetic diversity. Such links with genetic organization were observed for morphological and pomological characters (Ollitrault et al., 2003; Barrett and Rhodes, 1976), flavone constitution (Mizuno et al., 1991), peel oil volatile compounds (Liu et al., 2013a), carotenoid contents (Fanciullino et al., 2006), coumarin and furanocoumarin constitution (Dugrand-Judek et al., 2015) and fingerprinting of secondary metabolites (Matsukawa and Nito, 2017). It results from a generalized LD, when considering the global *Citrus* genus gene pool, also revealed from molecular marker analysis (Garcia-Lor et al., 2012). As mentioned before, this generalized LD should preclude GWAS considering only the natural germplasm. However, the importance of the interspecific component (between the ancestral taxa) in overall phenotypic polymorphism, opens the way for marker-traits association studies based on ancestral haplotype using composite populations resulting from diverse hybridizations.

In horticultural groups such as sweet and sour oranges, grapefruit, lemons and limes, vegetatively propagated by apomictic seeds or horticultural methods (grafting, cutting) the intra-group variability results from mutations, transposable element activation or epigenetic features. As we will discuss below, catching the molecular bases of this phenotypic variability generally needs specific approaches in relation with the considered mechanisms of diversification.

2.4 Ploidy manipulation is an important component of citrus breeding

Most of the citrus germplasm is diploid with a basic chromosome number of 9 (Krug, 1943). However, spontaneous reproductive features can lead to ploidy variation. Chromosome doubling of nucellar cell is relatively frequent in apomictic lines (Aleza et al., 2011), producing doubled-diploid genotypes. Unreduced (2n) gamete are produced both in pollen and ovules. Second division restitution (SDR) was found to be the main mechanisms of 2n ovules formation in mandarin (Cuenca et al., 2011, 2015), in tangors including clementine (Xie et al., 2014; Aleza et al., 2015) and lemon (Rouiss et al., 2017b) while first division restitution (FDR) was predominant in the pollen of a Clementine × Sweet orange hybrid (Rouiss et al., 2017a). In relation with the objectives of citrus genetic improvement and taking advantage of the natural mechanisms of polyploidization, ploidy manipulation became an important component of citrus genetics and breeding. For varieties, the main objective is to develop triploid seedless cultivars. For rootstock, the aim is to develop interesting traits in tetraploid hybrids and to improve adaptation to biotic and abiotic stresses. Thus, beside diploid hybrids, citrus breeders manage recombining triploid and tetraploid progenies requiring, as discussed below, specific tools and approaches for marker-traits association studies, MAS and GS.

3 Forty years of molecular markers development to study and exploit the citrus genome

Citrus has a relatively small genome size varying among ancestral taxa from 398 to 360 Mb/haploid genome for *C. medica* and *C. reticulata*, respectively (Ollitrault et al., 1994). *C. maxima* had an intermediate genome size of 383 Mb and the one of *C. sinensis* was estimated to be 372 Mb (Gmitter et al., 2012).

3.1 The dominant polymerase chain reaction-based markers

Citrus genome study started during the 1980s with isozymes markers (Torres et al., 1982). Several kinds of dominant nuclear markers based on polymerase chain reaction (PCR) were developed such as random amplified polymorphic DNA (RAPDs; Xiao et al., 1995; Luro et al., 1992), inter-simple sequence repeat (ISSR; Fang and Roose, 1997; Fang et al., 1997b, 1998b) and amplified fragment length polymorphisms (Fang et al., 2009; Liang et al., 2007; de Oliveira et al., 2007). These methods had the advantage of being easy to perform and do not require previous knowledge on citrus genome. They were used for germplasm studies (Krueger and Roose, 2003; Pang et al., 2007; Kumar et al., 2010; Biswas et al., 2010a,b; Yang et al., 2010; Lombardoa et al., 2012; Dorji and Yapwattanaphun, 2015; Munankarmi et al., 2018), nucellar/zygotic differentiation (Rao et al., 2007) and somatic hybrid genome characterization (Scarano et al., 2002; Guo and Deng, 2001; Fu et al., 2004), genetic mapping and marker-traits association (de Simone et al., 1998; Sankar and Moore, 2001; Choi et al., 2007; de Oliveira et al., 2007; Gulsen et al., 2010; Roose et al., 2000). However, today, their dominant character and the lack of knowledge of their sequence and position on the citrus genome strongly limit their usefulness compared with the new generation of co-dominant markers.

3.2 The mono-locus co-dominant markers

Restriction fragment length polymorphisms (RFLPs) were the first single locus co-dominant markers developed in citrus (Durham et al., 1992; Luro et al., 1996; Federici et al., 1998, 2000), but, due to technical difficulties and the development of co-dominant PCR markers, their application remained limited. Simple sequence repeat (SSRs) markers have been derived from genomic data (Kijas et al., 1995; Barkley et al., 2006; Froelicher et al., 2008; Ollitrault et al., 2010; Liu et al., 2013b) and from transcriptomic data (Chen et al., 2006; Luro et al., 2008; Liu et al., 2013b; Liang et al., 2015; Shimizu et al., 2016). They have been included in citrus genetic maps (Ruiz and Asins, 2003; Chen et al., 2008b; Lyon et al., 2007; Luro et al., 2008; Bernet et al., 2010; Raga et al., 2012; Ollitrault et al., 2012a; Cuenca et al., 2016). They were also used for the analysis of genetic diversity (Shimizu et al., 2016; Luro et al., 2001, 2012; Corazza-Nunes et al., 2002; Barkley et al., 2006; Garcia-Lor et al., 2012, 2015; Curk et al., 2016), the discrimination of zygotic and nucellar seedlings (Ruiz et al., 2000; Rao et al., 2008; de Oliveira et al., 2002), the control of the origin of plants obtained by induced gynogenesis and androgenesis (Froelicher et al., 2007; Germana et al., 2013; Aleza et al., 2009) and somatic hybridization (Chen et al., 2008a; Bassene et al., 2009), the molecular characterization of triploid cultivars (Aleza et al., 2010) and the analysis of the origin of 2n gametes (Luro et al., 2004; Chen et al., 2008b; Ferrante et al., 2010; Cuenca et al., 2011, 2015; Rouiss et al., 2017a,b).

With the development of NGS methods SNPs have become the most important resources for molecular marker development. They were mined from trancriptomic (Chen and Gmitter, 2013) or genomic data (Ollitrault et al., 2012b; Wu et al., 2014, 2018). Efficient SNP genotyping methods have been developed for scalable experiments using competitive allele amplification (KASPar© technology; Garcia-Lor et al., 2013b; Cuenca et al., 2013a). Curk et al. (2015, 2016) developed a set of KASPar SNP markers specific to the four ancestral taxa and studied the phylogenetic origin of the modern varieties. The ancestor diagnostic SNPs were also very useful to analyse the meiotic behaviour of allotetraploids and to identify zygotic plants in the seedlings of interspecific or intergeneric hybrids (Ollitrault et al., 2016; Bruyere et al., 2016). In Japan, special emphasis was given to the development of cleaved amplified polymorphic sequences targeting previously mined SNPs (Shimada et al., 2014; Omura and Shimada, 2016).

3.3 High-throughput genotyping

For high-throughput studies, several SNP arrays have been developed. Ollitrault et al. (2012b) focussed on markers useful to establish the reference genetic map of clementine and therefore heterozygous for this cultivar. They were mined in Clementine BAC-end sequences (Terol et al., 2008) to implement an Illumina GoldenGate assay including 1494 SNPs. Fujii et al. (2013) genotyped Japanese germplasm and recombining populations with an Illumina array of 384 SNPs while Yu et al. (2016) used a 1536-SNP Illumina GoldenGate assay to establish the genetic maps of Fortune and Murcott mandarins. Recently, two Affymetrix Axion SNP arrays with about 1.5 million and 56 000 SNPs were developed from the polymorphisms mined in 30 re-sequenced citrus accessions including the relative genera *Poncirus, Fortunella, Microcitrus and Eremocitrus* (Eck et al., 2016). GBS, RAD-sequencing and DARTSeq were also successfully developed in citrus and applied for germplasm analysis (Penjor et al., 2014; Oueslati et al., 2017; Ahmed et al., 2019), genetic mapping (Guo et al., 2015; Curtolo et al., 2017a,b; Huang et al., 2018), QTL studies (Curtolo et al., 2017a) and GWAS (Imai et al., 2018).

3.4 Markers for polyploid citrus studies

The genetics of polyploid species remains much more challenging than diploid genetics. Indeed, accurate polyploidy population genetic studies require the estimation of molecular marker allele copy number of heterozygous genotypes. Moreover, allelic dosage can affect gene expression and phenotype and its determination is therefore particularly important for marker-trait association studies (De Jong et al., 2003). Several methods have been developed to estimate allele dosage in polyploid citrus genotypes. For SSRs markers, the MAC-PR method (Esselink et al., 2004) was proposed to deal with differential amplification intensities among alleles in polyploid plants and was successfully transferred in citrus (Ferrante et al., 2010; Cuenca et al., 2011). For SNP markers, Cuenca et al. (2013a) demonstrated the efficiency of the KASPar SNP genotyping technique, to assign heterozygous allelic configurations within polyploid citrus populations. MAC-PR approach for SSRs markers and KASPar technology for SNPs were routinely applied for the study of 2n gamete origin and their genetic structures (Cuenca et al., 2015; Aleza et al., 2015; Rouiss et al., 2017b; Rouiss et al., 2017a), tetraploid meiosis analysis (Rouiss et al., 2018; Aleza et al., 2016; Ollitrault et al., 2016), centromere mapping (Aleza et al., 2015) and marker-trait association in a triploid progeny (Cuenca et al., 2013b). To achieve high throughput, Ahmed et al. (2019) developed a pipeline, based on a maximum likelihood analysis from the number of GBS reads, to infer ancestor doses along the genome of triploid and tetraploid individual. Beside molecular markers, the estimation of ploidy level by flow cytometry (Ollitrault and Michaux-Ferriere, 1992; Ollitrault et al., 1994) constituted a decisive step to manipulate efficiently the ploidy of the citrus genome. Indeed, it allowed the screening of large populations to identify spontaneous doubled diploids in polyembryonic seedlings (Aleza et al., 2011), to select triploids issued from 2n gametes in 2x × 2x hybridizations (Aleza et al., 2010) and to identify triploid and tetraploid plants in interploid progenies (2x × 4x and 4x × 2; Aleza et al., 2012a,b).

3.5 Markers of asexual diversification processes

Within vegetatively propagated horticultural groups such as sweet orange, where phenotypical diversity is not related with sexual recombination, targeted studies of transposable elements make it possible to reveal polymorphisms among varieties (Breto et al., 2001; Tao et al., 2005; Bernet and Asins, 2003; Bernet et al., 2004b) and transposition events directly linked with phenotypic variation such as the production of anthocyanin in blood oranges (Butelli et al., 2012) and apomixes in mandarins (Wang et al., 2017). IRAP and REMAP markers have also been used for studies of genetic similarity based on retro-transposon within the genus Citrus and its relatives (Biswas et al., 2010a,b).

4 Citrus genetic mapping

4.1 Early citrus genetic mapping work

Due to the important heterozygosity of citrus germplasm, most of the citrus genetic maps were developed from F1 crosses and segregation analyses allowed developing genetic maps for each of the parents and eventually consensus genetic maps (Table 1). Early genetic maps (1990, 2005) were reviewed by Ruiz and Asins (2003), Chen et al. (2008b) and Roose (2007). Many of them were based on intergeneric hybrids between *Citrus* and *Poncirus*, due to the importance of *Poncirus trifoliata* for rootstock breeding and particularly its immunity to CTV. Most of these maps suffered from relatively low numbers of analysed hybrids and from the multilocus and dominant nature of the markers (RAPD, ISSR, AFLP), even if a few isozymes and RFLPs were included. In most cases they resulted in more or less than nine linkage groups (LGs). Cai et al. (1994) using 189 markers (RAPD, RFLP, isozymes) were the first to propose a map with nine LGs from a small population of 65 hybrids resulting from an intergeneric backcross (*C. grandis* cv. Thong Dee × USDA 17-40 (*C. grandis* cv. Thong Dee × *P. trifoliata* cv Pomeroy)). It was extended to 310 markers using ISSR (Sankar and Moore, 2001). The first map of co-dominant markers grouped in nine LGs was based on 120 CAPS markers genotyped in a progeny of 125 BC1 hybrids of Kiyomi (*C. unshiu* cv. Miyagawa × *C. sinensis* cv. Trovita) × *C. unshiu* cv. Miyagawa (Omura et al., 2000). Subsequently, several maps were generated using co-dominant markers, particularly SSRs (Bernet et al., 2010; Chen et al., 2008b; Lyon et al., 2007) but failed to result in nine LGs due to insufficient marker numbers. During the same period, de Oliveira et al. (2007) and Gulsen et al. (2010) published new genetic maps of nine LGs mostly based in dominant markers, respectively, for Murcott tangor (227 AFLPs) and clementine and Orlando tangelos (with, respectively, 215 and 189 SRAP, RAPD, SSR, ISSR and POPG markers). However, none of these maps encompassed enough markers with published sequences to establish a reference citrus map which could be combined with whole-genome sequence data.

4.2 Saturated and reference genetic maps of citrus species

Given its aim to establish the citrus genome reference sequence from a haploid clementine, the International Citrus Genome Consortium (ICGC) identified the construction of a saturated genetic map of clementine as essential to improve the whole-genome sequence assembly in pseudomolecules (chromosomes).

Index

β-carotene 67

2,4-dichlorophenoxyacetic acid (2,4-D) 356–357

ABA. *see* Abscisic acid (ABA)
ABS. *see* Alternaria Brown Spot disease (ABS)
Abscisic acid (ABA) 357
Abscission chemicals 54
AC. *see* Activated charcoal (AC)
Academia Sinica 335
ACIAR. *see* Australian Centre for International Agricultural Research (ACIAR)
Activated charcoal (AC) 352
AFLP. *see* Amplified fragment length polymorphism (AFLP)
Agrobacterium tumefaciens 481
AIP. *see* Aminoindan-2-phosphonic acid (AIP)
Air-layering method 575
'Alborea' mandarin 188
Allahabad Safeda 393, 394, 426
Allotetraploids 160
Alternaria alternata 4, 196, 583
Alternaria Brown Spot disease (ABS) 195–196
American Heart Association 323
Aminoethoxyvinylglycine (AVG) 357
Aminoindan-2-phosphonic acid (AIP) 352
Amplified fragment length polymorphism (AFLP) 9, 12, 161, 479–480, 491, 492, 525, 532
Animal and Plant Health Inspection Service (APHIS) 79, 108, 124, 130–131
ANN. *see* Artificial Neural Network (ANN)
APCC. *see* Asian and Pacific Coconut Community (APCC)
APHIS. *see* Animal and Plant Health Inspection Service (APHIS)
APHIS CHRP Citrus Health Response Program 131
Aphis citricola 98
Arachis pintoi 298
Area-wide integrated pest management (AW-IPM) 105–106, 129–130
Aril browning 585
Arka Amulya 394
Artificial Neural Network (ANN) 57
Artificial pollination 333
Asexual propagation 418–419
Ashburner, Guy 254
Asian and Pacific Coconut Community (APCC). *see* International Coconut Community (ICC)
Asian citrus psyllid (ACP). *see Diaphorina citri*
Australian Centre for International Agricultural Research (ACIAR) 369
Autotetraploids 160
AVG. *see* Aminoethoxyvinylglycine (AVG)
Avocado cultivation
  cultivars 250–251
  fertility management
    minor elements 248
    nitrogen 244–247
    phosphorus 248
  high-density production 252–254
  irrigation management 248
    good-quality water 250
    scheduling 249–250
  overview 239–241
  pest management 255–256
  root rot management 254–255
  rootstocks 252
  soil management 241–244
Avocado propagation 231
  advances in micropropagation 221
    acclimatization 225
    culture initiation 222
    nodal culture 221–222

    rooting 224
    shoot induction 222–223
  clonal 217–219
  cultivation 216–217
  meristem culture for 225
    advances in 227–228
    woody plants 226–227
  micrografting for disease-free planting material 228–230
  overview 215–216
  tissue culture as sustainable alternative 220–221
  tissue culture for 219–220
AW-IPM. *see* Area-wide integrated pest management (AW-IPM)

Bacillus thuringiensis 480
Backcross breeding programme 536
Bacterial blight disease 583
Bacterial dieback disease (BDB) 534
Balsamocitrinae tribe 5
Banana Bunchy Top Virus 262
Banana production systems 311–313
  assessing gaps in resource efficiency 270–272
  climate and weather variability in 308–310
  cropping systems with trees 301–304
  ecological intensification gap 272–273, 275
  growing with other crops 297–301
  improving
    ecological intensification 281–284, 286
    identifying priorities for 281
    measuring potential 266
  life cycle assessment (LCA) and certification-based measurements 275–280
  mat density 295–297
  nutrient cycling/balance and soil health 304–305
    residue management 307–308
    using off-farm resources 306
    using on-farm resources 305–306
  overview 261–263
  selection, date and frequency 286–291
    mother plants selection 291–292
    planting material 292, 294
    planting/replanting dates 294
    sucker selection 294–295
  types 263–266
  yield gap analysis 266–270
'Bangkok Apple' 390, 392
Bayesian classifier 57
BC. *see* Biochar (BC)
BDB. *see* Bacterial dieback disease (BDB)
Biochar (BC) 352
Biological control
  of citrus postharvest decay 76
  of fruit flies 105
'Bio-Save® 10 LP' 75
Bisexual plants 549
Black spot and bacterial dieback disease 533–534
Blood lime 145
Brachiaria decumbens 298
Bridge crossing concept 531
Brontispa longissim 350
Brown citrus aphid. *see Toxoptera citricida*
Byrachandra 452

CABI. *see* Centre for Agriculture and Bioscience International (CABI)
Caging technique 474
Calamondin. *see Citrofortunella mitis*
California Citrus Program 109
California Department of Food and Agriculture 108–109
California Irrigation Management Information System (CIMIS) 249
Camp, A. F. 118
Candidates Phytoplasma aurantifolia 166
CAPS. *see* Cleaved amplified polymorphic sequence (CAPS)
Cas. *see* CRISP-associated proteins (Cas)
Cavendish monoculture 299
Cell specification 359
Cell suspension culture systems 357–358
Central Plantation Crops Research Institute (CPRI) 335
Centre for Agriculture and Bioscience International (CABI) 108
Centre for Insect Physiology and Ecology (ICIPE) 109
Ceratitis capitata 98–99, 583
Ceratitis rosa 99
CGRD. *see* Coconut Genetic Resources Database (CGRD)
Chilling injury 71
  preharvest factors affecting 72
  reducing symptoms
    fungicides 73
    modified atmospheres 74
    plant growth regulators 73
    temperature treatments 73
    waxes 74

Chinese Academy of Agricultural Sciences 109
Chinese lime. *see* Eustis lime
Chlorantraniliprole 583
Chlorine 77
Chloroplast (CPT) 163
CHMAs. *see* Citrus Health Management Areas (CHMAs)
CHRP. *see* Citrus Health Response Program (CHRP)
CIMIS. *see* California Irrigation Management Information System (CIMIS)
Citreae tribe 5
Citrinae tribe 5
Citrofortunella mitis 144
Citrus fruits
  genome 27–28
    citrus tristeza virus (CTV) immunity 24
    dominant polymerase chain reaction-based markers 9
    early genetic mapping 12
    genome-wide association studies (GWAS) 26
    genomic selection (GS) 26
    high-throughput genotyping 10
    inheritance by diploid gametes 19–20
    interspecific and intergeneric sexual compatibility 6
    MAS application for monogenic-controlled traits 24–25
    markers for polyploid citrus studies 11
    markers of asexual diversification processes 11–12
    mono-locus co-dominant markers 9–10
    non-Mendelian segregations and genetic determinism 18–19
    overview 3–5
    ploidy manipulation 8
    quantitative trait loci (QTLs) studies 25–26
    reference genome sequences 20–21
    re-sequencing data and exploitation for phylogenomy 21, 23
    reticulate evolution and facultative apomixes 6–8
    saturated and reference genetic maps 12, 18
    synteny 18
    taxonomic position 5–6
    zygotic/nucellar seedlings 24
  harvesting 59–60
    aids 47–52
    manual 44–47
    mechanical 52–56
    overview 43–44
    precision agriculture 57–58
    robotic 56–57
  see also Citrus pests; Lime breeding; Postharvest handling of citrus fruit
Citrus greening disease 44, 55, 59, 101–104, 117–118, 185
Citrus Health Management Areas (CHMAs) 122–124
Citrus Health Response Program (CHRP) 108, 131
Citrus leaf blotch virus (CLBV) 192
Citrus leafminer (CLM) 123, 125–126, 128–129
Citrus × limonia *osbeck* 144
Citrus macrophylla 3
Citrus pests 108–108
  Diaphorina citri ecology 101–104
  fruit flies management
    economic importance and control 104–105
    with sterile insect technique (SIT) 105–107
  overview 91–92
  tools in research
    modeling of species distribution (SDM) 98–100
    stable isotope analysis (SIA) 100–101
  types 92, 97–98
Citrus Research & Education Center 108
Citrus Research Institute 109
Citrus Research Program (CRB) 109
Citrus sinensis 43
Citrus tristeza virus (CTV) 4, 12, 24, 144, 169
CitRWP candidate gene 153
CK. *see* Cytokinins (CK)
Clauseneae tribe 5
CLBV. *see* Citrus leaf blotch virus (CLBV)
Cleaved amplified polymorphic sequence (CAPS) 492
Cleaved amplified polymorphisms 161
'Clementine' mandarin 186, 190, 193
Cleopatra mandarin 3–4
CLM. *see* Citrus leafminer (CLM)
Clonal propagation 476, 558

Clonal rootstocks 216–217
Clustered regularly interspaced short palindromic repeats (CRISPR) 192–193
Coconut
  breeding 337
    genetic resources 330–331
    mass selection and hybridization 331–333
    molecular breeding techniques 334–336
    origin and botany 326–330
    overview 323–324
    uses 324–326
  cultivation 324–326, 369
    elite genotypes production 350–351
    harvesting 364–365
    improving potential yield 348–349
    nursery and productive plantation management 360–364
    overview 345–348
    products and processing 365–368
    protecting from biohazards 350
    and somatic embryogenesis (SE) 351–352, 356–360
Coconut Genetic Resources Database (CGRD) 331
COGENT. *see* International Coconut Genetic Resources Network (COGENT)
Colchicine 152
Cold treatment 78–79, 86–87
Comité de Sanidad Vegetal (COSAVE) 109
Coorg Honey Dew 523
COSAVE. *see* Comité de Sanidad Vegetal (COSAVE)
Cover crops 298–300
CPRI. *see* Central Plantation Crops Research Institute (CPRI)
CPT. *see* Chloroplast (CPT)
CRB. *see* Citrus Research Program (CRB)
CRISP-associated proteins (Cas) 192–193
CRISPR. *see* Clustered regularly interspaced short palindromic repeats (CRISPR)
Cross-pollination 413
Cross protection 561–562
Cryopreservation 477
Cryptoxanthin 67
CsLOB1 gene 193
CsPDS gene expression 193
CTV. *see* Citrus tristeza virus (CTV)
CULTESA company 291
Cynodon dactylon 298
Cytokinins (CK) 222–223
Cytoplasmic factors control 156

DArT markers 189
DARTSeq 10, 18, 25
DE. *see* Differentially expressed (DE) genes
DeBach, Paul 92
Deblossoming 422
Deficit irrigation (DI) 504, 511
DGPS. *see* Differential global positioning system (DGPS)
DI. *see* Deficit irrigation (DI); Drip irrigation (DI)
Diagnostic SNPs (DSNPs) 23
Diaphorina citri 98, 99, 101–104, 120–123, 125–127, 129–131
Diaprepes abbreviatus 123
Differential global positioning system (DGPS) 45
Differentially expressed (DE) genes 336
Dioecious papaya varieties 525
Direct micro-expelling 366
Direct organogenesis 419
Division of Agriculture and Natural Resources 109
Division of Plant Industry 124
D-limonene 67
DNA markers 478, 510
DNA sequencing 5
Domestication process 97
Double grafting method 218
Drip irrigation (DI) 505, 580
Dry retting 367
DSNPs. *see* Diagnostic SNPs (DSNPs)

'Ecological Approach to Pest Control' 92
'Ecological Survey of Citrus Pests and Disorders' 118
EEM. *see* Extremely early maturing (EEM)
Electronic Data Information Source 119
Electronic detection 51
Ellendale mandarin 145
Emergy analysis 273, 275
EMS. *see* Ethylmethane sulphonate (EMS)
Eriwinia mallotivora 534
Erythrina poeppigiana 302
ESTs. *see* Expressed sequence tags (ESTs)
Ethyl formate 79
Ethylmethane sulphonate (EMS) 152
ETo. *see* Evapotranspiration (ETo)
Eustis lime 145
Evapotranspiration (ETo) 249–250

Expressed sequence tags (ESTs) 190, 336, 492
Extremely early maturing (EEM) 460

FAO. *see* Food and Agricultural Organization (FAO)
Farmyard manure (FYM) 581
FDR. *see* First division restitution (FDR)
Firm-fleshed type of jackfruit 437
First division restitution (FDR) 8, 19, 194–195
FISH. *see* Fluorescent in-situ hybridization (FISH)
Florida Department of Agriculture and Consumer Services 124
Fludioxonil 587
Fluorescent in-situ hybridization (FISH) 532
Foliar diagnosis 347
Food and Agricultural Organization (FAO) 84, 108
Fortune mandarin 4, 18–19
Fruit cracking 583–584
Fruit fly 424
  see also Citrus pests
Fruit sampling 104
Fumigation 79
Fusarium Tropical Race4 262, 273
FYM. *see* Farmyard manure (FYM)

GA. *see* Giberellic acid (GA)
GATA4. *see* Quadranucleotide repeats (GATA4)
G.B. Pant University of Agriculture and Technology 555
GBS. *see* Genotyping-by-sequencing (GBS)
GDD. *see* Growing degree days (GDD)
Gene expression analysis 164
Genetic mapping 10
Genetic-modified (GM) plants 193
Genome-wide association studies (GWAS) 4–5, 8, 10, 26
Genomic selection (GS) 5, 26
Genotyping-by-sequencing (GBS) 10, 11, 23, 25, 189
Geotrichum citri-aurantii 74
Germplasm analysis 10
GHG. *see* Greenhouse gas (GHG) emissions
Giberellic acid (GA) 499, 502, 511
Global positioning system (GPS) 45
GM. *see* Genetic-modified (GM) plants
Govind Bhallabh Pant University of Agriculture and Technology 535
GPS. *see* Global positioning system (GPS)
Grafting 418, 444, 576
Green citrus aphid. *see Aphis citricola*
Greenhouse cultivation 506–509
Greenhouse gas (GHG) emissions 277
Greenwaste mulches 242
Gros Michel 302–303
Growing degree days (GDD) 464
GS. *see* Genomic selection (GS)
Guava
  breeding 402
    floral biology 379–381
    genetic mapping 398–399
    genetic transformation 400–401
    heritability 383–385
    hybridisation 386, 390
    micropropagation 399–400
    molecular approaches 394, 396–398
    mutation 394
    objectives 381–383
    overview 377–379
    plant introduction 385–386
    polyploidy 390, 392–394
    selection 386
  cultivation
    climatic requirements and distribution 412–414
    composition, nutritional value and uses 414–415
    harvesting and postharvest operations 426–427
    irrigation and fertilization 422–423
    overview 411–412
    pests and diseases 423–425
    planting and cultivation techniques 419, 422
    propagation methods 415, 418–419
GWAS. *see* Genome-wide association studies (GWAS)
Gynodioecious papaya varieties 525

Half tetrad analysis (HTA) 19
Hand-pollination techniques 333
Harvesting aids
  mobile platforms
    ergonomics 47–48
    preventing accidents 51
    sorting and selection 51
  use
    deciding on 52
    for oranges 48–50
'Hass' cultivar 251

HDL. *see* High-density lipoprotein (HDL)
HDP. *see* High-density planting (HDP)
Herbicide-based weed control 298
High-density lipoprotein (HDL) 323
High-density planting (HDP) 411, 419
Higher Education Commission 151
High-throughput genotyping 5
High-throughput phenotyping 5
Hittalmani, S. V. 452
Honey Gold 523
Hortus Gold 523
HrpN recombinant protein 534
HTA. *see* Half tetrad analysis (HTA)
'Huaizhi' 459–460
Huanglongbing (HLB). *see* Citrus greening disease
Hybridization 473–474, 478

IARI. *see* Indian Agricultural Research Institute (IARI)
IBA. *see* Indole butyric acid (IBA)
ICAR. *see* Indian Council for Agricultural Research (ICAR)
ICC. *see* International Coconut Community (ICC)
ICC Advisory Committee on Health 369
ICGC. *see* International Citrus Genome Consortium (ICGC)
ICIA. *see* Instituto Canario de Investigaciones Agrarias (ICIA)
ICIPE. *see* Centre for Insect Physiology and Ecology (ICIPE)
IFAS. *see* Institute of Food and Agricultural Sciences (IFAS)
IFAS Florida Citrus Pest Management Guide 128
IIHR. *see* Indian Institute of Horticultural Research (IIHR)
Image classification methods 57
Indian Agricultural Research Institute (IARI) 382, 393, 523, 535, 555
Indian Council for Agricultural Research (ICAR) 523, 554
Indian Institute of Horticultural Research (IIHR) 447, 523
Indole butyric acid (IBA) 573, 575
Indonesian Palm Genome Project 334
'Indonesian Seedless' 390
Induced mutation breeding 186
Insecticide bait sprays 105
Institute of Food and Agricultural Sciences (IFAS) 108
Institute of Fruit Tree and Tea Science, NARO (NIFTS) 109
Instituto Canario de Investigaciones Agrarias (ICIA) 291
Instituto Valenciano de Investigaciones Agrarias (IVIA) 187
Integrated pest management (IPM) 92, 104
  abandoned citrus and 131–133
  in Florida 118–119
  Huanglongbing (HLB)
    arrival 120–123
    response to 123–124
  management practices in HLB era 125
    area-wide 129–130
    biological control 129
    chemical control 126–129
    cultural control 126
    pest monitoring 125–126
  overview 117–118
  quarantine and 130–131
  root weevil complex 123
Intergeneric hybridization 537
International Citrus Genome Consortium (ICGC) 12, 20–21
International Coconut Community (ICC) 324–325, 369
International Coconut Genetic Resources Network (COGENT) 330–331
International Conference on Coconut Oil 369
International Consortium for Citrus Genomics 190
International Plant Protection Convention (IPPC) 79–80
International Trade Center (ITC) 280
Inter-simple sequence repeats (ISSRs) 9, 12, 161, 480, 491, 525–526
Interspecific hybridization 444
Inter-varietal hybridization 333
Intraspecific somatic hybrids 476
In vitro micropropagation system 229
In vitro propagation 419
In vivo techniques 418–419
IPM. *see* Integrated pest management (IPM)
IPPC. *see* International Plant Protection Convention (IPPC)
Irradiation treatments 79–80
Isolated seed gardens technique 333
ISSRs. *see* Inter-simple sequence repeats (ISSRs)
ITC. *see* International Trade Center (ITC)

IVIA. *see* Instituto Valenciano de Investigaciones Agrarias (IVIA)
'IVIA-TRI707' 188

Jackfruit 455
  biology 439–440
  breeding and examples 441–442, 444
    genotypes classification 448–454
    Gumless type 447
    Konkan Prolific 447–448
    PalurJack/PLR Jack 2 446
    Palur/PLR 1 444
    Pechiparai/PPI 1 444, 446
    Swarna Halasu 446–447
  nutritional composition 440–441
  origin, distribution and uses 436–438
  overview 435
Janagere 449
Japanese mango greenhouses 509

Kabosu fruit 144
Kachahalli Roadside (Kempusiddappa) 449–450
Kachahalli Table type 12 450–451
Kaffir lime 145
KASPar SNP genotyping technique 11
'Keitt' cultivar 497, 502
'Kensington Pride' 490
KMN clustering 57

Lalbaugh Madhura 447
LCA. *see* Life cycle assessment (LCA)
LD. *see* Linkage disequilibrium (LD)
Leaf beetle. *see Brontispa longissim*
Lethal yellowing disease (LYD) 363
LGs. *see* Linkage groups (LGs)
Life cycle assessment (LCA) 275–280, 279–280, 281
Lime breeding 170
  economic importance and distribution 145–146
  germplasm collections, biodiversity and conservation 148–149, 151
  low productivity 148
  molecular approaches in improvement
    bioinformatics and genomics 164
    molecular markers and applications 161, 163–164
    reference genes selection 164, 166
    Ruby gene diversity and anthocyanin production 166–167
  transgenics 167, 169
  origin, classification, domestication and reproductive biology 139–140
  systems
    conventional and mutation 152
    cytogenetics 154
    ploidy manipulations and seedlessness 154–161
    polyembryony, apomixis and candidate gene(s) 152–154
  varieties 144–145
    acid limes 140–142
    Australian lime types 143
    hybrids 145
    Rangpur lime 144
    small-fruited acid citrus 143–144
    sweet limes 142–143
Limequat 145
Linkage disequilibrium (LD) 5, 8
Linkage groups (LGs) 18
Litchi
  cultivar quality and yield 461
  extension of production season 459–460
  improving tree management 461, 463
    flush growth cycle and flowering 464
    fruit set 465
    postharvest handling 465–467
    postharvest recovery 463
  overview 457–459
Lucknow-49 426
LYD. *see* Lethal yellowing disease (LYD)

MAB. *see* Marker-assisted breeding (MAB)
MAC-PR. *see* Microsatellite DNA allele counting–peak ratios (MAC-PR)
Macrodactylus pumilio 101
'Maguili' 459–461
Mandarin breeding 198
  conventional programs
    mutation breeding 186–187
    nucellar selections 185–186
    sexual hybridization 187–188
  overview 183–185
  tools for 188
    biotechnological 191–193
    genomic 190–191
    molecular 189–190
  triploid cultivars resistant to Alternaria brown spot disease 193–197
Mangoes
  breeding
    conventional methods 472–474

    - genetic engineering 480–481
    - molecular markers use 478–480
    - molecular methods 474–475
    - overview 471–472
    - in vitro techniques 475–478
  - cultivation 511–512
    - genetic considerations 490–493
    - overview 489
    - physiological aspects 493–496
    - techniques 497–510

MAP. *see* Modified atmosphere packaging (MAP)
Marker-assisted breeding (MAB) 396
Marker-assisted selection (MAS) 5, 24–26, 196–197, 334, 478
Mass trapping 105
Maxent. *see* Maximum entropy modelling (Maxent)
Maximum entropy modelling (Maxent) 99
Maximum likelihood analysis 11
MCT. *see* Medium chain saturated fatty acids (MCT)
Mealy bug infestation 560
Mechanical harvesting 52–55
  - automation 56
  - fruit detachment and quality 55–56

Mediterranean fruit fly. *see Ceratitis capitata*
Medium chain saturated fatty acids (MCT) 323
Meristem-tip culture process 227–228
Methyl bromide 79
Methyl jasmonate 587
Mexican lime (ML) 140–142
Microarray genotyping 5
Microcloning technique 218
Micropropagation 333
Microsatellite DNA allele counting—peak ratios (MAC-PR) 11
Microsatellites. *see* Simple sequence repeats (SSRs)
Mineralization process 247
Miniature inverted-repeat transposable element (MITE) 23, 25, 153
MITE. *see* Miniature inverted-repeat transposable element (MITE)
ML. *see* Mexican lime (ML)
Modeling of species distribution (SDM) 98–100, 99
Modified atmosphere packaging (MAP) 585, 587
Molecular marker systems 331
Monoembryonic mango 490–491
Monosalva, Patricia 252
Montreal Protocol on Substances that Deplete the Ozone Layer 79
MOSCAFRUT facility 106
Mulched avocados 243–244
Muniraju Ramachandra Hosur 453–454

Naphthalene acetic acid (NAA) 573, 575, 577
NAPPO. *see* North American Plant Protection Organization (NAPPO)
National Clonal Germplasm Repository of Citrus and Date (NCGRCD) 148
National Fruit Fly Program 106
National Institute of Nutrition 415
National Research Centre for Citrus 109
National Research Council 131
National Seed Project (NSP) jackfruit 451–452
Natural energy 273, 275
Naupactus cervinus 101
NCBI GenBank Database 335
NCGRCD. *see* National Clonal Germplasm Repository of Citrus and Date (NCGRCD)
Neoseiulus californicus 255
Next-generation sequencing (NGS) methods 5, 10, 18, 161, 164, 492, 510
NIFTS. *see* Institute of Fruit Tree and Tea Science, NARO (NIFTS)
'Niu kafa' 328
'Niu vai' 328
North American Plant Protection Organization (NAPPO) 108
NSP. *see* National Seed Project (NSP) jackfruit
Nursery grafting technique 229

'Orah' mandarin 187
Oranges. *see Citrus sinensis*
Organic waste 245
Organogenesis 477
'Orri' mandarin 187
Ozone 77

PAA. *see* Peracetic acid (PAA)
Paclobutrazol (PBZ) 502, 511
Papaya
  - breeding 538
    - back crossing 524
    - for disease resistance 527–534
    - germplasm collection 522–523

    - hybrids crossing and development 523–524
    - marker-assisted selection 524
    - mutation 524
    - origin and distribution 520–522
    - overview 519–520
    - programmes in India and Malaysia 534–537
    - selection 523
    - sex identification at seedling stage 524–527
  - cultivation 564
    - and climate requirements 555–557
    - fertilization 559–560
    - floral morphology, biology and pollination 550–551
    - genetics and plant breeding 551–555
    - overview 547–548
    - pests and diseases 560–563
    - plant morphology 548–549
    - propagation 557–558
    - raised bed sowing 558–559
    - ripening and harvesting 563
- Papaya black spot 519
- Papaya die back 520
- Papaya fruit fly. *see Toxotrypana curvicauda*
- Papaya ringspot virus (PRSV) 519, 522, 527–533, 537–538, 561–562
- Papaya Sex Determination Marker (PSDM) 526
- Parapheromones 105
- Parental heterozygosity restitution (PHR) 19
- Pareto-optimal solution search technique 54
- Partial root zone drying (PRD) 504, 580
- Pathogenesis-related (PR) genes 534
- PBZ. *see* Paclobutrazol (PBZ)
- PCR. *see* Polymerase chain reaction (PCR)
- Pectin methyl esterase (PME) 563
- PEG. *see* Polyethyleneglycol (PEG)
- PEMs. *see* Proembryonic masses (PEMs)
- *Penicillium digitatum* 74
- Peracetic acid (PAA) 77
- Persian lime (PL) 142
- PG. *see* Polygalacturonase (PG)
- PHB. *see p*-hydroxy benzoic acid (PHB)
- *Phomopsis psidii* 386
- Phosphonate fungicides 254
- Phosphorus solubilizing bacteria (PSB) 573
- PHR. *see* Parental heterozygosity restitution (PHR)
- *p*-hydroxy benzoic acid (PHB) 575
- *Phyllocnistis citrella* 97
- Phylogenetic origin and molecular markers 163–164
- Physical control of citrus postharvest decay 75–76
- *Phytophthora cinnamomi* 241–242, 244, 252
- *Phytophthora palmivora* 364
- Phytophthora root rot (PRR) 252, 254
- PL. *see* Persian lime (PL)
- PM. *see* Poultry manure (PM)
- PME. *see* Pectin methyl esterase (PME)
- Polyembryonic mango 490
- Polyethyleneglycol (PEG) 357
- Polygalacturonase (PG) 563
- Polymerase chain reaction (PCR) 9, 26, 161, 164, 397–398, 400, 478–479, 532, 572
- Polymorphic DNA markers 161
- Polyploidization 8
- Polyvinylpolypyrrolidone (PVPP) 352
- Polyvinylpyrrolidone (PVP) 352
- Pomegranate cultivation 589
  - advances in breeding 571–573
  - fruit thinning 584
  - irrigation and fertilization 578–581
  - overview 569–571
  - pest and disease management 581, 583
  - physiological disorder management 584–585
  - planting systems, training and pruning 576–577
  - postharvest handling 585, 587–588
  - propagation methods 573, 575–576
- *Poncirus trifoliata* 6, 12, 18
- Postharvest handling of citrus fruit 87–89
  - alternative decay control treatments 75–76
  - chilling injury 71
    - preharvest factors affecting 72
    - reducing symptoms 73–74
  - consumer and retail trends 80
    - chemical use and organics 83–84
    - nutrition and health 83
    - sustainability 84–86
    - taste 81–82
  - decay 74
  - degreening 69–70
  - food safety 77–78
  - fungicides 74–75
  - market access 78–80

  nutritional content 68–69
  origin and classification 67
  overview 65–67
  physiological storage disorders 70–71
  physiology 69
  sanitisers 76–77
Potassium fertilization 271
Poultry manure (PM) 581
PPQ Citrus Health Response Program 124
PRD. *see* Partial root zone drying (PRD)
PR genes. *see* Pathogenesis-related (PR) genes
Proembryonic masses (PEMs) 476
PRR. *see* Phytophthora root rot (PRR)
PRSV. *see* Papaya ringspot virus (PRSV)
Pruning 422
PSB. *see* Phosphorus solubilizing bacteria (PSB)
PSDM. *see* Papaya Sex Determination Marker (PSDM)
Pulp flesh gelling/translucency 562
PVP. *see* Polyvinylpyrrolidone (PVP)
PVPP. *see* Polyvinylpolypyrrolidone (PVPP)

QTLs. *see* Quantitative trait loci (QTLs)
Quadranucleotide repeats (GATA4) 526
Quantitative trait loci (QTLs) 4, 10, 25–26, 26, 334, 335, 397–399, 480

RAD-sequencing 10, 18, 25
RAF. *see* Randomly Amplified DNA Fingerprint (RAF)
Random amplified polymorphic DNA (RAPD) 9, 12, 396, 491, 525–526, 532
Randomly Amplified DNA Fingerprint (RAF) 532
Rangpur lime (RL) 144
RAPD. *see* Random amplified polymorphic DNA (RAPD); Rapid amplified polymorphic DNA (RAPD)
Rapid amplified polymorphic DNA (RAPD) 479–480
RBD. *see* Refined, bleached and deodourised (RBD)
RDI. *see* Regulated deficit irrigation (RDI)
Reference genome sequences 4
Refined, bleached and deodourised (RBD) 365
Regional Fruit Research Station (RFRS) 447
Regulated deficit irrigation (RDI) 503, 504
Respiration rate (RR) 585
Restriction fragment length polymorphism (RFLP) 9, 12, 491
RFRS. *see* Regional Fruit Research Station (RFRS)
RL. *see* Rangpur lime (RL)
Robotic harvesting 56–57
RR. *see* Respiration rate (RR)
Ruby activator 25
Rudrakshi 438

SADER. *see* Secretaría de Agricultura y Desarrollo Rural (SADER)
Sanitation 105
'Sanyuhong' 459–461
SAR. *see* Systemic acquired resistance (SAR)
'Satsuma' mandarin 185, 193
SCAR. *see* Sequence Characterized Amplified Region (SCAR)
SCOPUS database 467
SCoT. *see* Start codon targeted (SCoT)
SDI. *see* Sustained deficit irrigation (SDI)
SDM. *see* Modeling of species distribution (SDM)
SDR. *see* Second division restitution (SDR)
SE. *see* Somatic embryogenesis (SE)
Second division restitution (SDR) 8, 19–20, 194–195
Secretaría de Agricultura y Desarrollo Rural (SADER) 109
Seedlessness 157–158
Seedless Red Guava 390
Self-incompatibility 474
Self-pollination 348
Self-propelled fruit harvesters (SPFHs) 51
Semi-mechanized harvesting. *see* Harvesting aids
SENASICA. *see* Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria (SENASICA)
Sensors 57
Sequence Characterized Amplified Region (SCAR) 525
Sequence-related amplified polymorphic (SRAP) 397
Sequence-tagged microsatellite sites (STMS) 492
Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria (SENASICA) 109
Sesquiterpenes 67
Sexual propagation 418
Shoot-tip grafting in-vitro technique 185

Short tandem repeats (STRs) 526
SIA. *see* Stable isotope analysis (SIA)
Silver thiosulphate (STS) 357
SIMBA model 294, 304
Simple sequence length polymorphisms (SSLPs) 526
Simple sequence repeats (SSRs) 9, 11, 20, 24, 161, 163, 336, 396–398, 479, 491–492, 526, 572
Singapore/Ceylon jackfruit 438
Single nucleotide polymorphism (SNP) 5, 10, 20, 196–197, 492–493, 526
SIT. *see* Sterile insect technique (SIT)
Skin freckles 562
SL. *see* Sweet limes (SL)
SNP. *see* Single nucleotide polymorphism (SNP)
Soft computing methods 57
Soft-fleshed type of jackfruit 437
Soluble solids content (SSC) 81–82
Somatic embryogenesis (SE) 350, 419, 476
  challenge 351–352, 356–360
  molecular aspects in coconut 359–360
Somatic hybridization 156–157, 192, 476
Sour rot 74
Spanish breeding program 188
SPFHs. *see* Self-propelled fruit harvesters (SPFHs)
Spontaneous mutation breeding 187
Spontaneous polyploids 155
SRAP. *see* Sequence-related amplified polymorphic (SRAP)
Sri Lanka Brown Dwarf variety 333
Sri Lanka coconut breeding programme 333
SSC. *see* Soluble solids content (SSC)
SSLPs. *see* Simple sequence length polymorphisms (SSLPs)
SSRs. *see* Simple sequence repeats (SSRs)
Stable isotope analysis (SIA) 100–101
'Star Ruby' grapefruit 187
Start codon targeted (SCoT) 492
Sterile insect technique (SIT) 105–107
STMS. *see* Sequence-tagged microsatellite sites (STMS)
STRs. *see* Short tandem repeats (STRs)
STS. *see* Silver thiosulphate (STS)
'Stylar End Rot' 386
'Sudden Decline'disease 166
Supervised method 57
Support Vector Machine (SVM) 57
Sustainability 84–86
  and life cycle analysis 85–86
  postharvest technology in 84–85
Sustained deficit irrigation (SDI) 580
SVM. *see* Support Vector Machine (SVM)
Sweet limes (SL) 142–143
Sydney hybrid 145
Systemic acquired resistance (SAR) 534

TA. *see* Titratable acidity (TA)
Tahiti lime (TL) 142
Tamil Nadu Agricultural University (TNAU) 444, 446, 523, 535, 555
'Tango' mandarin 187
Tavares 145
Temporary immersion systems 358
Terpenes 67
Tetraploid ML meiosis and inheritance patterns 159–161
Titratable acidity (TA) 81
TL. *see* Tahiti lime (TL)
TNAU. *see* Tamil Nadu Agricultural University (TNAU)
Toxoptera citricida 98
Toxotrypana curvicauda 560
Transcriptome analysis 190–191
Trapping method 104–105
Tree Assistance Program 132
Trialeuroides variabilis 561
Triphasiinae tribe 5
Triploid breeding programs 188, 195
Triploid limes
  breeding manipulations 159
  origin and inheritance patterns 158–159
TROPgeneDB 335

UCR. *see* University of California Riverside (UCR)
UCR Avocado Rootstock Breeding Program 252
UF. *see* University of Florida (UF)
Ultra-high-density plantings 497–499
UN-ESCAP. *see* United Nations Economic and Social Commission for Asia and the Pacific (UN-ESCAP)
United Nations 280
United Nations Economic and Social Commission for Asia and the Pacific (UN-ESCAP) 324
United States Department of Agriculture (USDA) 79, 108, 118
University of California 109, 252
University of California Riverside (UCR) 148

University of Florida Agricultural Experiment Station 118
University of Florida Citrus Research and Education Center 118
University of Florida (UF) 108, 124
University of Queensland 227
University Putra Malaya 335
Unsupervised method 57
U.S. National Academy of Science 122–123
USDA. *see* United States Department of Agriculture (USDA)
USDA-ARS National Program Leaders 131

Variable number tandem repeat sequence (VNTRS) 479
Vasconcellea species 529–531, 538
VCO. *see* Virgin coconut oil (VCO)
Veerappa Surenahalli 453
VIGS. *see* Virus-induced gene silencing (VIGS)
Virgin coconut oil (VCO) 365–368
Virus-induced gene silencing (VIGS) 192
VNTRS. *see* Variable number tandem repeat sequence (VNTRS)

Wet retting 367
WGS. *see* Whole-genome sequencing (WGS)
Whitefly. *see Trialeuroides variabilis*
Whole-genome sequencing (WGS) 20–21
Witches Broom Disease 166
WorldClim free dataset 99
World Trade Organization 280

Xanthomonas axonopodis 583

Yardwaste 245–246

Zentmyer, George 252
Zinc deficiency 423, 580