Guide to Galapagos Seeds and Propagules

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Table of contents

Foreword

Access to information and the best possible scientific knowledge is essential in order to define both conservation priorities and adequate management decision-making. In a place as unique and well preserved as the Galapagos archipelago, the link between science and management is particularly relevant, as recognized by the Management Plan of the Protected Areas in Galapagos. In this context, this book is a practical demonstration that it is possible to turn scientific knowledge that is sometimes complex and ethereal, into something tangible, enjoyable and accessible to everyone.

The book captivated me, not only because I learned a lot about the subject but also because I consider it to be a practical, useful tool and above all, the perfect way to bring information with a deep scientific base to all citizens in general but described in a simple and understandable language for everyone. So, my congratulations to the authors for the great effort made to capture a large amount of their knowledge in a document, which will allow us to discover what lies behind those small corpuscles that we see sprouting from Galapagos plants, to which we pay very little or no attention, as they are not edible, toxic or marketable fruits and we might consider them unattractive or even of no interest at all. However, there are actually countless fascinating shapes and colors to discover, not to mention their enormous importance for the maintenance of the dynamics of ecosystems and with it the flow of services that these generate for human well-being.

The book begins with the most basic: explaining what a seed is, going through describing its types, sizes and shapes; the description of how they are kept in what we know as a seed bank, up to the description of a little-known "phenomenon" in the Galapagos: seed dispersal by different means. This book also describes the usefulness and methods that exist for its study, and ends with an extensive gallery of captivating images of seeds of different species that I invite you to review and discover, as there is an unsuspected world that the authors allow us to discover.

I am sure it will only be a matter of time before this book becomes a reference document for everyone regardless of their background, be they scientists, decision makers, public and private institutions, naturalist guides, students, teachers, the community in general and even tourists who, after reviewing this magnificent work, will have one more reason to visit the Galapagos and experience its magic. Therefore, I have the great pleasure of inviting readers to discover the surprising world of Galapagos seeds. With each of its pages, this book immerses us in a field that until now has been almost unexplored in the archipelago.

Washington Tapia Aguilera
Director of Conservation
Galapagos Conservancy

Why a seed guide for the Galapagos Islands?

Located on the equator about 1000 km off the west coast of South America, the Galapagos Islands have fascinated naturalists and scientists for centuries. The islands' long isolation has produced a high percentage of endemic species, creating unique ecosystems that were designated as the first UNESCO World Natural Heritage Site (UNESCO, 1972; Kier *et al.*, 2009). Unfortunately, such places are especially vulnerable to the detrimental effects of invasive species, climate change, and pressure from human populations, with the result being that many endemic species are also threatened or endangered (Hicks & Mauchamp, 1996; Mauchamp, 1997; Tye, 2020; IUCN, 2021). Successful conservation of natural vegetation and protection of these endemic plants must be based on an understanding of natural regeneration and the ecology of plant reproduction.

Seeds may be small and overlooked by a casual observer, but they exert powerful forces. They regenerate whole ecosystems and support complex food webs. They have been refined by natural selection to increase the persistence of plants and their genes over time and space (Cain *et al*., 2000). Seeds do not act alone, but rather enlist abiotic forces or animals to help them move. Giant tortoises and iguanas carry the seeds of many species across the Galapagos landscape (Blake *et al*., 2012; Traveset *et al*., 2016), an activity that has helped restore and maintain keystone populations of cactus (Gibbs *et al*., 2008). The fact that these seed-animal interactions can be co-opted by invasive species (Blake *et al*., 2015) merely reinforces their importance in successful plant reproduction. This is the ecological context within which seeds accomplish their mission of regeneration.

To understand the role of seeds in plant reproduction, we need to understand the physiology of seed germination and dormancy. Knowing the basic structure of seeds and fruits will also give us an insight into how plants interact with dispersal vectors as they move through the environment to places where they can originate the next generation of plants. This guide introduces seed and fruit structure within the ecological context of dispersal biology.

This guide is designed as a practical tool for visual identification of Galapagos seeds and propagules by non-botanists. This could initially seem like a challenge because seeds exhibit tremendous diversity. In addition, a system for describing morphology is not well developed for seeds as it is for example, for pollen grains. However, a careful examination of seed structure and appearance often allows identification to species if collection location is known (Martin & Barkley, 2018). In this guide we try to reduce technical language while helping readers to accurately identify the structures and species they encounter. We also categorize seeds into practical structural types that reflect adaptations for dispersal. Readers can identify seeds as they become acquainted with fruit and seed morphology: their shapes, colors, textures, and sizes shown in the photographs.

We hope the guide can be used as a reference for researchers who need to identify seeds and other propagules in ecological studies. We also hope the guide will introduce a broader public to botany and ecology, as we share our appreciation for the diversity and beauty of seeds. Perhaps in that way it can contribute to a more general awareness of the amazing biodiversity that surrounds us. Finally, the book might assist local authorities and conservation managers in their efforts to protect Galapagos ecosystems.

The first part of the book provides a general overview and description of seed and propagule structure, seed dispersal, and the study of seeds. This is followed by a reference section containing a map, pictures of seeds, and an index listing species by plant family and including their origin, conservation status, and distribution within Galapagos.

The structure of seeds and propagules

What is a seed?

Seeds are reproductive structures that result from ovule maturation in all spermatophytes (from the Greek word **σπέρμα**, sperma = "seed" and **φυτόν**, phyton = "plant"). In place of the unspecialized spores of non-seed plants, each seed contains a whole embryonic plant with energy and nutritional reserves inside a protective coat. Under appropriate conditions, each seed can develop into a new plant. Seeds were an evolutionary innovation of the Devonian period about 320 million years ago (Jiao *et al.*, 2011). The advantages of seed reproduction led first to the dominance of **gymnosperms** ("naked seeds"). Flowers and fruits first appeared over 130 million years ago with the arrival of the **angiosperms** ("enclosed seeds"). With other adaptations, the advantages of flowers for pollination and fruits for dispersal helped lead to the dominance of angiosperms in modern vegetation (Willis & McElwain, 2014).

In **angiosperms**, the **ovary** is the chamber that encloses the growing seeds, later developing into a dry or fleshy **fruit** and often facilitating dispersal. In **gymnosperms**, seeds are 'naked' on modified leaves rather than enclosed inside an ovary, but some still have dry or fleshy dispersal structures.

Based on their morphology, angiosperm seeds (*Figure 1a*) can be classified into two types: 1) **Dicotyledons** (or **dicots**) form the majority of flowering plants. Most dicots store food reserves for germination inside two embryonic leaves, known as **cotyledons** (*Figure 1a y b*). 2) **Monocotyledons** (or **monocots**) have a single cotyledon, which absorbs food stored outside the embryo in a tissue called endosperm (*Figure 1c*). Gymnosperms also store reserves in endosperm but can have more than 20 cotyledons. Distinguishing between monocots and dicots is useful, even though dicots are a paraphyletic group formed by several early diverging lineages (Stuessy 2010).

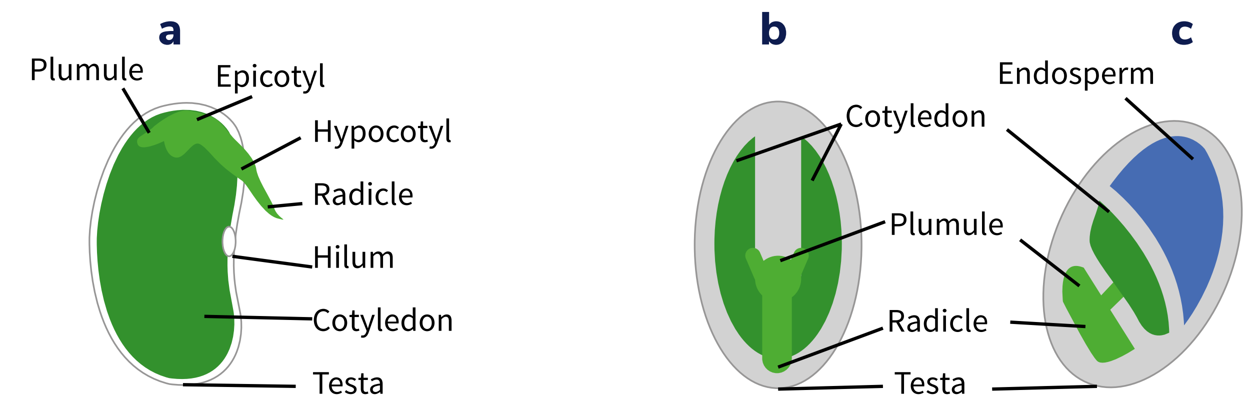


Figure 1. Seed structure. a) general seed morphology; b) internal morphology of a dicotyledon (dicot) seed; c) internal morphology of a monocotyledon (monocot) seed. Diagram by CDS Herbarium.

All seeds have the same basic structures. The **seed coat** or **testa** covers the seed and may provide mechanical protection or be a fleshy aril that aids dispersal. The **hilum** is the scar where the ovule was connected to the ovary wall. The **micropyle** is a pore in the seed coat located near the tip of the radicle, through which water enters and activates germination. The embryo itself consists of the **radicle** (the embryonic root), the **plumule** (the embryonic shoot with embryonic leaves), and the **cotyledons** (the "seed leaves") that contain energy reserves or absorb materials stored in the endosperm. The **epicotyl** and **hypocotyl** are the parts of the embryonic stem above, and below, the cotyledons, respectively (Harris & Harris, 2004).

Diversity of seed dispersal structures

The **pericarp** is the ovary wall that encloses angiosperm seeds. Evolution has modified its three layers (outer **exocarp**, middle **mesocarp,** and inner **endocarp)** to create the different fruits we see in Galapagos plants. These diverse structures interact with animals or the physical environment to help seeds move to a germination site. Differences in the structure and type of fruit often mean an animal disperser and a scientist encounter quite different parts of the same plant species.

Follicles, capsules and many **legumes** are types of **fruits** that open up to release the seeds they contain. In this case, both animals and ecologists typically encounter the seeds themselves.

In **fleshy fruits**, one or more layers of the pericarp develop into a soft, juicy, and often sweet tissue that is an attractive food for animals. In **berries**, seeds are embedded in fleshy mesocarp and endocarp. When an animal eats the berry, the fruit pulp with the seeds is digested, leaving the seeds in feces. In this case, the disperser eats the fruit, but the scientist encounters the seed in a scat. In peaches, olives, and mangoes, the mesocarp becomes fleshy and the endocarp is hard and stony; these are **drupes** (*Figure 2*). When an animal eats the fruit, its pulp is digested, leaving the **pit**, or **pyrene,** in its faeces or on the ground. Here again the disperser encounters the fruit, but in this case the scientist finds the pyrene with a hidden seed still inside. The seed emerges only when it germinates. Since scientists are likely to see the pyrene rather than the seed itself, these are pictured separately in the guide.

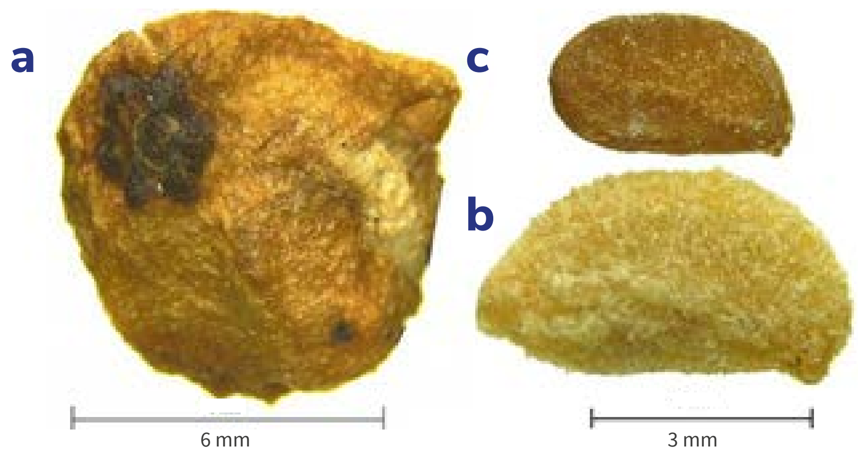


Figure 2. Right: *Chiococca alba* (Rubiaceae). a): the fruit, a drupe, b): one of the pyrenes inside the drupe, c): the seed extracted from pyrene. Photos by: CDS Herbarium. **Left:** Galapagos vegetarian finch (*Platyspiza crassirostris*) ingesting the drupes of the endemic "palo santo" (*Bursera graveolens*) on the island of Santa Cruz. Photo by: Ruben Heleno.

Some dry fruits, **schizocarps**, are split apart into separate pieces called **mericarps** (*Figure 3*). Many people in Galapagos are familiar with the "goat's head" or "puncture vine" ("cacho de chivo"), *Tribulus cistoides*, whose mericarps are armed with sharp spikes. A few species disperse other parts of a fruit separately. For example, each *Tournefortia* fruit releases four hard 'nutlets' after the flesh is digested. Some legumes, like those of *Desmodium,* split into 1-seeded segments. The guide contains a section with pictures of mericarps, pyrenes, and other fruit parts.

Figure 3. Left: *Sida ciliaris* (Malvaceae). a): fruit, a schizocarp, b): mericarp, c): seeds extracted from mericarp. Photo by CDS Herbarium. **Right:** Galapagos mockingbird (*Mimus parvulus*) eating the juicy pulp of *Opuntia* fruits on the island of Pinta. Photo by: Ruben Heleno.

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Members of the sedge family (Cyperaceae*)* produce a simple fruit called an **achene** that contains a single seed. Species in the sunflower family (Asteraceae) produce a similar fruit called a **cypsela** (*Figure 4*), which often has a modified calyx, the **pappus,** attached to the fruit itself. The hairs, bristles, or awns in the pappus can be important in dispersal as we will see below. In these cases, the whole fruit functions in dispersal so these are pictured separately in the guide.

Lastly, some species disperse more complicated structures. In the grass family, the pericarp fuses to the seed coat, forming a fruit called a **grain**, or **caryopsis**. As a result, there is often little reason to distinguish between the fruit and the seed. In grasses, floral bracts may be dispersed with the grain, so ecologists encounter whole flowers. In other species, a whole spike or spikelet is dispersed with its grain(s) inside (*Figure 5*). Sandburs, *Cenchrus*, are a common example. These are pictured separately in the guide.

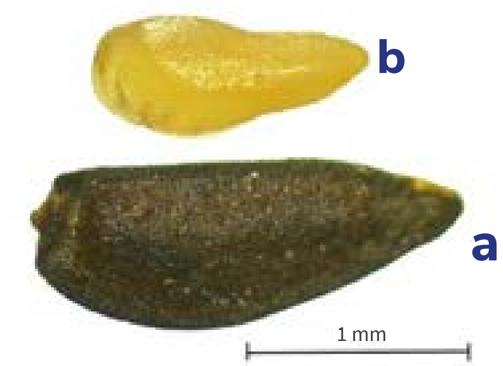


Figure 4. Left: *Acmella sodiroi* (Asteraceae). a): fruit, an achene (cypsela), b): seed extracted from fruit. Photo by CDS Herbarium.
Right: Galapagos Giant Tortoise *(Chelonoidis porteri)* at El Chato, Santa Cruz. Photo by: Joshua Vela CDF.

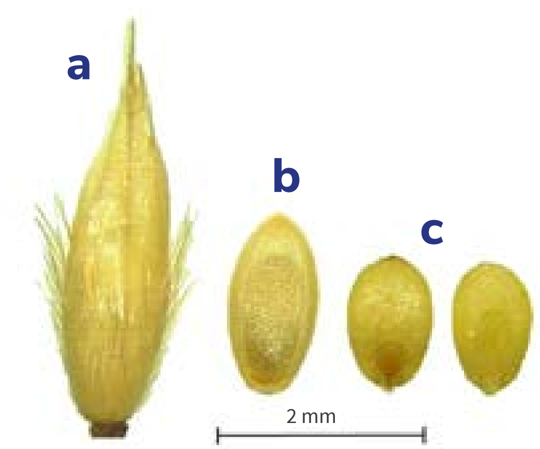


Figure 5. Left: *Coix lacryma-jobi* inflorescences with large round female spikelets and smaller male spikelets. Photo by María del Mar Trigo. **Right:** *Eriochloa pacifica* (Poaceae). a): propagule is an inflorescence, a spikelet; b): a single flower or floret; c): caryopsis from both sides. Photo by: CDS Herbarium.

The term **propagule** can be used to describe any of these dispersal structures. Seeds are visible in about half the genera in the photographic database from which we selected images for the guide (*Figure 6*). These are seeds released from capsules (the fruit of more than 100 genera), as well as those from legumes and follicles. In this group we also include seeds dispersed inside berries, since ecologists often find the seed after the fruit's flesh has been digested. The other three groups of propagules are found with roughly the same frequency. In the photos, you may notice that the seeds removed from protective propagules like pyrenes, mericarps and dry fruits are often delicate structures.

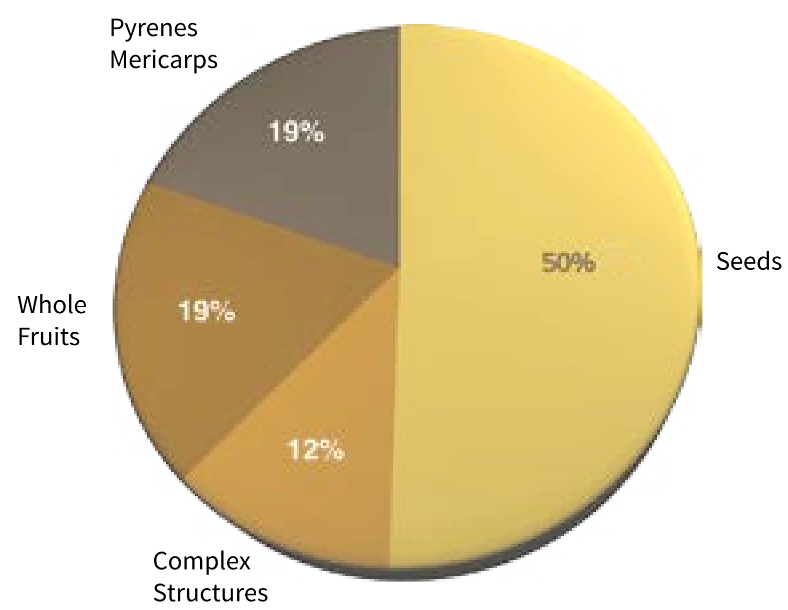


Figure 6. Left: A seed of the red mangrove (*Rhizophora mangle*) ready to start growing after being dispersed by seawater on the island of Genovesa. **Right:** Frequency of propagule types among 394 genera on our photographic database. See text for explanation of groups. **Below:** The famous seeds of *Tribulus cistoides* on the island of Daphne Major. Photos by: Ruben Heleno.

The ecology of dispersal

Trade-offs between seed size and number

The size, number and shape of seeds are modified by natural selection. All these characteristics directly affect the plant's main objective: the production of new recruits that will maximize the probability of species perpetuation. This plant **"fitness"** is principally determined by the plant's ability to disperse over both space (i.e., across the landscape) and time (i.e., across seasons and years). Seed size, shape, color, and surfaces are all important attributes in determining seed fate and therefore the long-term regeneration of plant communities.

There is a trade-off between facilitating dispersal and maximizing seed germination and growth. Larger seeds contain more energy reserves for the embryo, so they have a greater chance of germination and seedling survival, smaller seeds can be more easily dispersed over greater distances (Tiffney, 1984).

In this way, seed size is a compromise between providing reserves and at the same time allowing effective dispersal. Some plants fall at the extremes of this spectrum. For example, the remarkable fruits of the Seychelles Coco-de-Mer weigh over 25 kg and provide enough reserves for seedlings to survive in an extremely poor environment directly under the mother plant (Edwards *et al.,* 2015). The evolution of fleshy fruits provides other strategies for parental resource allocation. Plants with fleshy fruits use resources in fruit pulp to reward animals that may carry seeds over long distances. Other structural adaptations require investments of materials and energy to promote dispersal by abiotic vectors such as marine currents or wind (Ridley, 1930; Heleno & Vargas, 2015).

Another important trade-off involves the number of seeds an individual can produce (Moles *et al.,* 2007). Producing more successful seeds clearly increases the plant's chances of propagating into the next generation. However, since resources are limited, plants face a compromise between the number of seeds they produce and the reserves allocated to each seed. In other words, either produce fewer large seeds with greater chances of survival or more small seeds with lower survival probabilities (Moles *et al.,* 2007).

Seed surface is also important for seed survival, dispersal, and germination. For instance, the seed coat must be thick enough to protect the seeds from mechanical damage, dehydration and the gastric juices of frugivores (Traveset 1998), but must not be so thick as to hinder germination. Seed color and texture may prevent a seed from being conspicuous and help avoid the attention of seed predators (Beckman and Muller-Landau 2011). However, seeds of *Abrus precatorious* are protected by internal toxins, and advertise their toxicity with a bright red color. Seed shape and ornamentation can affect their longevity in the seed bank, but are particularly important in promoting the dispersal across the landscape (Van der Pijl, 1982).

Diversity in modes of dispersal

Seed movement (dispersal) from the parent plant to the final recruitment site is a key process through which plants find favorable conditions for germination and growth (Traveset *et al*. 2014). By dispersing their seeds across the landscape, plants can colonize available habitats, expand their species distribution, and escape high competition and predation near the parent plant (Janzen, 1971; Howe & Smallwood, 1982). Dispersal vectors that move seeds vary greatly in their "effectiveness", defined as their net contribution to plant recruitment (Schupp *et al*., 2010). Natural selection may develop adaptations for an effective vector that results in successful and reliable seed dispersal. Groups of plant adaptations that facilitate seed dispersal by specific vectors are called **dispersal syndromes.** The following dispersal syndromes include both biotic (animal) and abiotic vectors.

Anemochory - wind dispersal: small dry seeds can remain airborne for long periods if they have structures that increase surface area and friction with the air (van der Pijl 1982). The wing of mahogany seeds and the hairy seed coat of milkweed seeds (*Figure 7*) both facilitate wind dispersal. In many Asteraceae, the modified calyx (pappus) often consists of bristles or hairs that help the fruit float in the air. In other cases, seeds are covered by a cottony mass as seen in some poplar trees (*Populus*), willow (*Salix*) or cattail (*Typha*). Tumbleweeds, or runner plants, are a particular case of anemochory in which the entire plant is blown along the soil surface, releasing its seeds as it hits the ground.

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Figure 7. Seeds of the tropical milkweed *(Asclepias curassavica)*, an introduced species in Galapagos, which have seeds with a plume of soft hair that promotes dispersal by wind. Photos by: María del Mar Trigo and Ruben Heleno.

Hydrochory - dispersal by water currents. Fruits adapted to dispersal by water normally have impermeable membranes and low density tissues with air or oil chambers that allow the propagules to float. The fibrous mesocarp of coconut drupes (*Cocos nucifera*) is lighter than seawater so the fruits can float for long periods on the sea surface and cross long stretches of ocean. Coconuts have another remarkable adaptation to help them germinate in an inhospitable salty environment once washed ashore: they transport some fresh water as watery endosperm (coconut water). Dispersal by ocean currents is a special case of hydrochory, named **thalassochory** (from the Greek word for "sea") (van der Pijl 1982).

Ballochory – explosive dispersal mechanisms. This is an uncommon yet highly impressive, way to disperse seeds over short distances (Dalling, 2002). In a few plants, fruit maturation creates pressures or tensions within the fruit. A fortuitous event, such as a passing animal or the impact of a raindrop, will release accumulated tension and throw the seeds from the fruit. The dynamite tree, *Hura crepitans*, shoots its seeds as far as 45 m away from the parent plant (Swaine & Beer, 1977). Since this does not require any external dispersal vector, it is also called **autochory** (self-dispersal). Short-distance dispersal mechanisms like ballochory and gravity are important for plant regeneration but can have little effect on long range movement.

Zoochory – dispersal by animals. Most seeds in the tropics are transported by the action of animals. In **endozoochory,** seeds are ingested, carried inside the animal and deposited after moving through the animal's gut. In **epizoochory,** the seeds adhere to the animal's surface and are transported externally. Plant anatomy can promote one or the other of these ecological strategies. Fleshy fruits of endozoochorous plants give frugivorous animals an energetic or nutritional reward of water, energy or nutrients, often advertised with attractive odors or colours. Animals ingest the fruit, consume the reward, and deposit viable seeds in their feces. In contrast, epizoochorous propagules have a surface covered in sticky substances or mechanical structures such as hooks, spikes, or hairs. These help the propagule adhere to passing animals, particularly on animals' fur and feathers (Sorensen, 1986). Animal dispersal has the added advantage that animal behavior can seek out suitable habitat and suitable germination sites for the seeds (Howe & Smallwood, 1982; Wenny, 2001; Green *et al.,* 2009).

Dispersal by ants **(myrmecochory)** is a special type of epizoochory where seeds are deliberately transported by ants which consume appendages called **elaiosomes** (literally "fat bodies") that are rich in nutritive oils (Van der Pijl, 1982). Ants collect these seeds and carry them to their nest where they consume the elaiosomes and abandon the viable seed (García *et al*., 2012). While the distance a seed moves is short, evidence suggests ant dispersal may help the seeds avoid predation and disperse to a favorable, nutrient-rich germination site (Giladi, 2006).

The coupling between seed dispersal traits (i.e. syndromes) and their actual dispersal mechanisms is not a strict one (Vargas *et al*., 2012; Heleno & Vargas, 2015). Many types of seeds, with widely varying morphology, can be dispersed externally or internally by animals. This has been observed repeatedly, for example, in the mud adhered to waterfowl (Porter, 1983; Viana *et al*., 2016). When seeds are transported by vectors other than the ones that they are apparently adapted to, this movement is called **non-standard dispersal.**

Dispersal vectors differ greatly in their importance for plant biogeography. Ballochory and myrmecochory accomplish short-distance dispersal but have no potential for colonization of remote habitats like isolated islands. Long-distance dispersal can be accomplished by anemochory, thalassochory and zoochory. For Galapagos, evidence suggests that ocean currents (thalassochory) have been more important than wind (anemochory) in carrying propagules from the South American continent to the archipelago (Fajardo *et al*., 2019). However, the presence of a large number of plant species without specific adaptations to long-distance dispersal on many oceanic archipelagos across the world, including Galapagos, suggests that non-standard dispersal might be more common that generaly assumed (Higgins *et al*., 2003; Heleno & Vargas, 2015). Moreover, many seeds moved by the sea had adaptations for dispersal by other vectors, suggesting that non-standard long-distance dispersal is especially important in the biogeography of plants (Higgins *et al.,* 2003; Nogales *et al*., 2012).

Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Seed Dormancy

Another key advantage of seeds is promoting the survival of plant genes through adverse conditions when survival of adult plants would be unlikely (Baskin & Baskin, 2004). Inside seeds, plant genes can remain protected for days or years inside a seed that germinates only when suitable conditions occur. This happens on a yearly basis in annual plants, but latency (or dormancy) periods can be much longer, as in the successful germination of 2000-year-old seeds as *Phoenix dactylifera* L. (Sallon *et al.,* 2008). In some cases germination occurs as soon as the seed encounters favorable conditions, but in true dormancy seeds remain viable and dormant despite periods of favorable conditions (Baskin & Baskin, 2004). Types of dormancy differ in their control mechanisms. Dormancy may be triggered by some internal physiological mechanism or by the structure of the seed coat or embryo (Fenner, 2000). Frequently, seed germination can be delayed due to seed dehydration, embryo immaturity, or by chemical or physical factors (Murdoch, 2014).

As a direct consequence of seed dormancy, there are frequently many viable seeds in the soil (*Figure 8*). This accumulation is called a soil seed bank and is a 'safety deposit' of plant biodiversity. Seed banks are absolutely vital for rapid regeneration after perturbations such as floods and wildfires. If perturbation like an intense fire destroys the seed bank, regeneration can only occur as seeds arrive from elsewhere by dispersal.

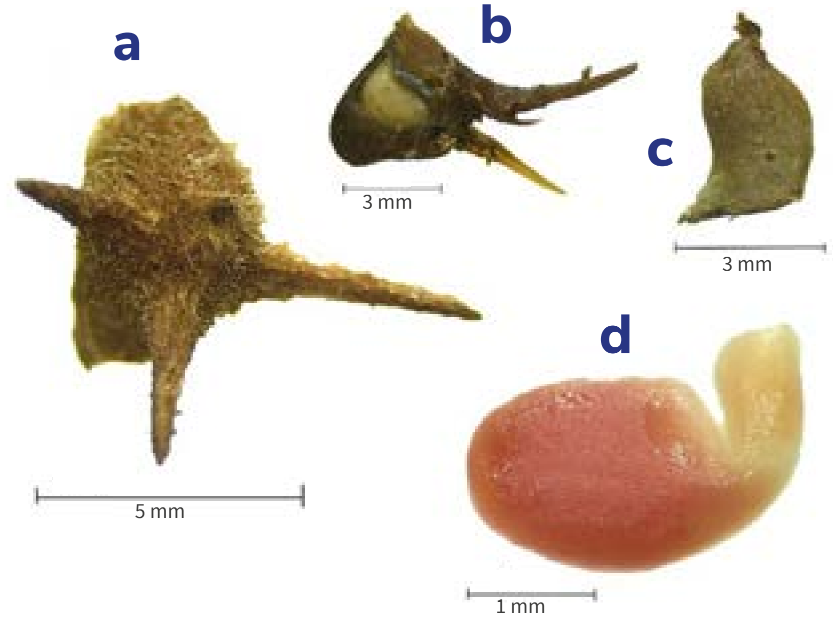


Figure 8. Viability test for *Lecocarpus lecocarpoides* seed stored more than a year after collection from the parent plant. a) whole propagule; b) dissected propagule showing achene and embryo (seed) embedded within bract; c) achene extracted from propagule; d) embryo removed from achene whose pink color indicates viability in tetrazolium test (ISTA, 1985). Photos by: Patricia Jaramillo Díaz and Rafael Pulido, CDF.

Seed dispersal in Galapagos

The Galapagos flora consists of about 560 native vascular plant species, of which 32% are endemic to the archipelago, and over 800 are introduced alien plant species (Bungartz *et al*., 2012; Atkinson *et al*., 2017; Toral-Granda *et al.,* 2017; Jaramillo *et al*., 2018). This native-rich flora includes a large variety of seeds, propagules, and dispersal mechanisms. For example, the common yellow-flowered *muyuyo* tree (*Cordia lutea*) produces drupes consumed and dispersed by birds and lava lizards (Heleno *et al*., 2013). The drupe's pulp is also very sticky and adheres well to the bodies of large animals such as tortoises and seabirds (Nogales *et al*., 2017). As in other insular floras, a large proportion of plant species (approximately 36%) produce propagules without any specific adaptation to long-distance dispersal, with all long-distance dispersal syndromes occurring with relatively similar frequencies (approximately 15%) (Vargas *et al*., 2012).

Because large terrestrial mammals are typically absent on oceanic islands, birds (*Figure 9*) and reptiles are the primary seed dispersers in the Galapagos Islands (Heleno *et al.,* 2011; Heleno *et al.,* 2013). To develop successful conservation and restoration strategies for these threatened interactions, we must understand the dependence of plant and animal populations on seed dispersal and frugivory (Gardener *et al.,* 2013). Loss of dispersers can be more destructive for plants on oceanic islands due to the simplicity and fragility of their native ecosystems (Traveset *et al*., 2014).

Figure 9. Bird dispersal of fleshy fruits. a) fleshy fruits of the introduced invasive blackberry (*Rubus niveus*); b) fleshy fruits of the endemic *Varronia leucophlyctis*; c) a large ground finch (*Geospiza magnirostris*), a typical granivore, trying to break the pyrene of the endemic *Cordia lutea*; d) Galapagos flycatcher (*Myiarchus magnirostris*), a typical insectivorous bird, dispersing the seed of the endemic *Zanthoxylum fagara.* Photos by: Ruben Heleno.

Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

The study of seed dispersal in Galapagos occurred in three stages. During most of the 20th century, there was a great focus on the importance of co-evolution between birds and seeds (Wiener, 1995; Grant & Grant, 2014). A second stage was marked by the description of seed consumption by focal animal species, and the evaluation of the effect on animal ingestion of seed germination (*Figures 10, 11*). The third stage was marked by the accumulation of large datasets that allowed detailed studies of spatial and community-level patterns of seed dispersal (Heleno *et al*., 2011; Vargas *et al.,* 2012; Heleno *et al.,* 2013; Blake *et al.,* 2015).

Despite the absence of obligate frugivores in the archipelago, native and introduced plants disperse a vast number of seeds. From giant tortoises to insectivorous birds, almost all vertebrates consume and disperse seeds (Guerrero & Tye, 2011; Heleno *et al.,* 2011; Blake *et al.,* 2012; Heleno *et al.,* 2013; Traveset *et al*., 2016).

Figure 10. Left: A scat of a Galapagos giant tortoise *(Chelonoidis hoodensis)* found on Española island with four seedlings of manzanillo *(Hippomane mancinella)* growing in the nutritious subtrate after fruits were ingested by a tortoise. On the right, a detail of a ripe manzanillo fruit. Photos by: Ruben Heleno y María del Mar Trigo.

Basic and applied seed science

Because of their role in regenerating of plant communities and, consequently, in the persistence of whole ecosystems, seeds are an important object of study in disciplines such as botany, zoology, ecology, and conservation biology. Additionally, fruits and seeds constitute an important component of human diets and provide chemical compounds frequently used in medicines and cosmetics. In all these disciplines, a broad range of research methods is used to study different seed components (*Figure 11*). In ecology, the identification of seeds in animal droppings, on the ground, or transported by humans, can provide insight into ecological relations or conservation threats. Although molecular techniques are increasingly used, macroscopic identification of seeds remains a vital tool in ecology (Phillips & McGrew, 2013; Srivathsan *et al*., 2015). Such identification is only possible if there are appropriate reference collections available, usually maintained by seed banks and herbaria.

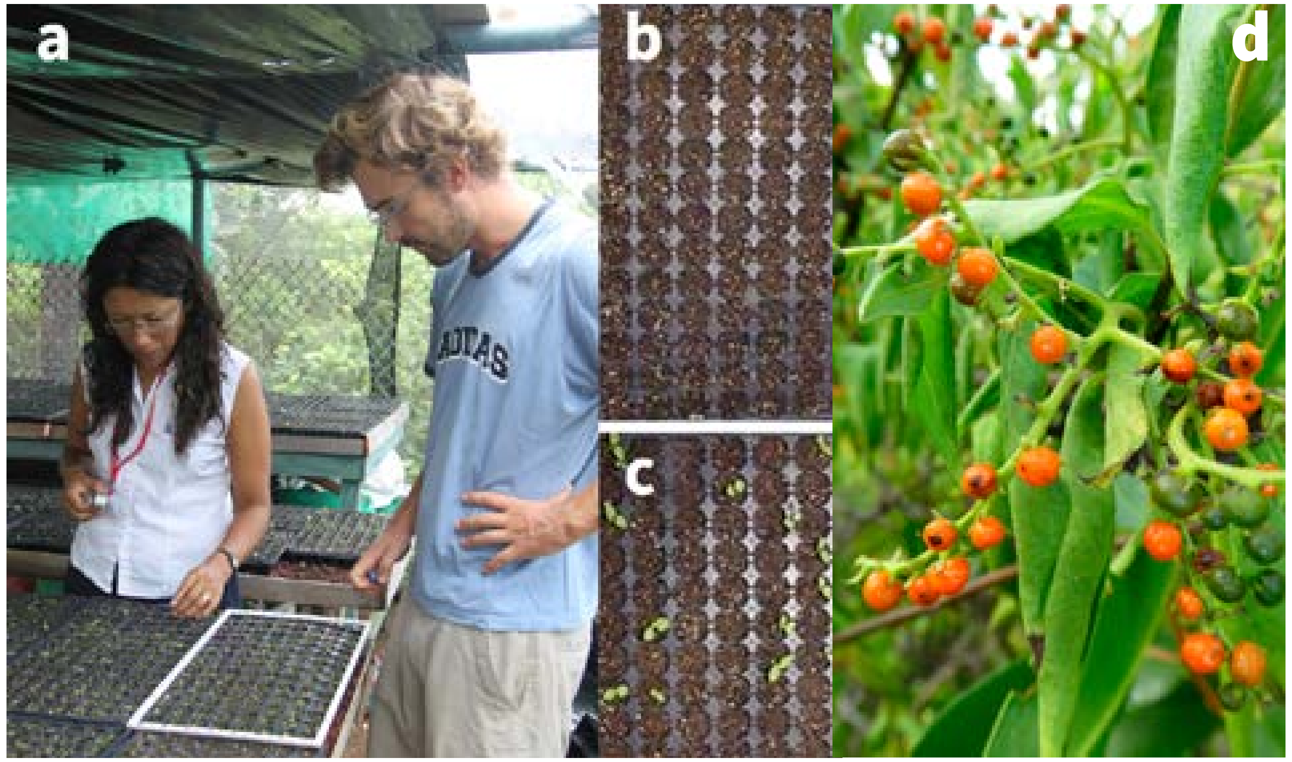


Figure 11. Seed germination experiments at the Charles Darwin Research Station. a) authors Patricia Jaramillo Diaz and Ruben Heleno conducting seed research; b) tray with seeds of *Tournefortia psilostachya* sown immediately after being collected from the mother plant; c) tray with *T. psilostachya* seeds sown after being recovered from scats of lava lizard (*Microlophus albermarlensis*); and d) detail of a fruits of *T. psilostachya.* Photos by: Patricia Jaramillo and Ruben Heleno.

Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Seed Banks

Earlier, we used the term "seed bank" to refer to viable seeds present in the soil. Here we refer to **seed bank repositories** that collect and store seeds to preserve both the seeds themselves and the genetic heritage they represent. The largest seed collection in the world is the one amassed by the “Millennium Seed Bank Partnership” led by the Kew Royal Botanical Gardens, England. More than 95 countries have already contributed over 2 billion seeds from about 35,000 plant species, representing 13% of the wild plant species in the world (van Slageren, 2003; Lewis-Jones, 2019).

The collection and storage of seeds from agricultural plants has been pivotal for the domestication of plants over the last 10,000 years. During this ancient activity, varieties that produced greater yields were artificially selected each generation, producing the cultivars we know and consume today. However, the modern seed trade has become dominated by a few companies in a highly aggressive global market, where irreparable loss of agricultural genetic diversity has occured (Howard, 2009). As a result, some farmers have revived the practice of collecting and exchanging local varieties (Fowler and Mooney, 1990), even though their efforts are losing ground to the global seed economy (Howard, 2009).

Up to a quarter of the world's known wild plant species may be currently endangered because of direct and indirect human activities (Burger *et al*., 2012; IUCN, 2021). This has motivated conservationists, researchers and governmental institutions worldwide to collect and store wild seeds and preserve their genetic diversity. These seeds are stored in seed banks, often associated with botanic gardens and universities, for future ecological restoration and scientific research.

Galapagos Seed and Fruit Herbarium

The Galapagos seed and fruit collection is hosted and curated by the CDS Herbarium of the Charles Darwin Research Station, Charles Darwin Foundation (*Figure 12*). This collection, property of the Ecuadorian Government and the Galapagos National Park, currently (2021) consists of seeds from 1200 species, including endemic, non-endemic natives and introduced plants.

This seed collection has been a collaborative effort of Station staff and scientists studying seeds. Studies of plant-animal interactions require scientists to identify seeds, so a reference collection of identified seeds was created by herbarium and Foundation staff to support those efforts. In turn, many seeds identified in those studies have been added to the Herbarium collection. In this way the growth of the collection represents the work of many scientific collaborators. It now includes seeds collected directly from plants as well as those that were dispersed by birds, tortoises, iguanas, and other species. These plant-animal studies have added significantly to our ecological knowledge of Galapagos (Blake *et al.*, 2012; Blake *et al.*, 2015; Traveset *et al.*, 2016). Like all parts of the herbarium, this is an ongoing project with the goal of producing the knowledge necessary to support management decisions.

Figure 12. Materials from the reference collection of seeds kept by the Charles Darwin Foundation in Puerto Ayora, Galapagos. Photo by: Juan Manuel García.

Photographs of seeds and propagules

The following collection of photographs has been assembled to show the range of seed morphology within the Galapagos flora. We have included native species and species introduced accidentally or on purpose by humans to the islands. We also made an effort to emphasize endemic species, especially those threatened or of particular conservation concern (IUCN, 2021). We have included both rare and common species, including some invasive species. This collection represents a wide geographic range in the archipelago, from various research projects and samples from the CDS Herbarium (*Figure 13*). All Photos were taken by the herbarium staff and volunteers and are property of the CDS Herbarium.

Photographs are ordered according to the four main types of propagules found in the field (*Figure 6*), namely: the **Seeds** group includes species in which seeds are released from dry fruits, fleshy fruits in which dispersed seeds are found in scats, and a few grains dispersed like seeds; **Whole fruits** act as propagules in the second group; **Pyrenes, mericarps, fruit parts** show the propagules of species where seeds are dispersed within part of a fruit; and **more complex structures** include the florets or spikes dispersed by grasses as well some accessory fruits that contain extrafloral structures. Within each group, species are sorted alphabetically.

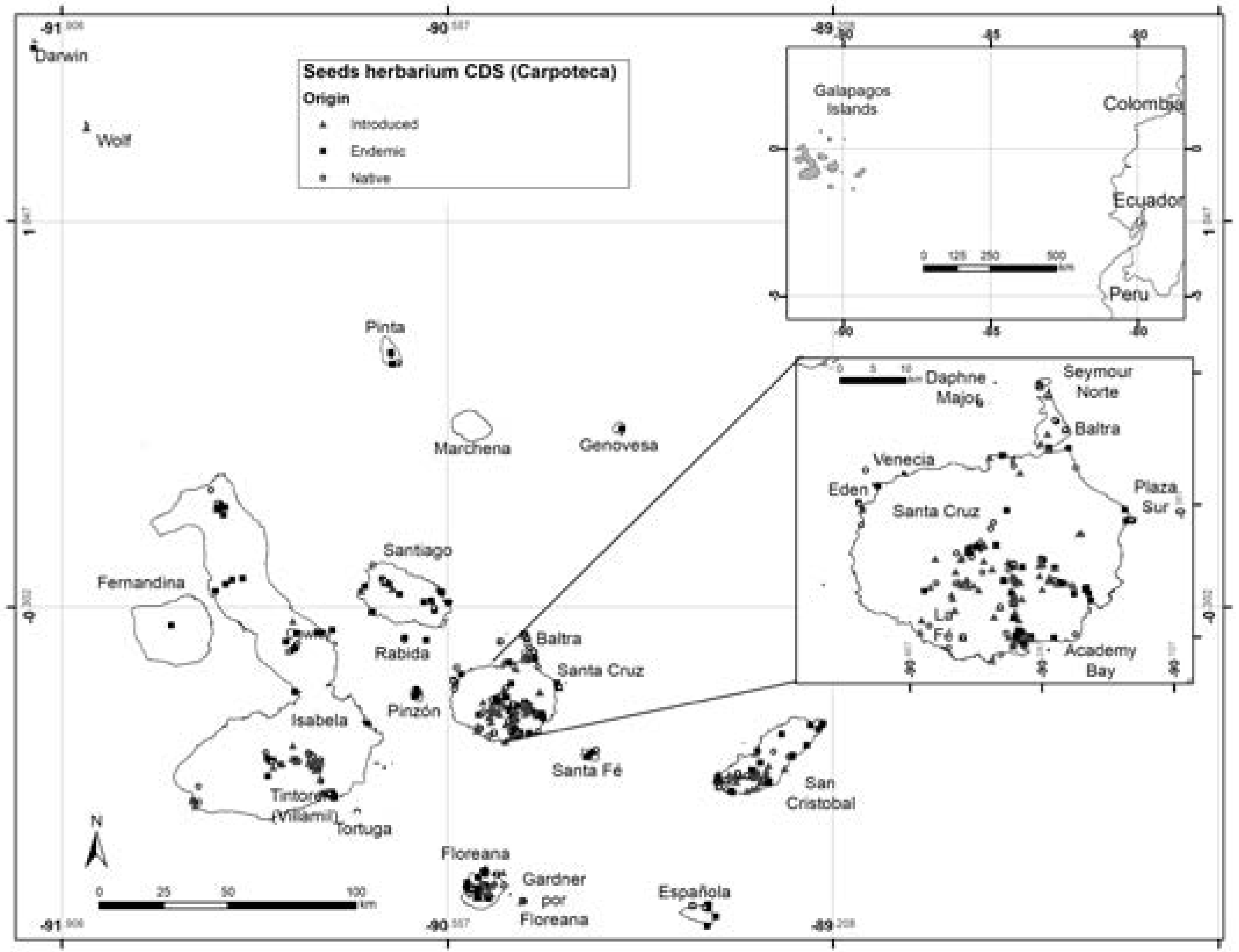


Figure 13. Distribution of collections in the seed and fruit herbarium of the Charles Darwin Research Station. Map by Byron Delgado.

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Abrus precatorius

Abutilon depauperatum

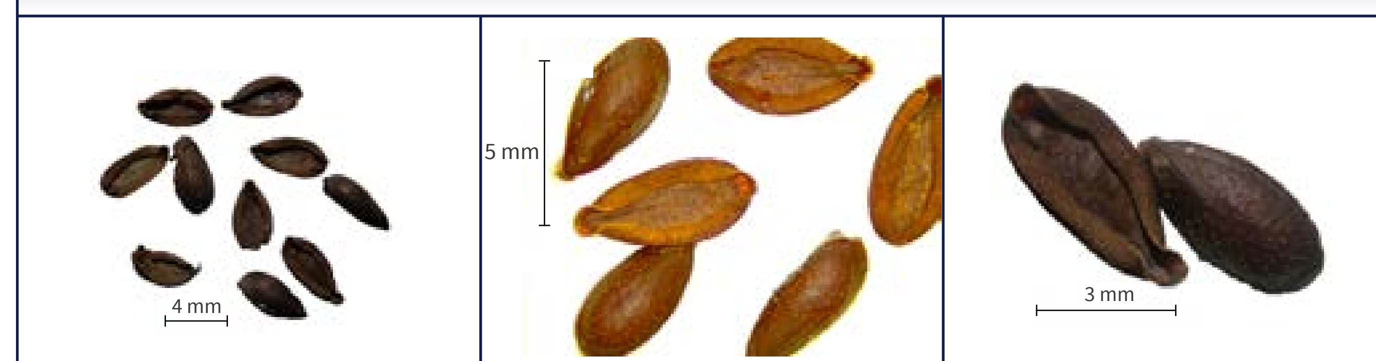
Acacia nilotica

Acacia rorudiana

Acalypha wigginsii

Amaranthus sclerantoides

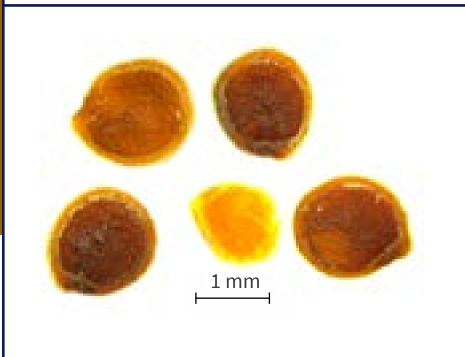
Asclepias curassavica



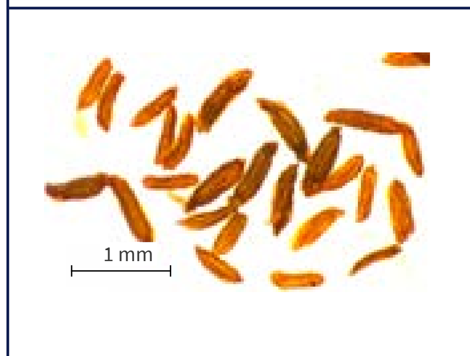
Bastardia viscosa

Seeds

Blechum pyramidatum

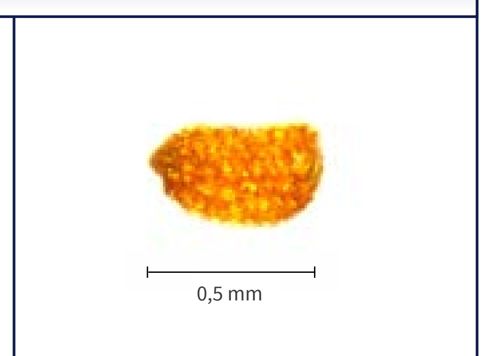


Bryophyllum pinnatum



Calandrinia galapagosa

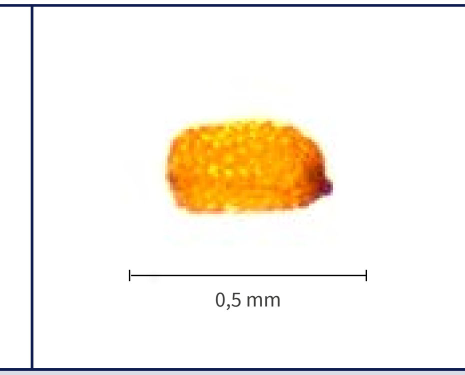
Capraria biflora



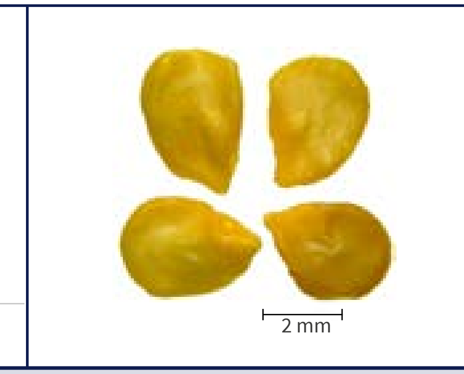
Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Seeds

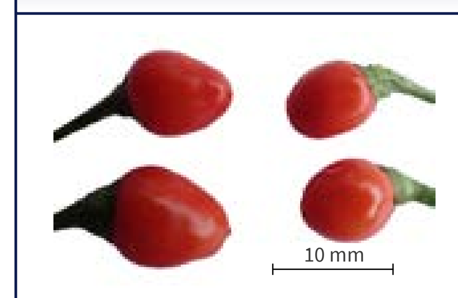
Capraria peruviana

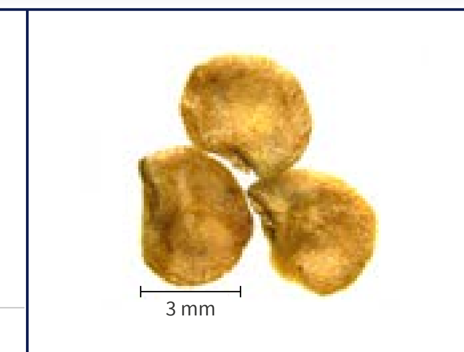


Capsicum annuum L.

Fruit (Berry)


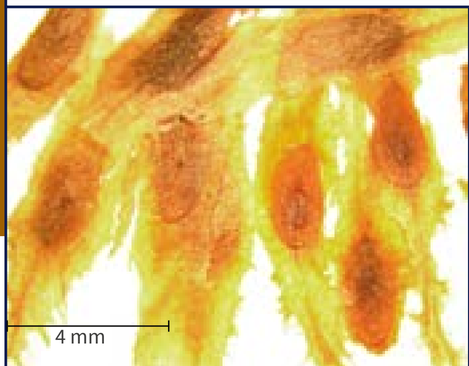
Capsicum galapagoense

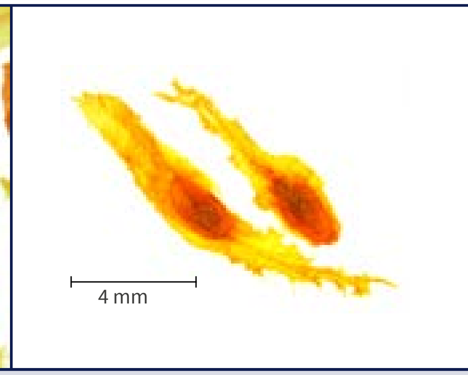


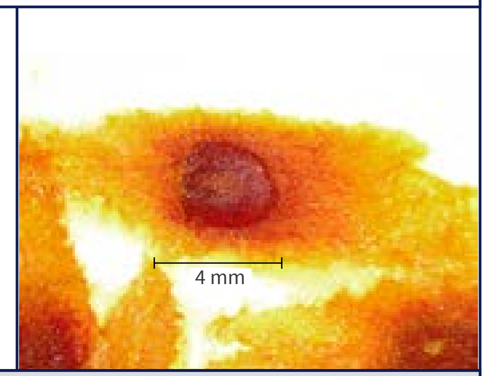
Fruit (Berry)


Cardiospermum galapageium

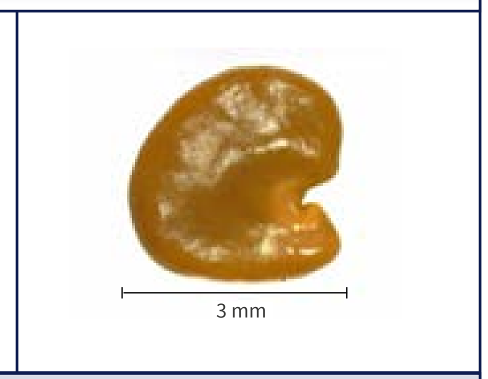
Cinchona pubescens







Crotalaria pumila

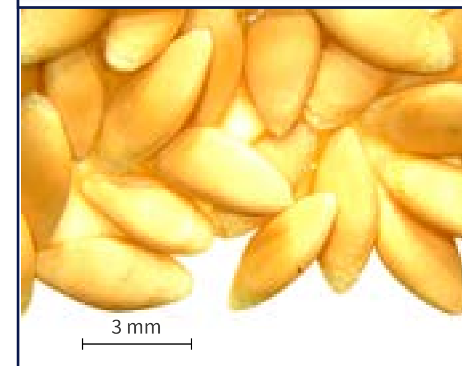


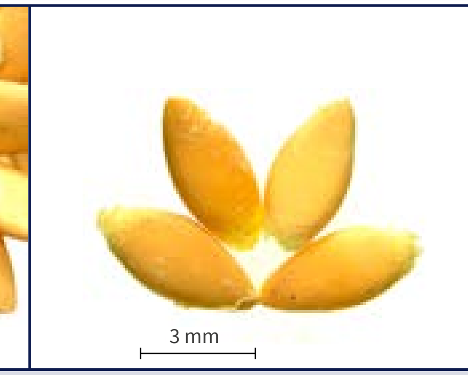
Crotalaria retusa

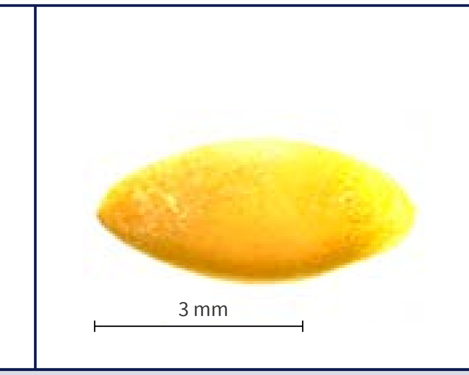
Croton scouleri var. scouleri

Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

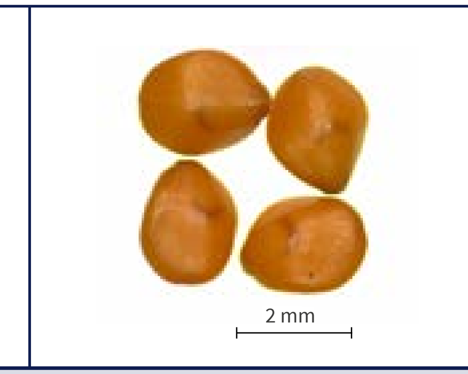
Cucumis dipsaceus





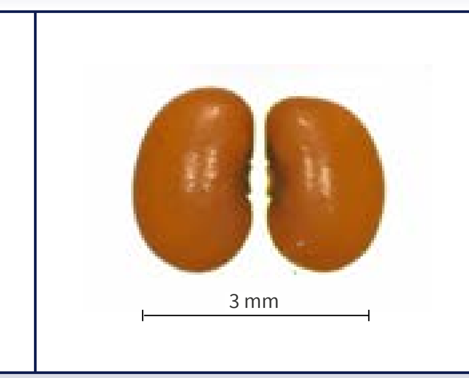


Desmanthus virgatus (L.) Willd

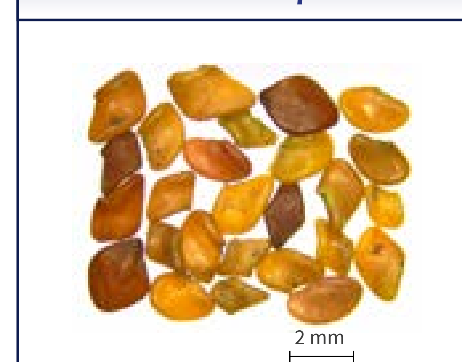


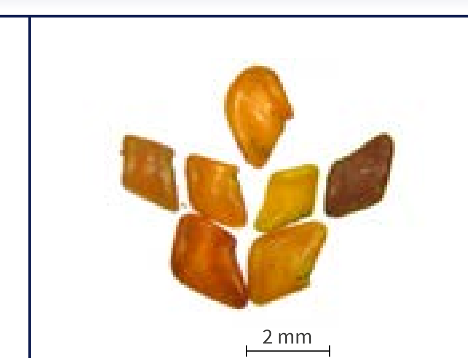
Desmodium incanum

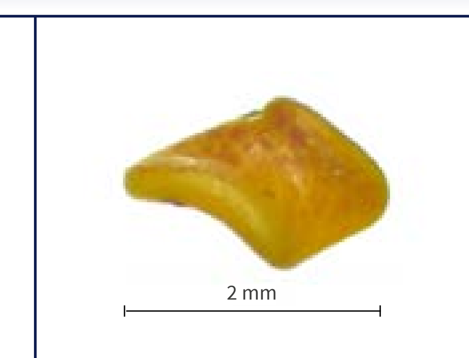
Fruit (Legume), Seeds



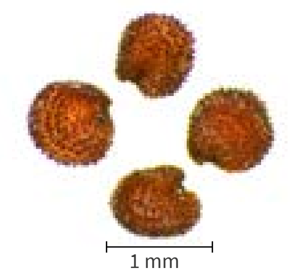
Desmodium procumbens

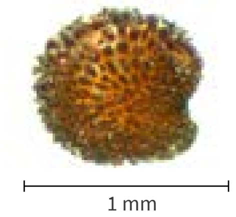




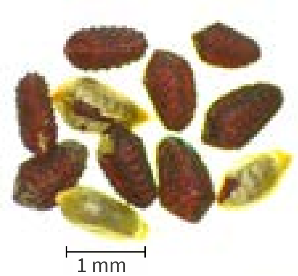


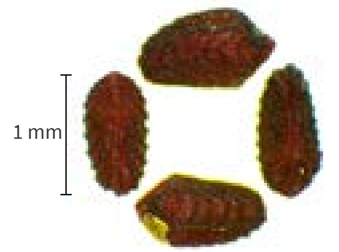
Drymaria monticola

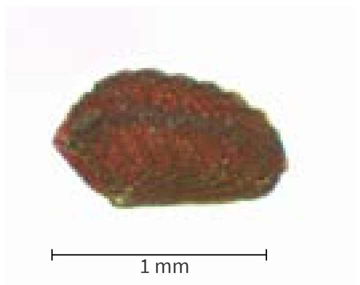




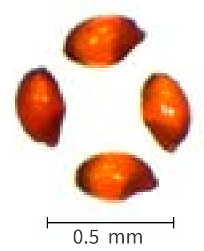
Eleusine indica



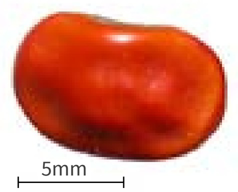


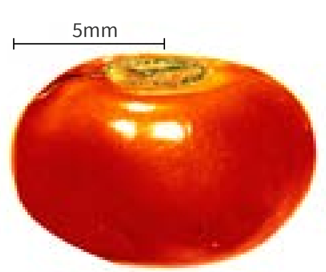


Eragrostis ciliaris



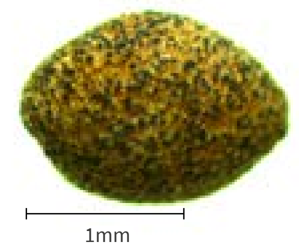
Erythrina velutina





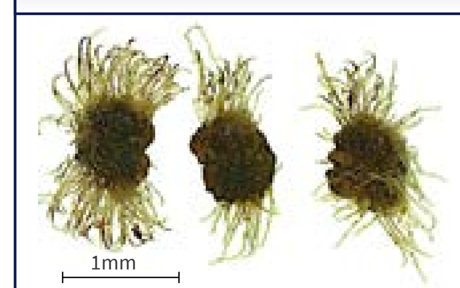
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Evolvulus convolvuloides

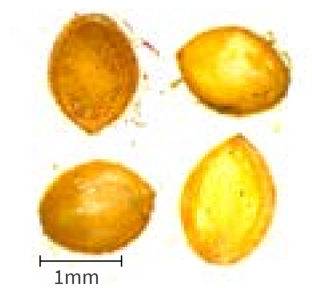


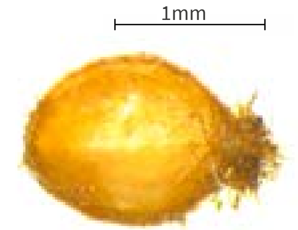
Galactia striata

Galium galapagoense

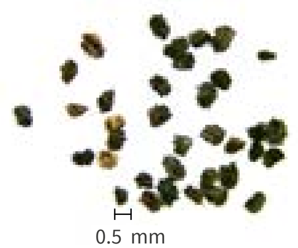


Fruit (schizocarp)



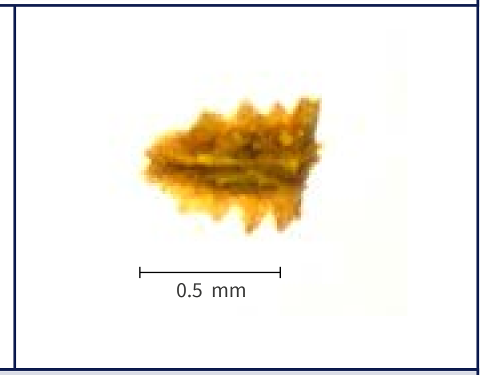


Galvezia leucantha subsp. leucantha

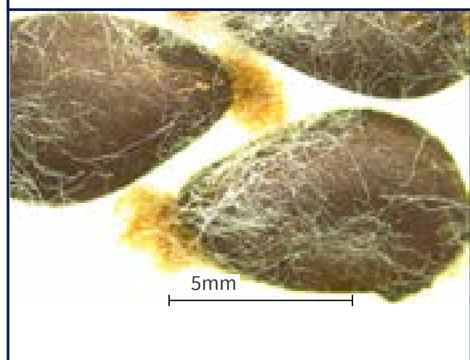


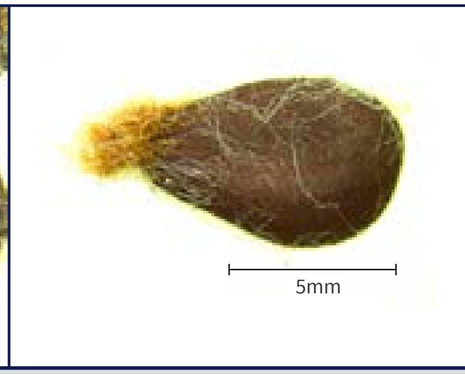
Seeds

Galvezia leucantha subsp. pubescens

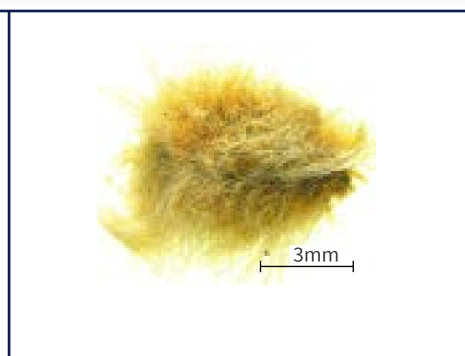


Gossypium barbadense





Gossypium darwinii

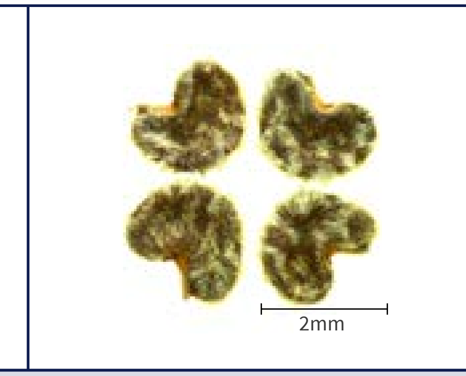


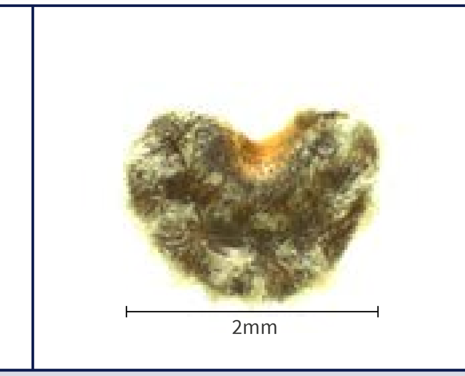
Gossypium klotzschianum

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

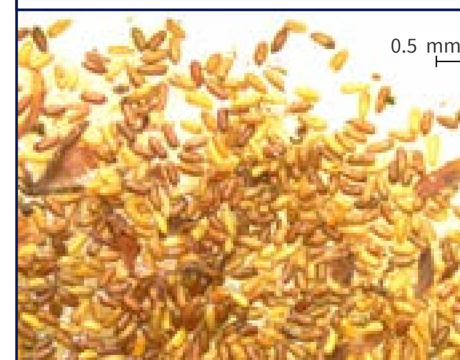
Seeds

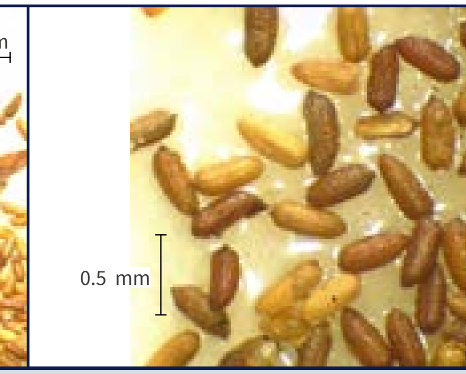
Herissantia crispa

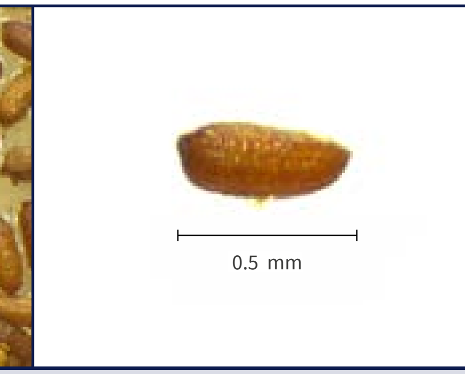




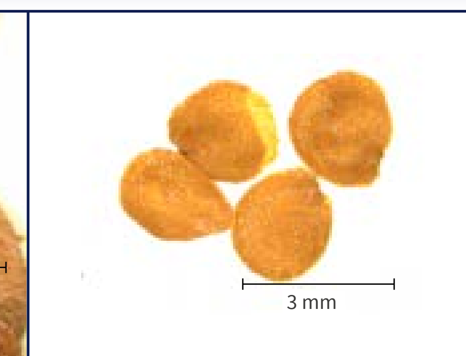
Hypericum thesiifolium



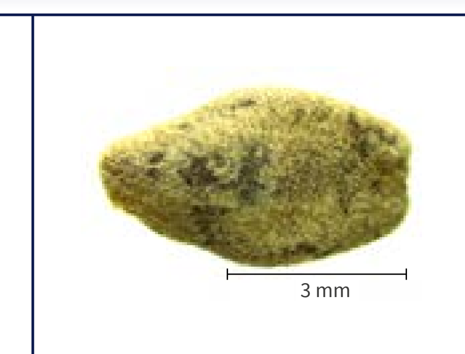




Iochroma ellipticum



Ipomoea incarnata



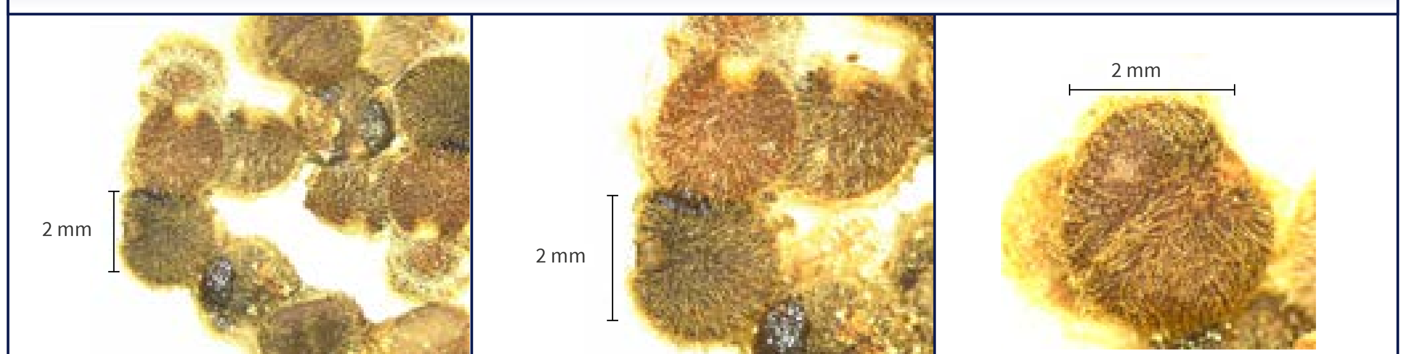
Seeds

Ipomoea pes-caprae

Ipomoea triloba

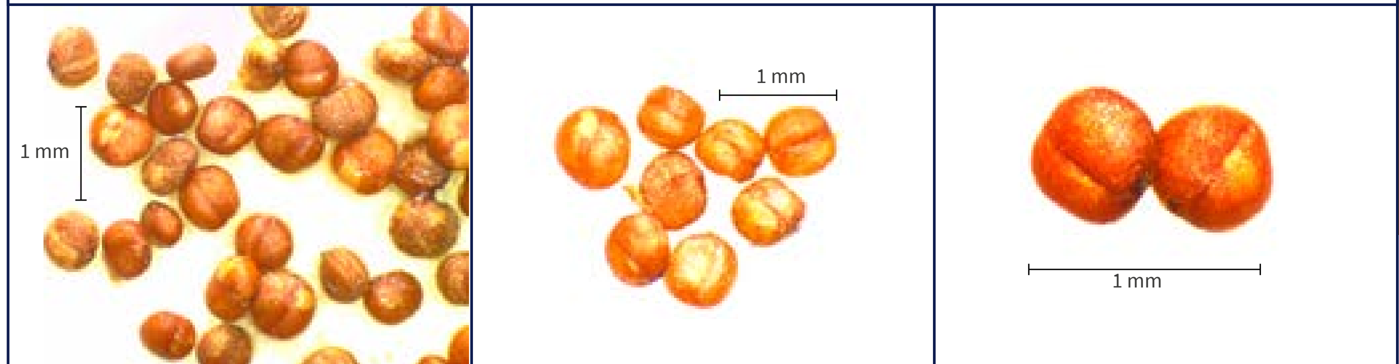
Jasminocereus thouarsii var. *delicatus*

Justicia galapagana

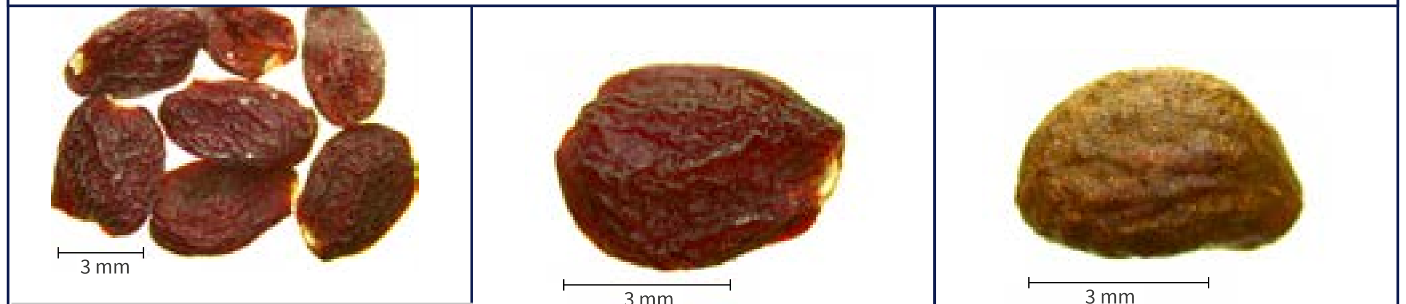


Seeds

Ludwigia leptocarpa



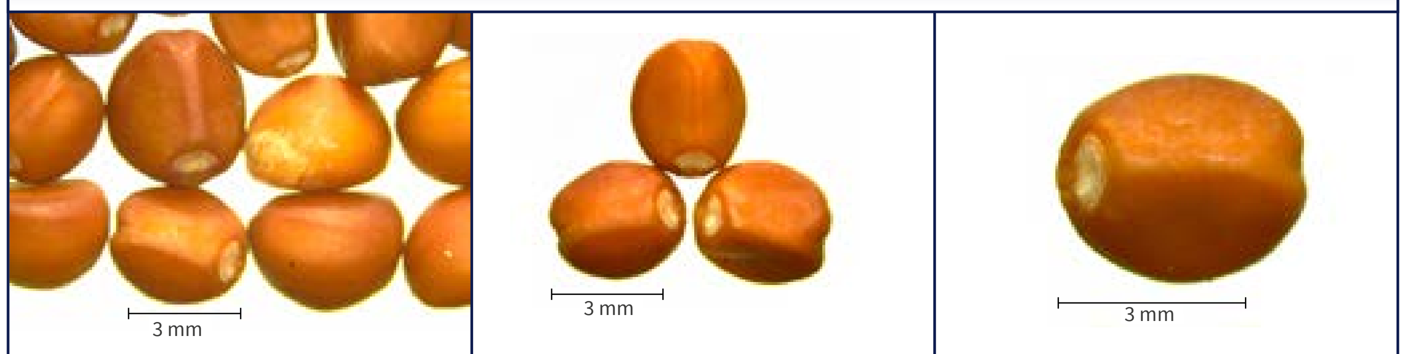
Maytenus octogona



Seeds with red aril

Mentzelia aspera

Merremia aegyptia



Miconia robinsoniana

Fruit (berry), seeds in pulp

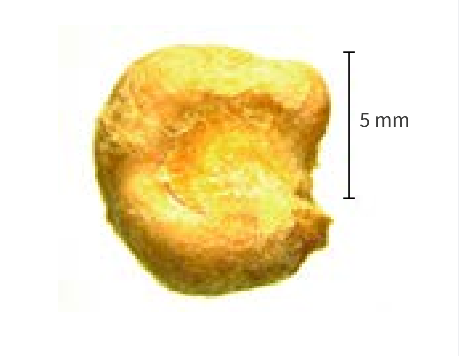
Momordica charantia

Opuntia echios var gigantea

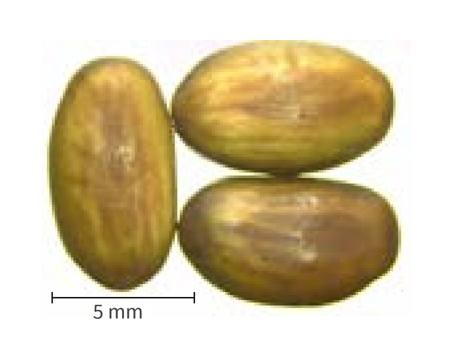
Opuntia galapageia

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Opuntia megasperma var. megasperma



Parkinsonia aculeata



Passiflora colinvauxii

Passiflora edulis

Seeds

Passiflora foetida

Pernettya howellii

Phyllanthus caroliniensis subsp. *caroliniensis*

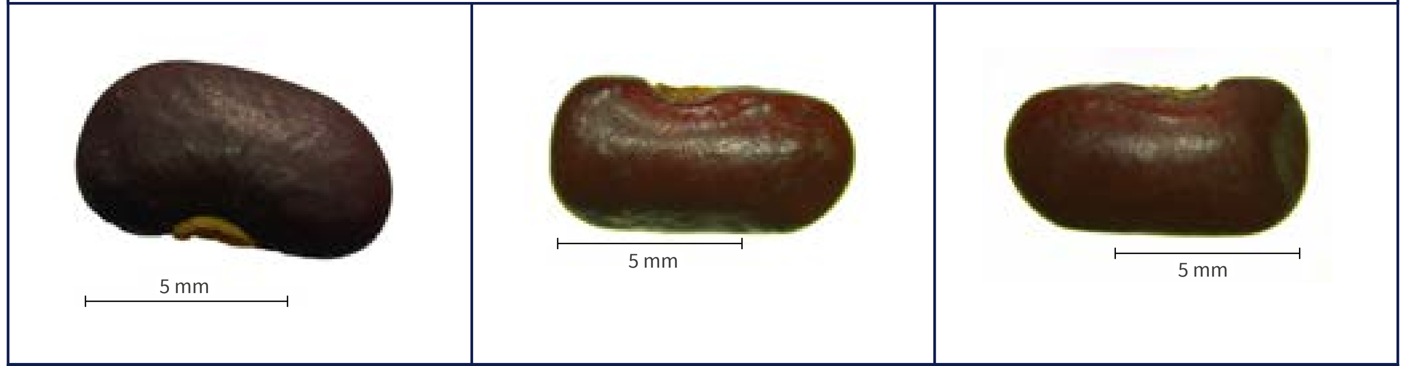
Physalis galapagoensis

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Seeds

Physalis pubescens

Piscidia carthagenesis



Plantago major

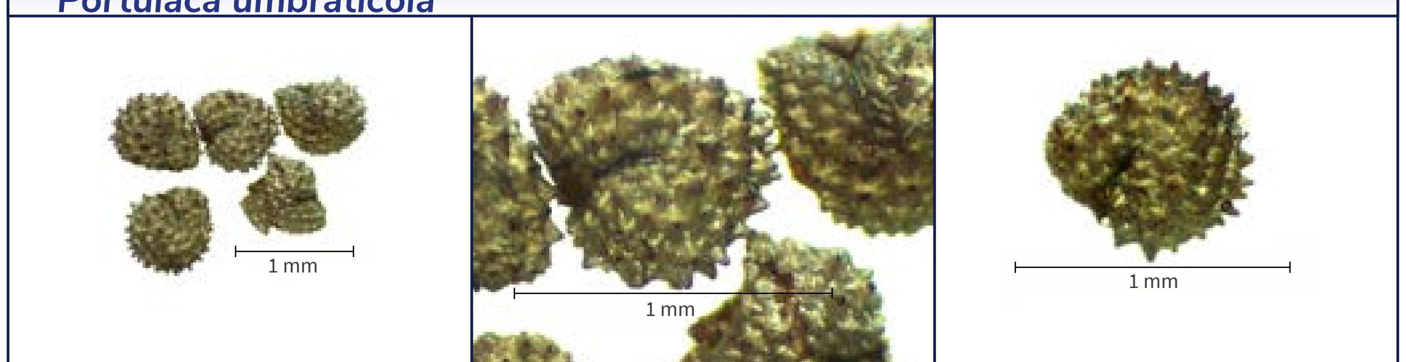
Seeds within fruit (capsule)

Pleuropetalum darwinii

Polygala andersonii

Portulaca oleracea

Portulaca umbraticola



Prosopis juliflora

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Jaramillo, P., Shepherd, J. & Heleno, R.

Seeds

Psidium galapageium

Fruit (berry) | Seeds | Seed

Psidium guajava

Rhynchosia minima

Ricinus communis

Senna occidentalis

Sesuvium portulacastrum

Sisyrinchium galapagense

Solanum americanum

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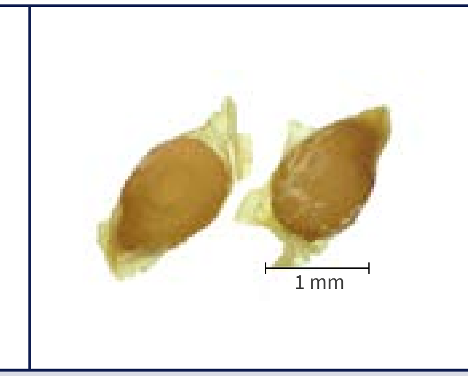
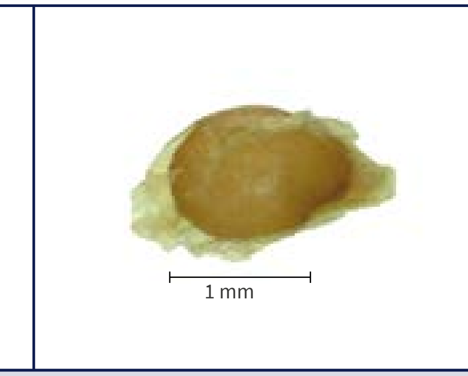
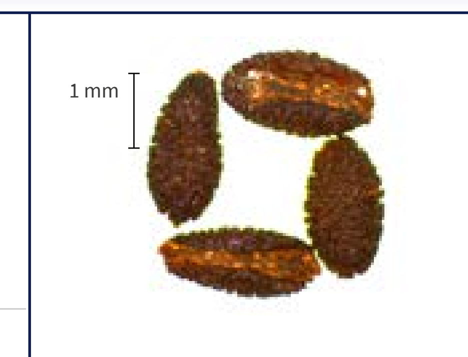
Solanum cheesmaniae



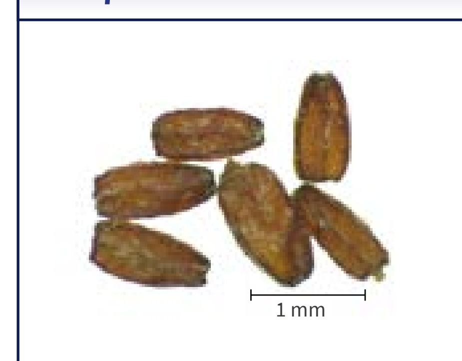


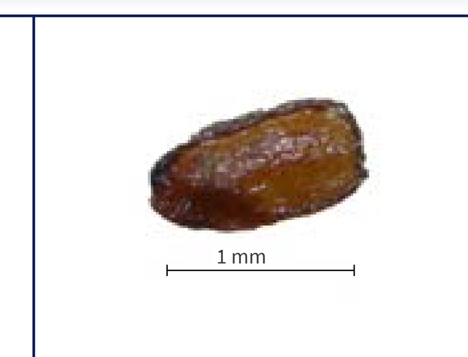
Solanum pimpinellifolium

Spermacoce remota

Fruits, seeds


Sporobolus indicus



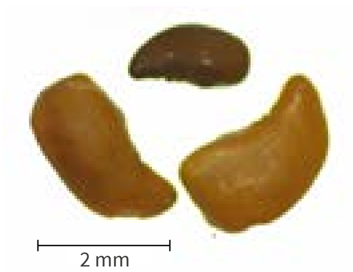


Seeds

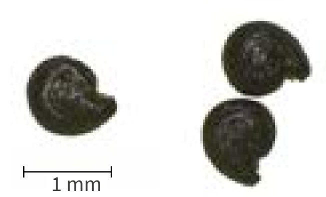
Seeds

Stylosanthes sympodiales

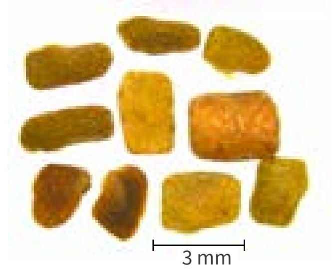
Fruit (Legume), Seeds



Talinum paniculatum



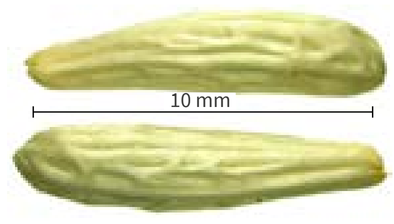
Tephrosia decumbers Benth.

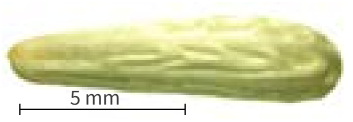


Thunbergia fragrans

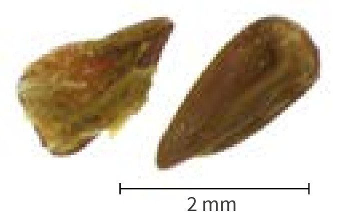
Trianthema portulacastrum

Vallesia glabra var. glabra

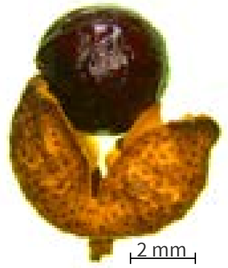




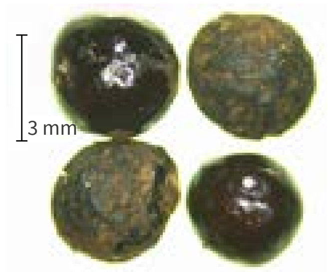
Waltheria ovata



Zanthoxylum fagara



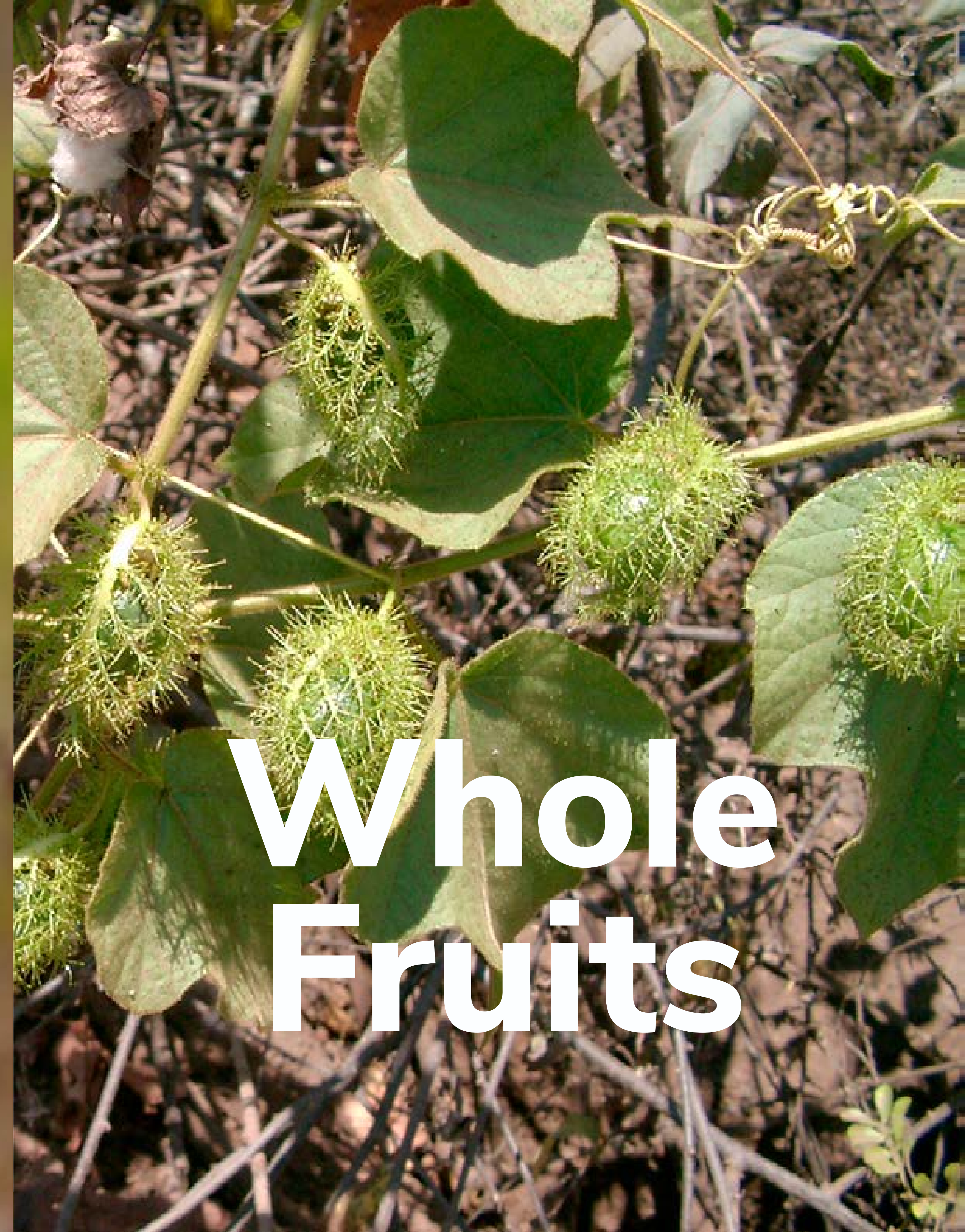
Fruit (Follicle)



Seeds

Seed without testa

Seeds

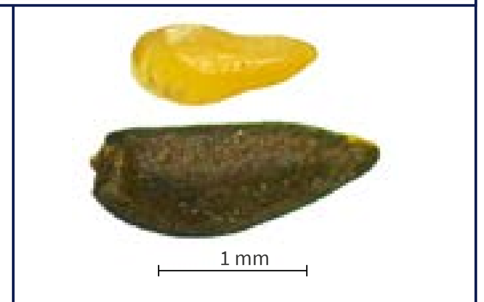


Whole Fruits

Acmella sodiroi

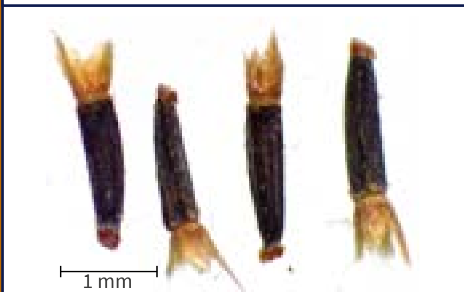
Fruits (cypsela)

Fruits

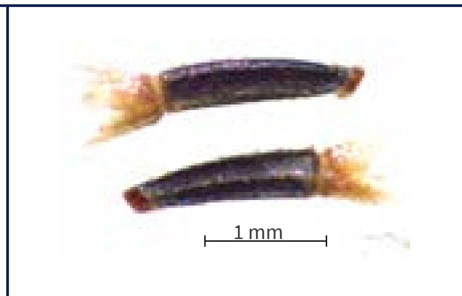


Seed, fruit

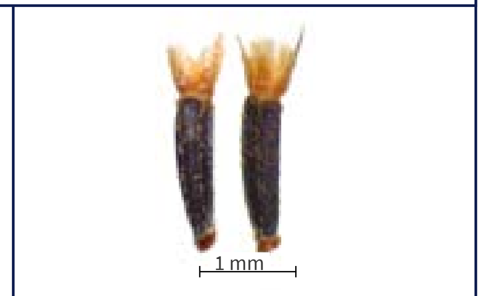
Ageratum conyzoides



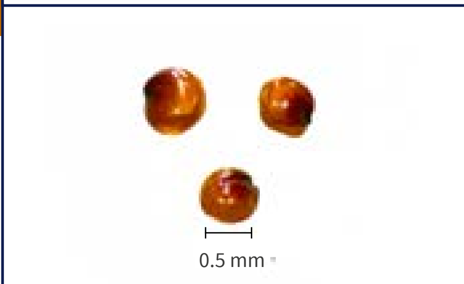
Fruits (cypsela)



Fruits



Alternanthera nesiotes



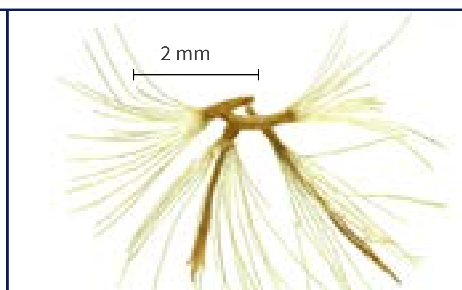
Fruits (achene)

Fruits

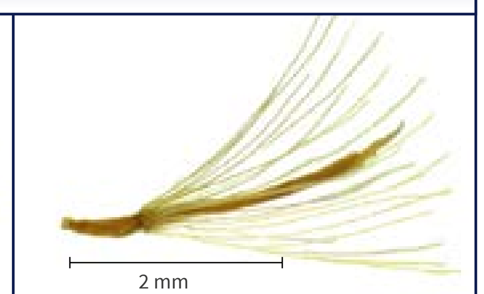
Fruit

Baccharis steetzii

Fruits (cypsela)



Fruits



Fruit

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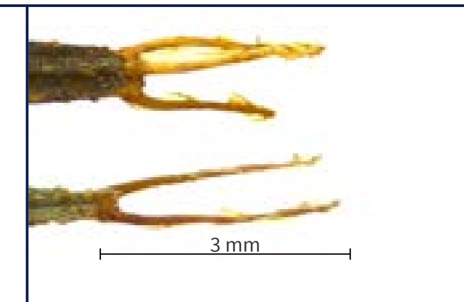
Bidens pilosa

Fruits (cypsela)



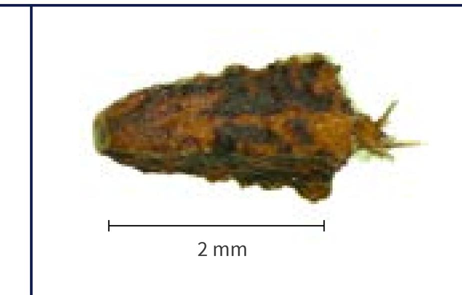
Fruits, pappus

Seed, fruit

Blainvillea dichotoma

Fruits (cypsela)

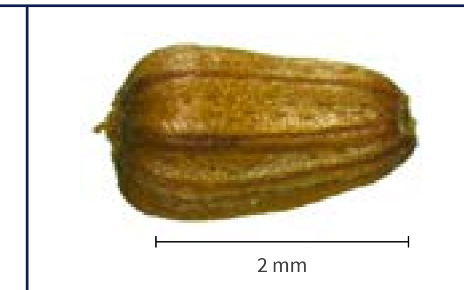
Fruits



Fruit

Centratherum punctatum

Fruits (cypsela)

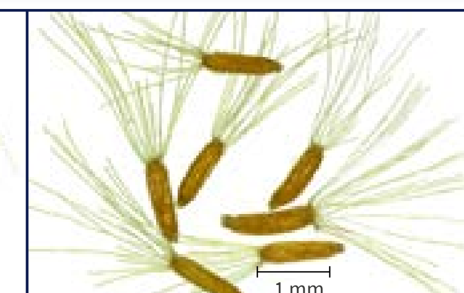


Fruit

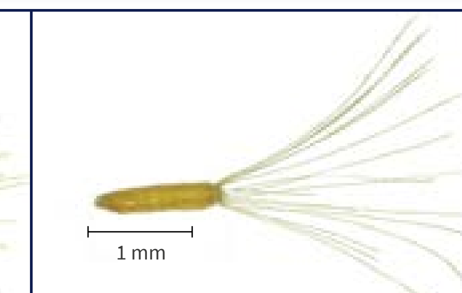
Fruit, seed

Conyza bonariensis

Fruits (cypsela)



Fruits



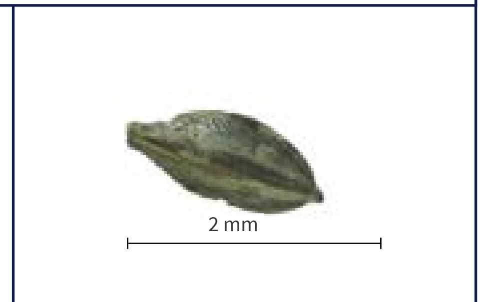
Fruit

Whole Fruits

Cyperus confertus

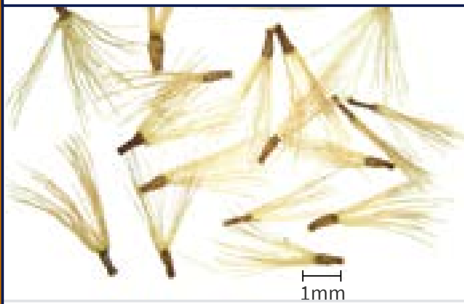
Fruits (achene)

Fruits

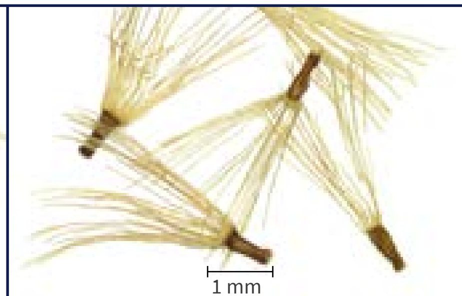


Fruit

Darwiniothamnus lancifolius



Fruits (cypsela)

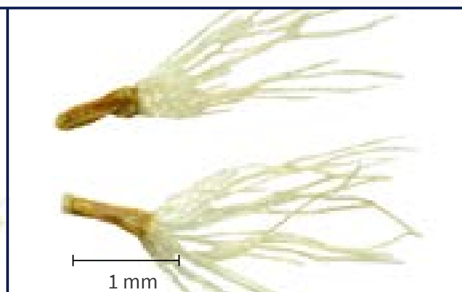


Fruits

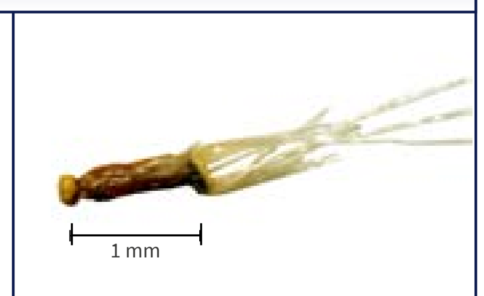
Fruit

Darwiniothamnus tenuifolius

Fruits (cypsela)

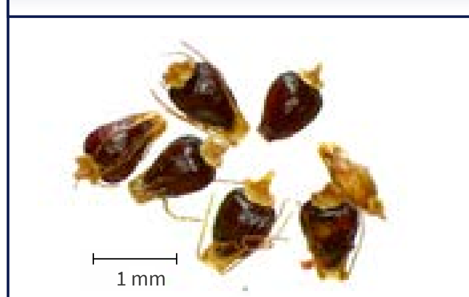


Fruits

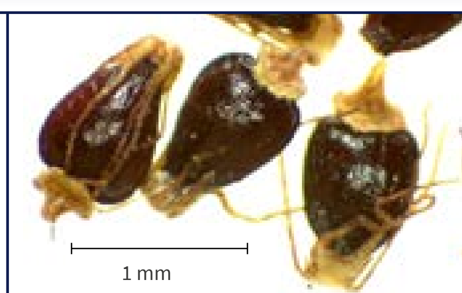


Fruit

Eleocharis maculosa



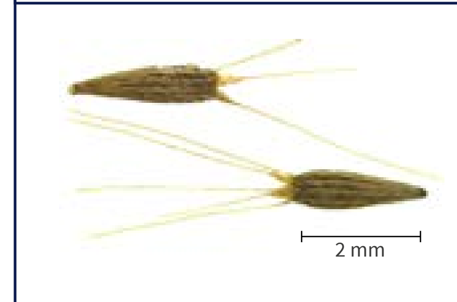
Fruit (achene) + perianth



Fruits

Seed, fruit

Elephantopus mollis



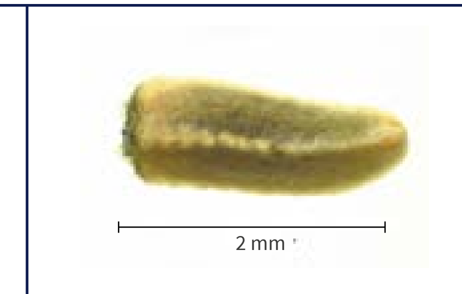
Fruits (cypsela)

Fruits

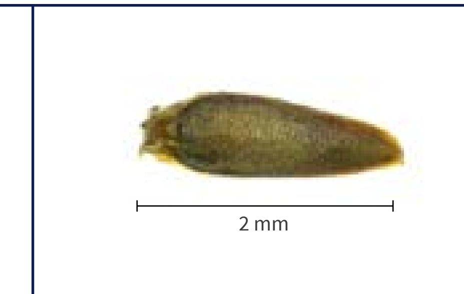
Seed, fruit

Encelia hispida

Fruits (cypsela)



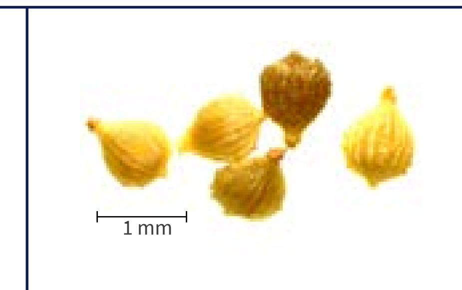
Fruit



Fruit

Fimbristylis dichotoma

Fruits (achene)



Fruits

Fruits

Froelichia juncea

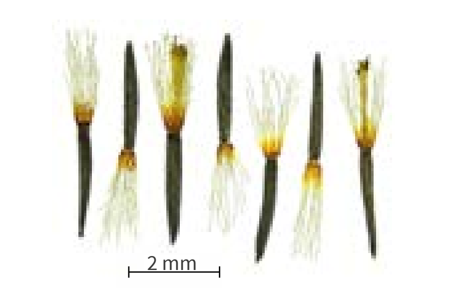
Fruits (achene)

Fruits

Fruit

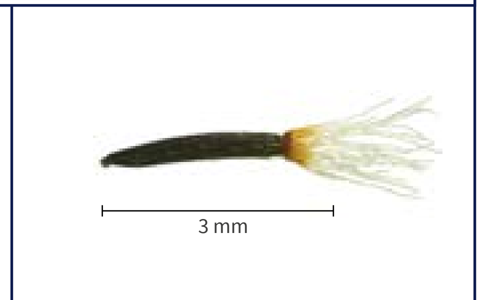
Whole Fruits

Pectis tenuifolia



Fruits (cypsela)

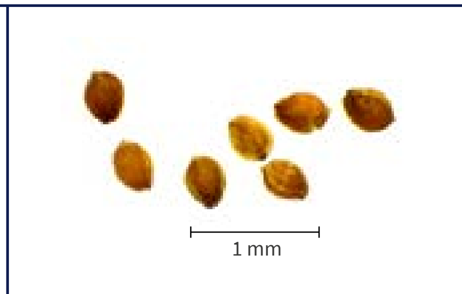
Fruits



Fruit

Pilea baurii

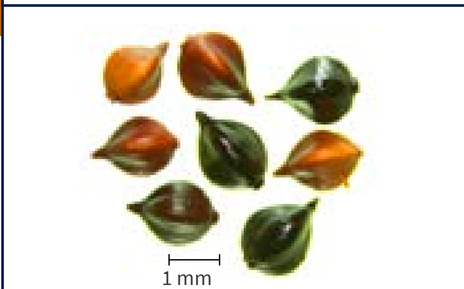
Fruits (achene)



Fruits

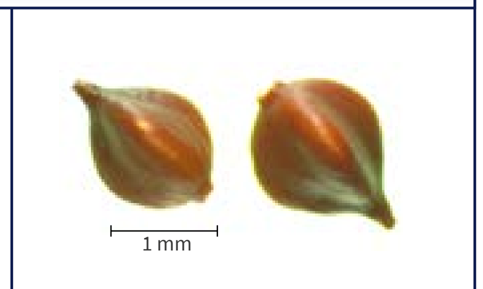
Fruits

Polygonum opelousanum



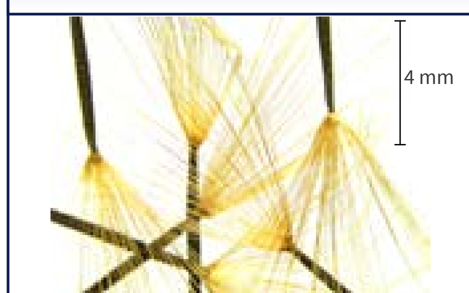
Fruits (achene)

Fruits

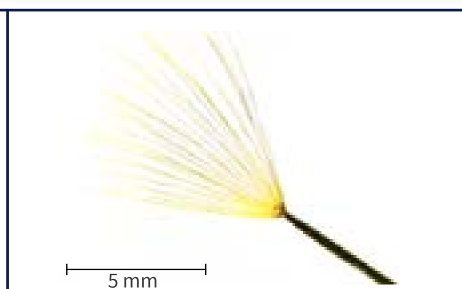


Fruits

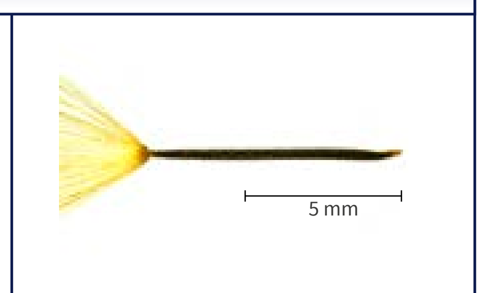
Porophyllum ruderale ssp. macrocephalum



Fruits (cypsela)

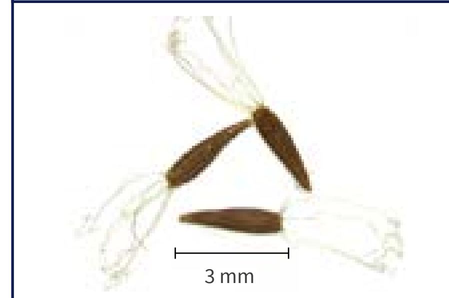


Fruit

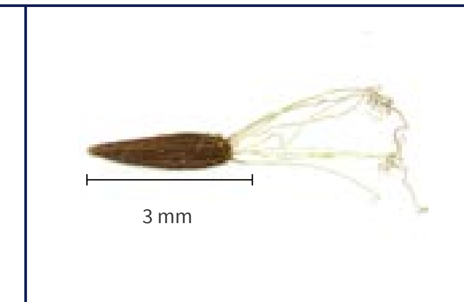


Fruit

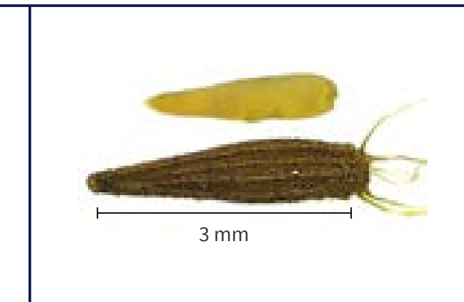
Pseudelephantopus spiralis



Fruits (cypsela)

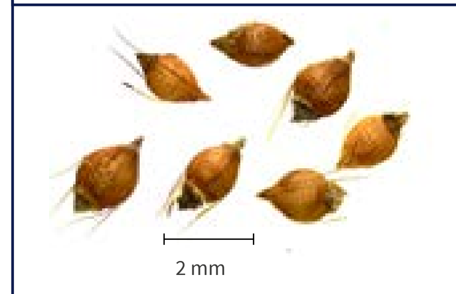


Fruit

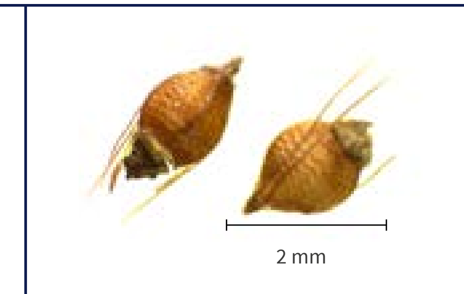


Seed, fruit

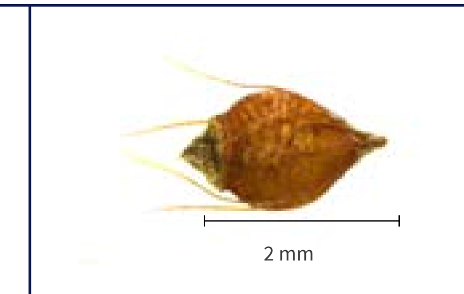
Rhynchospora rugosa



Fruits (achene)



Fruits

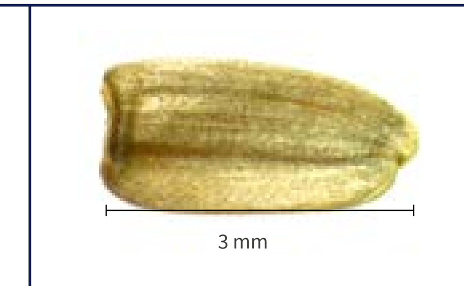


Fruit

Scalesia affinis

Fruits (cypsela)

Fruits



Fruit

Scalesia atractyloides

Fruits (cypsela)

Fruits

Fruit

Whole Fruits

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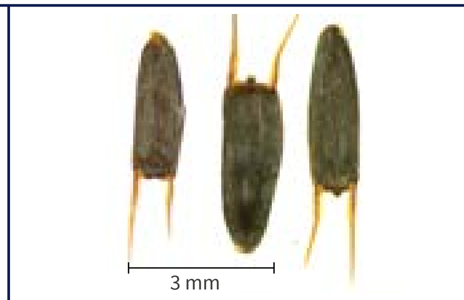
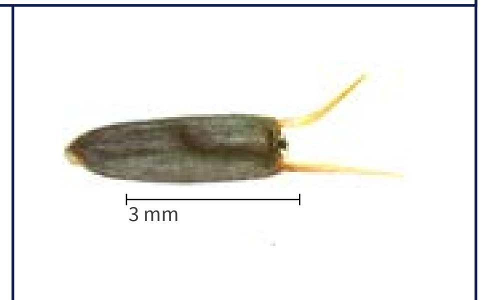
Whole Fruits

Scalesia cordata

Fruits (cypsela)



Fruits



Fruit

Scalesia divisa

Fruits (cypsela)

Fruits

Fruit

Scalesia gordilloi

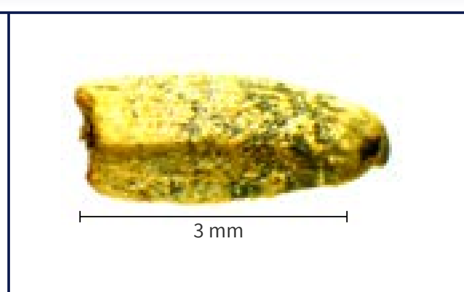
Fruits (cypsela)

Fruits

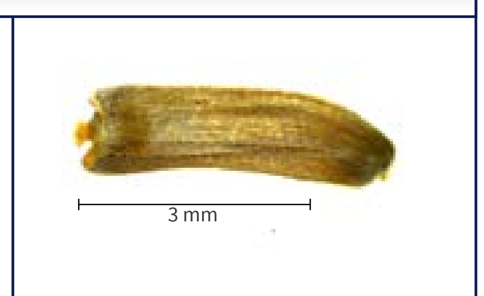
Fruit

Scalesia helleri

Fruits (cypsela)



Fruit



Fruit

Scalesia incisa

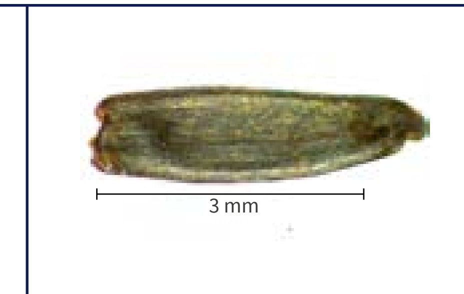
Fruits (cypsela)

Fruit

Fruit

Scalesia microcephala

Fruits (cypsela)



Fruit

Fruit

Scalesia pedunculata

Fruits (cypsela)

Fruits

Fruit

Scalesia retroflexa

Fruits (cypsela)

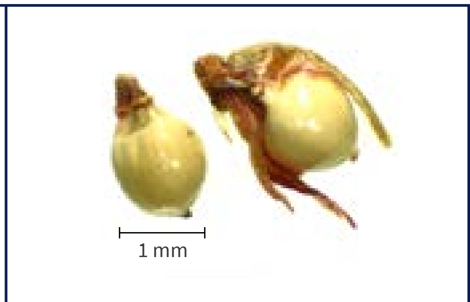
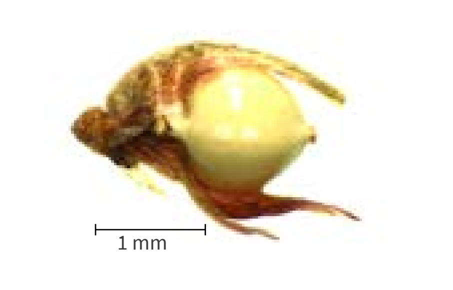
Fruits

Fruit

Whole Fruits

Whole Fruits

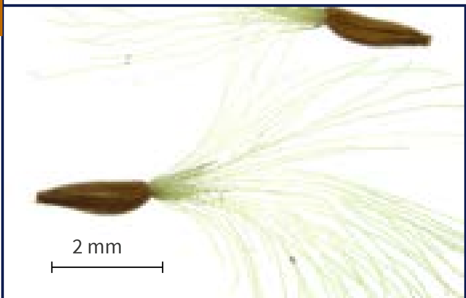
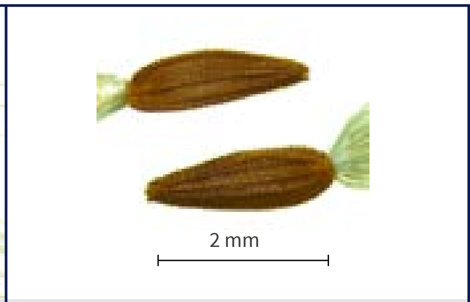
Scleria distans

		
Fruits (achene)	Fruits + perianth	Fruits + perianth

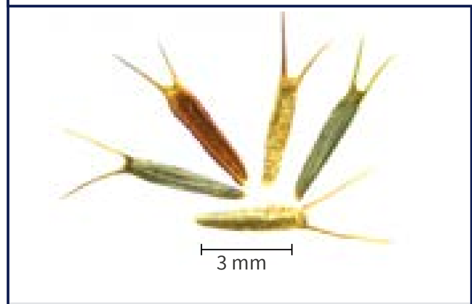
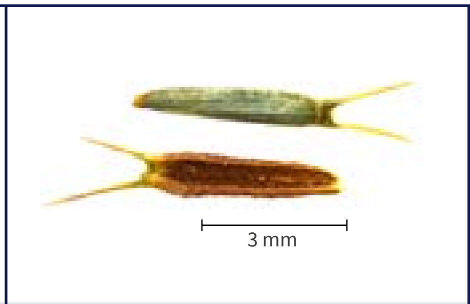
Scleria melaleuca

		
Fruits (achene)	Fruits	Fruit, seed

Sonchus oleraceus

		
Fruits (cypsela)	Fruits	Seed, fruit

Synedrella nodiflora

		
Fruits (cypsela)	Fruits	Seed, fruit

Pyrenes, Mericarps, Fruit Parts

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Pyrenes, Mericarps, Fruit Parts

Bursera graveolens

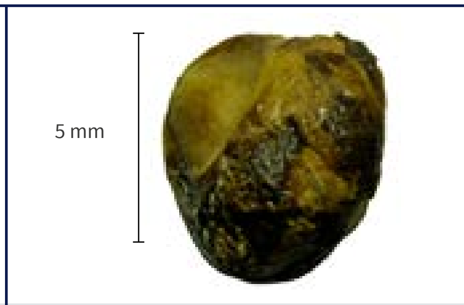
Fruit (drupe)

Pyrene

Seed

Bursera malacophylla

Pyrene

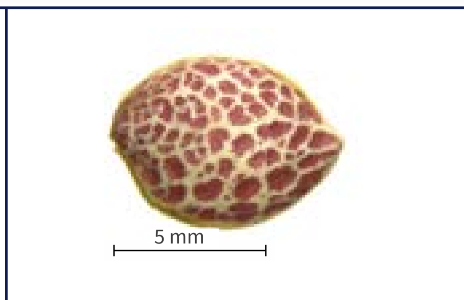


Pyrene

Pyrene

Castela galapageia

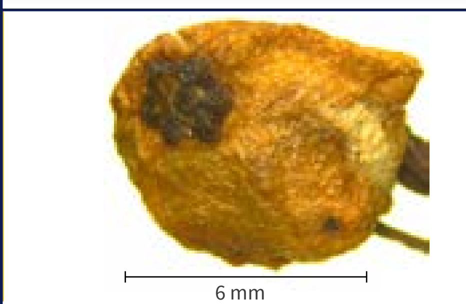
Fruit (drupe)



Pyrene

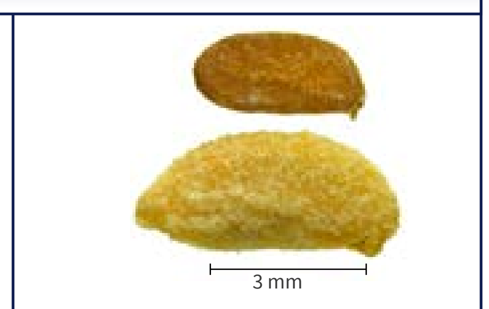
Pyrene, seed

Chiococca alba



Fruit (drupe)

Fruit, pyrene



Pyrene, seed

Citharexylum gentryi

Fruit (drupe)

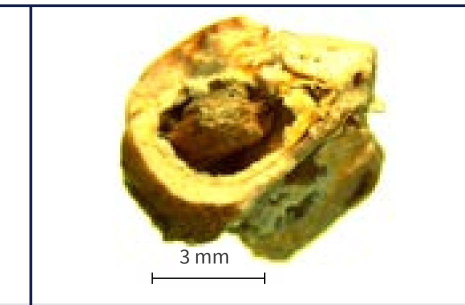
Pyrene

Pyrene

Cordia lutea

Fruit (drupe)

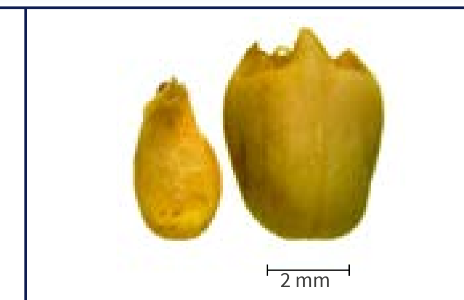
Pyrene



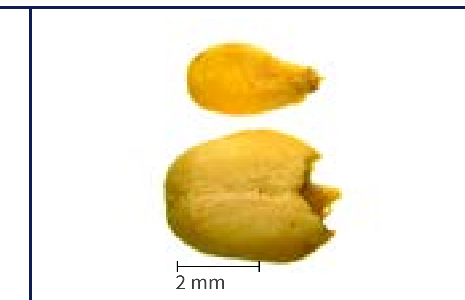
Seed in pyrene

Grabowskia boerhaaviaefolia

Fruit (drupe)



Seed, pyrene



Pyrene, seed

Heliotropium angiospermum

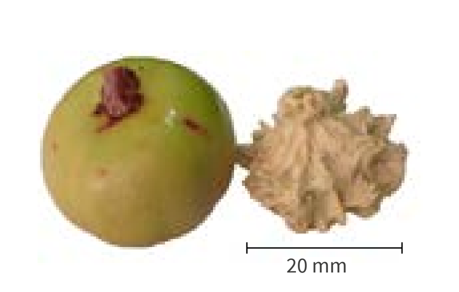
Fruit (nutlets)

Fruit, nutlets

Nutlet

Pyrenes, Mericarps, Fruit Parts

Hippomane mancinella



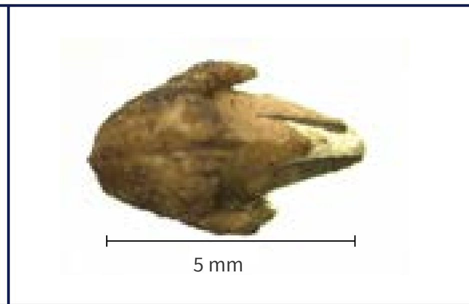
Fruit (drupe), pyrene

Pyrene

Seed

Lantana camara

Fruit (drupe)



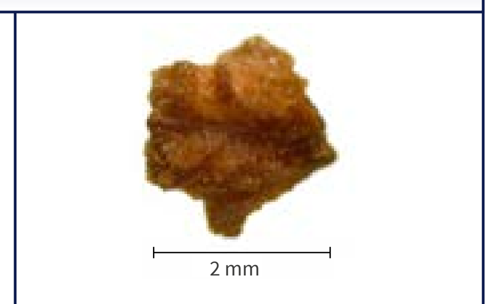
Pyrene

Pyrene

Lantana peduncularis

Pyrenes

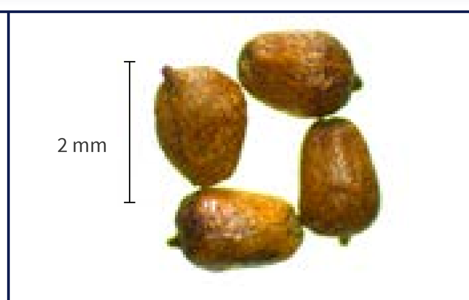
Pyrenes



Pyrene

Lippia rosmarinifolia

Fruit (drupe), pyrene



Pyrenes

Pyrene

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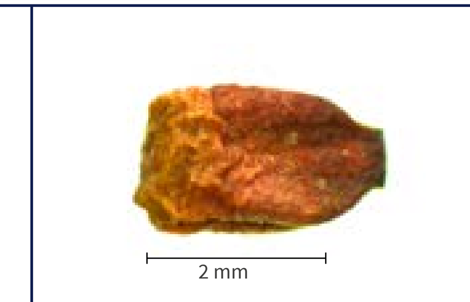
Phoradendron berteroanum

Inflorescences, fruits

Fruits (drupes)



Fruit

Psychotria rufipes

Fruits (drupes)

Pyrene, seed

Seed

Psychotria angustata

Fruit (drupe)

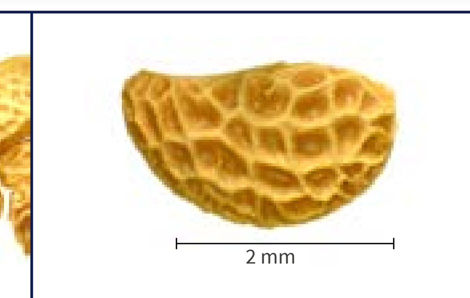
Drupe/pyrene

Drupe/pyrene

Rubus niveus

Pyrenes

Pyrenes

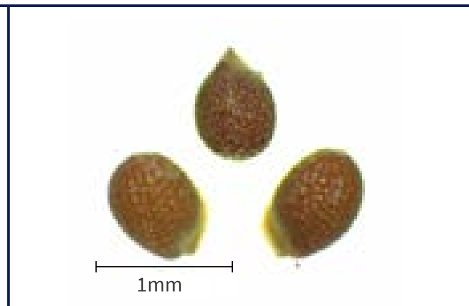


Pyrene

Pyrenes, Mericarps, Fruit Parts

Salvia prostrata

Nutlets



Nutlets

Nutlet

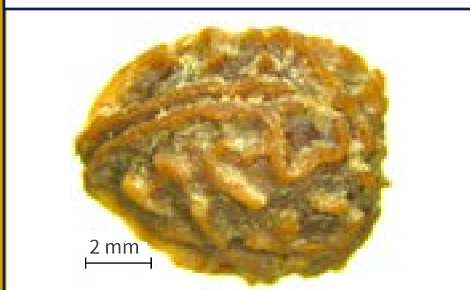
Salvia pseudoserotina

Nutlets

Nutlets

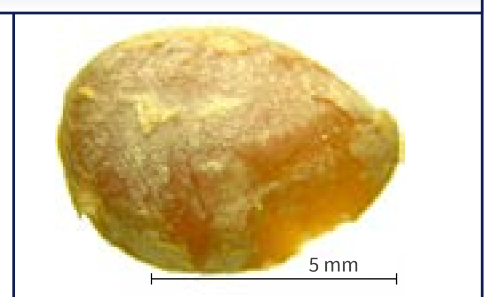
Nutlet

Scaevola plumieri



Pyrene

Pyrene



Seed

Scutia spicata var. pauciflora

Fruit (drupe)

Pyrene

Pyrene

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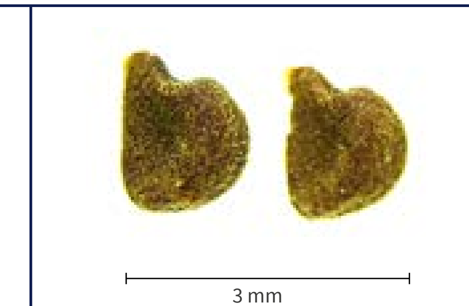
Sida ciliaris

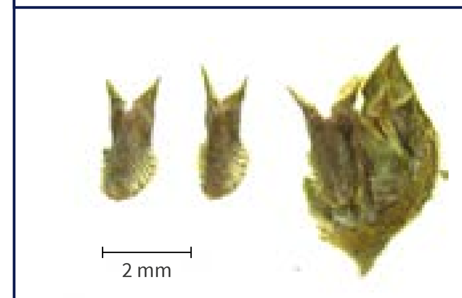
Fruit (schizocarp)

Mericarp

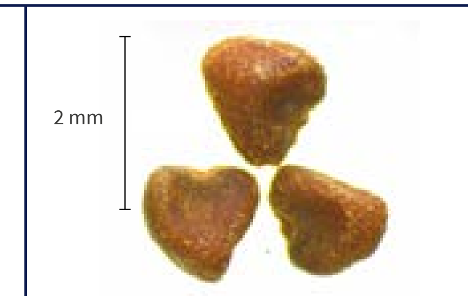


Seeds

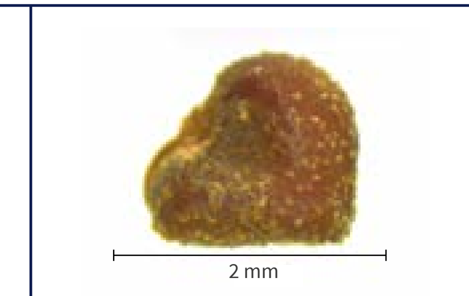
Sida hederifolia



Fruit (schizocarp), mericarps



Seeds



Seed

Sida rhombifolia

Fruit (schizocarp)

Seeds, mericarps

Seeds

Sida spinosa

Mericarps

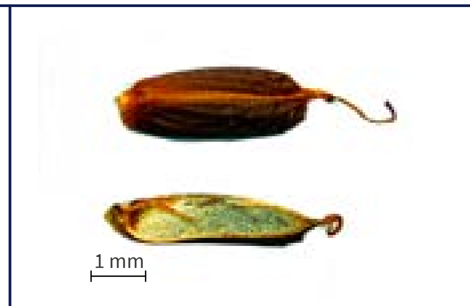
Mericarps, seeds

Seeds

Pyrenes, Mericarps, Fruit Parts

Stachytarpheta cayennensis

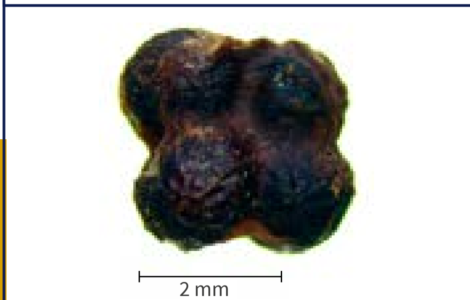
Fruits, schizocarp + calyx



Fruit, mericarp

Mericarps, seed

Tournefortia psilostachya



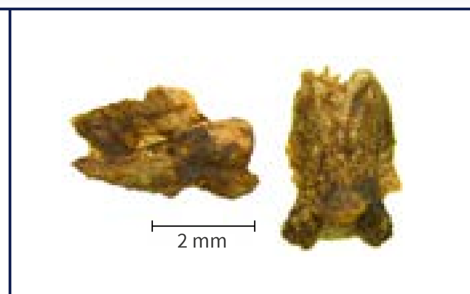
Fruit (drupe), pyrene

Pyrenes

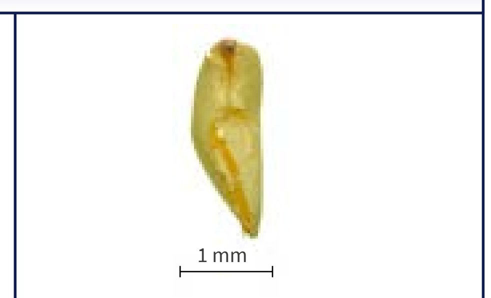
Pyrenes

Tournefortia pubescens

Fruit (drupe), pyrene



Pyrene



Seed

Tournefortia rufo-sericea

Pyrenes

Pyrenes

Seed, part of pyrene

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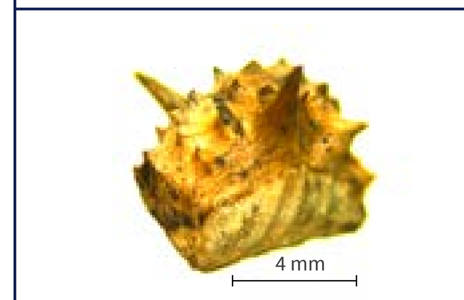
Trema micrantha

Fruit (drupe)

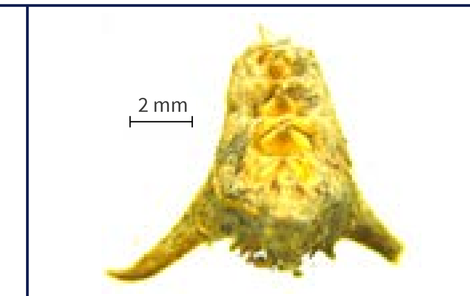
Pyrenes

Pyrene

Tribulus cistoides



Mericarp



Seeds in Mericarp

Seeds

Varronia leucophlyctis

Fruit (drupe)

Pyrenes

Pyrene

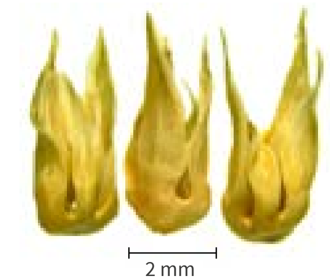
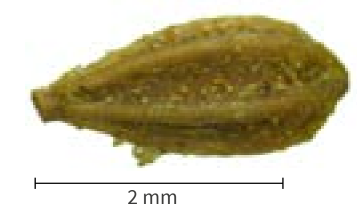
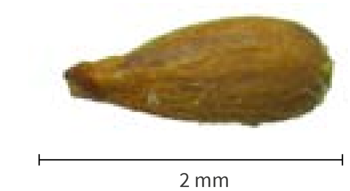
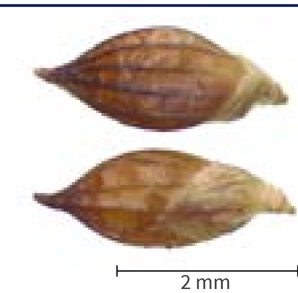
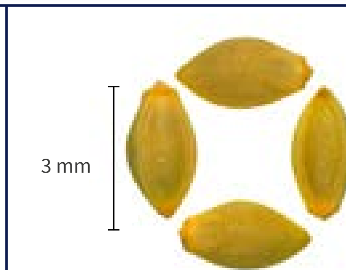
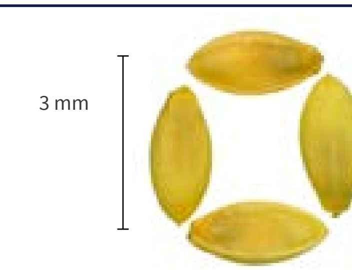
Volkameria mollis

Fruit (drupe)

Pyrenes

Seed, pyrene

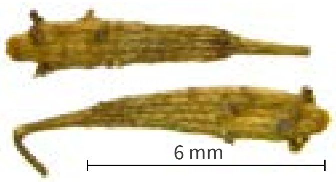
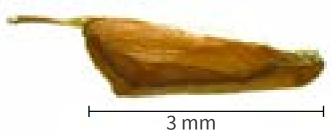
Pyrenes, Mericarps, Fruit Parts

Anthephora hermaphrodita		
		
Propagule (spike)	Seeds with floral remains	Grain (achene)
Boerhavia coccinea		
		
Accessory Fruits (anthocarp)	Fruit	Seed
Brachiaria multiculma		
		
Propagule (spikelet)	Florets	Florets
Brachiaria mutica		
		
Propagule (spikelet)	Florets	Florets

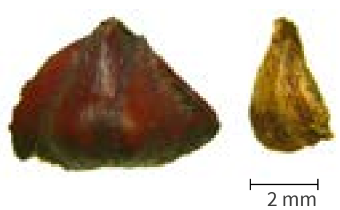
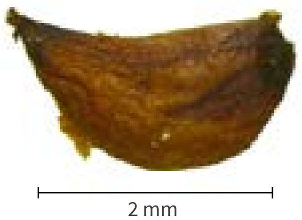
Cenchrus platyacanthus

		
Propagule (spike)	Propagule, spikelet, floret, grain	Spikelet, floret, grain

Commicarpus tuberosus

		
Accessory Fruit (anthocarp)	Fruit	Seed

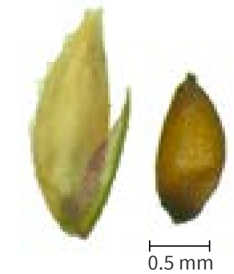
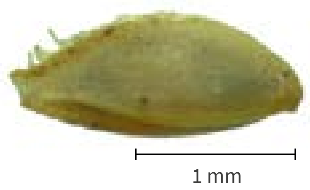
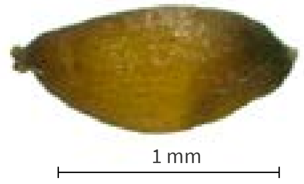
Conocarpus erectus

		
Accessory Fruits (anthocarp)	Fruit, Pyrene	Seed

Cryptocarpus pyriformis

		
Accessory Fruit (anthocarp)	Seed, fruit	Seed

Cynodon dactylon

		
Propagule (spikelet), grain	Caryopsis (palea, lemma)	Grain

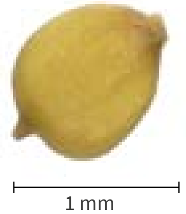
Digitaria horizontalis

		
Propagule (spikelet)	Floret, grain	Grain

Eriochloa pacifica

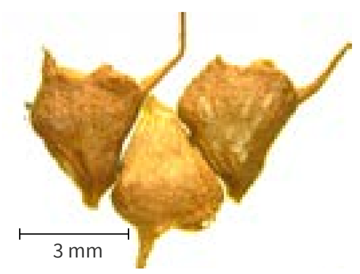
		
Propagule (spikelet)	Spikelet, floret, grain	Floret, grains

Kyllinga brevifolia

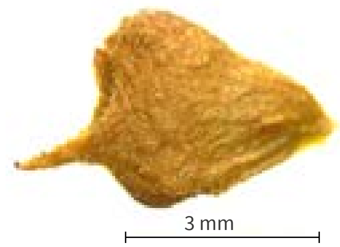
		
Propagule (spikelet)	Fruits, achene	Fruit

Lecocarpus darwinii

Propagule (bract+achene)



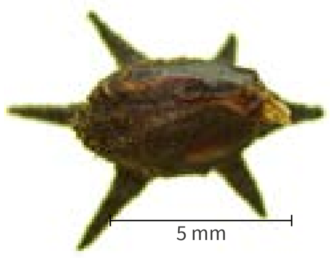
Propagule



Propagule

Lecocarpus lecocarpoides

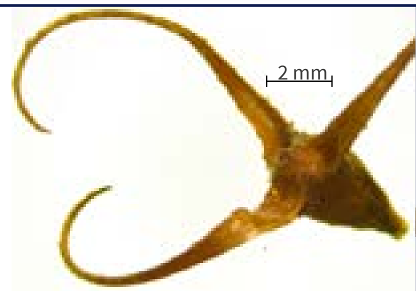
Propagules (bract+achene)



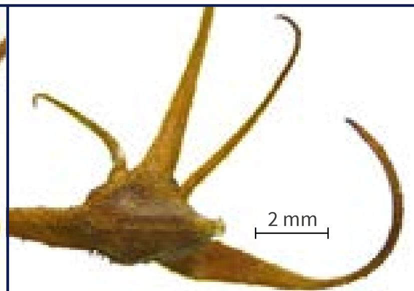
Propagule

Fruit (achene)

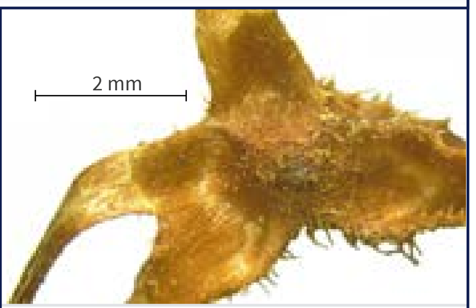
Lecocarpus leptolobus



Propagule (bract+achene)

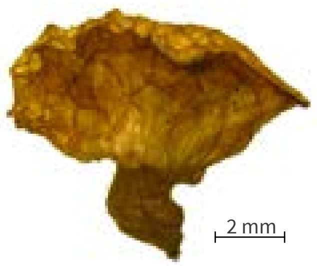


Propagule



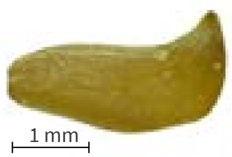
Propagule

Lecocarpus pinnatifidus



Propagule (bract+achene)

Propagules



Seed

More Complex Structures

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Jaramillo, P., Shepherd, J. & Heleno, R.

Panicum maximum

Propagule (spikelet)

Grains, florets

Grain

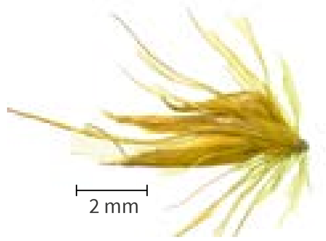
Paspalum conjugatum

Propagule (spikelet)

Propagule, floret

Floret

Pennissetum purpureum



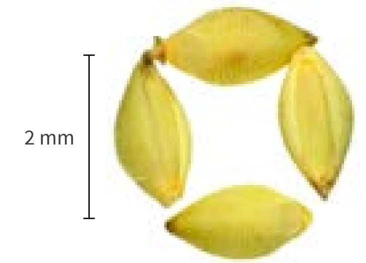
Propagule (spike)

Spikelet, floret, grains

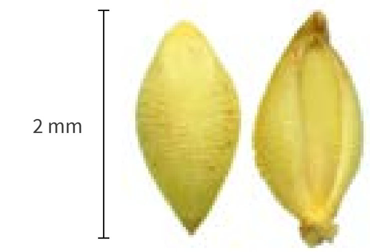
Grains

Setaria setosa

Florets



Florets



Florets

More Complex Structures

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The book reflects the effort of a large team of collaborators of the Charles Darwin Research Station over the years. We are particularly indebted to Angel Cajas, Antonio Picornell, Anne Guézou, Ana Guerrero, Alan Tye, Arturo Izurieta, Anna Traveset, Catarina Heleno, Manuel Nogales, Pablo Vargas, Danielle Mares, Frank Bungartz, Freddy Cabrera, María del Mar Trigo, Patricia Silva, María Guerrero, Rafael Pulido, Stephen Blake and Washington Tapia. Special thanks to Patricia Isabela Tapia and Esme Plunkett for reviewing the English version of this document, to María del Mar Trigo and Sarita Mahtani-Williams for revising, translating and editing into Spanish. Maria José Barragán and Rebecca Ditgen made helpful comments on an earlier version of the manuscript. We are also thankful for the initial support of project REDGAL coordinated by Anna Traveset (Institut Mediterrani D'Estudis Avançats-CSIC), and for the constant support of the Galapagos National Park Directorate (GNPD). The permanent loan of a stereo microscope with digital camera by the GTRI (Giant Tortoise Restoration Initiative - GC and the GNPD) greatly increased the quality of images. We also greatly thank the GTRI for largely contributing to increasing the amount of seeds in the collection through several research projects related to the seed dispersal by giant tortoises and their diet on different islands.

This publication is contribution number 2291 of the Charles Darwin Foundation for the Galapagos Islands. This work is a pioneer scientific contribution in Ecuador and contains the most complete seed catalog for native, endemic and introduced species from the CDS Herbarium and from several research projects on plant-animal interactions.

References

Atkinson, R., Guézou, A. & Jaramillo, P. (2017). Siémbrame en tu Jardín - Kanpa sisapampapi tarpuway - Plant me in your Garden. Jardines nativos para la conservación de Galápagos - Galapagos suyu kuskata kamankapak sisapampakuna - Native gardens for the conservation of Galapagos. Fundación Charles Darwin: Islas Galápagos-Ecuador.

Baskin, J. & Baskin, C. (2004). A classification system for seed dormancy. Seed Science Research 14(1): 1-16.

Beckman, N. G. & Muller-Landau, H. C. (2011). Linking fruit traits to variation in predispersal vertebrate seed predation, insect seed predation, and pathogen attack. Ecology 92(11): 2131-2140.

Blake, S., Guézou, A., Deem, S. L., Yackulic, C. & Cabrera, F. (2015). The Dominance of Introduced Plant Species in the Diets of Migratory Galapagos Tortoises Increases with Elevation on a Human Occupied Island. Biotropica 47(2): 246-258.

Blake, S., Wikelski, M., Cabrera, F., Guezou, A., Silva, M., Sadeghayobi, E., Yackulic, C. & Jaramillo, P. (2012). Seed dispersal by Galápagos tortoises. Journal of Biogeography: 1961-1972.

Bungartz, F., Ziemmeck, F., Tirado, N., Jaramillo, P., Herrera, H. & Jiménez-Uzcátegui, G. (2012).The neglected majority- biodiversity inventories as an integral part of conservation biology. In The Role of Science for Conservation, Vol. 4, 22 (Eds M. Wolff and M. Gardener).

Burger, J. R., Allen, C. D., Brown, J. H., Burnside, W. R., Davidson, A. D., Fristoe, T. S., Hamilton, M. J., Mercado-Silva, N., Nekola, J. C., Okie, J. G. & Zuo, W. (2012). The macroecology of sustainability. PLOS Biology 10(6): 1-7.

Cain, M. L., Milligan, B. G. & Strand, A. E. (2000). Long-distance seed dispersal in plant populations. American Journal of Botany 87(9): 1217-1227.

Catusse, J., Job, C. & Job, D. (2013).Proteomics reveals a potential role of the perisperm in starch remobilization during sugarbeet seed germination. In Seed Development: OMICS Technologies toward Improvement of Seed Quality and Crop Yield, 1-16 (Eds G. K. Agrawal and R. Rakwal). Springer Science+Business Media Dordrecht 2013.

Dalling, J. W. (2002).Ecología de Semillas. In Ecología y Conservación de Bosques Neotropicales, 345-375 (Eds M. R. Guariguata and G. H. Catan). Costa Rica: Cartago, Costa Rica.

Edwards, P. J., Fleischer-Dogley, F. & Kaiser-Bunbury, C. N. (2015). The nutrient economy of *Lodoicea maldivica*, a monodominant palm producing the world's largest seed. New Phytologist 206(3): 990-999.

Fenner, M. (2000). Seeds: the ecology of regeneration in plant communities. 2nd Edition. CABI.

Fowler, C. & Mooney, P. R. (1990). Shattering: food, politics, and the loss of genetic diversity. University of Arizona Press: Tucson.

García, M. B., Espadaler, X. & Olesen, J. M. (2012). Extreme reproduction and survival of a true cliffhanger: The endangered plant *Borderea chouardii* (Dioscoreaceae). PLoS ONE 7(9).

Gardener, M. R., Trueman, M., Buddenhagen, C., Heleno, R., Jäger, H., Atkinson, R. & Tye, A. (2013). A pragmatic approach to the management of plant invasions in Galapagos In Plant Invasions in Protected Areas, Vol. 7, 349-374 (Eds C. F. Llewellyn, P. Petr, D. M. Richardson and P. Genovesi). Invading Nature - Springer Series in Invasion Ecology, vol 7. Springer, Dordrecht.

Gibbs, J. P., Márquez, C. & Sterling, E. J. (2007). The Role of Endangered Species Reintroduction in Ecosystem Restoration: Tortoise–Cactus Interactions on Española Island, Galápagos. Restoration Ecology 16(1): 88-93.

Giladi, I. (2006). Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. Oikos 112: 481-492.

Grant, P. & Grant, M. (2014). 40 Years of Evolution: Darwin's Finches on Daphne Major Island. Princeton University Press, Princeton.

Green, A. K., Ward, D. & Griffiths, M. E. (2009). Directed dispersal of mistletoe (*Plicosepalus acaciae*) by Yellow-vented Bulbuls (*Pycnonotus xanthopygos*). J. Ornithol 150: 167-173.

Guerrero, A. M. & Tye, A. (2011). Native and Introduced birds of Galapagos as dispersers of Native and Introduced plants. Ornitología Neotropical 22: 207–217.

Harris, J. G. & Harris, M. W. (2001). Plant Identification Terminology: An Illustrated Glossary. Spring Lake Pub.

Heleno, R., Blake, S., Jaramillo, P., Traveset, A., Vargas, P. & Nogales, M. (2011).Frugivory and seed dispersal in the Galapagos: what is the state of the art? In Integrate Zoology, Vol. 6, 88-106.

Heleno, R., Olensen, J. M., Nogales, M., Vargas, P. & Traveset, A. (2013). Seed dispersal networks in the Galapagos and the consequences of alien plant invasions. Proceedings of the Royal Society of Biological Sciences.

Heleno, R. & Vargas, P. (2015). How do islands become green?. Global Ecology and Biogeography 24: 518–526DOI:.

Hicks, D. J. & Mauchamp, A. (1996). Evolution and conservation biology of the Galápagos opuntias (Cactaceae). Haseltonia (4): 89-102.

Higgins, S. I., Nathan, R. & Cain, M. L. (2003). Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84(8): 1945–1956.

Howard, P. H. (2009). Visualizing Consolidation in the Global Seed Industry: 1996–2008. Sustainability 1(4): 1266-1287.

Howe, H. F. & Smallwood, J. (1982). Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228.

IUCN (2021).The IUCN Red List of Threatened Species. www.iucnredlist.org. Downloaded on 04 March 2021.

Janzen, D. H. (1971). Seed predation by animals. Annual Review of Ecology and Systematics 2(1): 465-492.

Jaramillo, P., Guézou, A., Mauchamp, A. & Tye, A. (2018).CDF Checklist of Galapagos Flowering Plants - FCD Lista de especies de Plantas con flores de Galápagos. In Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin(Eds F. Bungartz, H. Herrera, P. Jaramillo, N. Tirado, G. Jiménez-Uzcátegui, D. Ruiz, A. Guézou and F. Ziemmeck). Puerto Ayora, Galapagos: Charles

Darwin Foundation / Fundación Charles Darwin.
Jiao, Y. N., Wickett, N. J., Ayyampalayam, S., Chanderbali, A. S., Landherr, L., Ralph, P. E., Tomsho, L. P., Hu, Y., Liang, H. Y., Soltis, P. S., Soltis, D. E., Clifton, S. W., Schlarbaum, S. E., Schuster, S. C., Ma, H., Leebens-Mack, J. & de Pamphilis, C. W. (2011). Ancestral polyploidy in seed plants and angiosperms. Nature 473(7345): 97-113.
Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J. & W., B. (2009). A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences of the United States of America (PNAS) 106(23): 9322-9327.
Lewis-Jones, K. E. (2019). Holding the wild in the seed: Place, escape, and limnality at the Millenium Seed Bank Partnership. Anthropology Today 35(2): 3-7.
Martin, A. (2018). Seed Identification Manual. Cambridge University Press, London, England: University of California Press.
Mauchamp, A. (1997). Threats from alien plant species in the Galapagos Islands. Conservation Biology 1 1(1): 260-263.
Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T. & Westoby, M. (2007). Global patterns in seed size. Global Ecology and Biogeography 16(1): 109-116.
Murdoch, A. (2014).Seed dormancy. In Seeds: The ecology of regeneration in plant communities, 151-177 (Ed R. S. Gallagher). Oxfordshire, UK: CABI.
Nogales, M., González-Castro, A., Rumeu, B., Traveset, A., Vargas, P., Jaramillo, P., Olesen, J. M. & Heleno, R. (2017). Contribution by Vertebrates to Seed Dispersal Effectiveness in the Galapagos Islands: A Community-Wide Approach. Ecology 98(8): 2049-2058.
Nogales, M., Heleno, R., Traveset, A. & Vargas, P. (2012). Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. New Phytologist 194(2): 313-317.
Phillips, C. A. & McGrew, W. C. I. (2013). Identifying Species in Chimpanzee (*Pan troglodytes*) Feces: A Methodological Lost Cause? International Journal of Primatology 34: 792–807.
Porter, D. M. (1983).Vascular plants of the Galapagos: origins and dispersal. In Patterns and Evolution of Galapagos Organisms, 33-96 (Eds R. I. Bowman, M. Berson and A. I. Leviton). San Francisco, California: AAAS, Pacific Division.
Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C. & Job, D. (2012). Seed Germination and Vigor. Annual Review of Plant Biology: 507-734.
Ridley, H. N. (1930). The Dispersal of Plants Throughout the World. Ashford, Kent: L. Reeve & Company, Limited.
Sallon, S., Solowey, E., Cohen, Y., Korchinsky, R., Egli, M., Woodhatch, I., Simchoni, O. & Kislev, M. (2008). Germination, genetics, and growth of an ancient Date seed. Science 320.
Schupp, E. W., Jordano, P. & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188: 333–353.
Sorensen, A. E. (1986). Seed dispersal by adhesion. Annual Review of Ecology and Systematics 17: 443-463.
Srivathsan, A., Sha, J. C. M., Vogler, A. P. & Meier, R. (2015). Comparing the effectiveness of metagenomics and metabarcoding for diet analysis of a leaf-feeding monkey (*Pygathrix nemaeus*). Molecular ecology Resources 15(2): 250–261.
Stuessy, T. F. (2010). Paraphyly and the origin and classification of angiosperms. Taxon 59(3): 689-693.
Swaine, M. D. & Beer, T. (1977). Explosive Seed Dispersal in *Hura crepitans* L. (Euphorbiaceae). New Phytologist 78(3): 695-708.
Tiffney, B. H. (1984). Seed size, dispersal syndromes, and the rise of the Angiosperms - evidence and hypothesis. Annals of the Missouri Botanical Garden 71(2): 551-576.
Toral-Granda, M. V., Causton, C., Jäger, H., Trueman, M., Izurieta, J. C., Araujo, E., Cruz, M., Zander, K., Izurieta, A. & Garnett, S. T. (2017). Alien species pathways to the Galapagos Islands, Ecuador. PLoS ONE 12(9): e0184379.
Traveset, A. (1998). Effect of seed passage through vertebrate frugivores' guts on germination: a

Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

review. Perspectives in Plant Ecology, Evolution and Systematics 1(2): 151–190.
Traveset, A., Heleno, R. H. & Nogales, M. (2014).The ecology of seed dispersal. In Seeds: The ecology of regeneration in plant communities, 62-93 (Ed R. S. Gallagher). Oxfordshire, UK: CABI.
Traveset, A., Nogales, M., Vargas, P., Rumeu, B., Olesen, J., Jaramillo, P. & Heleno, R. (2016). Galápagos land iguana (*Conolophus subcristatus*) as a seed disperser. Integrative Zoology 11(3): 207-2013.
Tye, A. (2006).The status of the endemic flora of Galapagos: the number of threatened species is increasing. In Galapagos Report 2006-2007, 97-103 (Eds DPNG, FCD and INGALA). Puerto Ayora, Isla Santa Cruz.
UNESCO (1972).Convention concerning the protection and of the World Cultural and Natural Heritage. 17 Paris, France.
van der Pijl, L. (1982). Principles of dispersal in higher plants. Springer Science & Business Media: Springer-Verlag, Berlin.
van Slageren, M. W. (2003). The Millenium Seed Bank: building partnerships in arid regions for the conservation of wild species. Journal of Arid Environments 54: 195-201.
Vargas, P., Heleno, R., Traveset, A. & Nogales, M. (2012). Colonization of the Galápagos Islands by plants with no specific syndromes for long-distance dispersal: a new perspective. Ecography 35(1): 33-43.
Viana, D. S., Santamaría, L. & Figuerola, J. (2016). Migratory birds as global dispersal vectors. Trends in Ecology & Evolution 31(10): 763-775.
Weiner, J. (1994). The beak of the finch: the story of evolution in our time. New York: Knopf Doubleday Publishing Group.
Wenny, D. G. (2001). Advantages of seed dispersal: A re-evaluation of directed dispersal. Evolutionary Ecology Research 3(1): 51-74.
Willis, K. & McElwain, J. (2014). The evolution of plants. Oxford, UK: Oxford University Press.

Appendix

The Index is a list of all plant species included in this book, as well as their origin status in the Galapagos, the conservation status in the archipelago (NA-not applicable, NT-near threatened, LC-least concern, VU-vulnerable, EN-endangered, CR-critically endangered), their distribution across the main islands (Dar-Darwin, Esp-Espanola, Fer-Fernandina, Flo-Floreana, Gen-Genovesa, Isa-Isabella, Mar-Marchena, Pin-Pinta, Piz-Pinzon, SCri- San Cristobal, SCru- Santa Cruz, SFe- Santa Fe, San-Santiago, Wolf-Wolf), Group of Photos (Seed; Fruit-Whole Fruits; Pyr-Pyrenes, Mericarps, Fruit Parts; Comp-More Complex Structures), and Page Number (Jaramillo et al., 2018).

Family	Species	Origin in Galapagos	Conser-vation	Distribution in Galapagos	PhotoGroup
Acanthaceae	*Blechum pyramidatum* (Lam.) Urb.	Native	-	Fer, Flo, Isa, Pin, SCri, SCru, San	Seed, 28
Acanthaceae	*Justicia galapagana* Lindau	Endemic	NT	Fer, Flo, Isa, Pin, SCri, SCru, San	Seed, 36
Acanthaceae	*Thunbergia fragrans* Roxb.	Introduced	-	SCri	Seed, 46
Aizoaceae	*Sesuvium portulacastrum* (L.) L.	Native	-	Fer, Flo, Isa, Mar, Pin, SCri, SCru, SFe, San	Seed, 44
Aizoaceae	*Trianthema portulacastrum* L.	Native	-	Esp, Flo, Gen, Isa, Pin, Piz, SCri, SCru, SFe, San	Seed, 47
Amaranthaceae	*Alternanthera nesiotes* I.M Johnst.	Endemic	EN	Flo	Fruit, 50
Amaranthaceae	*Amaranthus sclerantoides* (Andersson) Andersson	Endemic	LC	Dar, Esp, Flo, Gen, Isa, Pin, Piz, SCri, SCru, SFe, San, Wolf	Seed, 27
Amaranthaceae	*Froelichia juncea* B.L. Rob. & Greenm.	Endemic	VU	Isa, SCru, San	Fruit, 53
Amaranthaceae	*Pleuropetalum darwinii* Hook. f.	Endemic	VU	Isa, SCru, San	Seed, 41
Apocynaceae	*Vallesia glabra var. glabra* (Cav.) Link	Native	-	Esp, Flo, Isa, SCri, SCru, San	Seed, 47
Asclepiadaceae	*Asclepias curassavica* L.	Introduced	-	Flo, Isa, SCri, SCru, San	Seed, 27
Asteraceae	*Acmella sodiroi* (Hieron.) R.K. Jansen	Introduced	-	Pin, SCri, SCru	Fruit, 50
Asteraceae	*Ageratum conyzoides* L.	Native	-	Flo, Isa, Pin, SCri, SCru, San	Fruit, 50
Asteraceae	*Baccharis steetzii* Andersson	Endemic	EN	Flo, Isa, SCri, Scru	Fruit, 50
Asteraceae	*Bidens pilosa* L.	Doubtfully Native	-	Fer, Flo, Isa, SCri, SCru, San	Fruit, 51
Asteraceae	*Blainvillea dichotoma* (Murray) Stewart	Native	-	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, SFe, San	Fruit, 51
Asteraceae	*Centratherum punctatum* Cass.	Introduced	-	Isa, SCri, SCru	Fruit, 51
Asteraceae	*Conyza bonariensis* (L.) Cronquist	Introduced	-	Fer, Flo, Isa, SCri, SCru, San	Fruit, 51
Asteraceae	*Darwiniothamnus lancifolius* (Hook. f.) Harling	Native	EN	Fer, Isa, Scru	Fruit, 52
Asteraceae	*Darwiniothamnus tenuifolius* (Hook. f.) Harling	Native	EN	Scru	Fruit, 52
Asteraceae	*Elephantopus mollis* Kunth	Introduced	-	SCri	Fruit, 53
Asteraceae	*Encelia hispida* Andersson	Native	EN	Flo, Isa, SCri, SFe, San	Fruit, 53
Asteraceae	*Lecocarpus darwinii* Adsersen	Endemic	EN	SCri	Comp, 72
Asteraceae	*Lecocarpus lecocarpoides* (Rob. & Greenm.) Cronquist & Stuessy	Endemic	EN	Esp	Comp, 72
Asteraceae	*Lecocarpus leptolobus* (Blake) Cronquist & Stuessy	Endemic	CR	SCri	Comp, 72
Asteraceae	*Lecocarpus pinatifidus* Decne	Endemic	CR	Flo	Comp, 72
Asteraceae	*Pectis tenuifolia* (DC.) Sch. Bip.	Endemic	LC	Esp, Fer, Flo, Gen, Isa, Pin, SCri, SCru, SFe, San	Fruit, 54
Asteraceae	*Porophyllum ruderale subsp. macrocephalum* (DC.) R.R. Johnson	Introduced	-	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, San	Fruit, 54
Asteraceae	*Pseudelephantopus spiralis* (Less.) Cronquist	Introduced	-	Flo, Isa, SCri, SCru, San	Fruit, 55
Asteraceae	*Scalesia affinis* Hook. f.	Endemic	VU	Flo, SCru	Fruit, 55
Asteraceae	*Scalesia atractyloides* Arn.	Endemic	CR	San	Fruit, 55
Asteraceae	*Scalesia cordata* Stewart	Endemic	EN	Isa	Fruit, 56
Asteraceae	*Scalesia divisa* Andersson	Endemic	EN	SCri	Fruit, 56
Asteraceae	*Scalesia gordilloi* O. Hamann & Wium-And.	Endemic	CR	Scri	Fruit, 56
Asteraceae	*Scalesia helleri* B.L. Rob.	Endemic	VU	SCru	Fruit, 56
Asteraceae	*Scalesia incisa* Hook. f.	Endemic	EN	SCri	Fruit, 57
Asteraceae	*Scalesia microcephala* Robinson	Endemic	EN	Fer, Isa	Fruit, 57
Asteraceae	*Scalesia pedunculata* Hook. f.	Endemic	VU	Flo, Isa, SCri, Scru	Fruit, 57
Asteraceae	*Scalesia retroflexa* Hemsl.	Endemic	CR	SCru	Fruit, 57
Asteraceae	*Sonchus oleraceus* L.	Introduced	-	Fer, Flo, Isa, SCri, SCru, San	Fruit, 58
Asteraceae	*Synedrella nodiflora* Gaertn.	Introduced	-	Flo, Isa, SCri, SCru, San	Fruit, 58
Boraginaceae	*Cordia lutea* Lam.	Native	-	Esp, Flo, Gen, Isa, Mar, Pin, Piz SCri, SCru, SFe, San, Wolf	Pyr, 61
Boraginaceae	*Heliotropium angiospermum* Murray	Native	-	Esp, Fer, Flo, Gen, Isa, Pin, Piz, SCri, SCru, SFe, San, Wolf	Pyr, 61

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Boraginaceae	*Tournefortia psilostachya* Kunth	Native	-	Esp, Flo, Isa, Pin, Piz, SCri, SCru, San	Pyr, 66
Boraginaceae	*Tournefortia pubescens* Hook. f.	Endemic	LC	Fer, Flo, Isa, Piz, SCri, SCru, San, Wolf	Pyr, 66
Boraginaceae	*Tournefortia rufo-sericea* Hook. f.	Endemic	VU	Fer, Flo, Isa, Pin, SCri, SCru, San	Pyr, 66
Boraginaceae	*Varronia leucophlyctis* Hook. f.	Endemic	DD	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, SFe, San	Pyr, 67
Burseraceae	*Bursera graveolens* (Kunth) Triana & Planch	Native	-	Dar, Esp, Fer, Flo, Gen, Isa, Mar, Pin, SCri, SCru, SFe,	Pyr, 60
Burseraceae	*Bursera malacophylla* B.L. Rob.	Native	VU	Mar, Scru, San	Pyr, 60
Cactaceae	*Jasminocereus thouarsii var. delicatus* (E.Y. Dawson) E.F. Anderson & Walk.	Endemic	VU	SCru, San	Seed, 36
Cactaceae	*Opuntia echios var. gigantea* Howell	Endemic	EN	SCru	Seed, 38
Cactaceae	*Opuntia galapageia* Hemsl.	Endemic	EN	Isa, Pin, Piz, San	Seed, 38
Cactaceae	*Opuntia megasperma var. mesophytica* J. Lundh	Endemic	CR	SCri	Seed, 39
Caesalpinaceae	*Parkinsonia aculeate* L.	Native	-	Esp, Flo, Isa, Piz, SCri, SCru	Seed, 39
Caesalpinaceae	*Senna occidentalis* (L.) Link	Native	-	Flo, Isa, SCri, SCru, San	Seed, 44
Caryophyllaceae	*Drymaria monticola* Howell	Native	EN	SCru, San	Seed, 32
Celastraceae	*Maytenus octogona* (L'Her.) DC	Native	-	Esp, Fer, Flo, Isa, Piz, SCri, SCru, SFe, San	Seed, 37
Clusiaceae	*Hypericum thesiifolium* Kunth	Native	-	Isa, SCri, SCru, San	Seed, 35
Combretaceae	*Conocarpus erectus* L.	Native	-	Fer, Pin, SCri, SCru, San	Comp, 70
Convolvulaceae	*Evolvulus convolvuloides* (Willd. ex Schult.) Stearn	Native	-	Esp, Flo, Isa, Pin, Piz, SCri, SCru, SFe, San	Seed, 33
Convolvulaceae	*Ipomoea incarnata* (Vahl) Choisy	Native	LC	Fer, Gen, Isa, Pin, Piz, SCru, San, Wolf	Seed, 35
Convolvulaceae	*Ipomoea pes-caprae* (L.) R. Br.	Native	-	Fer, Gen, Isa, Mar, Pin, SCri, SCru	Seed, 36
Convolvulaceae	*Ipomoea triloba* L.	Native	--	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, San, Wolf	Seed, 36

Convolvulaceae	*Merremia aegyptia* (L.) Urb.	Native	-	Dar, Esp, Flo, Gen, Isa, Mar, Pin, Piz, SCri, SCru, SFe, San	Seed, 37
Crassulaceae	*Bryophyllum pinnatum* (Lam.) Oken	Introduced	-	Flo, Isa, SCri, SCru	Seed, 28
Cucurbitaceae	*Cucumis dipsaceus* Ehrenb. ex Spach	Introduced	-	Esp, Flo, Isa, SCri, SCru	Seed, 31
Cucurbitaceae	*Momordica charantia* L.	Introduced	-	Isa, SCri, SCru	Seed, 38
Cyperaceae	*Cyperus confertus* Sw.	Native	-	Esp, Fer, Flo, Gen, Isa, Mar, Pin, Piz, SCri, SCru, SFe, San, Wolf	Fruit, 52
Cyperaceae	*Eleocharis maculosa* (Vahl) Roem. & Schult.	Native	-	Isa, SCru, San	Fruit, 52
Cyperaceae	*Fimbristylis dichotoma* (L.) Vahl	Native	-	Esp, Flo, Isa, Mar, SCri, SCru, San	Fruit, 53
Cyperaceae	*Kyllinga brevifolia* Rottb.	Native	-	Flo, Isa, SCri, SCru, San	Comp, 71
Cyperaceae	*Rhynchospora rugosa* (Vahl) Gale	Native	-	Isa, SCru, San	Fruit, 55
Cyperaceae	*Scleria distans* Poir.	Native	-	SCru	Fruit, 58
Cyperaceae	*Scleria melaleuca* Rchb. Ex Schltdl. & Cham.	Native	-	Isa, SCri, SCru, San	Fruit, 58
Ericaceae	*Pernettya howellii* Sleumer	Endemic	EN	Isa, Scru	Seed, 40
Euphorbiaceae	*Acalypha wigginsii* G.L. Webster	Endemic	CR	Isa, Scru	Seed, 27
Euphorbiaceae	*Croton scouleri var. scouleri* Hook. f.	Endemic	LC	Esp, Fer, Flo, Gen, Isa, Mar, Pin, SCri, SCru, SFe, San	Seed, 30
Euphorbiaceae	*Hippomane mancinella* L.	Native	-	Flo, Isa, SCri, SCru, San	Pyr, 62
Euphorbiaceae	*Phyllanthus caroliniensis subsp. caroliniensis* Walter	Native	-	Fer, Flo, Isa, Pin, SCri, SCru, San	Seed, 40
Euphorbiaceae	*Ricinus communis* L.	Introduced	-	Flo, Isa, SCri, SCru	Seed, 43
Fabaceae	*Abrus precatorius* L.	Introduced	-	Flo, SCru	Seed, 26
Fabaceae	*Crotalaria pumila* Ortega	Native	-	Esp, Fer, Flor, Isa, Pin, Piz, SCri, SCru, SFe, San	Seed, 30
Fabaceae	*Crotalaria retusa* L.	Introduced	-	SCri, SCru	Seed, 30
Fabaceae	*Desmodium incanum* DC.	Doubtfully Native	-	Fer, Flo, Gen, Isad, Pin, SCri, SCru, San	Seed, 31
Fabaceae	*Desmodium procumbens* (Mill.) Hitchc.	Native	-	Esp, Fer, Flo, Gen, Isa, Mar, Pin, Piz, SCri, SCru, SFe, San, Wolf	Seed, 31

Fabaceae	*Erythrina velutina* Willd.	Native	-	Darwin, Gen, Isa, SCru, San, Wolf	Seed, 32
Fabaceae	*Galactia striata* (Jacq.) Urb.	Native	-	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, SFe, San	Seed, 33
Fabaceae	*Piscidia carthagenesis* Jacq.	Native	-	SCri, SCru	Seed, 41
Fabaceae	*Rhynchosia minima* (L.) DC.	Native	-	Esp, Fer, Flo, Gen, Isa, Mar, Pin, Piz, SCri, SCru, SFe, San	Seed, 43
Fabaceae	*Stylosanthes sympodiales* Taub.	Native	-	Fer, Flo, Gen, Isa, Mar, Pin, Piz, SCri, SCru, San	Seed, 46
Fabaceae	*Tephrosia decumbers* Benth.	Native	-	Esp, Fer, Flo, Isa, Pin, SCri, SCru, SFe, San	Seed, 46
Goodeniaceae	*Scaevola plumieri* (L.) Vahl	Native	-	Flo, Isa, SCri, SCru	Pyr, 64
Iridaceae	*Sisyrinchium galapagense* Ravenna	Endemic	EN	Flo, Isa, SCri, SCru	Seed, 44
Lamiaceae	*Salvia prostrata* Hook. f.	Endemic	EN	Flo, Scri, San	Pyr, 64
Lamiaceae	Salvia pseudoserotina Epling	Endemic	EN	Flo, Isa, Scru	Pyr, 64
Lamiaceae	*Volkameria mollis* (Kunth) Mabb. & YW Yuan	Endemic	VU	SCru	Pyr, 67
Loasaceae	*Mentzelia aspera* L.	Native	-	Esp, Flo, Gen, Isa, Pin, Piz, SCri, SCru, SFe, San	Seed, 37
Malvaceae	*Abutilon depauperatum* (Hook. f.) Andersson ex B.L. Rob.	Endemic	LC	Esp, Fer, Flo, Gen, Isa, Mar, Pin, Piz, SCri, SCru,	Seed, 26
Malvaceae	*Bastardia viscosa* (L.) Kunth	Native	-	Esp, Flo, Isa, Pin, Piz, SCri, SCru, SFe, San	Seed, 27
Malvaceae	*Gossypium barbadense* L.	Introduced	-	Esp, Fer, Flo, Isa, SCri, SCru	Seed, 34
Malvaceae	*Gossypium darwinii* G. Watt	Endemic	LC	Esp, Fer, Flo, Isa, Mar, Pin, SCri, SCru, San	Seed, 34
Malvaceae	*Gossypium klotzschianum* Andersson	Endemic	NT	Isa, Mar, SCri, SCru	Seed, 34
Malvaceae	*Herissantia crispa* (L.) Brizicky	Native	-	Flo, Isa, Pin, SCri, SCru, San	Seed, 35
Malvaceae	*Sida ciliaris* L.	Introduced	-	Flo, Isa, SCri, SCru	Pyr, 65
Malvaceae	*Sida hederifolia* Cav.	Native	-	Flo, Isa, Pin, Piz, SCri, SCru, San	Pyr, 65

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Malvaceae	*Sida rhombifolia* L.	Introduced	-	Flo, Isa, SCri, SCru, San	Pyr, 65
Malvaceae	*Sida spinosa* L.	Native	-	Esp, Flo, Gen, Isa, Pin, Piz, SCri, SCru, San	Pyr, 65
Melastomataceae	*Miconia robinsoniana* Cogn.	Endemic	EN	SCri, SCru	Seed, 38
Mimosaceae	*Acacia nilotica* (L.) Willd. Ex Delile	Endemic	-	SCri, SCru	Seed, 26
Mimosaceae	*Acacia rorudiana* Christoph.	Endemic	VU	Esp, Flo, Isa, SCri, SCru, San	Seed, 26
Mimosaceae	*Desmanthus virgatus* B.L. Turner	Native	-	Esp, Flo, Isa, Pin, Piz, SCri, SCru	Seed, 31
Mimosaceae	*Prosopis juliflora* (Sw.) DC.	Native	-	Esp, Flo, Isa, Pin, Piz, SCri, SCru, SFe, San	Seed, 42
Myrtaceae	*Psidium galapageium* Hook. f.	Endemic	EN	Fer, Isa, Pin, Scri, Scru, San	Seed, 43
Myrtaceae	*Psidium guajava* L.	Introduced	-	Flo, Isa, SCri, SCru	Seed, 43
Nyctaginaceae	*Boerhavia coccinea* Mill.	Native	-	Esp, Fer, Flo, Isa, Pin, SCri, SCru, SFe, San	Comp, 69
Nyctaginaceae	*Commicarpus tuberosus* (Lam.) Standl.	Native	-	Esp, Flo, Isa, Piz, SCri, SCru, San	Comp, 70
Nyctaginaceae	*Cryptocarpus pyriformis* Kunth	Native	-	Esp, Fer, Flo, Gen, Isa, Mar, Pin, SCri, SCru, SFe, San	Comp, 70
Onagraceae	*Ludwigia leptocarpa* (Nutt.) H. Hara	Native	-	SCri, SCru, San	Seed, 37
Passifloraceae	*Passiflora colinvauxii* Wiggins	Endemic	VU	SCru	Seed, 39
Passifloraceae	*Passiflora edulis* Sims	Introduced	-	Flo, Isa, SCri, SCru	Seed, 39
Passifloraceae	*Passiflora foetida* L.	Endemic	-	Flo, Isa, SCru	Seed, 40
Plantaginaceae	*Plantago major* L.	Introduced	-	Flo, Isa, SCri, SCru, San	Seed, 41
Poaceae	*Anthephora hermaphrodita* (L.) Kuntze	(Doubtfully Native)	-	Fer, Flo, Isa, SCri, SCru, SFe, San	Comp, 69
Poaceae	*Brachiaria multiculma* (Andersson) Laegaard & Renvoize	Endemic	LC	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, SFe, San	Comp, 69
Poaceae	*Brachiaria mutica* (Forssk.) Stapf	Introduced	-	Isa, SCri, SCru	Comp, 69
Poaceae	*Cenchrus platyacanthus* Andersson	Endemic	LC	Esp, Fer, Flo, Gen, Isa, Mar, Pin, SCri, SCru, SFe, San	Comp, 70
Poaceae	*Cynodon dactylon* (L.) Pers.	Introduced	-	Flo, Isa, SCri, SCru	Comp, 71

Poaceae	*Digitaria horizontalis* Willd.	Introduced	-	Esp, Flo, Gen, Isa, Pin, SCri, SCru, San	Comp, 71
Poaceae	*Eleusine indica* (L.) Gaertn.	Introduced	-	Esp, Flo, Isa, SCri, SCru, San	Seed, 32
Poaceae	*Eragrostis ciliaris* (L.) R. Br.	Native	-	Fer, Flo, Gen, Isa, Mar, Pin, SCri, SCru, San	Seed, 32
Poaceae	*Eriochloa pacifica* Mez	Native	-	SCri, SCru	Comp, 71
Poaceae	*Panicum maximum* Jacq.	Introduced	-	Flo, Isa, SCri, SCru	Comp, 73
Poaceae	*Paspalum conjugatum* Bergius	Doubtfully Native	-	Esp, Flo, Isa, Pin, SCri, SCru, San	Comp, 73
Poaceae	*Pennissetum purpureum* Schumach	Introduced	-	Flo, Isa, SCri, SCru	Comp, 73
Poaceae	*Setaria setosa* (Sw.) P. Beauv.	Native	-	Esp, Fer, Flo, Isa, Mar, Pin, Piz, SCri, SCru, SFe, San, Wolf	Comp, 73
Poaceae	*Sporobolus indicus* (L.) R. Br.	Native	-	Esp, Fer, Isa, Pin, SCri, SCru, San	Seed, 45
Polygalaceae	*Polygala andersonii* B.L. Rob.	Endemic	NT	Isa, SCru, San	Seed, 42
Polygonaceae	*Polygonum opelousanum* Riddell ex Small	Native	-	Flo, Isa, SCri, SCru, San	Fruit, 54
Portulacaceae	*Calandrinia galapagosa* H. St. John	Endemic	CR	Scri	Seed, 28
Portulacaceae	*Portulaca oleracea* L.	Doubtfully Native	-	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, SFe, Wolf	Seed, 42
Portulacaceae	*Portulaca umbraticola* Kunth	Introduced	-	Flo, Isa, SCru, SFe	Seed, 42
Portulacaceae	*Talinum paniculatum (*Jacq.) Gaertn.	Introduced	-	Flo, SCri, SCru	Seed, 46
Rhamnaceae	*Scutia spicata var. pauciflora* (Hook. f.) M.C. Johnst.	Endemic	LC	Esp, Flo, Isa, SCri, SCru, SFe, San	Pyr, 64
Rosaceae	*Rubus niveus* Thunb.	Introduced	-	Flo, Isa, SCri, SCru, San	Pyr, 63
Rubiaceae	*Chiococca alba* (L.) Hitchc.	Native	-	Fer, Flo, Isa, Mar, Pin, Piz, SCri, SCru, San	Pyr, 60
Rubiaceae	*Cinchona pubescens* Vahl	Introduced	-	SCru	Seed, 30
Rubiaceae	*Galium galapagoense* Wiggins	Endemic	EN	Flo, Isa, SCri, SCru, San	Seed, 33
Rubiaceae	*Pschotria rufipes* Hook. f.	Endemic	VU	Fer, Flo, Isa, Pin, SCri, SCru, San	Pyr, 63
Rubiaceae	*Psychotria angustata* Andersson	Endemic	CR	Flo	Pyr, 63

Rubiaceae	*Spermacoce remota* Lam.	Native	-	Fer, Flo, Isa, SCri, SCru, San	Seed, 45
Rutaceae	*Zanthoxylum fagara (*L.) Sarg.	Native	-	Flo, Isa, Pin, Piz, SCri, SCru, San	Seed, 47
Sapindaceae	*Cardiospermum galapageium* B.L. Rob. & Greenm.	Endemic	VU	Flo, Isa, SCri, SCru	Seed, 29
Scrophulariaceae	*Capraria biflora* L.	Native	-	Flo, Isa, SCri, SCru	Seed, 28
Scrophulariaceae	*Capraria peruviana* Benth.	Native	-	Flo, Isa, Piz, SCri, SCru	Seed, 29
Scrophulariaceae	*Galvezia leucantha subsp. leucantha* Wiggins	Endemic	EN	Fer, Isa	Seed, 33
Scrophulariaceae	*Galvezia leucantha subsp. pubescens* Wiggins	Endemic	CR	San	Seed, 34
Simaroubaceae	*Castela galapageia* Hook. f.	Endemic	LC	Esp, Fer, Flo, Isa, Pin, piz, SCri, SCru, SFe, San	Pyr, 60
Solanaceae	*Capsicum annuum* L.	Introduced	-	Flo, Isa, SCri, SCru, San	Seed, 29
Solanaceae	*Capsicum galapagoense* Hunz.	Endemic	EN	Isa, SCru	Seed, 29
Solanaceae	*Grabowskia boerhaaviaefolia* (L. f.) Schltdl.	Native	-	Esp, Flo, Pin, Piz, SCri, SCru, Sfe, San	Pyr, 61
Solanaceae	*Iochroma ellipticum* (Hook. f.) Hunz	Endemic	VU	Flo, Isa, SCri, SCru, San	Seed, 35
Solanaceae	*Physalis galapagoensis* Waterf.	Endemic	LC	Esp, Fer, Flo, Isa, SCri, SCru, San	Seed, 40
Solanaceae	*Physalis pubescens* L.	Native	-	Esp, Fer, Flo, Isa, Pin, Piz, SCru, SFe, San	Seed, 41
Solanaceae	*Solanum americanum* Mill.	Doubtfully Native	-	Esp, Fer, Flo, Isa, Pin, Piz, SCri, SCru, San, Wolf	Seed, 44
Solanaceae	*Solanum cheesmaniae* (Riley) Fosberg	Endemic	NT	Fer, Flo, Isa, SCri, SCru, San	Seed, 45
Solanaceae	*Solanum pimpinellifolium* L.	Introduced	-	SCru	Seed, 45
Sterculiaceae	*Waltheria ovata* Cav.	Native	-	Esp, Fer, Flo, Gen, Isa, Mar, Pin, SCri, SCru, SFe, San	Seed, 47
Ulmaceae	*Trema micrantha* (L.) Blume	Doubtfully Native	-	Flo, Isa, Pin, SCru, San	Pyr, 67
Urticaceae	*Pilea baurii* B.L. Rob.	Endemic	LC	Fer, Flo, Isa, Pin, Piz, SCri, SCru, San	Fruit, 54
Verbenaceae	*Citharexylum gentryi* Moldenke	Introduced	-	SCru	Pyr, 61
Verbenaceae	*Lantana camara* L.	Introduced	-	Flo, Isa, SCri, SCru	Pyr, 62

Fundación Charles Darwin Foundation GALAPAGOS
Guide to Galapagos Seeds and Propagules
Jaramillo, P., Shepherd, J. & Heleno, R.

Verbenaceae	*Lantana peduncularis* Andersson	Endemic	LC	Esp, Fer, Flo, Gen, Isa, Mar, Pin, SCri, SCru, SFe, San	Pyr, 62
Verbenaceae	*Lippia rosmarinifolia* Andersson	Endemic	CR	Fer, Flo, Isa, Pin, San	Pyr, 62
Verbenaceae	*Stachytarpheta cayennensis* (Rich.) Vahl	Introduced	-	Flo, Isa, SCri, SCru	Pyr, 66
Viscaceae	*Phoradendron berteroanum* (DC.) Griseb.	Endemic	LC	Fer, Flo, Isa, Pin, SCri, SCru, San	Pyr, 63
Zygophyllaceae	*Tribulus cistoides* L.	Doubtfully Native	-	Dar, Esp, Fer, Flo, Gen, Isa, Pin, SCri, SCru, San	Pyr, 67

Index

Guide to Galapagos Seeds and Propagules

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