Annonas: cherimoya, atemoya and sweetsop.

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HORTICULTURAL REVIEW

The genus *Annona*: Botanical characteristics, horticultural requirements and uses

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Abstract

An overview of the genus *Annona* in the Family Annonaceae is provided in this review. The mainly neotropical family of trees and lianas has numerous commercial fruits that are eaten fresh, processed, or used as popular medicines. The family has 109 recognized genera and from 2,300 to 2,500 species. The taxonomy, morphology, and cytology of *Annona* spp. are discussed. The genus *Annona* has the most fruits of commercial importance, including the cherimoya (*A. cherimola* Mill.), soursop (*A. muricata* L.), sugar apple (*A. squamosa* L.), ilama (*A. diversifolia* Saff.), pond apple (*A. glabra* L.), biriba (*A. mucosa* Jacq. formerly *Rollinia deliciosa* Saff.), and hybrids such as the atemoya (*A. squamosa* × *A. cherimola*).

1 | INTRODUCTION

The edible fruits of the family Annonaceae are found primarily in the genus *Annona*. A number of these fruits have significant commercial value including the cherimoya (*A. cherimola* Mill.), soursop (also known as the guanábana or graviola) (*A. muricata* L.), the sweetsop or sugar apple (*A. squamosa* L.), the ilama (*A. diversifolia* Saff.), biriba (*A. mucosa* Jacq. formerly *Rollinia deliciosa* Saff.), and the hybrid atemoya (*A. squamosa* × *A. cherimola*). The fruit are normally consumed fresh, though their short postharvest life often limits marketing. The processed pulp, which is widely available in frozen or aseptically processed form, is in high demand by the juice industry, as well as for use in marmalades, ice creams, bakery products, and sweets. Extracts from the seeds have insecticidal and pharmacological uses. The fruits have high nutritional value due to an abundance of carbohydrates and high concentrations of calcium, phosphorus, iron, thiamine, niacin, riboflavin and, in some cases, ascorbic acid and carotene.

The species *A. cherimola*, *A. muricata*, and *A. squamosa* and others in the same family, together with many hybrids, are valued locally as important genetic resources for food and for their wide uses in popular medicines. The medicinal uses depend upon the diverse chemical makeup of the different fruits and foliage from the wide range of *Annona* species. Their unique essential oils are also widely used in the perfume industry (Pinto et al., 2005). The trees provide wood for the timber industry.

Commercially, the more common species are planted worldwide on a limited scale. These plantings are typified by less-than-ideal tree management leading to very low yields and poor quality, except for cherimoya, sugar apple and the hybrid atemoya. Other specific exceptions are sweetsop in Taiwan (Lin et al., 2014), custard apple (*A. reticulata* or *Annona* hybrids) in Australia (Nissen & George, 2002) and *A. squamosa* in Southeast Asia (Wongs-Aree & Noichinda, 2011). The absence of in-depth horticulture research and limited characterization of available germplasm collections has limited commercialization in the warm tropics.

2 | TAXONOMY, MORPHOLOGY, AND CYTOLOGY

2.1 | Taxonomy

The family Annonaceae A.L. Jussieu is found in the tropics and subtropics of both the old and new world. Annonaceae is one of the most diverse and primitive angiosperms, reported to contain from 110 to 200 genera and from 2,300 to 2,500 species (Awachare et al., 2018; Doyle & Le Thomas, 1997; Le Thomas & Doyle, 1996). Though found mainly in the tropics, a few species do occur in temperate zones. It is estimated that about 900 species are from the Caribbean and Central America, 450 from tropical Africa and close to 1,200 species from tropical Asia and Australia (Chatrou, 1999; Couvreur et al., 2011; Guo et al., 2017). The *Annonaceae* belongs to the Order Magnoliales, though Dahlgren et al. (1985) considered that the family belongs to the Order Annonales, with two suborders of 10–13 families. The family is the largest and most diverse within the Magnoliales with an abundant of species richness, low extinction rate, and diversity of habitats.

Annonaceae is one of the most primitive families within the spermatophytic (syn. Phanerogamous) plants and sometimes is called Annoniflorae, because species frequently have an indefinite number of free floral parts and spiral stamens. The family has many primitive and archaic morphological features and many species have survived mass extinctions and are regarded as "living fossils" (Couvreur et al., 2011; Soltis & Soltis, 2004). They are closely related to the core Magnoliaceae but differ by having a ruminate endosperm, lack of stipules, and are separated by the fact that they grow and develop at low latitudes and altitudes. The family is closely related to the Winteraceae due to their lack of vessels in the vascular bundles, to the Myristicaceae for their free stamens, and from the Lauraceae and Calycanthaceae because of their hypogynous flowers (Mabberley, 1993). The Annonaceae family limits are very well defined, but it is difficult to divide the family into natural genera groupings. However, the family is often divided into two subfamilies or clades: Monodoroideae and Annonoideae (Couvreur et al., 2011; Guo et al., 2017).

The genus *Annona* is the second largest genus in the family with about 60 species distributed through tropical America and four species in Africa (Maas et al., 2019). Safford (1911, 1914) considered the genus *Annona* to be comprised of around 50 species and divided them into five groups, and each group into sections. Subsequently there were some additions by Schatz (1992). However, up to 120 other species considered to be in this genus may not fit into this classification, with many potentially being synonyms (Table 1).

Soursop (*Annona muricata*, L.) has been chosen as the lectotype for the genus *Annona* as described by Carl Linnaeus.

Core Ideas

- *Annona* taxonomy is discussed.
- *Annona* horticultural practices are considered.
- *Annonas*' pest and diseases are discussed.

The genus has undergone numerous taxonomic changes in its boundaries, such as the creation of *Rollinia* as a separate genus. The taxonomy of the genus *Annona* has been revised (Couvreuer et al., 2011; Rainer, 2001, 2006). The 44 species in the genus *Rollinia* (Maas et al., 1992) were returned to the genus *Annona* as originally described by Nikolaus Joseph von Jacquin in 1764 (Couvreur et al., 2012; Rainer, 2006). *Rollinia* was regarded as an orphan genus with significant overlap with the genus *Annona* though not significantly collected in situ to clarify their taxonomy, botanical relationships and species evolution, with molecular studies not supporting its rank as a distinct genus (Chatrou et al., 2012; Maas et al., 2011; Rainer, 2006). The most current list of approved names and synonyms for *Annona* is presented in Table 1 and can be accessed at the Catalogue of Life (Banki et al., 2021). The confused nature of the *Rollinia* spp. can be appreciated by the many synonyms for what are now regarded as a single *Annona* spp. (Table 1). The overlap in species characteristics and the presence of hybrids makes species boundaries difficult to define. Further molecular studies will clarify the relationship between species and lead to a more well-defined classification.

2.2 | Morphology

The Annonaceae are trees, shrubs, and vines (liana) with aromatic foliage, resinous channels in their stems, and a septate medulla or pith. The stems have alternate simple leaves that occur in two rows, with deciduous or persistent stipules. Flowers are super axillary, regular, solitary or in fragrant racemes, being bisexual (rarely unisexual), protogynous (because the stigmas lose their receptivity before pollen dispersal), actinomorphic and hypogenous. There are three vertical perianths that are brown or pale yellow-green. There are three sepals, six petals in two series of three petals; generally, valvate; numerous stamens agglomerated in spirals, with adnate anthers of short and thick filaments, with the gynoecium on top of them with many pistils. The ovary is superior with one-to-many ovules. The fruit are berries, capsules or a dry fruit, though in some genera the pistils are located in an elongated receptacle that transforms into an aggregated and pulpous fruit. Seeds of a complicated structure, but with the endosperm ruminated or cracked (Brummitt, 1992; Folorunso & Olorode, 2006; Gottsberger, 1999; Mabberley, 1993; Purseglove, 1968).

TABLE 1 Accepted species within the genus *Annona*, according to Maas et al. (2011) and modified from *The Catalog of Life* (Banki et al., 2021). The list includes the species formerly in the genus *Rollinia* (Rainer, 2006). The Lectotype for the genus is *A. muricata* L

Genus and common name	Accepted name and synonyms
Annona acuminata Saff.	Accepted. *Annona echinata* Hemsl.
Annona acutiflora Mart.	Accepted.
Annona amazonica R. E. Fr.	Accepted. *Annona amazonica* var. *lancifolia* R. E. Fr., *Rollinia amazonica* R. E. Fr.
Annona ambotay Aubl.	Accepted.
Annona andicola (Maas & Westra) H. Rainer	Accepted. *Rollinia andicola* Maas & Westra
Annona angustifolia Huber	Accepted.
Annona annonoides (R. E. Fr.) Maas & Westra	Accepted. *Rollinia annonoides* R. E. Fr.
Annona antioquensis Linden	Accepted.
Annona asplundiana R. E. Fr.	Accepted.
Annona atabapensis Kunth	Accepted.
Annona atemoya Mabb.	Accepted.
Annona aurantiaca Barb. Rodr.	Accepted. *Annona coriacea* var. *amplexicaulis* S. Moore
Annona bahiensis (Maas & Westra) H. Rainer	Accepted. *Rollinia bahiensis* Maas & Westra
Annona bicolor Urb.	Accepted. *Annona bicolor* f. *concolor* R. E. Fr.
Annona billbergii R. E. Fr.	Accepted.
Annona bimaculate (Distant, 1884)	Accepted.
Annona boliviana (R. E. Fr.) H. Rainer	Accepted. *Rollinia boliviana* R. E. Fr.
Annona brasiliensis Carvalho & Schaffner, 1977	Accepted.
Annona bullata A. Rich.	Accepted.
Annona burchellii R. E. Fr.	Accepted.
Annona cacans Warm. – araticum-cagão	Accepted.
Annona cacans subsp. *glabriuscula* (R. E. Fr.) H. Rainer	Accepted. *Annona quaresma* Dutra ex R. E. Fr.
Annona calcarata (R. E. Fr.) H. Rainer	Accepted. *Rollinia calcarata* R. E. Fr.
Annona calophylla R. E. Fr.	Accepted.
Annona campestris R. E. Fr.	Accepted.
Annona cancellata Mart.	Accepted.
Annona cascarilloides C. Wright ex Griseb.	Accepted. *Annona elliptica* R. E. Fr.
Annona centrantha (R. E. Fr.) H. Rainer	Accepted. *Rollinia centrantha* R. E. Fr.
Annona cercocarpa Saff.	Accepted.
Annona cherimola Mill. – cherimoya, chirimoriñon	Accepted. *Annona cutifolia* Saff. Ex R. E. Fr., *A. cherimola* var. *loxensis* Linden., *A. odorata* Linden., *A. pubescens* Salisb., *A. tripetala* Aiton
Annona cherimolioides Triana & Planch.	Accepted. *Annona ambotay* subsp. *occidentalis* R. E. Fr., *A. cherimolioides* var. *amplifolia* Triana & Planch.
Annona chiriquensis Linden	Accepted.
Annona conica Ruiz & Pav. Ex G. Don	Accepted. *Annona amambayensis* Hassl. Ex R. E. Fr.
Annona cordifolia (Szyszyl.) R. E. Fr.	Accepted. *Annona scandens* var. polychyla Diels., Ambiguous synonym of *A. cordifolia* Poepp. Ex Szyszyl. *Rollinia cordifolia* Szyszyl.
Annona coriacea Mart.	Accepted. *Annona geraensis* Barb. Rodr., *A. coriacea* var. *cuneata* R. E. Fr.
Annona cornifolia A. St.-Hil.	Accepted. *Annona walkeri* S. Moore
Annona crassiflora Mart. – araticum do cerrado, marolo	Accepted. *Annona macrocarpa* Barb. Rodr., *A. rodriguesii* Barb. Rodr.
Annona crassivenia Saff.	Accepted.
Annona cristalensis (Alain) Borhidi & Moncada	Accepted.
Annona crotonifolia Mart.	Accepted. *Annona velutina* A. St.-Hil. & Tul.
Annona cubensis R. E. Fr.	Accepted.

(Continues)

TABLE 1 (Continued)

Genus and common name	Accepted name and synonyms
Annona cuspidata (Mart.) H. Rainer	Accepted. *Rollinia cardiantha* Diels., *R. cuspidata* Mart., *R. pachyptera* Diels., *R. sphaerantha* R. E. Fr., *R. uniflora* R. E. Fr.
Annona danforthii (Standl.) H. Rainer	Accepted. *Rollinia chocoenis* R. E. Fr., *R. chocoënsis* R. E. Fr., *R. danforthii* Standl.
Annona deceptrix (Westra) H. Rainer	Accepted.
Annona deminuta R. E. Fr.	Accepted.
Annona densicoma Mart.	Accepted.
Annona dioica A. St.-Hil.	Accepted. *Annona cuyabaensis* Barb. Rodr., *A. dioica* var. *mattogrossensis* R. E. Fr.
Annona dodecapetala Lam.	Accepted.
Annona dolabripetala Raddi	Accepted. *Annona minensis* Glaz., *A. xestropetala* Spreng., *Rollinia dolabripetala* (Raddi) R. E. Fr., *R. grandifolia* Klotzsch ex Mart., *R. longifolia* A. St.-Hil. *R. minensis* (Glaz.) R. E. Fr.
Annona dolichopetala (R. E. Fr.) H. Rainer	Accepted. *Rollinia dolichopetala* R. E. Fr., *R. dolichopetala* var. *Divergens* R. E. Fr., *R. dolichopetala* var. *Suberecta* R. E. Fr.
Annona dolichophylla R. E. Fr.	Accepted.
Annona duckei Diels	Accepted.
Annona dunalii Wall.	Accepted.
Annona echinata Dunal	Accepted. *Annona tenuifolia* A. DC., *A. poeppigiana* Saff. Ex R. E. Fr., *Rollinia tenuifolia* A. DC. Ex Steud.
Annona ecuadorensis R. E. Fr.	Accepted.
Annona edulis (Triana & Planch.) H. Rainer	Accepted. *Rollinia edulis* Triana & Planch., *R. edulis* var. *acuta* R. E. Fr., *R. edulis* var. *macropus* R. E. Fr.
Annona ekmanii R. E. Fr.	Accepted.
Annona emarginata (Schltdl.) H. Rainer	Accepted. *Rollinia emarginata* Schltdl., *R. glaucescens* Sond., *R. glaziovii* R. E. Fr., *R. hassleriana* R. E. Fr., *R. intermedia* R. E. Fr., *R. longipetala* R. E. Fr., *R. occidentalis* R. E. Fr. *Rollinia odoriflora* Rojas Acosta, *R. sonderiana* Walp. *Rollinia emarginata* var. *Longipetala* (R. E. Fr.) R. E. Fr.
Annona excellens R. E. Fr.	Accepted
Annona exsucca DC.	Accepted. *Rollinia brevipes* R. E. Fr., *R. broadwayi* R. E. Fr. *Rollinia exsucca* (DC.) A. DC., *R. gardneri* R. E. Fr. *Rollinia glaucescens* Miq., *R. incurva* S. Moore *Rollinia multiflora* Splitg., *R. procera* R. E. Fr. *Rollinia puberula* A. DC., *R. resinosa* Spruce ex Benth. *Rollinia surinamensis* R. E. Fr., *R. tinifolia* Klotzsch *Rollinia exsucca* subsp. *elongata* R. E. Fr., *R. exsucca* subsp. *resinosa* (Spruce ex Benth.) R. E. Fr.
Annona fendleri (R. E. Fr.) H. Rainer	Accepted. *Rollinia fendleri* R. E. Fr. *Rollinia subracemosa* Pittier
Annona ferruginea (R. E. Fr.) H. Rainer	Accepted. *Rollinia ferruginea* (R. E. Fr.) Maas & Westra
Annona foetida Mart.	Accepted. *Annona trunciflora* R. E. Fr.
Annona fosteri (Maas & Westra) H. Rainer	Accepted. *Rollinia fosteri* Maas & Westra
Annona frutescens R. E. Fr.	Accepted.
Annona fuscata Carvalho & Schaffner, 1977	Accepted.
Annona gardneri R. E. Fr.	Accepted.
Annona gigantophylla (R. E. Fr.) R. E. Fr.	Accepted.
Annona glabra L. – pond apple, swamp apple, alligator apple, monkey apple, anona lisa, anon de agua, cayube	Accepted. Synonym: *Annona australis* A. St.-Hil., *A. chrysocarpa* Lepr. Ex A. Rich., *A. humboldtiana* Kunth., *A. humboldtii* Dunal., *A. klainii* Pierre ex Engl. & Diels., *A. laurifolia* Dunal., *A. palustris* L., *A. peruviana* Humb. & Bonpl. Ex Dunal., *A. uliginosa* Kunth

(Continues)

TABLE 1 (Continued)

Genus and common name	Accepted name and synonyms
Annona glauca Schumach. & Thonn.	Accepted.
Annona glauca var. *minor* Robyns & Ghesq.	Accepted.
Annona glaucophylla R. E. Fr.	Accepted.
Annona globiflora Schltdl.	Accepted. *Annona fruticosa* Sessé & Moç.
Annona glomerulifera (Maas & Westra) H. Rainer	Accepted. *Rollinia glomerulifera* Maas & Westra
Annona gracilis R. E. Fr.	Accepted.
Annona haematantha Miq.	Accepted.
Annona haitiensis R. E. Fr.	Accepted.
Annona haitiensis subsp. *appendiculata* R. E. Fr.	Accepted
Annona havanensis R. E. Fr.	Accepted.
Annona hayesii Saff. Ex Standl.	Accepted.
Annona helosioides (Maas & Westra) H. Rainer	Accepted. *Rollinia helosioides* Maas & Westra
Annona herzogii (R. E. Fr.) H. Rainer	Accepted. *Rollinia herzogii* R. E. Fr.
Annona hispida (Maas & Westra) H. Rainer	Accepted. *Rollinia hispida* Maas & Westra
Annona holosericea Saff.	Accepted.
Annona hypoglauca Mart.	Accepted. *Annona tessmannii* Diels
Annona hystricoides A. H. Gentry	Accepted.
Annona inconformis Pittier	Accepted.
Annona insignis R. E. Fr.	Accepted.
Annona ionophylla Triana & Planch.	Accepted. *Annona conophylla* Müll. Berol.
Annona iquitensis R. E. Fr.	Accepted.
Annona jahnii Saff., - catuche cimarron, pepino de monte, pepuro	Accepted. *Annona guaricensis* Pittier., *A. ulei* R. E. Fr.
Annona jamaicensis Sprague	Accepted.
Annona jucunda (Diels) H. Rainer	Accepted. *Rollinia jucunda* Diels., *R. peruviana* Diels., *R. rigidiflora* R. E. Fr.
Annona lepida Carvalho & Schaffner, 1977	Accepted.
Annona leptopetala (R. E. Fr.) H. Rainer	Accepted. *Rollinia leptopetala* R. E. Fr., *R. leptopetala* var. *Angustifolia* R. E. Fr.
Annona liebmanniana Baill. – cawesh, poshe-te, wild red custard apple, anona del monte	Accepted. *Annona scleroderma* Saff., *A. testudinea* Saff.
Annona longiflora S. Watson	Accepted.
Annona longipes Saff.	Accepted.
Annona macrocalyx R. E. Fr.	Accepted.
Annona macroprophyllata Donn. Sm. – Ilama, Anona blanca, izlama	Accepted. *Annona diversifolia* Saff.
Annona maiscula Carvalho & Gomes, 1972	Accepted.
Annona malmeana R. E. Fr.	Accepted.
Annona malmeana var. *Vestita* R. E. Fr.	Accepted.
Annona mammifera (Maas & Westra) H. Rainer	Accepted. *Rollinia mammifera* Maas & Westra
Annona manabiensis Saff. Ex R. E. Fr.	Accepted.
Annona maritima (Záchia) H. Rainer	Accepted. *Rollinia maritima* Záchia
Annona membranacea R. E. Fr.	Accepted.
Annona mimica Carvalho & Schaffner, 1977	Accepted.
Annona moaensis Léon & Alain	Accepted.
Annona montana Macfad. – mountain soursop, guanabana cimarrona, guanabano cimarron, false graviola, corosol zombi, duragua, araticum	Accepted. *Annona montana* f. *marcgravii* (Mart.) Porto., *A. marcgravii* Mart., *A. sphaerocarpa* Splitg.
Annona monticola Mart.	Accepted. *Annona grandifolia* A. St.-Hil. & Tul., *A. pisonis* Mart.

(Continues)

TABLE 1 (Continued)

Genus and common name	Accepted name and synonyms
Annona monticola var. *Brevipetiolata* R. E. Fr.	Accepted.
Annona mucosa Jacq. – Rollinia, Anona	Accepted. Ambiguous synonym *Annona biflora* Sessé & Moç. and *A. biflora* Ruiz & Pav. Ex G. Don., *A. reticulata* var. *mucosa* (Jacq.) Willd., *A. muscosa* Aubl., *A. obtusiflora* Tussac., *A. obtusifolia* DC., *Annona parviflora* Ruiz & Pav., *A. parviflora* Ruiz & Pav. Ex G. Don., *A. pterocarpa* Ruiz & Pav. Ex G. Don., *A. pteropetala* Ruiz & Pav., *A. pteropetala* Ruiz & Pav. Ex R. E. Fr., *Rollinia biflora* Ruiz & Pav. Ex G. Don., *R. curvipetala* R. E. Fr., *R. deliciosa* Saff. *Rollinia jimenezii* Saff., *R. micrantha* G. Don *Rollinia mucosa* (Jacq.) Baill., *R. neglecta* R. E. Fr. *Rollinia orthopetala* A. DC., *R. permensis* Standl. *Rollinia pterocarpa* G. Don., *R. pulchrinervia* A. DC. *Rollinia sieberi* A. DC., *R. mucosa* subsp. *aequatorialis* R. E. Fr., *Rollinia mucosa* subsp. *portoricensis* R. E. Fr., *Rollinia mucosa* var. *macropoda* R. E. Fr., *R. mucosa* var. *neglecta* (R. E. Fr.) R. E. Fr.
Annona muricata L. – soursop, graviola, guyabano, guanábana, catuche, corosol, sunni, nejo	Accepted. *Annona bonplandiana* Kunth., *Annona cearaensis* Barb. Rodr., *Annona muricata* f. *mirabilis* R. E. Fr., *Annona muricata* var. *Borinquensis* Morales ex Urb., *Annona portoricensis* M. Gómez.
Annona murrayi Carvalho & Schaffner, 1977	Accepted.
Annona neglecta R. E. Fr.	Accepted. *Annona axillaris* Ruiz ex R. E. Fr., *Annona oligocarpa* R. E. Fr.
Annona neoamazonica H. Rainer	Accepted.
Annona neochrysocarpa H. Rainer	Accepted. *Rollinia chrysocarpa* Maas & Westra
Annona neoecuadorensis H. Rainer	Accepted. *Rollinia ecuadorensis* R. E. Fr.
Annona neoelliptica H. Rainer & Maas	Accepted. *Rollinia elliptica* R. E. Fr.
Annona neoinsignis H. Rainer	Accepted. *Rollinia insignis* R. E. Fr., *Rollinia insignis* var. *pallida* R. E. Fr.
Annona neolaurifolia H. Rainer	Accepted. *Rollinia laurifolia* Schltdl., Rollinia *laurifolia var. divergens R. E. Fr., Rollinia laurifolia* var. *erecta* R. E. Fr., *Rollinia laurifolia* var. *laurifolia Rollinia laurifolia* var. *longipes* R. E. Fr., *Rollinia laurifolia* var. *reflexa* R. E. Fr., *Rollinia laurifolia* f. longipes (R. E. Fr.) R. E. Fr.
Annona neosalicifolia H. Rainer	Accepted. *Rollinia salicifolia* Schltdl.
Annona neosericea H. Rainer	Accepted. *Rollinia sericea* (R. E. Fr.) R. E. Fr., *Rollinia dolabripetala* var. *sericea* R. E. Fr., *Rollinia sericea* var. *longisepala* R. E. Fr.
Annona neoulei H. Rainer	Accepted. *Annona microcarpa* Ruiz & Pav. Ex G. Don., *Rollinia microcarpa* (Ruiz & Pav. Ex G. Don) R. E. Fr., *Rollinia ulei* Diels
Annona neovelutina H. Rainer	Accepted. *Rollinia velutina* Marle
Annona nipensis Alain	Accepted.
Annona nitida Mart.	Accepted.
Annona nutans (R. E. Fr.) R. E. Fr.	Accepted. *Annona nano-fruticosa* Herzog., *Annona spinescens* var. *nutans* R. E. Fr.
Annona oblongifolia R. E. Fr.	Accepted.
Annona oxapampae Maas & Westra	Accepted. *Rollinia pachyantha* Maas & Westra
Annona pachyantha (Maas & Westra) H. Rainer	Accepted.
Annona palmeri Saff.	Accepted.
Annona paludosa Aubl.	Accepted.
Annona papilionella (Diels) H. Rainer	Accepted. *Rollinia microsepala* Standl., *Rollinia papilionella* Diels., *Rollinia pittieri* Saff.
Annona paraguayensis R. E. Fr.	Accepted.
Annona paraënsis R. E. Fr.	Accepted. *Annona sericea* var. *angustifolia* Mart.
Annona parviflora (A. St.-Hil.) H. Rainer	Accepted. *Rollinia parviflora* A. St.-Hil., *Rollinia parviflora* var. *angustifolia* Mart., *Rollinia parviflora* var. *latifolia* Mart.
Annona pavonii G. Don	Accepted
Annona pickelii (Diels) H. Rainer	Accepted. *Rollinia pickelii* Diels
Annona pittieri Donn. Sm.	Accepted
Annona poeppigii (Mart.) Maas & Westra	Accepted. *Rollinia poeppigii* Mart.

(Continues)

TABLE 1 (Continued)

Genus and common name	Accepted name and synonyms
Annona praetermissa Fawc. & Rendle	Accepted
Annona prevostiae H. Rainer	Accepted
Annona primigenia Standl. & Steyerm.	Accepted. *Annona reticulata* var. *primigenia* (Standl. & Steyerm.) Lundell
Annona pruinosa G. E. Schatz	Accepted
Annona punicifolia Triana & Planch.	Accepted
Annona purpurea Moç. & Sessé ex Dunal. – soncoya, chincuya, catiguire, turagua, manire	Accepted. *Annona incolucrata* Baill., *Annona manirote* Kunth., *Annona prestoei* Hemsl.
Annona quinduensis Kunth	Accepted
Annona recurvata Carvalho & Schaffner, 1977	Accepted
Annona rensoniana (Standl.) H. Rainer	Accepted. *Rollinia cherimolioides* R. E. Fr., *Rollinia membranacea* Triana & Planch., *Rollinia mexicana* Standl. *Rollinia rensoniana* Standl., *Rollinia standleyi* R. E. Fr.
Annona reticulata L. – custard apple, bullock's heart, anona, anona rosada, corazon, corazon de buey, anona rosada	Accepted. *Annona excelsa* Kunth., *Annona laevis* Kunth., *Annona longifolia* Sessé & Moç., *Annona lutescens* Saff., *Annona micrantha* Bertero ex Spreng., *Annona riparia* Kunth
Annona rigida R. E. Fr.	Accepted
Annona rosei Saff.	Accepted. *Annona domingensis* R. E. Fr., *Annona dumetorum* R. E. Fr.
Annona roxburghiana Wall.	Accepted.
Annona rufinervis (Triana & Planch.) H. Rainer	Accepted. *Rollinia rufinervis* Triana & Planch.
Annona rugulosa (Schltdl.) H. Rainer	Accepted. *Rollinia rugulosa* Schltdl., *Rollinia rugulosa* subsp. *australis* R. E. Fr.
Annona saffordiana R. E. Fr.	Accepted. *Annona fagifolia* Saff.
Annona salicifolia Ekman & R. E. Fr.	Accepted.
Annona salzmannii A. DC. – beach sugar apple	Accepted. *Annona impressivenia* Saff. Ex R. E. Fr.
Annona sanctae-crucis S. Moore	Accepted.
Annona sariffa Roxb. Ex Hensch.	Accepted.
Annona scandens Diels	Accepted.
Annona schunkei (Maas & Westra) H. Rainer	Accepted. *Rollinia schunkei* Maas & Westra
Annona sclerophylla Saff.	Accepted. *Annona sulcata* Urb.
Annona senegalensis Pers. – Graines, African custard apple, wild soursop	Accepted. *Annona africana* L., *Annona chrysophylla* Bojer
Annona senegalensis var. *Areolata* Le Thomas	Accepted. *Annona arenaria* Thonn., *Annona arenaria* var. *obtusa* Robyns & Ghesq., *Annona senegalensis* var. deltoides Robyns & Ghesq.
Annona senegalensis var. *Glabrescens* Oliv.	Accepted.
Annona senegalensis subsp. *oulotricha* Le Thomas	Accepted. *Annona senegalensis* var. *arenaria* (Thonn.) Sillans., *Annona senegalensis* var. *oulotricha* Le Thomas
Annona senegalensis subsp. *senegalensis*	Accepted. *Annona senegalensis* var. *chrysophylla* (Bojer) Sillans., *Annona senegalensis* var. *latifolia* Oliv., *Annona senegalensis* var. *porpetac* (Baill.) Diels., *Annona porpetac* Boivin ex Baill.
Annona sericea Dunal	Accepted. *Annona jenmanii* Saff., *Annona trinitensis* Saff.
Annona spinescens Mart.	Accepted. *Annona squamosa f. parvifolia* Kuntze
Annona spraguei Saff.	Accepted. *Annona uncinata* Sprague
*Annona squamosa*L. – sugar apple, sweetsop, riñón, anona blanca, fruta de condesa, corosolier, ecailleux	Accepted. *Annona asiatica* L., *Annona cinerea* Dunal., *Annona forskahlii* DC., *Annona glabra* Forssk.
Annona stenophylla Engl. & Diels	Accepted, *Annona cuneata* (Oliv.) R. E. Fr., *Annona friesii* Robyns & Ghesq.
Annona stenophylla subsp. *Cuneata* (Oliv.) N. Robson	Accepted. *Annona senegalensis* var. *Cuneata* Oliv.
Annona stenophylla subsp. *longepetiolata* (R. E. Fr.) N. Robson	Accepted. *Annona longepetiolata* (R. E. Fr.) Robyns & Ghesq., Annona *longepetiolata* var. *precaria* Robyns & Ghesq.

(Continues)

TABLE 1 (Continued)

Genus and common name	Accepted name and synonyms
Annona stenophylla subsp. *nana* (Exell) N. Robson	Accepted. *Annona nana* var. *katangensis* Robyns & Ghesq., *Annona nana* var. *oblonga* Robyns & Ghesq., *Annona nana* var. *sessilifolia* Exell., *Annona nana* var. *subsessilifolia* (Engl.) Exell & Mendonça., *Annona senegalensis* var. *rhodesiaca* Engl. & Diels. *Annona nana* Exell
Annona stenophylla subsp. *stenophylla*	Accepted. *Annona stenophylla* var. *nana* R. E. Fr.
Annona sylvatica A. St.-Hil.	Accepted. *Annona exalbida* Vell., *Annona fagifolia* A. St.-Hil. & Tul., *Annona silvestris* Vell., *Rollinia exalbida* (Vell.) Mart., *Rollinia fagifolia* A. St.-Hil., *Rollinia sylvatica* (A. St.-Hil.) Mart.
Annona symphyocarpa Sandwith	Accepted. *Annona tenuipes* R. E. Fr
Annona tenuiflora Mart.	Accepted. *Annona humilis* Benth.
Annona tomentosa R. E. Fr.	Accepted.
Annona tuberosa Noronha	Accepted.
Annona ubatubensis (Maas & Westra) H. Rainer	Accepted. *Rollinia ubatubensis* Maas & Westra
Annona urbaniana R. E. Fr.	Accepted.
Annona variabilis Carvalho & Schaffner, 1977	Accepted.
Annona vepretorum Mart.	Accepted.
Annona volubilis Lundell	Accepted. *Annona rufa* Lundell
Annona warmingiana Mello-Silva & Pirani	Accepted. *Annona coriacea* var. *pygmaea* Warm., *Annona pygmaea* (Warm.) Warm.
Annona williamsii (Rusby ex R. E. Fr.) H. Rainer	Accepted. *Rollinia williamsii* Rusby ex R. E. Fr., *Rollinia williamsii* Rusby
Annona xylopiifolia A. St.-Hil. & Tul.	Accepted. *Rollinia lanceolata* R. E. Fr., *Rollinia warmingii R.* E. Fr., *Rollinia xylopiifolia* (A. St.-Hil. & Tul.) R. E. Fr., *Rollinia xylopiifolia* var. *lanceolata* (R. E. Fr.) R. E. Fr.

The leaves of the genus *Annona* are firm and coriaceous, deciduous or persistent, without stipules. The super-axillary flowers are solitary or in racemes, frequently opposed to the leaves. The calyx usually tubular and trimerous enclosing six petals in two series, sometimes the internal series represented by defective petals or scales with many stamens with mass pulpous filaments and pollinic sacs present. Many mass pistils have one ovule. The fruit is a large fleshy multiple fruit (syncarp), formed by the fusion of pistils and receptacles (Bailey, 1951; Spjut, 1994).

The majority of *Annona* species have a chromosome number of $2n = 14$, with *A. glabra* a tetraploid with $2n = 28$. Because the frequency of chiasma (crossovers) occurrence is high in *A. glabra*, and there is an absence of multivalents during meiosis, *A. glabra* is possibly of amphidiploid origin (Nakasone & Paull, 1998). A chromosome-level reference genome has been published of soursop (*A. muricata*) that found low heterozygosity (0.06%) which agrees with the limited variation found in soursop cultivars (Strijk et al., 2021). This low level of heterozygosity is common in cultivated species with a reduction in species population size and may limit approaches to genetic improvement.

3 | GENETIC RESOURCES – SELECTION AND CULTIVAR DEVELOPMENT

3.1 | Genetic resources

The *Annona* species are diverse and those of importance to horticulture could be utilized in genetic breeding programs to improve the characteristics of currently used selections. However, as a result of genetic erosion, species that are present in the wild and even in cultivation are threatened. Human pressure on natural ecological habitats has contributed to the loss of some wild species, and the introduction of new and improved cultivars has often replaced traditional varieties, further eroding the genetic variability that has accumulated over thousands of years of natural evolution and direct human domestication (Ferreira & Pinto, 2005).

Mendes-Ferrão (1992) and Ferreira and Pinto (2005) indicated that the genus *Annona* includes many species that originated on diverse continents. However, cultivars commercially grown for their fruits, generally originated primarily from the Antilles and Central America, with some from South America and Southeast Asia. Selected varieties have been cultivated since pre-Columbian times. The genetic material that is needed for the establishment of germplasm collection banks, allowing access for future breeding work will, therefore, come from diverse geographical sources.

In general, wild *Annona* spp. have a more limited distribution than cultivated forms, so it is difficult to determine the place of origin of the cultivars. Also, information on phenotypic variability is directly related to the economic importance of the fruit crop within the genus (Ponce, 1978).

Seeds of soursop and sweetsop are reported to be orthodox (World Agroforestry Centre, 2009) and can be stored at low temperatures at low moisture contents. However, cherimoya seeds only remain viable for a few years (Duarte et al., 1974). Nonetheless, the genetic resources (particularly seed) of the most important commercial species have not been collected systematically, except for the collections made by Zill's Nurseries in Central America (Belize, Guatemala, Yucatán, etc.) (Mahdeem, 1990a, 1990b, 1990c, 1990d; Zill & Mahdeem, 1998), and small collections in Spain, the Philippines, Ecuador, Australia, and India. More prospecting is necessary to collect both wild and cultivated species, so their phenotypes can be characterized, and their botanical status clarified. Such collections would also allow research that is necessary to explain the evolutionary processes involved and the botanical relationships among the different types. Further, their potential uses as medicines needs to be evaluated (Ferreira & Pinto, 2005; Morton, 1987; Smith et al., 1992).

3.2 | Selection and improvement

Seed propagation of *Annona* spp. has led to significant variation in tree and fruit phenotype, especially in fruit color, fruit weight, total soluble solids concentration, and seed number. Furthermore, productivity is often low, around 7–8 t ha^{-1} (Ray, 2002), with wide variation between individual trees due to outcrossing. Asexual (clonal) propagation of elite selections is necessary to increase yields and fruit quality. However, with some exceptions, most commercial production is based upon seedlings. This seedling diversity provides an opportunity for genetic improvement and the selection of individual trees as scions for better adapted genotypes for local climates and soil conditions.

A hybridization program, using controlled pollinations among superior seedlings, cultivars or different species, can increase phenotypic diversity and allow the selection of potential new clones with desirable characteristics. It is necessary to choose the best parents, based on available information, to carry out the required controlled cross-pollinations (Table 2). The resultant hybrids with optimal characteristics must be vegetatively propagated to maintain their characteristics (Paiva & Fioravanço, 1994).

Studies to understand the genetic diversity and inheritance of desirable traits in atemoya and cherimoya have been suggested by Ellstrand and Lee (1987), Rahman et al. (1999), and Perfectti and Pascual (1998). Multiple breeding strategies on atemoya have included the use of polyline crosses between selected lines and commercial cultivars, interspecific crosses (*A. cherimoya*, *A. squamosa*, *A. reticulata*, *A. diversifolia*, and atemoya) and auto-tetraploid induction which have provided progeny for evaluation and advanced selections with specific characteristics to use for superior selection (George, Broadley, et al., 2002). Building on previous genetic diversity and inheritance research, selection criteria should include considerations of tree morphology, yield capacity, fruit quality, postharvest storage life characteristics and disease and pest susceptibility (Table 3) (George, Broadley, et al., 2002; Paiva & Fioravanço, 1994; Vanhove, 2008).

3.3 | Hybridization

Genetic improvement in *Annona* species has been very limited. In both Florida and The Philippines, many crosses were made among different species (Wester, 1910, 1913, 1915, 1916) and one of the results was the hybrid atemoya selected from a cross between *Annona cherimola* × *A. squamosa* (George, Nissen, et al., 2002; George & Paull, 2008). Findings from interspecific crosses in Queensland, Australia, of *A. diversifolia* and *A. reticulata* showed that progeny of *A diversifolia* inherited strong apical dominance and poor fruit setting ability. Progeny of atemoya × *A. reticulata* and cherimoya × *A reticulata* produced late-maturing fruit in spring. Inheritance of flowering and fruit characteristics of *A reticulata* produced progeny which flowered in autumn and matured fruit in late spring under the subtropical conditions of Australia. Progeny produced fruit with high levels of internal grittiness (stone cells). Crossing with red skinned types produced fruit with pink-red flesh and skin color. Further crossings with *A. cherimoya* and either red skinned *A. squamosa* or red skinned atemoya types are now producing cultivars with acceptable fruit quality characteristics. Furthermore, *A. cherimoya* seedlings and hybrids have produced a number of dwarf and semi-dwarf progeny and a few with flower and fruit characteristics similar to *Rollinia deliciosa* (George, Broadley, et al., 2002).

Genome duplication or polyploidy is especially frequent in hybrids and very valuable in many crops. The hybrid atemoya has been reported as being diploid. Flow cytometry analysis of a progeny obtained from an interspecific cross between *A. cherimoya* and *A. squamosa* showed an unusual ploidy variability that was also confirmed by karyotype analysis. Intraspecific crosses of *A. cherimoya* showed polyploid genotypes and the hybrid atemoyas from the interspecific cross showed 35% of triploids from a total of 186 genotypes

TABLE 2 Characteristics of different fruit species and cultivars that could be used as parents (after George et al., 1999)

Species	Cultivar or selection	Origin	Desirable characteristic
A. squamosa	Red Sugar	Florida, USA	Husk red color
	Noi	Thailand	Fruit very large, yellow husk
	Accession '6633′	Unknown	Seedless
	Lobo	The Philippines	Fruit large, sweet, few seeds
	Seedless	The Philippines, Cuba/Florida	Seedless
	LeahReese	Florida, USA	Very large, green-peel, high quality
A. diversifolia	Imery	Florida, USA	Fruit husk and pulp pink
	Púrpura	Florida, USA	Pink husk
A. reticulata	Camino Real	Florida, USA	Pulp and husk red, smooth peel
	Fairchild Púrpura	Florida, USA	Purpuric husk
	Dr León	Florida, USA	Pulp and husk orange
	Young	Java, Indonesia	Sweet fruits, tender pulp
A. cherimola	Citamex	Mexico	Orange husk
	Sin semilla	Peru and Ecuador	Seedless

TABLE 3 Selection criteria for breeding and selection programs aimed at improving Annona spp. (after Paiva & Fioravanço, 1994; George et al., 2002a; Vanhove, 2008)

Plant descriptors	Fruit characteristics
Leaf characteristics (size, shape, color)	Location of fruit on the tree
Juvenile period (planting or grafting and the time to first flowering)	Good fruit set
Crown shape	Fruit size, shape (good symmetry), and uniformity to meet market requirements
Height and tree growth habit	Fruit peduncle length
Trunk branching characteristics – good fruit-bearing laterals	Good taste
Flower density	Low seed number per 100 g of flesh
Production period	Large proportion of pulp
Regularity of production	Peel type: smooth or with protrusions and the protrusion size
Productivity (kg ha^{-1}, kg per tree)	Peel thickness and color, and ease of peeling
Flowering to ripe fruit duration (d)	Pulp quality (acidity, sugar content, taste, color, fiber)
Disease and insect susceptibility	Pulp oxidation (none to severe)
Responses to environmental stress (temperature, water stress)	Resistance to fruit rot
	Resistance to chilling injury
	Good postharvest storage life

analyzed. Interspecific hybrids could have implications to explain the emergence of polyploidy and as valuable information for crop improvement in the Annonaceae (Martin et al., 2019).

Atemoya inherited the *A. squamosa* glabrous leaf characteristics and the large leaf size of *A. cherimola*. The flowering and fruiting times are similar to *A. squamosa*, but the skin, pulp and seed characters are from both parents, and inherited to different degrees in each hybrid seedling that is produced. It should be noted that the term atemoya has also been applied to *Annona* hybrids between atemoya × *A. reticulata*, *A. cherimola* × *A. reticulata*, and between either *A. squamosa* or *A. cherimola* with either as the male or female parent (Goenaga & Jenkins, 2016).

In Egypt, a hybrid between *Annona squamosa* × *A. cherimola*, named 'Cherimata' is commercially grown (Ezzat et al., 1974). Further, 'Red Israel', a natural hybrid from *A. cherimola* × *A. reticulata* has been grown commercially. Some research has been conducted with tetraploids induced by colchicine, but most of the progeny were unproductive (Islam, 1953, 1960). 'Cutemoya', a hybrid of atemoya × *A. reticulata*, was selected in India where it is considered to have many desirable characters when compared with other *Annona* cultivars and hybrids (Kumar & Jalikop, 2000).

Little has been published on the heredity of specific plant and fruit characters in *Annona* but some correlation studies have shown probable associations between different plant characteristics. For example, Cull and Lindsay (1995) have shown a relationship between shoot growth and tree vigor vs. fruit size where, in general, weak shoots produce small fruit, which is a problem with the atemoya cultivar African Pride.

Hybridization studies using selected *Annona* spp. (*A. muricata, A. squamosa, A. glabra, A. montana, A. reticulata*, and *A. mucosa*) have been conducted in Malaysia (Khalid, 2002) where all of the species were crossed, complete with their reciprocals. In some of these crosses, fruit were produced but the seeds were not viable except for fruits from two of the crosses: *A. muricata* × *A. montana* and *A. mucosa* × *A. muricata*. The F_1 hybrids of *A. muricata* × *A. montana* produced plants that flowered but were without fruit, whereas the F_1 hybrids of *A. mucosa* × *A. muricata* had fruit similar to those of *A. mucosa* (formerly *Rollinia mucosa*).

Jalikop (2010a) studied the inheritance of four characteristics of atemoya (*Annona cherimola* × *A. squamosa*) × *A. reticulata* crosses. Leaf color (green or dark green), leaf insertion angle (erect or fragile and dropping), leaf apex form (round or sharp), and season of leaf fall (early, middle, or late) segregated into discreet phenotypic classes. Foliage characters showed simple Mendelian inheritance. Based on the parent's phenotype, the population segregation and the genetic proportions obtained, allelic symbols were assigned to the four leaf characteristics. Leaf color and leaf position were controlled by interactions among duplicate dominant genes. Green leaves were produced by individuals with single genes or with both dominant genes (A-, B-, A-bb, aaB-), whereas dark green were those with recessive genes (aabb). Individuals with erect leaves were C-D-, C-dd, ccD-, and the ones with dropping leaves are ccdd. Leaf tips that could be round (Rr) or acuminate (rr) were determined by a single gene. The progeny segregation for early (J^EJ^E), intermediate (J^EJ^L) or late leaf fall (J^LJ^L), suggested codominant alleles. These studies provide some basis for the genetic improvement of *Annona* fruits through defining selection criterion for these characters.

Annona reticulata has been hybridized with atemoya (*A. cherimola* Mill. × *A. squamosa* L.), and 250 tri-species hybrids were studied for 28 traits (12 tree traits and 16 fruit traits) (Jalikop, 2010b). The objectives were to determine useful genes from the three edible *Annona* species and to determine the extent of variation in the progeny. The heterozygous nature of *Annona* spp. and simultaneous segregation of three distant genomes resulted in tremendous heterogeneity in the progenies. The fitness of the progenies ranged from very vigorous to very weak, with a wide range of values for tree height (1.75–5.9 m), canopy spread (1.15–5.07 m) and trunk circumference (11–38.5 cm). The occurrence of diverse and novel segregants for tree shape and branching pattern suggested the possibility of identifying efficient ideotypes. Variation in fruit shape, skin color and skin surface smoothness, in addition to total soluble solids (17–32%), acidity (0.16–2.2%), and number of seeds per 100 g of fruit (3–49) showed exciting opportunities existed in terms of selecting for desirable traits (see Figure 1). Among the segregating population were slow fruit-ripening genotypes that required up to 12 d from harvesting to the ripe stage. Interestingly, some recombinants produced fruit resembling *A. glabra* and *A. muricata* fruit, suggesting that one or the other parental species of the trihybrid could be progenitor of these two nonparental species. These results demonstrate that *A. reticulata* is potentially a valuable source of a variety of novel traits.

In considering potential crosses, a desirable hybrid might be possible from a cross between cherimoya and soursop (*A. cherimola* × *A. muricata*). This cross could combine the soursop large fruit size and acidity with the sweetness, taste, and pulp texture of the cherimoya. Such efforts to make the cross between soursop and cherimoya (or with ilama or the sugar apple) have so far been unsuccessful, implying a larger genetic distance between the soursop and the other *Annona* spp. (Nakasone & Paull, 1998; Samuel et al., 1991). A breeding program in Australia has also included in its objectives, to have seedless (parthenocarpic) atemoya and cherimoya (George et al., 1999).

Hybrids have been obtained with other *Annona* spp. For example, in interspecific crosses of *A. diversifolia* × *A. reticulata*, the progeny inherited the high apical dominance characteristic of *A. diversifolia* and its tendency for fruit set. The fruit quality was good with symmetrical fruit having good taste (George et al., 2008). In Florida, breeding studies with pink colored cultivars indicated that this color could be due to a simple or double recessive gene (George et al., 2008).

UPGMA analysis of 28 *Annona* genotypes showed distinct groups within the *Annona* spp. hybrid types, *A. cherimoya, A. squamosa*, and *A. reticulata*. Under Australian conditions, *A. cherimoya* types and *A reticulata* types have low natural fruit set, <3%, with *A. squamosa* regularly having >20% and the hybrid type 'KJ Pinks' averaging 41% in some seasons. Phylogenetic relationships using 15 polymorphic SSR markers found that five *Annona* spp. hybrid genotypes were indistinguishable. However, increased natural fruit set of a hybrid type, KJ Pinks may be a single point mutation, warranting further studies to determine selection of high natural fruit set genotypes (George et al., 2008). In Israel, RAPD markers were used to suggest genetic relationships among cherimoya, sugar apple, and atemoya cultivars (Ronning & Schnell, 1995).

The progeny of crosses between atemoya × A. *reticulata* and *A. cherimola* × *A. reticulata* produced late-maturing fruit typical of that from *A. reticulata*. Many selections of this

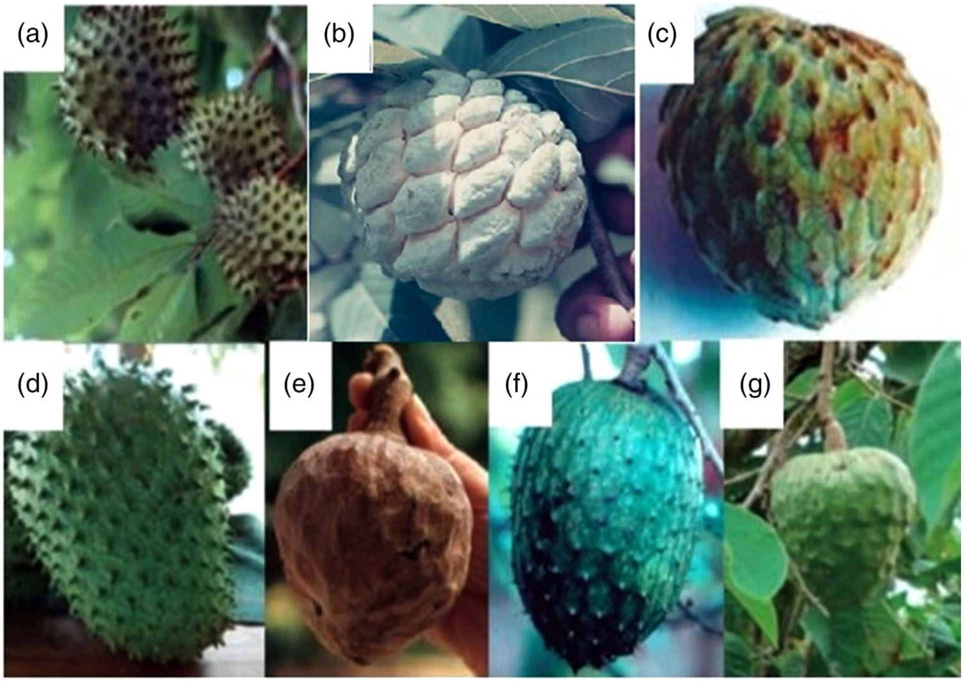

FIGURE 1 Annona fruit vary widely in size, smoothness and skin color. (a) *Annona purpurea* – Soncoya; (b) *Annona squamosa* – Sweetsop; (c) Atemoya selected hybrid, *Annona squamosa* × *Annona cherimola*; (d) *Annona muricata* – Soursop; (e) *Annona retriculata* – Custard apple; (f) *Annona montana* – Mountain soursop; (g) *Annona cherimola* – Cherimoya. (*Source*: the authors.)

hybrid in Australia, as in Florida, were rejected due to poor fruit quality fruit, with the progeny having the sandy (gritty) pulp of *A. reticulata*, possibly due to lignified sclerenchyma cells (George et al., 2008).

4 | HORTICULTURAL CHARACTERISTICS

4.1 | Soil and climatic requirements

The climatic and soil requirements for most of the commercially important *Annona* species are typical of those used for the production of tropical fruit crops. Most *Annona* spp. are well adapted to altitudes below 1,000 msl, and annual rainfall >1,000 mm with a dry period during flowering, and an average annual temperature of 25–28 °C (Table 4). Soils of medium fertility, with good drainage in areas with slopes <7%, are required (Avilán & Leal, 1984). The exception is the cherimoya, as it is adapted to both tropical and subtropical zones. In the tropics, cherimoya is found between 1,000 and 3,000 msl, depending on the latitude, with an annual average temperature <20 °C and with soils of medium fertility and good drainage (Owens, 2003). Atemoya, sugar apple, guanabana, and custard apple (*A. reticulata*) trees appear to tolerate a wide range of soil pH (e.g., 5.5–8.5) (Pinto et al., 2005). Tolerance to flooded or constantly wet soils varies by

TABLE 4 Behavior and response of seven Annona fruit species when grown under high humidity, cold, dry conditions and poor drainage (after Escobar & Sanchez, 1992; Núñez-Elisea et al., 1998, 1999)

Species	High humidity	Cold	Dry	Poor drainage
A. muricata	T	S	R	T
A. glabra	T	S	R	R
A. cherimola	T	R	S	S
A. cherimola	S	S	R	S
A. squamosa	R	S	R	S
A. reticulata	R	S	R	R
A. diversifolia	S	R	R	S

Note. R = Resistant, S = Susceptible, T = Tolerant.

Annona spp. (Núñez-Elisea et al., 1998, 1999). Seedlings of *A. glabra* and *A. muricata* tolerated 12 mo of soil flooding (Núñez-Elisea et al., 1998) whereas seedling sugar apple and grafted 'Gefner' atemoya onto seedling sugar apple rootstocks had no flood tolerance.

In Colombia, Escobar and Sanchez (1992), based upon available data, evaluated seven *Annona* spp. for their suitability as rootstocks in different soils and environmental conditions and concluded that *A. muricata* was the best.

Information on the tolerance of *Annona* spp. to saline soils and/or saline irrigation water is limited. Some observations suggested *A. squamosa* has some salinity tolerance (see Pinto et al., 2005), however, Marler and Zozor (1996) reported sugar apple seedlings had little to no physiological tolerance to mild salinity.

In Australia, sudden death of young, grafted custard apples cultivars and decline in mature trees was due to bacterial wilt (*Ralstoria solanacearum*. Syn. *Pseudomonas solanacearum* biovar 3), limiting custard apple production in subtropical regions. Trees grafted on *A. squamosa* rootstock were highly susceptible to bacterial wilt compared with trees grafted on *A. cherimoya* that had a good level of resistance. *Annona cherimoya* rootstocks provided a level of economic disease control for custard apple orchards in subtropical regions (Mayers & Hutton, 2008). The *A. cherimoya* cultivar White proved to have the highest resistance and grows equally well at both high and low soil temperatures producing more dry matter, which may explain why it also exhibits resistance to bacterial wilt compared with hybrid species (*A. cherimoya* × *A. squamosa*), *A. squamosa*, and *A. glabra* (George & Nissen, 1987b). Furthermore, cuttings of (*A. cherimoya* × *A. squamosa*) 'African Pride' under tropical conditions had dry matter production and distribution affected, compared with growth under subtropical conditions; dry matter partitioning to the leaves increased, whereas that to the stem and roots decreased. This suggests high leaf/root ratios may increase physiological stress within the plant making it more susceptible to root rot disease (George & Nissen, 1987c).

Temperate has little or no effect on fruit set of *Annona* spp. hybrids in Australia, but high vapor pressure deficit (VPD) caused a severe reduction in both flowering and fruit set. High temperature conditions and soil moisture stress moderately reduced fruit set and increased fruit internal disorders due to reduced transpiration (George & Nissen, 1988, 2002; Nissen & George, 2002).

4.2 | Propagation

Most *Annona* spp. can be seed propagated. However, grafting and budding ensure propagation of desirable parent traits (Table 5). Selection of the compatible scion–rootstock combinations is critical and complicated (Núñez-Elisea et al., 1998; Pinto et al., 2005). Micropropagation is possible (George & Nissen, 1987a; Lemos & Blake, 1996). *Annona* seeds normally remain viable for a few weeks to many months and some species are regarded as being recalcitrant. The recommendation is to sow seeds as soon as possible after extraction from the fruit. Germination takes around 30 d, but gibberellic acid (GA) applications (10,000 ul L^{-1}) can increase germination rate and accelerate seedling growth (Nakasone & Paull, 1998; Pinto, 1975).

When grafting and budding are used, the principal problem is scion/rootstock incompatibility among the different *Annona* spp. (Campbell, 1985; Pinto et al., 2005). Incompatibility causes economic losses in commercial nurseries. The problem is complex as some cultivars are compatible with a particular rootstock whereas others are not. For example, the atemoya cultivars Bradley and Page are compatible with *A. reticulata* rootstock, but 'Gefner' is partially incompatible (Table 6). Sanewski (1991) has also recorded incompatibility among scions and rootstocks in species of *Annona* and the *Annona* spp. formerly in *Rollinia*, specifically among *Annona* cultivars. Further research is necessary to better understand the mechanisms involved with this incompatibility.

Asexually propagation is critical for atemoya as it is a hybrid. The rooting of cuttings or the use of air layers has been shown to have a low success rate (Araque, 1967; Baraona & Sancho-Barrantes, 1992; Figueroa, 1978; Leal & Rodríguez, 1981; Mason & Andrews, 1992; Ramkhelawan, 2008), hence budding is the preferred propagation method (George & Nissen, 1987a; Ogden et al., 1981; Ramkhelawan, 2008). However, in commercial *Annona* plantations, because budding and grafting require specialized skills, the added cost is sometimes not seen as being justified.

In general, air-layering (marcotting) has shown only limited success with cherimoya and sugar apple but was highly successful for pond apple (Núñez-Elisea et al., 2000; Pinto et al., 2005). The success of air-layering custard apple and soursop has not been documented. When in vitro propagation is used, the choice of the mother plants, based upon appropriate selection criteria is critical (Bridg, 2000). For the fresh market or the pulp, nectar, and juice industries, the criteria must be established by mutual agreement to meet both grower and market demands as to what are the most important factors. The major issues for good root production of soursop explants in vitro have been the avoidance of phenolic oxidation of the cut end of the shoot, difficulty in eliminating exogenous and endogenous contaminants without tissue damage, and minimizing variability (Rincón et al., 1999).

4.3 | Flowering and fruiting

Annona spp. are characterized by an indeterminate growth habit and associated axillary flowering (Chomicki et al., 2017). Excessive vegetative growth does not significantly interfere with flower initiation as compared with plants with a determinate growth habit (Nakasone & Paull, 1998). However, George et al. (1989) reported hand-pollinated fruit set was significantly less following a major vegetative flush compared with that following a minor flush in 'African Pride' atemoya. Furthermore, marked sensitivity of *Annona* spp. hybrids stomata to low relative humidity (RH) reduced flowering, fruit set and effected fruit quality (the occurrence of internal disorders) (George & Nissen, 1988, 2002; Nissen & George, 2002).

Sugar apple, cherimoya, and atemoya have hermaphroditic protogynous dichogamous flowers which drastically reduces

TABLE 5 Propagation methods used for Annona spp. and the typical success rates (modified from George & Nissen, 1987a)

Propagation method	***Annona* species/hybrid (common name)** *A. squamosa* × *A. cherimola* (atemoya)	*A. squamosa* (sugar apple)	*A. cherimola* (cherimoya)	*A. muricata* (soursop, guanabana)
Seedlings				
Genetic variability	Variable	Uniform	Variable	Uniform
Use	Not recommended	Good	Rootstock	High
Cuttings	Some cultivars	Low success rate	Low success rate	Good
Air layers	Unknown	High with modification	Unknown	Unknown
Micropropagation	Possible	Unknown	Unknown	Unknown
Typical success rates				
Cuttings	<5%	<8%	<5%	>60%
Budding	>70%	>70%	>70%	>70%

TABLE 6 Grafting success of different Annona rootstock/scion combinations in Florida (modified from Campbell, 1985)

Rootstocks	**Scions** *A. squamosa* × *A. cherimola* (atemoya)	*A. diversifolia* (ilama)	*A. muricata* (soursop)	*A. squamosa* (sugar apple)
A. squamosa × *A. cherimola* (atemoya)	+	?	0	?
A. cherimola (cherimoya)	?	0	0	?
A. reticulata	+	?	–	?
A. diversifolia (ilama)	0	+	0	0
A. montana	0	0	+	0
A. glabra	+	–	?	–
A. muricata (soursop)	–	0	+	–
A. squamosa (sugar apple)	+	?	–	+

Note. +, good budding in most cases.?, union with scion but is unknown if it will be prolonged; –, budding failed; 0, No information.

the chances of self-pollination (Noonan, 1953). Flowers first undergo a female phase where stigmas are receptive to pollen followed by a male phase when the anthers dehisce pollen, but the stigmas are no longer receptive (Nadel & Peña et al., 1994). When flowers of *Annona* spp. (soursop, sweetsop, cherimoya, etc) develop, it is possible to distinguish the following four phases (Fioravanço & Caleffi-Paiva, 1994):

1. *Unopened flower*: This phase can last 10–15 d; flowers usually increasing in size during this period.
2. *Pre-female stage*: The petal points are separated, but not to their base; the stigmas are receptive, but not easily accessible to pollinators. This state lasts for 5–20 h.
3. *Female stage*: The petal bases are separated and allow access by small pollinators. In most instances this happens after midday (13 h). The stigmas are receptive during the first 23–24 h of the total period of flower opening that typically lasts for around 26 h.
4. *Male flower stage*: This takes place at the end of the female stage, the petals open for 20 min, and then the stamens release the pollen. In the absence of high winds that can lead to pollen desiccation, the pollen stays viable for around 24 h.

In contrast, in the warm subtropical environment of southern Florida, the sugar apple and atemoya female flowers are receptive (female phase) from about 0800–1100 h and during the mid- to late afternoon male flowers dehisce (male phase) pollen (Nadel & Peña, 1994). Arizaleta and Parés (2003) showed that the synchronized sequence of *A. muricata* flower development from initiation to flowering took about 40 ± 2.8 d and could be divided into five stages, one more than Fioravanço and Caleffi-Paiva (1994). These events are similar to those reported by Escobar and Sanchez (1992) in Colombia.

Flowering continues over a considerable period with male and female flowers opening every afternoon on every tree. During some flowering periods of a single cultivar, there can be almost perfect synchronism among all the flowers on a tree. Every afternoon all the flowers are either in the male or

TABLE 7 The advantages and disadvantages of hand pollination to improve fruit quality and yield characteristics of Annona spp. (after Fioravanço & Caleffi-Paiva, 1994)

Advantages	Disadvantages
Fruit set guaranteed	Specialized hand labor needed for pollen collection, preparation and pollination
Potential yields greater than 10 t ha^{-1}	Pollinated fruit located only on lower branches
Fruit size increased	Good tree form required – specialized pruning needed
Fruit shape more symmetrical	Tree size needs to be limited
Greater harvest efficiency (fruit accessible from the ground)	Fruit may have more seeds

in the female stage on alternate days. This synchrony of the flowering stages limits self-pollination.

In areas where the temperature is >32 ˚C, female and male flowers can be present on the same day, with pollen released in the same afternoon that the female flowers are receptive (Sanewski, 1991; Schroeder, 1943; Thakur & Singh, 1965). Besides dichogamy (Schroeder, 1943; Thakur & Singh, 1965), other factors restrict the pollination of *Annona* spp. The flower anatomy, with the large petals which have a short and narrow peduncle, slow anthesis (especially in the outer whorl), along with heterostyly and the low number of visits by pollinators, all reduce pollination success. These restraints on pollination can lead to incomplete pollination, misshapen fruit, reduced fruit set and low fruit yield. Hand pollination is frequently practiced improving fruit quality (shape, size) and fruit yield per tree, though it increases production costs (Escobar & Sánchez, 1992).

Natural pollination of cherimoya, sugar apple and atemoya is affected by various Nitidulid beetle species (Coleoptera: Nitidulidae) (Gazit et al., 1982; George et al., 1989; Nadel & Peña, 1994; Nagel et al., 1989). Nine to 10 Nitidulid species were reported to visit atemoya and sugar apple flowers in Florida (Nadel & Peña, 1994), four species were found visiting cherimoya and atemoya trees in Israel (Gazit et al., 1982) and, in Australia, George et al. (1989) demonstrated that fruit set was significantly higher for Nitidulid pollinated 'Gefner' and 'Pink Mammoth' atemoyas trees with noncovered flowers. Similarly, sugar apple and atemoya fruit set increased significantly with the number of Nitidulid beetle visits under both Florida and Israeli conditions.

Hand pollination is commonly practiced to increase the potential for commercially viable *Annona* fruit production (Nakasone & Paull, 1998; Noonan, 1953; Paull & Duarte, 2012; Pinto et al., 2005) (Table 7). Pollen for hand pollination may be collected for most *Annona* spp. by harvesting flowers at the female opening stage or the early stage of male flowering (Escobar & Sánchez, 1992; Figueroa, 1978; Fioravanço & Caleffi-Paiva, 1994; Guzmán, 1991; Nietsche et al., 2003, 2009; Popenoe, 1961). The early-male stage flowers collected in the early afternoon (13–15 h) are held in a paper bag or in a tray in a cool shaded area at room temperature. The petals can be removed by hand. The collected flowers develop to the male stage within 16–18 h when the released pollen is collected. Twenty to 30 flowers produce enough pollen for 50–60 flowers (Fioravanço & Caleffi-Paiva, 1994). In contrast, dehiscing male flowers (early and mid-stage) may be collected, in the early morning, the petals removed, and the pollen used immediately. Sometimes the crude pollen (anthers and pollen) collected is cleaned by passing it through a 2- to 3-mm mesh sieve – gentle hand pressure is sufficient to separate the pollen grains from the anthers. The pollen can be stored in a refrigerator for a day at 3–7 ˚C and applied the following day (Pereira, Crane, Montas, et al., 2014). Viable pollen is yellow-orange and pollen that is black or dark yellow is discarded as being over-mature. A hand lens or a dark paper background can be used to confirm if the pollen is viable before it is stored. Hand pollination is normally carried out in the morning from 0700 to noon, when the pollen is taken from the refrigerator and rapidly applied using a camel-hair brush or atomizer to recently opened flowers when the stigma is most receptive. Stored pollen can subsequently be held in an ice bag to limit loss in viability before application.

Early investigations on the use of plant growth regulators (PGRs) (e.g., gibberellic acid and naphthalene acetic acid) to increase *Annona* fruit set and seedless fruit resulted less fruit set than hand pollination and/or led to smaller, mishappen, lower pulp quality fruit (Campbell, 1979; Saavedra, 1979). More recently, the use of a combination of PGRs (e.g., promalin, gibberellic acid, naphthalene acetic acid) with or without hand pollination on 'Gefner' atemoya resulted in a similar percent fruit set as with hand pollination, smaller and later fruit but with good fruit quality (Pereira, Crane, Nietsche, et al., 2014; Pereira, Santos, et al., 2014). Three applications of gibberellic acid at 500 ul L^{-1} plus hand pollination of Gefner atemoya resulted in larger fruit with fewer seeds and three applications of 1,500 ul L^{-1} of gibberellic acid alone produced seedless fruit of good quality (Santos et al., 2016). Similarly, 'Red' and 'Lessard Thai' sugar apple flowers treated with three applications of gibberellic acid (1,000 ul L^{-1}) alone or with hand pollination resulted in high percent fruit set (≥90%) (Pereira et al., 2019). Gibberellic acid treatment plus hand pollination produced fruit that had similar fruit quality as hand pollinated only Red and Lessard Thai sugar apple fruit.

4.4 | Fruit growth and ripening

Fruit of all *Annona* spp. show a double sigmoidal growth type (Bruinsme & Paull, 1984; Escobar & Sanchez, 1992; Mosca et al., 1999; Worrell et al., 1994). The fruit are climacteric with a marked respiratory peak and have autocatalytic ethylene production during ripening. Ripening rate is rapid after harvest (Mosca et al., 1999; Wong-Aree & Noichinda, 2011).

In some production areas, commercial *Annona* spp. flower and fruit continually throughout the year with generally a major production peak that is determined by temperature and water stress (Nakasone & Paull, 1998). In Taiwan, the sweetsop fruiting period can be altered by pruning in either the summer or winter as flowering occurs on the basal end of a growing branch (Anonymous, 1995; Lo, 1987; Yang, 1987). In Florida, the period of commercial harvest varies by the *Annona* grown. For example, sugar apples are harvested from August through October, 'Gefner' atemoya from September through December, and guanabana from early summer to early fall (Crane et al., 2009). Fruit thinning can also be used to extend the fruiting period. Cherimoya fruiting can also be altered by summer pruning in Chile (Razeto & Diaz de Valdes, 2001).

4.5 | Uses

A number of the genera within the Annonaceae produce edible fruit including *Annona, Uvaria*, *Asimina*, *Duguetia, Fusae*, and *Porcelia*. Other species in the *Annona*, *Cananga*, and *Xylopia* are cultivated for their essential oils and insecticidal compounds from leaves, seeds, roots, and stems (Schultes & Raffauf, 1990). Among the New World native people, the Annonaceae are used as medicines with infusions of leaves, stems, and branches being used to treat fevers, urinary and kidney disorders, and rheumatism. This has led to research on the different classes of chemical constituents such as alkaloids, flavonoids, and acetoquinones found in the Annonaceae for their pharmalogical properties (Attiq et al., 2017; Chatrou, 1999; Morton, 1966, 1973, 1987; Pumiputavon et al., 2019). The flavonoids and alkaloids in the Annonaceae also have insecticidal and antibacterial properties, and are used for the medicinal treatment of malaria, skin diseases, parasitic worms and eye inflammation (Mabberley, 1993; Schultes & Raffauf, 1990; Vásquez & Gentry, 1989). It has been shown that acetoquinones from soursop have anti-cancerous and anti-VIH/AIDS properties leading to numerous studies and the development of commercial products (Hadisaputri et al., 2021; Pumiputavon et al., 2019).

The wood from trees within the Annonaceae is hard and flexible, and is used for house building, fishing rods, toys, and paddles (Chatrou, 1999) and for agroforestry (ICUC, 2002; Vásquez & Gentry, 1989). Forest dynamic studies in areas where the largest number of species are present, reveal that the Annonaceae are usually among the five most important families in terms of species diversity and abundance (Foster, 1990; León & Monsalve, 2006; Valencia et al., 1994).

5 | CONCLUSIONS

The Annonaceae is one of the most primitive families in the plant kingdom. It has more than 140 genera and close to 2,500 species, mostly in the tropics with only a few species in the temperate zone. It is comprised of numerous commercial fruits that are consumed fresh, processed, or used in popular remedies. The family includes numerous genera and species of commercial fruits mainly from tropical America, but in general, its taxonomical revision is necessary as there are numerous synonyms.

The genus *Annona* has many fruits of commercial importance that are grown mostly in tropical zones and in some subtropical regions. Greater effort is needed to collect both wild and cultivated species and cultivars or types, so that they can be characterized and their botanical status determined. In general, selection and improvement of commercial species has been very limited. The climatic and soil requirements, for most of the *Annona* commercially grown, are similar to other tropical fruit crops, with the exception of the cherimoya, which is adapted to both tropical and subtropical areas. Fruit of all *Annona* spp. are climacteric with a rapid ripening after harvest. Besides their use for fruit production, *Annona* spp. are used for their essential oils, insecticidal compounds, medicinal compounds, and wood.

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Freddy Leal: Investigation.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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