

ANNONA GLABRA L., A KEY SWAMP TREE: ECOLOGICAL, FUNCTIONAL, AND ETHNOBOTANICAL ASPECTS FOR CONSERVATION AND RESTORATION

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Abstract

Freshwater wetlands are among the most threatened ecosystems in the world, with more than 60 % loss in Mexico. *Annona glabra* L. dominates many neotropical freshwater swamps but remains poorly studied despite its ecological importance. The aim of this work was to conduct a comprehensive review of the biological, ecological, and ethnobotanical aspects of *A. glabra* and to assess its role as a key wetland species and its potential for medicinal applications, ecological restoration, and climate change adaptation. The research was carried out in La Mancha-Diada and El Salado, Veracruz, Mexico, with comparative data from La Mancha-CICOLMA. We combined a bibliographic review with field measurements (2018-2019) of tree density, diameter at breast height, height, and monthly litter collection. In addition to environmental parameters: hydrology and salinity. The results demonstrated that *A. glabra* exhibits flood tolerance and moderate salinity resistance through morphological adaptations (aerenchyma, adventitious roots, hypertrophied lenticels), maintaining photosynthesis during flooding. Tree density reached 833 individuals/ha, with a basal area of 188.94 m²/ha. Annual litterfall averaged 12.4 t/ha, and seed production reached 3.7 million seeds/ha/year. Ethnopharmacological analyses revealed antimicrobial, anti-inflammatory, anticancer, and larvicidal properties. Functioning as a “freshwater mangrove,” *A. glabra* is crucial for ecosystem services. It shows high potential for ecological restoration but requires management due to its invasive capacity. Sea level rise and salinization represent a significant threat, underscoring the need for urgent conservation strategies.

Keywords: Ecological restoration, ecology, freshwater swamps, pond apple, tropical wetlands, wetland conservation

Resumen

Los humedales de agua dulce están entre los ecosistemas más amenazados del mundo, con más del 60 % de pérdida en México. *Annona glabra* L. domina muchas selvas inundables neotropicales, pero permanece poco estudiada a pesar de su importancia ecológica. El objetivo del trabajo fue realizar una revisión integral de los aspectos biológicos, ecológicos y etnobotánicos de *A. glabra* y evaluar su papel como especie clave de humedales y su potencial para aplicaciones medicinales, restauración ecológica y adaptación al cambio climático. La investigación se realizó en La Mancha-Diada y El Salado, Veracruz, México, con datos comparativos de La Mancha-CICOLMA. Combinamos revisión bibliográfica con mediciones de campo (2018-2019) de densidad arbórea, diámetro a la altura del pecho, altura y colecta mensual de hojarasca. Además de parámetros ambientales: hidrología y salinidad. Los resultados demostraron que *A. glabra* exhibe tolerancia a las inundaciones y resistencia moderada a la salinidad mediante adaptaciones morfológicas (aerénquima, raíces adventicias, lenticelas hipertrofiadas), manteniendo la fotosíntesis durante la inundación. La densidad arbórea alcanzó 833 individuos/ha, con un área basal de 188.94 m²/ha. La hojarasca anual promedió 12.4 t/ha, y la producción de semillas 3.7 millones de semillas/ha/año. Los análisis etnofarmacológicos revelaron propiedades antimicrobianas, antiinflamatorias, anticancerígenas y larvicidas. Al funcionar como un “mangle de agua dulce”, *A. glabra* es crucial para los servicios ecosistémicos. Muestra un alto potencial para restauración ecológica, pero requiere manejo por su capacidad invasora. El aumento del nivel del mar y la salinización representan una amenaza significativa, subrayando la necesidad de estrategias de conservación urgentes.

Palabras clave: Anona, conservación de humedales, ecología, humedales tropicales, restauración ecológica, selva inundable.

Wetlands provide habitat for thousands of species of aquatic and terrestrial plants and animals. These ecosystems are considered valuable for flood protection, biodiversity conservation, water quality improvement, climate change mitigation through soil carbon sequestration, shoreline erosion control, natural product extraction (including commercial fisheries), aesthetic value, and as sites for research, education, and recreation. Nevertheless, they are disappearing three times faster than other ecosystems and are the planet's most threatened (United Nations 2025). In Mexico, 60 % of wetlands have disappeared or are severely degraded (Landgrave & Moreno-Casasola 2012). Human activities that impact wetlands include filling, grading, and removing vegetation for various land uses, such as building construction, agriculture, and cattle grazing. Many of these activities alter drainage patterns and water levels, thereby affecting the functioning of wetlands.

Freshwater swamps are wooded wetlands characterized by flooded or saturated soils for part of the growing season and slow-moving water or standing water. They are often found in low-lying areas near rivers or lakes (floodplains) or in land depressions and can vary in size and type (Niembro-Rocas *et al.* 2010, Moreno-Casasola *et al.* 2012). Too many people still consider swamps or forested wetlands wastelands that should be exploited and/or drained to control pests or converted to other uses (Mitsch & Gosselink 2015). Millions of hectares are still lost every year. Forested swamps, in particular, are under pressure worldwide from logging and overexploitation and are being drained for other uses (Burton 2009). In Mexico, wetlands are frequently used for cattle raising; in some areas, exotic grasses are introduced as fodder (Moreno-Casasola *et al.* 2009). Infante-Mata (2011) considers them one of the most threatened wetlands in the Gulf of Mexico.

Coastal wetlands are among the most vulnerable ecosystems to rising sea levels resulting from global climate change (Friess *et al.* 2022). The rising sea level will alter their hydrology, suggesting a more significant intrusion of saline water into previously freshwater wetlands (Li & Pennings 2018). This represents another critical factor affecting the structure and functioning of freshwater swamps, which can potentially modify species composition and ecosystem processes.

The importance of *Annona glabra* in tropical wetlands lies in its status as a dominant tree in many Neotropical freshwater swamps (Figure 1). In many others, it is an accompanying species, often found in association with *Pachira aquatica* Aubl. (Infante-Mata *et al.* 2011, Moreno-Casasola *et al.* 2012). Despite being one of the most widespread Annonaceae species in tropical America, it has been understudied both in Mexico and globally. The generic name, *Annona*, was derived from the Arawak Indian word “anor”, which refers to the edible fruit sweetsop (*Annona squamosa* L.). The specific name, *glabra*, is derived from the Latin word for “smooth” and refers to the smooth texture of the fruit (Brown & Mark 2013).

The justification for the study lies in its ecological functions and adaptive capacity; understanding *A. glabra* is crucial for ensuring the conservation and restoration of wetlands. This paper aims to compile information, both published and unpublished, to facilitate an understanding of its importance, ecological behavior, uses, and existing knowledge gaps.

We aim to conduct a comprehensive review of the geographic, morphology, taxonomic, biological, ecological, and ethnobotanical aspects of *A. glabra*, assessing its significance as a keystone species in wetland ecosystems and its potential for medicinal applications, environmental restoration, and adaptation to climate change.

Materials and methods

Study sites. Research was conducted at three freshwater swamps in Veracruz, Mexico (Figure 2): La Mancha-CICOLMA (19° 35' 52.91" N, 96° 22' 53.81" W; Actopan municipality) on the north side of Laguna La Mancha in a reserve of the Centro de Investigaciones Costeras La Mancha (CICOLMA- Instituto de Ecología A.C.); La Mancha-Diada (19° 34' 06.91" N, 96° 22' 46.40" W; Actopan municipality) on the southern side of the laguna, on private property; and El Salado (19° 02' 04.40" N, 95° 59' 01.52" W; Alvarado municipality). All sites are situated in dune depressions, receiving freshwater input from groundwater and seasonal flooding.



Figure 1. Photograph of a swamp dominated by *Annona glabra* in La Mancha-Diada, Veracruz. Photograph by Mariano Guevara.

Forest structure and growth measurements. At La Mancha-Diada, three permanent plots of 10×10 m were established in June 2018 within a monospecific *A. glabra* swamp, following the methodology described by Infante-Mata *et al.* (2011). All trees within the plots were tagged and measured for diameter at breast height (DBH; at 1.3 m) and total height using the similar triangles method. If a tree was multicaulous, each stem was considered to be an individual. Buttressed trees were measured with a ladder 10 cm above the top of the buttresses. Measurements were repeated in June 2019 to assess annual growth. We calculated tree density and basal area per hectare. Forest structure data from La Mancha-CICOLMA and El Salado were obtained from previous studies conducted between 2008 and 2009 using 9-12 plots of 10×10 m per site (Infante-Mata *et al.* 2011).

Litterfall production. Litterfall collection was conducted at different periods at each site due to the nature of this long-term study. At La Mancha-CICOLMA and El Salado, fifteen plastic mesh traps (52 cm diameter, 0.2123 m^2) were installed at each site 1 m above the ground, and litterfall collection was carried out monthly from November 2005 to October 2006 (Infante-Mata *et al.* 2012). Each litterfall sample was sorted by leaf, flower, fruit, seed, and stem structure, after Richardson & Vymazal (2001). Litter was stored in paper bags, dried in an electric oven (70°C , 48 h), and weighed with an OHAUS balance (mod. CT200). The dry weight per trap was converted to grams per square meter (g/m^2) for each month and to tons per hectare (t/ha) for annual comparisons. At La Mancha-Diada, five circular litter traps (52 cm in diameter, 0.2123 m^2) were placed systematically in each plot ($n = 15$ total). Monthly collections were conducted from July 2018 to July 2019 following the same processing methodology.

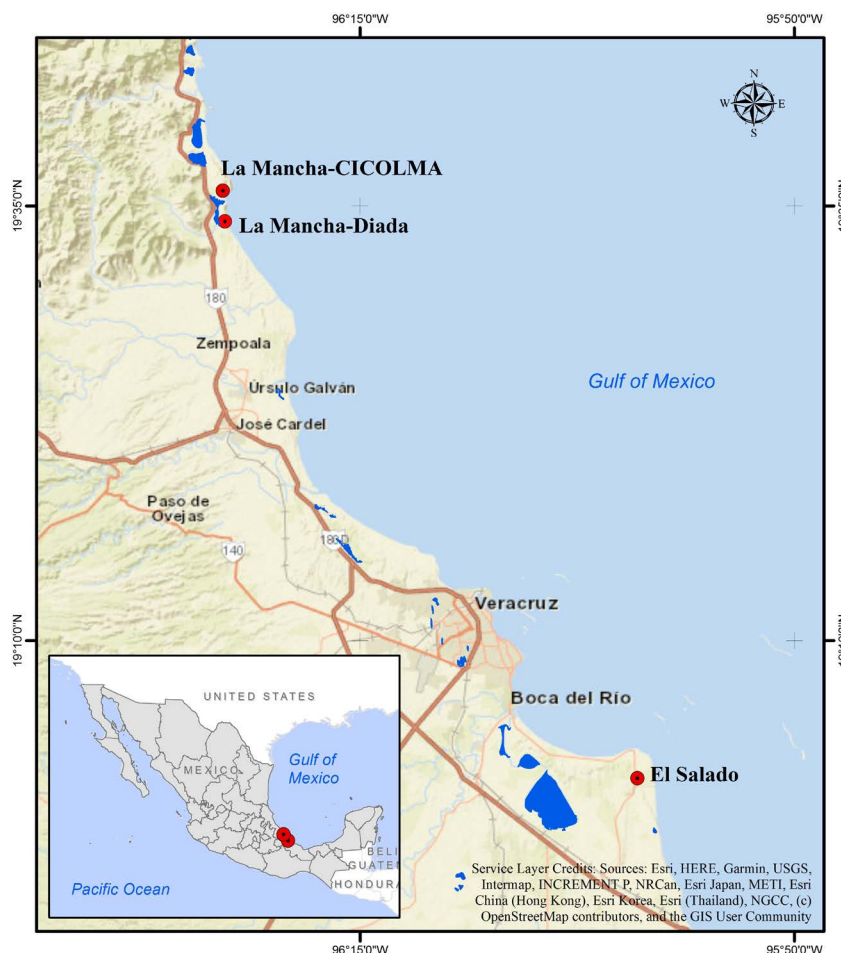


Figure 2. Map showing the location of the three sampling sites in the state of Veracruz, in the Gulf of Mexico: La Mancha-CICOLMA, La Mancha-Diada, and El Salado.

Environmental monitoring. Water level and interstitial water salinity were measured monthly at La Mancha-Diada from June 2018 to August 2020 using a conductivity meter (HANNA HI 9033). At La Mancha-CICOLMA and El Salado, monitoring shallow wells were constructed using PVC pipe 13 mm in diameter, 3 m long, and inserted 1.5 m deep into the soil. The lower 20 cm of each pipe were slotted at 2-cm intervals and wrapped with Nytex™ microfilament mesh, held in place with stainless steel wire. Water level was measured using a water-level tape (Solinst Mini 101) from November 2005 to October 2006. Each study site had 10 monitoring wells, placed adjacent to litter traps. Salinity was measured with a YSI 550 multiparameter at each site during both seasons. The flooding regime was characterized based on seasonal patterns related to rainfall and lagoon dynamics, with hydroperiod curves plotted for the means of monitoring wells (with standard error) for each site.

Literature review and mixed methodological approach. This study integrates a literature review with new empirical data. The bibliographic search was conducted on Scopus, Web of Science, and Google Scholar using the search term “*Annona glabra*”. Retrieved documents were selected based on relevance and reliability, categorized by topic (geography, morphology, taxonomy, ecology, physiology, ethnobotany, restoration), and analyzed for information synthesis. This mixed approach enables the evaluation of geographic, taxonomic, biological, ecological, and ethnobotanical aspects of *A. glabra*, the determination of its importance as a keystone species, and an analysis of its potential for medicinal applications, environmental restoration, and climate change adaptation.

Results

Geographic distribution and habitat. Globally, *A. glabra* grows in freshwater wetlands, near coastal mangrove swamps, freshwater swamps, wet hammocks, other seasonally ponded wetlands, sloughs and strands, and inland along watercourses and on riverbanks.

This species is distributed in Tropical and Subtropical America, ranging from Mexico to Ecuador on the west side and to southern Brazil on the east, as well as the West Indies. It is also found in West and West Central Tropical Africa (Figure 3). It appears to have naturally colonized West Africa from seeds transported on water from Tropical America (Brown & Mark 2013). It has been introduced into parts of China, Southeast Asia, India, Queensland, several islands in this region, and the Galápagos (Plants of the World Online 2025b). In Australia, *A. glabra* is classified as an invasive species that impacts mangroves and wetlands (Queensland Government 2025).

In Mexico, *A. glabra* is distributed in Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca, Chiapas, Tamaulipas, Veracruz, Tabasco, Campeche, Yucatán, and Quintana Roo (eFloraMex 2025). It dominates depressional wetlands and is also found in floodplain forests surrounding lakes and lagoons. Its presence correlates with high water tables and specific edaphic conditions, like sandy or sandy-loam soils mixed with clay, with low fertility (low C and N), high water content, and low salinity levels (Infante-Mata *et al.* 2011). Diversity indices, species associations, and soil parameters exhibit regional variability linked to the geomorphological setting (Infante-Mata 2011, Infante-Mata *et al.* 2011). The common names in English are pond apple, corkwood, monkey apple, swamp apple, or alligator apple, and in Spanish, it is known as corcho, palo de corcho, anona, and anona silvestre.

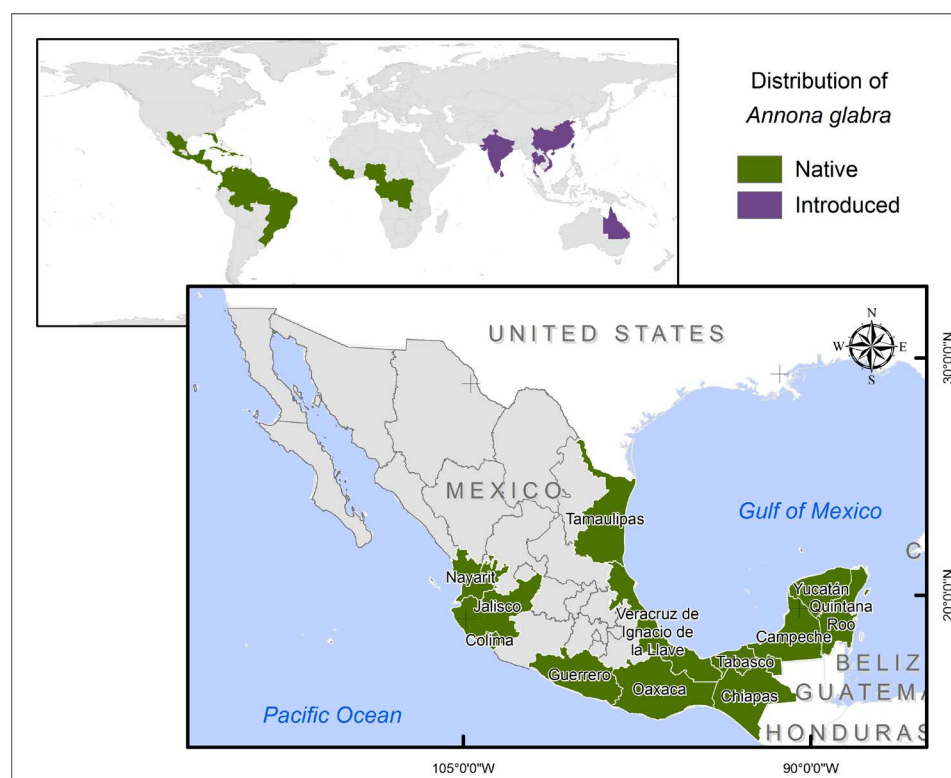


Figure 3. Global and regional distribution of *Annona glabra*. The upper map shows the worldwide distribution with native range (green) in Tropical and Subtropical America, from Mexico to southern Brazil, the West Indies, and West and West Central Tropical Africa. Introduced populations (purple) are found in Asia, Australia, and the Pacific Islands (Plants of the World Online 2025b). The lower map details the distribution in Mexico, where the species occurs in coastal states along both the Pacific Ocean and Gulf of Mexico, including Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca, Chiapas, Tamaulipas, Veracruz, Tabasco, Campeche, Yucatán, and Quintana Roo (eFloraMex 2025).

Morphology and taxonomic description. Vegetative morphology.- *Annona glabra* is a semi-deciduous tree typically growing 5-12 meters in height, with single or multi-stemmed trunks displaying swollen bases in saturated soils ([Figure 4A](#)). Leaves are simple, alternate, oblong to elliptic (10-15 cm × 5-8 cm), glabrous, leathery, and dark green above with entire margins. The species exhibits a dorsiventral mesophyll with specialized stomata and structural reinforcements that are adapted to hydric stress ([Figure 4B](#)).

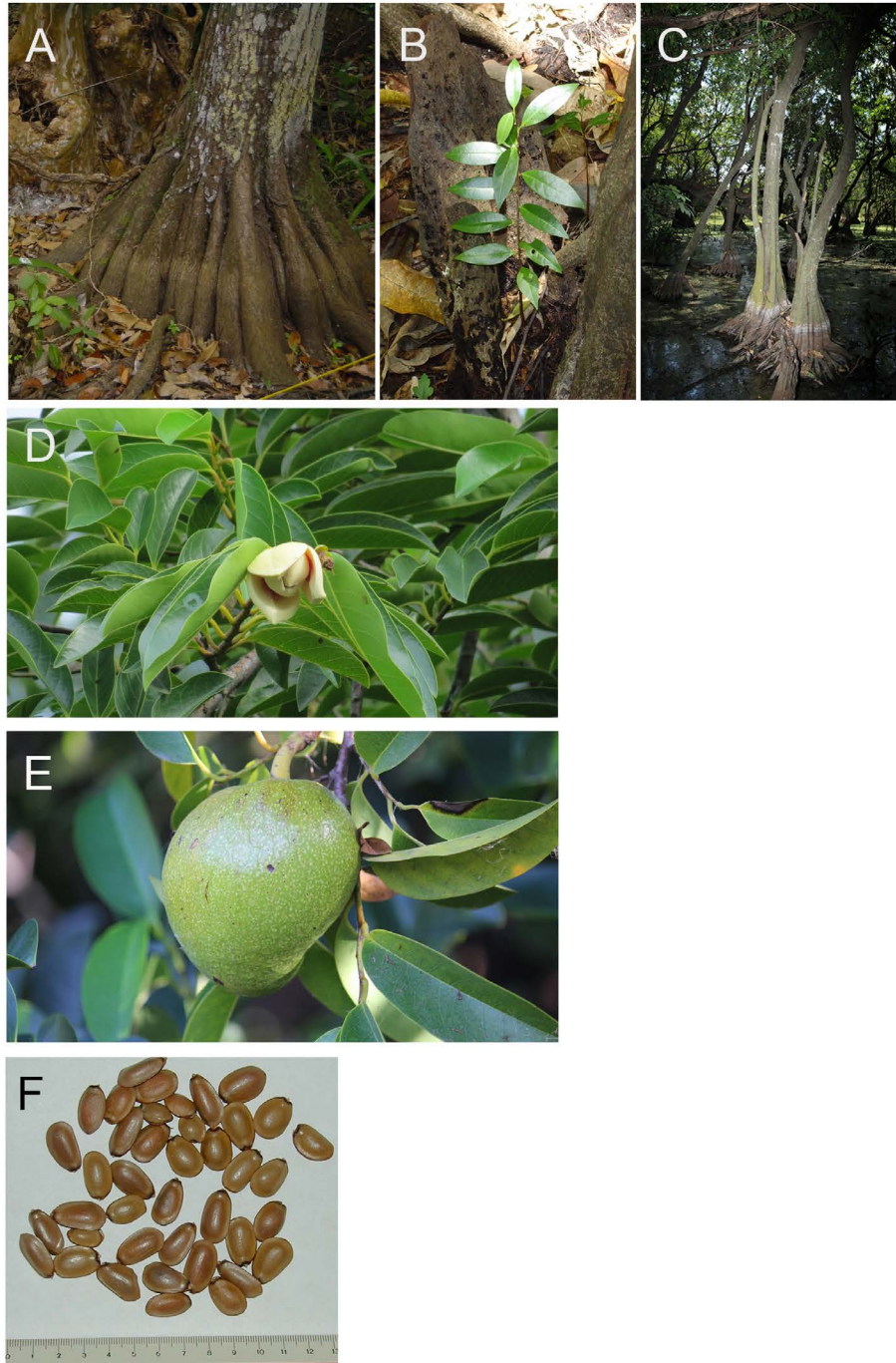


Figure 4. Photos showing the morphology of *Annona glabra*. A) tree base showing buttress roots, B) leaves of seedling, C) tree trunks showing the flooding level, D) flower and leaves, E) fruit, F) seeds. Photographs by Edgar Abel Sánchez-García (E), Dulce Infante-Mata (B, F) and Gerardo Sánchez-Vigil (A, C, D).

Root morphology and anatomy.- The root system is shallow and extensively branched, featuring spongy tissue with extensive aerenchyma that enables oxygen diffusion to submerged tissues (Figure 4C). Under flooding, roots develop secondary aerenchyma, adventitious roots, and hypertrophied lenticels (Santos *et al.* 2015, India Biodiversity Portal 2025). The vascular tissue contains a net-like parenchyma system enhancing transport under submerged conditions, providing tolerance to chronic inundation and episodic droughts (Yáñez-Espinoza & Terrazas 2001). More than two-thirds of the plant's hydraulic resistance is located in the roots, which offsets their low conductivity by increasing root quantity (Zotz *et al.* 1997).

These hydraulic and anatomical traits provide not only tolerance to chronic inundation but also resilience to episodic droughts, suggesting dual adaptation to brackish habitats with fluctuating water levels.

Floral and reproductive traits.- *Annona glabra* bears solitary, bisexual flowers on axillary pedicels. Each flower has three fleshy sepals and six thick, yellow-green petals arranged in two whorls. Numerous stamens and free carpels are enclosed within the petals (Figure 4D). The flowers are protogynous and adapted for beetle pollination, although artificial pollination may be employed in cultivated settings where pollinators are absent (Cañizares Zayas 1969).

Flowering occurs asynchronously, with up to three annual peaks. However, according to Lestari & Sofiah (2015), it is highly synchronized within populations and positively influenced by humidity and moderate rainfall. Fruiting typically peaks during the wet season.

Fruit and seed morphology.- The fruit is a syncarpium, formed by the fusion of multiple free carpels and the fleshy receptacle, measuring up to 15 cm in length and green to yellowish at maturity. The fruit floats and is dispersed via hydrochory and, to a lesser extent, frugivory (Figure 4E) (Westcott *et al.* 2008).

Seeds are numerous, cinnamon-colored, oblong, and smooth, with sizes ranging from 12 to 19 mm in length and 4 to 8 mm in thickness (Figure 4F). Anatomical studies reveal the presence of ruminant endosperm -an infolding of the seed coat into the endosperm- which is a defining feature of Annonaceae seeds and aids in taxonomic classification (Van Setten & Koek-Noorman 1992, Lestari & Pratiwi 2022).

Taxonomic remarks.- The genus *Annona* comprises 171 species, many of which are economically significant (Plants of the World Online 2025a). *Annona glabra* is taxonomically distinguished by its elliptic leaves, syncarpic fruit, extensive aerenchyma, and highly specialized root and seed anatomy. Its ability to grow in flooded and saline environments makes it ecologically distinct from upland relatives such as *Annona cherimola* Mill or *Annona squamosa* L.

Taxonomic synonyms.- Synonyms for *A. glabra* are: *Annona australis* A.St.-Hil., *A. chrysocarpa* Lepr., *A. chrysocarpa* Lepr. ex Guill. & Perr., *A. klainei* Pierre ex Engl. & Diels, *A. klainei* var. *moandensis* De Wild., *A. klainii* Pierre ex Engl. & Diels, *A. klainii* var. *moandensis* De Wild., *A. laurifolia* Dunal, *A. palustris* L., *A. palustris* var. *grandifolia* Mart., *A. peruviana* Humb. & Bonpl. ex Dunal, *A. uliginosa* Kunth, *Asimina arborea* Raf., *Cassia ketschta* Hasselq., *Guanabanus palustris* M. Gómez.

Types of wetlands where Annona glabra is established. In Veracruz, three types of freshwater swamps have been characterized: those dominated by *P. aquatica* (often with *A. glabra* as companion species), those dominated by *A. glabra*, and those dominated by various *Ficus* species. The first type tolerates extended inundation periods and stronger water flow, while *Ficus* swamps occupy the opposite extreme (Moreno-Casasola & Infante-Mata 2010). *Annona glabra* also forms associations with *Chrysobalanus icaco* L. in southern Veracruz and Tabasco (Lot 2004), and monotypic stands along the Palizada River in Campeche (Ocaña & Lot 1996). In the Yucatan Peninsula, it occurs in permanently water-saturated forested communities (Romero-Soler & Cetzal-Ix 2015).

In Florida, *A. glabra* occurs at margins of sloughs, streams, and lakes, often with bald cypress trees (*Taxodium distichum* (L.) Rich.), with the largest populations in the Everglades (Brown & Mark 2013). Throughout its range, *A. glabra* forms diverse wetland associations from monospecific stands to mixed communities with species such as

Pterocarpus officinalis Jacq. and various mangrove associates, particularly common in Caribbean swamp forests and Central American coastal wetlands (Armenteros *et al.* 2007, Galford *et al.* 2018). In the Pacific lowlands of Panama, Ibáñez (2006) has recorded 10-m-high swamps dominated by *A. glabra*, sometimes associated with the palm *Elaeis oleifera* (Kunth) Cortés.

Association with edaphic and hydrological conditions.- Information on the ecology of these freshwater swamps has been obtained mainly for Veracruz. Table 1 shows a description of the environmental characteristics of the swamps in La Mancha-CICOLMA and El Salado. It indicates geomorphological settings, water input, and water salinity, showing that they are freshwater forested wetlands located in depressions.

Table 1. Environmental characteristics of the studied freshwater swamps in the coastal plain of Veracruz, Mexico. Values are presented as means $\pm$ S.E. Both sites are located in accumulative intradunal depressions with phreatic water flow. La Mancha-CICOLMA shows higher species diversity ($H' = 3.4$) with 44 species, while El Salado has lower diversity ($H' = 2.7$) with 20 species. Water salinity remains low at both sites (< 0.5 g/L), confirming their freshwater status. Redox potential values indicate reduced soil conditions typical of flooded environments. Data taken from Infante-Mata *et al.* (2011).

	La Mancha-CICOLMA	El Salado
Geomorphology ¹	Accumulative intradunal depression	Accumulative intradunal depression
Soil type ¹	Humic Gleysoil	Histogleic Arenosol
Associated water flow	Phreatic water	Phreatic water
Mean annual temperature ² (°C)	25	24
Annual precipitation ² (mm)	1156	1592
Superficial water salinity ³ (g/L)	0.47 $\pm$ 0.08	0.27 $\pm$ 0.02
Water pH ³	7.3 $\pm$ 0.06	7.1 $\pm$ 0.06
Groundwater salinity ³ (g/L)	0.40 $\pm$ 0.07	0.27 $\pm$ 0.02
Flood time (% of year with water above surface of soil)	75	50
Redox potential ⁴ (mV)	104 $\pm$ 11	58 $\pm$ 30
Bordering ecosystems	Tropical dry forest, dune lake and marshes, dune vegetation	Tropical dry forest, watermelon cultivars
Tree height (m)	10-12	10-15
Shannon diversity index H*	3.4 $\pm$ 0.13	2.7 $\pm$ 0.10
Species number ⁵	44	20

¹Data obtained from field work in each study area. ²Eric III (IMTA 2007). ³The salinity was measured with a YSI 550 multi-parameter at each site. ⁴Measured with platinum electrodes, a reference electrode, and a digital pH/ORP Barnant meter. Dry season, June 2006. ⁵Total species number by tropical forested wetland (trees, shrubs, lianas, epiphytes, and herbs).

Forest structure, hydrology, and dynamics. Floristic composition and vegetation structure.- In La Mancha-CICOLMA, the canopy (10-12 m) was dominated by *A. glabra* with several accompanying tree species. Tree density was 2,421 ind./ha with a basal area of 32.7 m²/ha (Table 2). *Annona glabra* showed the highest relative importance value (RIV) (159.11 %). Species with the highest RIVs were *A. glabra* (159.11 %), *Salix humboldtiana* Willd. (13.61 %), *Ficus insipida* subsp. *insipida* (12.28 %), and *F. cotinifolia* Kunth (11.58 %). The tree diameter classes best represented in this swamp are found in the 3-13 cm class, with an estimate of 1,146 ind./ha, slightly under 48 %; the 13.1-23 cm class, with 1,107 ind./ha (46 %) and the 23.1-53 cm class, with 130 ind./ha (5.4 %). No trees over 53 cm DBH were found (Infante-Mata *et al.* 2011).

El Salado exhibited similar patterns, with a tree density of 2,230 ind./ha and a basal area of 74.73 m²/ha. *Pachira aquatica* (129.28 %) and *A. glabra* (53.41 %) showed the highest RIVs (Infante-Mata *et al.* 2011).

Table 2. Forest structure parameters showing density, basal area, and importance value index (IVI) for the ten most important tree species in La Mancha-CICOLMA and El Salado swamps in Veracruz, Mexico. Total tree density is similar between sites, but Salado shows more than double the basal area. Data taken from Infante Mata *et al.* (2011).

LA MANCHA-CICOLMA			
Species	Absolute density	Basal area	Importance value
	(ind. ha ⁻¹)	(m ² ha ⁻¹)	(%)
<i>Annona glabra</i> L.	1677	22.96	159.11
<i>Salix humboldtiana</i> Willd.	38	2.86	13.61
<i>Ficus insipida</i> Willd. subsp. <i>insipida</i>	69	1.47	12.28
<i>Ficus cotinifolia</i> Kunth.	38	0.59	11.58
<i>Diospyros virginiana</i> L.	54	0.91	11.55
<i>Tabebuia rosea</i> (Bertol) DC.	62	0.38	10.27
<i>Ginoria nudiflora</i> (Hemsl.) Koehne	46	0.85	7.78
<i>Trichilia havanensis</i> Jacq.	31	0.30	7.12
<i>Piper amalago</i> L.	77	0.19	7.03
<i>Pachira aquatica</i> Aubl.	15	0.13	4.30
<i>Enterolobium cyclocarpum</i> Jacq. (Griseb.)	8	0.95	4.85
<i>Bursera simaruba</i> (L.) Sarg.	31	0.07	4.76
<i>Coccoloba liebmannii</i> Lindau	15	0.20	4.52
<i>Vachellia cornigera</i> (L.) Seigler & Ebinger	38	0.07	5.08
<i>Cestrum dumetorum</i> Schltdl.	15	0.03	4.02
Total of the other species (12)	207	0.74	32.14
Total	2421	32.7	300
EI SALADO			
Species	Absolute density	Basal area	Importance value
	(ind. ha ⁻¹)	(m ² ha ⁻¹)	(%)
<i>Pachira aquatica</i> Aubl.	810	56.61	129.28
<i>Annona glabra</i> L.	550	9.87	53.41
<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	140	0.31	22.21
<i>Dalbergia brownei</i> (Jacq.) Schinz	230	1.76	19.57
<i>Piper divaricatum</i> G.Mey.	150	0.038	15.40
<i>Pristimera celastroides</i> (Kunth) A.C.Sm.	130	0.149	12.93
<i>Sapium lateriflorum</i> Hemsl.	70	0.116	11.92
<i>Ficus insipida</i> Willd. subsp. <i>insipida</i>	20	4.41	8.53
<i>Diospyros virginiana</i> L.	30	1.11	8.00
<i>Combretum albidum</i> G.Don	50	0.332	7.86
Total of the other species (3)	50	0.0279	10.89
Total	2,230	74.73	300

In La Mancha-Diada, a total of 25 adult individuals of *A. glabra* were recorded within the 300 m² area sampled. In 2018, the mean DBH was 53.34 ± 0.27 cm, and the mean height was 12.33 ± 0.11 m. In 2019, DBH increased to 53.71 ± 0.27 cm and height to 12.45 ± 0.11 m, indicating minimal but consistent growth across individuals. These values correspond to an estimated tree density of 833 ind./ha and a basal area of 188.94 m²/ha.

Hydrology: flood regime and salinity.- In La Mancha-Diada, the flood pattern exhibited two peaks in water level throughout the year. The first occurred during the rainy season (September-October), while the second took place during the winter months (November-February), when the sandbar of Laguna La Mancha closed. The water level gradually rises due to the continuous inflow of freshwater from the Caño Gallegos River, which feeds the mangroves of the coastal lagoon ([Figure 5](#)).

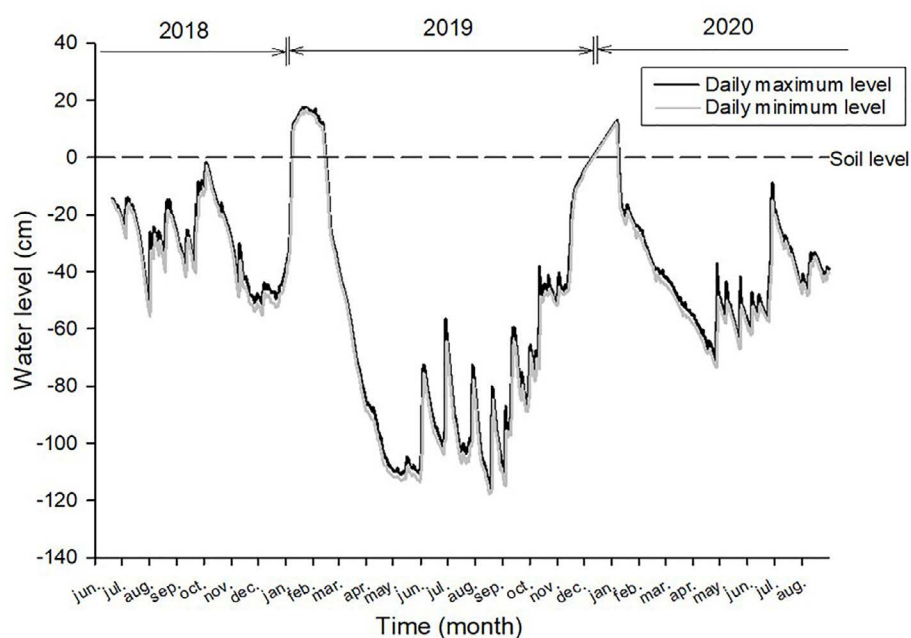


Figure 5. Hydroperiod for freshwater swamp dominated by *Annona glabra* in La Mancha-Diada from June 2018 to August 2020. The dashed line is ground level, and the solid lines indicate the daily maximum (black) and minimum (gray) levels of the hydroperiods.

The recorded interstitial water salinity in La Mancha-Diada was 5.9 ± 0.87 parts per thousand (ppt), classifying this wetland as oligohaline according to the classification by Montagna *et al.* (2013). The average water level was 11.6 ± 1.18 cm above the soil surface.

Ecological dynamics and functionality. Phenology and productivity.- In the Gulf of Mexico, *A. glabra* undergoes leaf shedding from November to January, coinciding with the cold front season. Leaf regrowth takes place between February and March, while flowering begins simultaneously and continues until June. Fruit development spans from March to August, with mature fruits falling just before the onset of the rainy season. Upon contact with water, the fruit pulp disintegrates, releasing seeds that remain buoyant during floods. As water levels recede, the seeds settle onto the soil and germinate (Infante-Mata 2004).

This reproductive strategy is closely linked to hydrological dynamics and demonstrates remarkable efficiency. Seeds initially float during flood periods and settle as waters recede, creating opportunities for seedling establishment on exposed soils. Controlled experiments in Pantanos de Centla reported germination rates above 86 % for *A. glabra* seeds after mechanical scarification, with germination beginning around days 6-8 and extending over several

weeks. The species shows phanerocotylar epigeal germination, producing robust seedlings with high survival rates (Zamora-Cornelio *et al.* 2010).

Recruitment potential is enhanced by seed buoyancy and longevity in aquatic systems. In Queensland, *A. glabra* seeds remained afloat for more than 12 months in both fresh and salt water, with an average germinability of 38 % after one year, increasing the chances for long-distance hydrochorous dispersal (Setter *et al.* 2008). Seedling physiology supports this resilience through adaptations that enhance flood tolerance. In experiments with 56 days of flooding, all seedlings survived, showing significant increases in total biomass and root:shoot ratios, while maintaining high stomatal conductance and photosynthetic activity under inundation (Mielke *et al.* 2005).

In La Mancha-Diada litterfall production showed apparent monthly variation. The annual litterfall production averaged 12.4 ± 0.05 t/ha/yr. The peak production was observed during November and December, coinciding with the season of strong winds due to winter cold fronts. [Table 3](#) presents the DBH and height of trees across both years, while [Figure 6](#) illustrates monthly litterfall dynamics.

Table 3. Mean DBH and height of *Annona glabra* trees in 2018 and 2019 in La Mancha-Diada.

Year	Mean DBH (cm)	SE DBH	Mean Height (m)	SE Height
2018	53.34	0.27	12.33	0.11
2019	53.71	0.27	12.45	0.11

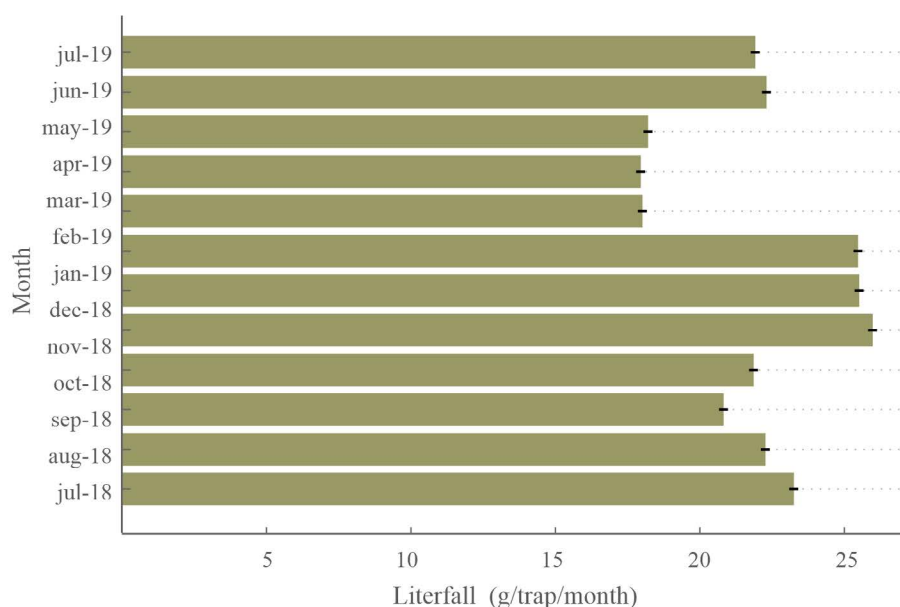


Figure 6. Monthly litterfall production (mean $\pm$ 1 SE) recorded in 15 traps across the monospecific *Annona glabra* swamp in La Mancha-Diada, from July 2018 to June 2019.

The tree *A. glabra* accounts for 35.24 % of the productivity in La Mancha-CICOLMA and 9.31 % in El Salado. Decaying leaves and stems were recorded from November to March and from June to October (Infante-Mata *et al.* 2012). The fruits occurred in March in La Mancha and in December and January in El Salado. In both sites, from March to June, the litterfall from *A. glabra* decreased, and flower production occurred during the dry season (February to June) ([Figure 7](#)).

The total productivity of litterfall in one year in La Mancha-CICOLMA was 9.7 ± 0.6 t/ha/yr, while in El Salado, it was higher, 12.5 ± 1.1 t/ha/yr ([Figure 8](#)). The wetlands of both sites had the lowest water levels (below the soil surface) during the dry season from March to June. The hydrology of La Mancha-CICOLMA and El Salado was strongly dependent on groundwater (Infante-Mata *et al.* 2011, 2012).

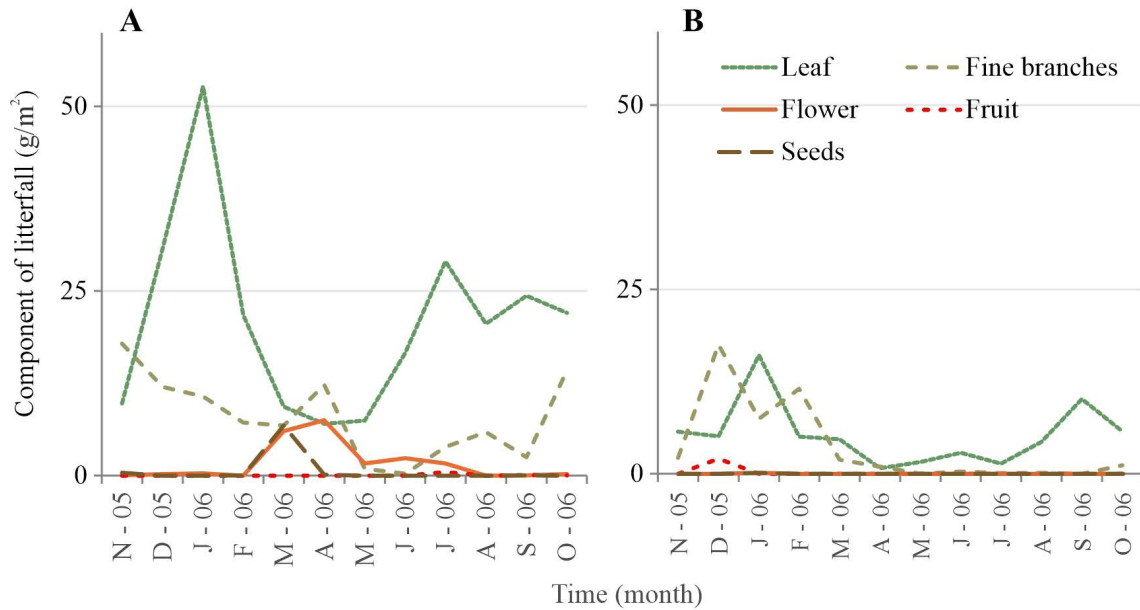


Figure 7. Monthly contribution per litterfall component (g/m/month) by *Annona glabra*. A) La Mancha-CICOLMA and B) El Salado. North winds season (November-February), dry season (March-June), and rainy season (July-October). Unpublished data.

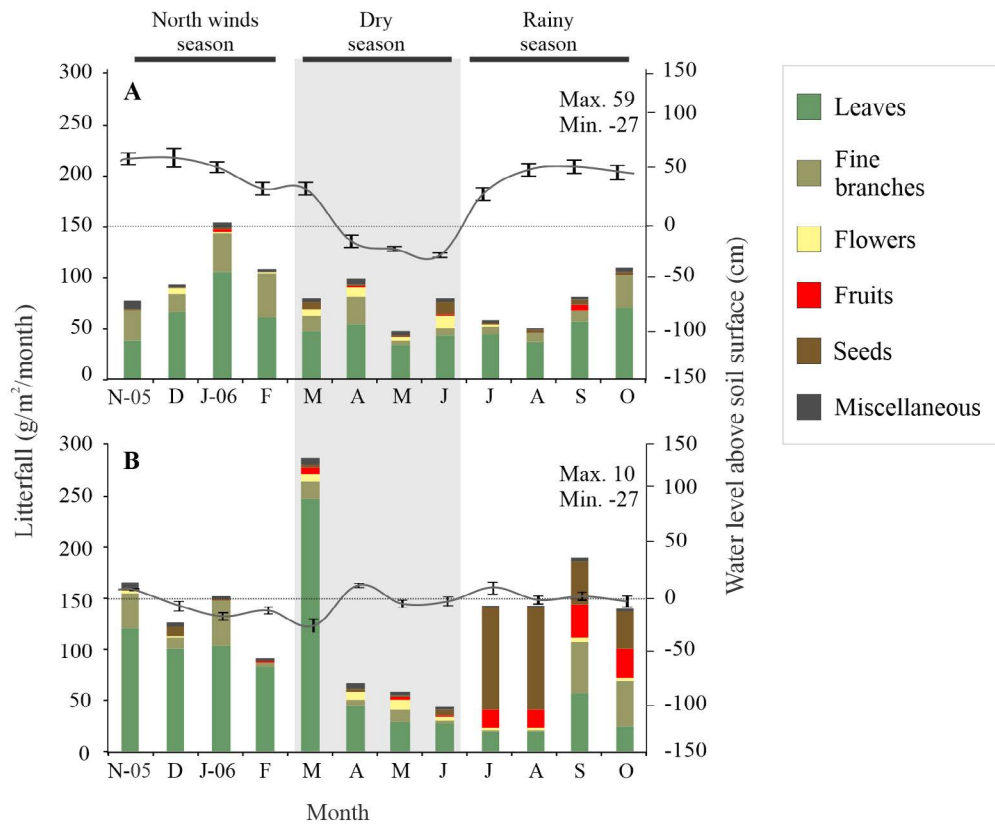


Figure 8. Monthly contribution per litterfall component (g/m/month). The hydroperiod curves for the mean of ten monitoring wells (standard error bars) from each swamp are shown. Maximum (Max.) and minimum (Min.) water levels are indicated by site, along with the seasons throughout the year. A) La Mancha- CICOLMA and B) El Salado. The dotted line indicates ground level. Data taken from Infante-Mata *et al.* (2012).

The litterfall contribution differed depending on the biological life form. In La Mancha-CICOLMA and El Salado, arboreal material contributed 85 and 90 % to the litter, respectively, while lianas contributed less than 10 % (Figure 9, Infante-Mata *et al.* 2012). Liana development is limited in *A. glabra*-dominant wetlands, as these plants are deciduous and remain leafless for two to three months, thereby providing temporary canopy support for lianas. This temporary canopy opening also allows seedlings of other species or *A. glabra* to have favorable light conditions for growth in annual pulses until they reach the height of adult trees and have the potential to grow taller than established trees.

In Everglades restoration trials, seedlings showed high survival along experimental hydrological gradients, performing better in higher and moderately flooded microsites than in persistently inundated ones (Stoffella *et al.* 2010). High planting densities promoted greater total biomass without reducing survival, underscoring the species adaptability in restoration contexts (Stoffella *et al.* 2022). These traits (high germination rates, prolonged buoyancy, hydrochorous dispersal, flood tolerance, and growth plasticity) make *A. glabra* a dominant recruiter in Neotropical wetlands, supporting a theory of temporary patch succession that allows plants to grow through pulses.

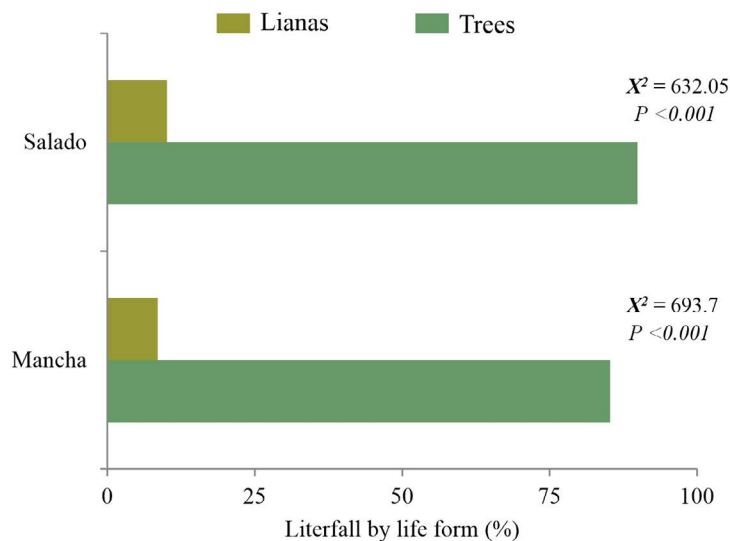


Figure 9. Contribution of different life forms to total annual litterfall production in two freshwater swamps of Veracruz, Mexico: La Mancha-CICOLMA, and El Salado. Data taken from Infante-Mata *et al.* (2012).

Decomposition. The decomposition of *A. glabra* litter was evaluated in the swamps of La Mancha-CICOLMA and El Salado from July 2012 to July 2013; average data are presented. A total of 180 litterfall bags were placed, and 18 bags were removed at 15, 30, 45, 60, 90, 150, 210, 270, 330, and 390 days after placement. The degradation of *A. glabra* litter at 390 days was 89 % (Figure 10). The degradation coefficient of *A. glabra* litter was 0.0199 ± 0.002 k/d and the estimated time for 50 % degradation of leaf material was $T_{50} = 34.7$. This indicates that the reincorporation into the soil occurs continuously throughout the year.

Reproduction and regeneration. Pollination. *Annona glabra* exhibits a protogynous and entomophilous pollination system consistent with the ancestral traits present in the Annonaceae family. Like most Annonaceae, its flowers are hermaphroditic but temporally dichogamous: the female (pistillate) stage precedes the male (staminate) phase. This behavior reduces the probability of self-pollination and favors cross-pollination (Silberbauer-Gottsberger *et al.* 2003, Goodrich & Raguso 2009).

The flowers are solitary, axillary, and composed of three thick sepals and six fleshy petals arranged in two whorls. Flowers emit a strong, fruity-acetonic scent, consisting primarily of volatile compounds such as 3-pentanyl acetate and 1,8-cineole; they function as attractants for beetle pollinators (Goodrich & Raguso 2009). These volatiles mimic the odor of fermenting fruit, a known attractant for certain beetle guilds (Silberbauer-Gottsberger *et al.* 2003, Jürgens

2009). The scent profile is dynamic and varies during floral ontogeny, particularly between the female and male phases. During the pistillate stage, flowers are more fragrant and thermogenic, enhancing scent dispersal and pollinator attraction (Goodrich 2012).

Pollination in *A. glabra* is primarily mediated by beetles (cantharophily), particularly nitidulid and dynastine beetles, which are attracted to the floral scent; they enter the flower chamber during the pistillate phase (Gottsberger 1999, Silberbauer-Gottsberger *et al.* 2003). Once inside, the beetles remain trapped as the flower transitions to the staminate phase, during which pollen is released. These beetles often feed on pollen or sterile floral tissues. Their confinement within the flower ensures efficient pollen transfer when they exit to visit another receptive flower. A temporary chamber enclosing the reproductive organs and the visiting beetles is formed by the petals curving inward during anthesis. Thus, the flower's structure facilitates this process. This chamber promotes pollen deposition on the beetles' bodies and limits premature pollen loss or escape by the insect before the flower's male phase (Gottsberger 1989).

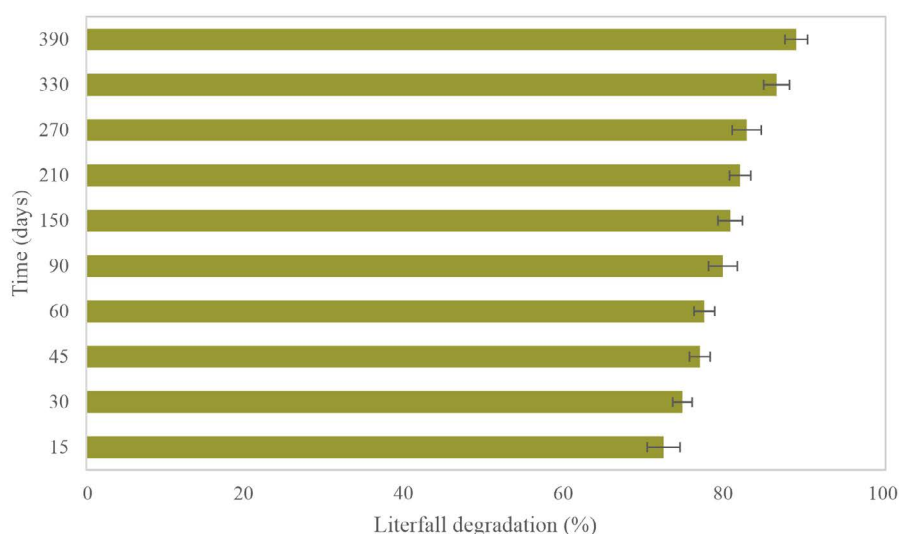


Figure 10. Litterfall degradation of *Annona glabra* leaves over time. Bars represent the mean value for sites La Mancha-CICOLMA and El Salado, from July 2012 to July 2013. Unpublished data.

Historical and contemporary observations have shown that in cultivation, *A. glabra* and related species benefit from artificial pollination. Wester (1910), at the beginning of the last century, showed that manual pollination significantly increased fruit set in *Annona* species with asynchronous anthesis. These findings remain remarkably relevant in regions where natural pollinators are absent, or their populations are insufficient. Artificial pollination involves collecting pollen during the late afternoon (staminate phase) and transferring it to stigmas during the early morning (pistillate phase), thereby optimizing the timing for maximum receptivity.

In Veracruz, under tropical conditions, *A. glabra* flowers asynchronously and repeatedly throughout the year, with up to three flowering events per year (Lestari & Sofiah 2015). This strategy enhances reproductive success across varying climatic conditions, thereby increasing opportunities for outcrossing in the genus *Annona*. The reproductive success of this system depends on maintaining a stable community of pollinators, which is closely linked to local temperature and humidity dynamics (Gottsberger 1999, 2016).

Dispersal (hydrochory, zoochory).- The primary dispersal mechanism of *A. glabra* is via water, making hydrology a fundamental aspect of its dispersal, germination, and seedling establishment strategies (Infante-Mata 2004, Infante-Mata & Moreno-Casasola 2005). In the Gulf of Mexico, fruit development occurs from March to August, coinciding with the transition from the dry season to the rainy season (Infante-Mata *et al.* 2012). Similarly, in Queensland's

coastal region (northeastern Australia), fruit production spans from January to May, aligning with local flood events; seeds are likewise dispersed by water (Mason *et al.* 2008). This species exhibits high seed productivity, with each fruit containing approximately 100 seeds (Infante-Mata 2004). A single hectare dominated by *A. glabra* can produce up to 3.7 million seeds annually (Setter *et al.* 2008). Upon ripening, fruits fall to the ground. If the site remains unflooded, the endosperm disintegrates, releasing seeds onto the soil surface. In flooded conditions, the fruit floats, and the endosperm breaks down in the water, releasing seeds that can also float. Fruits typically disintegrate within two weeks after falling into the water (Setter *et al.* 2008). Seeds have been observed to float and retain viability for over 12 months in both freshwater and saltwater (Setter *et al.* 2008). However, studies suggest limited long-distance dispersal, with most seeds stranding near their origin (Mason *et al.* 2008).

Although less frequent, seed dispersal can also occur via animals. The fruits attract various fauna that consume the pulp and seeds, thereby acting as dispersal vectors. In Australia, feral pigs and other wild animals consume this fruit, and the seeds are dispersed over great distances in their droppings. Specifically, in northeastern Australia, the marsupial agile wallaby (*Macropus agilis* Gould 1842) feeds on fruits, and seeds excreted in its droppings remain viable, achieving germination rates of up to 73 % within four months (Setter & Patane 2011).

Additionally, the native bird, the southern cassowary (*Casuarius casuarius* Linnaeus, 1758), has been documented consuming and dispersing *A. glabra* seeds (Westcott *et al.* 2008). Recently, consumption of *A. glabra* fruits by toque macaque monkeys (*Macaca sinica* Linnaeus 1771) was reported in the mangroves of Sri Lanka's Muthurajawela swamp and Negombo lagoon, on the Indian Ocean coast (Rog & Sinovas 2024). In the Caribbean Sea, *A. glabra* has been reported as an essential food source for reptiles, such as the green iguana (*Iguana iguana* Linnaeus 1758) and the slider turtle (*Trachemys stejnegeri* Schmidt 1928), in Puerto Rico (Burgos-Rodríguez *et al.* 2016). In the Gulf of Mexico, animal-mediated dispersal of *A. glabra* has not been documented. However, in the Shark River Estuary, Florida Everglades, American alligators (*Alligator mississippiensis* Daudin 1802) have been observed consuming *A. glabra* fruits. These reptiles function as seed predators rather than dispersers, as no germination occurred after seeds passed through their digestive tract (Rosenblatt *et al.* 2014). In central Veracruz, Mexico, during the dry season when resources are limited, coyotes (*Canis latrans* Say 1823) have been recorded feeding on fruits and potentially acting as seed dispersers (EA Sánchez-García 2019, unpublished data); however, the germination capacity of seeds in coyote feces remains unevaluated. The secondary dispersal mechanism could be ecologically significant in regions where hydrological dispersal is constrained.

Germination and seedling establishment.- Following dispersal, once floodwaters recede and water levels drop, the seeds settle onto the soil, and germination begins. *A. glabra* seeds typically initiate germination within two weeks of reaching the ground (Infante-Mata & Moreno-Casasola 2005, Sánchez-García *et al.* 2023a). Germination in this species is enhanced under moist soil conditions and direct sunlight, with reported success rates exceeding 80 % (Infante-Mata & Moreno-Casasola 2005, Zamora-Cornelio *et al.* 2010, Sánchez-García *et al.* 2023a). However, seed viability declines proportionally with the time spent floating or buried in soil, leading to significantly reduced germination (Infante-Mata & Moreno-Casasola 2005, Setter *et al.* 2008, Sánchez-García *et al.* 2023a). *Annona glabra* produces recalcitrant seeds, which germinate only under favorable environmental conditions (Infante-Mata 2004). Consequently, they do not form persistent seed banks (Setter *et al.* 2004).

Seedlings of *A. glabra* show high survival under varied flooding and light conditions, although growth is optimal under mesic, high-light environments without herbivory (Infante-Mata *et al.* 2019). Post-germination, *A. glabra* seedlings face a critical six-month race against the rising water table. Only those achieving sufficient height growth to keep leaves above floodwater will survive submersion stress during the subsequent inundation period.

Adaptations to flooding.- *Annona glabra* exhibits a complex array of morphological, physiological, and phenological adaptations that underlie its high tolerance to prolonged flooding, a trait central to its success in tropical and subtropical wetlands. These adaptations manifest early in seeds and seedling development and are critical both for individual survival and for the species' potential in ecological restoration. One of the earliest responses to inundation is the rapid

development of hypertrophied lenticels at the stem base, occurring typically within the first week of submersion. These structures facilitate gas exchange under hypoxic conditions (Ojeda *et al.* 2004, Mielke *et al.* 2005). *Annona glabra* also produces adventitious roots, swollen basal stems, and aerenchyma in submerged tissues, facilitating internal oxygen transport and tolerance to anoxic environments (Zotz *et al.* 1997, Núñez-Elisea *et al.* 1998), which gives its trunk a distinctive and attractive appearance. Unlike many flood-sensitive species, *A. glabra* maintains high stomatal conductance and stable net photosynthetic rates during inundation. Mielke *et al.* (2005) observed a 152 % increase in stomatal conductance after 56 days of continuous flooding. Meanwhile, photosynthesis remained steady, even in older leaves, supporting continued growth and carbon assimilation under stress. These physiological traits help explain the species' ability to accumulate biomass during periods of flooding. Seedlings exhibit a growth pattern characterized by early stem thickening, followed by rapid vertical elongation. This strategy allows emergent leaf exposure above the waterline within the first six months' post-germination—a critical threshold for survival under prolonged inundation (Sánchez-García *et al.* 2022b). However, seedling development can be significantly hindered by herbivory; Infante-Mata (2004) documented growth suppression under saturated conditions due to the presence of lepidopteran larvae. Flooding alters soil redox potential, increasing the bioavailability of iron (Fe^{2+}) and manganese (Mn^{2+}), which *A. glabra* effectively assimilates. Nonetheless, under non-flooded calcareous soils, it often exhibits iron deficiency symptoms unless supplied with high levels of chelated Fe (Ojeda *et al.* 2004), indicating its physiological dependence on reduced conditions for optimal micronutrient uptake. Field-scale experiments in the Everglades confirm the species' ecological amplitude. Stoffella *et al.* (2022) found that *A. glabra* not only survived but also increased its relative biomass in high-flood zones over an eight-year period, while less flood-tolerant species declined. This resilience across hydrological gradients affirms its ecological versatility and suitability for wetland restoration, particularly in areas prone to chronic flooding. These traits collectively position *A. glabra* as a “fresh-water or brackish water mangrove”, functionally analogous to coastal mangrove species. Its robust flood tolerance, capacity for structural adaptation, and physiological plasticity make it a prime candidate for use as rootstock in waterlogged agricultural systems or as a framework species in forested wetland restoration.

Adaptations to salinity. *Annona glabra* exhibits notable adaptations to salinity, enabling its establishment and survival in coastal wetlands, estuarine margins, and brackish environments where many other woody species fail. Its salt tolerance mechanisms include both morphological traits and physiological resilience, positioning it as a strategic species for restoration and landscaping in areas subject to seawater intrusion and increasing soil salinity.

Morphological and physiological adaptations.—A key morphological feature contributing to salinity tolerance is the presence of thick cuticular wax on the adaxial and abaxial surfaces of its broad leaves. This wax layer reduces water loss through transpiration and minimizes salt uptake through the leaf surface (Liu *et al.* 2016). In contrast to salt-sensitive species such as bald cypress (*T. distichum*), which show rapid mortality under root-submerged saline conditions, *A. glabra* maintains growth and leaf turgor even when roots are fully submerged in solutions containing 15,000 ppm NaCl—a concentration typical of brackish water. This leaf morphology and the underlying physiological differences may be the mechanisms that make *A. glabra* significantly more tolerant to salt stress than *T. distichum* (Liu *et al.* 2016).

Experimental comparisons have confirmed *A. glabra*'s exceptional salinity tolerance: while *T. distichum* seedlings exhibited 100 % mortality after nine days of complete root submersion in saline conditions, *A. glabra* seedlings continued to grow normally under identical treatments (Liu *et al.* 2016). This differential survival is attributed not only to anatomical differences but also to the species' internal water relations, low transpiration rates, and robust osmotic adjustment capacity. Native to Florida, *A. glabra* is frequently found in the interface between freshwater swamps and saline environments, including mangrove margins. It often coexists with species such as *Avicennia germinans* (L.) L and *Laguncularia racemosa* (L.) C.F. Gaertn., tolerating moderate salinity without sacrificing reproductive capacity. Its buoyant fruits contribute to hydrochorous seed dispersal, enhancing colonization of saline floodplains and coastal depressions (Austin 2001). Iron chlorosis is frequently observed in upland settings due to reduced Fe^{2+} availability in

soils that are oxidized. However, the anaerobic conditions of saturated or brackish soils improve iron solubility and uptake, thereby indirectly favoring its performance in saline wetlands (Ojeda *et al.* 2004, Liu *et al.* 2016).

Ecological interactions. Epiphytes.- Several studies on epiphyte populations on *A. glabra* trees have been conducted on Barro Colorado Island, Panama. 47 epiphyte species were found on *A. glabra* trees both in 1994 and 2002. The most frequent families were Orchidaceae, with 25 species; Araceae, with 17; Bromeliaceae, with eight; and Polypodiaceae and Moraceae, each with seven. The most frequently recorded species were *Dimerandra emarginata* (G. Mey.) Hoehne, and *Caularthron bilamellatum* (Rchb. f.) R.E. Schult., *Tillandsia bulbosa* Hook., and *Niphidium crassifolium* (L.) Lellinger (Laube & Zotz 2007). In a later study, Einzmann *et al.* (2021) documented an ongoing increase in abundance and diversity at both the epiphyte metacommunity level on *Annona* trees and at the level of epiphyte communities growing on individual *A. glabra* tree stands.

Ghost orchid (*Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe) grows on swamp trees such as *Fraxinus caroliniana* Mill. and *A. glabra* in Florida, as well as on three additional species in Cuba. Mújica *et al.* (2018) reported 241 individuals in Cuba, with 30.3 % being seedlings, nearly twice the seedling percentage found in Florida (16.4 %). In Florida, its roots hosted a *Ceratobasidium* endophyte, suggesting that the orchid prefers moist, corrugated bark that supports this fungus, essential for seed germination.

Zotz & Vollrath (2002) tested the hypothesis that observed interspecific differences in the vertical distributions of three epiphyte species (bromeliads) are determined at a very early stage of ontogeny. They used *A. glabra* trees as a host species for substrates differing in orientation and relative position within the host's crown. No evidence of differential mortality across different substrate types was found for any of the three species, suggesting that spatial distribution patterns are determined even earlier, likely due to species differences in seed dispersal or germination.

Associated fauna and flora.- In Cuba, the Snakebird or Darter (*Anhinga anhinga anhinga* Linnaeus 1758) nested in El Venero, a shallow wetland dominated by *A. glabra* and *Conocarpus erectus* L. Antunez & Denis (2013) described nesting behavior and hatching success. The Cuban populations of the Common Black-Hawk (*Buteogallus anthracinus* Deppe 1830) were studied in the mangroves and semi-deciduous gallery forests, which are formed by the Cuban royal palm (*Roystonea regia* (Kunth) O.F. Cook), beach hibiscus (*Hibiscus tiliaceus* L.), and pond apple (*A. glabra*). Wiley & Garrido (2005) concluded that *Buteogallus anthracinus* was a full species endemic to Cuba, Isla de Pinos, and many of the cays of the Cuban Archipelago.

The Snail Kite (*Rostrhamus sociabilis* Vieillot 1817) is a raptor of conservation interest. Ferrer-Sánchez *et al.* (2018) investigated nesting activity in the Gran Humedal del Norte, in Ciego de Ávila, a Ramsar site in Cuba. All nests were built on living bushes of *A. glabra* that formed in emerging keys within the lagoons, with a water depth of 1.0-1.2 m adjacent to the nests. The Snail Kite is widely distributed in America. Still, changes to hydrological regimes caused by human activity and climate change endanger populations of freshwater snails (*Pomacea* spp.), which are a primary food source in their diet. Of the nests found, 67 % contained eggs and/or chicks; 40 % contained only eggs, 33 % contained only chicks, and 20 % contained both. In general, Snail Kites remain reproductively active the entire year and depend on the existence and abundance of food and adequate water levels in the lagoons.

In Southern Havana, in swamps dominated by *Roystonea regia* Britton, *Callophyllum antillanum* Britton, *Calyptrotrichia occidentalis* (Sw.) H.E. Moore, and *A. glabra*, the endangered fern *Maxonia apiifolia* (Sw.) C. Chr. was re-found. It is a hemiepiphyte fern native to Cuba and Jamaica, which was considered possibly extinct in Cuba (Rodríguez-Cala *et al.* 2018).

The sawgrass (*Cladium jamaicense* Crantz) forms extensive, largely monospecific stands within the coastal swamps of the Caribbean region. Imbert & Delbé (2006) assessed the floristic and structural changes that might occur within these marsh communities once the setting of fires has been discontinued. The discontinuation of the fire regime induced alterations in the vertical structure of the vegetation and changes in the marsh flora, promoting woody species over herbaceous species. Three groups of potentially colonizing woody species were defined. The first group consisted of either mangrove or swamp species, which were consistently found near the forest edges.

The second comprised flood- and salt-tolerant species, widespread over the marshes and present either in the swamp forest (*A. glabra*, *Ficus citrifolia* Mill.) or in the mangrove forest (*L. racemosa*). The third group consisted of upland, light-demanding, pioneer species. Thus, slow but significant forest recovery occurs when fire setting has been discontinued.

Herbivory. Infante-Mata (2004) and Infante-Mata *et al.* (2019) assessed *in situ* impacts of herbivory by Lepidoptera larvae on the seedling growth responses of two swamp tree species, *A. glabra* and *P. aquatica*, at La Mancha-CICOLMA. Seedling survival and growth were analyzed in the presence/absence of herbivory and under two levels of soil saturation. Seedlings of *A. glabra* and *P. aquatica* showed unique responses. *A. glabra* was heavily attacked by herbivores, and its growth rate was severely limited (0.017 ± 0.003 g/d) compared with that of plants that were isolated from herbivores (0.032 ± 0.004 g/d). Leaf area and total dry weight of *A. glabra* seedlings declined in response to herbivory. *P. aquatica* seedlings also exhibited lower leaf area in response to herbivory, but their dry weight was unaffected (Figure 11). The herbivory treatment revealed that the seedlings of *A. glabra* were highly susceptible, while those of *P. aquatica* experienced minimal damage from herbivores.

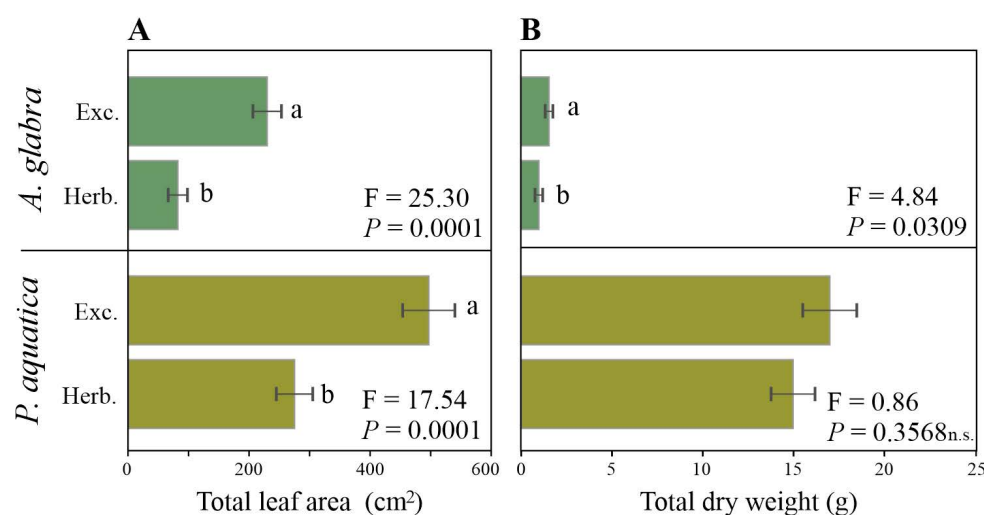


Figure 11. Seedling response of *Annona glabra* and *Pachira aquatica* when exposed to herbivory *in situ* in the swamps of La Mancha-CICOLMA. Different letters indicate significant differences between treatments (N=80). A) The leaf area of seedlings under excluded conditions (Exc.) and herbivory (Herb.). B) Total dry weight of seedlings under these two conditions. Data taken from Infante-Mata (2004).

Martin *et al.* (2011) analyzed the effects of feeding on leaves by adult root weevil (*Diaprepes abbreviatus* Linnaeus, 1758, Coleoptera: Curculionidae). Flooding on leaf gas exchange [net CO₂ assimilation (*A*), transpiration (*E*), and stomatal conductance (*g_s*)], plant growth (stem diameter, root, stem, leaf, and total plant dry weights, and plant height) and adult host plant preference (feeding damage and oviposition) were determined on *A. glabra*, trees using outdoor screen cages. For pond apple, *A* of infested trees were minimally affected by flooding, except after five weeks. Flooding reduced root dry weight, but it was the only growth variable that differed significantly between treatments. Despite the good flood tolerance of the species, the lack of sufficient time for morphological plant adaptations to flooding (i.e., increased stem aerenchyma tissue and enlarged and adventitious roots; Núñez-Elisea *et al.* 1998) to develop during the relatively short flooding period in this study may have resulted in reduced root weights of flooded *A. glabra* trees. There was no significant interaction between flooding and insect infestation, except for the variable *A*. No significant differences were found between infested and non-infested plants in terms of leaf gas exchange or growth variables. There were no significant differences in feeding damage or number of egg clusters between non-flooded and flooded trees; mean rates of leaf damage were low (3.6 ± 2.0 %). Hence, the conclusion is

that *A. glabra* was not a favorable host for this Coleoptera type in the present study. Trees can support root weevil larval development, but do not seem to attract adults nor serve as suitable feeding or oviposition sites.

Propagation and uses. Propagation methods.- *Annona glabra* can be propagated by both sexual and asexual means, with each method offering distinct advantages for conservation, horticulture, and restoration purposes. While sexual propagation is more common and straightforward, there have been advances in vegetative techniques. Options for producing genetically uniform or stress-tolerant plants under variable environmental conditions have increased.

Seed propagation is the most widely used method, with seeds classified as recalcitrant, exhibiting high germination rates (up to 88 %) after three months of flotation (Infante-Mata & Moreno-Casasola 2005, Setter *et al.* 2008). Seeds do not exhibit dormancy and germinate within 10-20 days under suitable conditions (Ferreira *et al.* 2019). Under nursery conditions, seedlings respond well to slow-release fertilizers (Gettys & Sutton 1999).

Vegetative propagation through grafting is a widely used technique for maintaining desirable genotypes. *Annona glabra* serves as a compatible rootstock for economically significant *Annona* species, particularly *Annona muricata* L. and *Annona reticulata* L., in flooded or saline soils, often providing dwarfing effects useful in orchard systems (de Carvalho *et al.* 2001). Cutting propagation shows moderate success with rooting rates up to 94 % during summer using semi-hardwood cuttings and indolebutyric acid (IBA) treatment, though success declines significantly in colder months (Scaloppi Junior & Martins 2003).

Traditional and potential uses. Plants have been used in traditional medicine by numerous societies. They are the natural sources of bioactive compounds used to treat various life-threatening diseases. *Annona glabra* possesses various phytochemicals (Kusmardiyani *et al.* 2020) in the fruits and stems (Chang *et al.* 1998 2000, Chen *et al.* 2004), leaves (Liu *et al.* 1998 a, b, Lee *et al.* 2015), and seeds (Wu *et al.* 2012). It can be used to treat various diseases (Kusmardiyani *et al.* 2020, D'Elia Oliveira *et al.* 2022, Sinchana *et al.* 2024). Among the numerous active compounds found in this species are mainly flavonoids, glycosides, saponins, tannins, steroids, acidic compounds, and anthraquinones. Recently, a novel class of bioactive compounds, known as annonaceous acetogenins, has garnered significant interest (Sinchana *et al.* 2024).

Numerous research papers have examined the pharmacological properties of traditional uses, including anti-leishmanial activity, antimicrobial activity, anticancer activity, anti-inflammatory activity, burn-healing properties, larvicidal efficacy, and antioxidant activity. Sinchana *et al.* (2024) describe several pharmacological activities:

a) Anti-leishmanial activity. Leishmaniasis is a tropical and neglected disease caused by the protozoan parasites of the genus *Leishmania*. Alkaloids are substances that exhibit leishmanicidal activity in *A. glabra* (Araujo *et al.* 2021).

b) Anti-cancer activity. Leaf extracts have been shown to inhibit the proliferation of human leukemia cells (Cochrane *et al.* 2008, Liu *et al.* 2016). Annoglacins A and B suppressed the proliferation of pancreatic carcinoma and human breast cell lines. These acetogenin fractions were isolated from leaves. On the other hand, the seed extract induces necrosis and apoptosis in both sensitive and resistant leukemia cells (Zhang *et al.* 2004). It has long been used in traditional medicine as an anti-cancer agent.

c) Anti-inflammatory activity. The acetone extract of the leaves showed therapeutic value in treating the inflammatory phase of cancer (Siebra *et al.* 2009, Sophiya *et al.* 2020).

d) Anti-microbial activity. Experimental results revealed that the antimicrobial potency of the extract exhibits superior antimicrobial efficacy compared to conventional antibiotics against different strains of *Pseudomonas aeruginosa* Schroeter 1872, *Escherichia coli* Migula 1895, *Staphylococcus aureus* Rosenbach 1884, *Aspergillus niger* van Tieghem 1867, and *Candida albicans* (C.P. Robin, 1853) Berkhout 1923 (Sivangnanam & Krishna Rao 2016, Mokhtar *et al.* 2022, Khalaf *et al.* 2023). *Pseudomonas aeruginosa* is an important pathogen in opportunistic infections in humans. *Annona glabra*-derived compounds, particularly flavonoids, may help treat infections caused by this pathogen (Galvão *et al.* 2016, Mokhtar *et al.* 2022).

e) Burn healing properties. The alginate films impregnated with the leaf extract exhibited wound-healing activity, enhancing the rate of wound contraction (Le Son & Tram 2013).

f) Larvicidal efficacy. In recent mosquito control programs, larvicides have been the primary tool. Larvicidal bioassays using leaf extracts revealed that *Aedes albopictus* (Skuse 1894) is more susceptible than *Aedes aegypti* Linnaeus 1762, but it was an effective larvicide against both species. Amarasinghe *et al.* (2020) consider it a potent larvicide for controlling the dengue vector. Ethanol stem bark extract also exhibited a larvicidal effect on both dengue mosquito larvae (Thang *et al.* 2012, Sinchana *et al.* 2024).

g) Fungicide efficacy. *Fusarium* species are the cause of diseases in various crops worldwide, resulting in significant economic losses. Seed extracts can be a potential source of metabolites with fungicidal activity and have proven to be an alternative control for *Fusarium solani* (Martius) Saccardo 1881 (Martínez *et al.* 2024).

h) Insecticidal efficacy. It has been found to have an effect on wood protection against termites. Seed extract was toxic to dry-wood termites (*Cryptotermes cynocephalus* Light 1921) and to subterranean termites (*Coptotermes curvignathus* Holmgren 1913) (Priadi *et al.* 2021). Seeds and leaves are insecticidal; leaves placed in hen nests kill lice on the fowl. The crushed seed was cooked with coconut oil and applied to remove head lice in the past (Thang *et al.* 2012).

A beneficial fiber is obtained from the bark. It is sometimes used locally. It has also been reported as animal food and as a poison (Plants of the World Online 2025b).

It has been used in traditional medicine to treat various ailments, including fever, constipation, ulcers, tumors, and cancer. The leaves and young stems, sometimes combined with those of *Passiflora foetida* L., are boiled to make a tea used to repel worms and nematodes. The bark and leaves, combined with the bark and leaves of *A. squamosa*, are used as sedatives and cardiogenic infusions.

In Mexico, Aguilar-Contreras & Xolalpa-Molina (2002) recorded the use of roots to control diabetes. It has been recorded that it is most commonly used to treat dysentery, particularly in Quintana Roo. They administer the burned root or the juice of the leaves to the patient, and small leaves are also placed on the patient's stomach. In cases of diabetes, the underground parts are prepared as an infusion and administered orally. As an antidiarrheal, the leaves are ground along with other unspecified plants, boiled, and then infused into tea. The buds can be crushed and toasted for the same purpose and then infused into tea. It is also used for blood clots, hemorrhage in women, scalds, sores, or blisters in the mouth, and hiccups (Biblioteca Digital de la Medicina Tradicional Mexicana 2025).

Thang *et al.* (2012) consider it a kind of survival food. It is edible and can be made into jam. In the Maldives, it is a popular ingredient in fresh fruit drinks. The fruit was a vital food source for early Native Americans and settlers. Ripened *A. glabra* fruits contain ample phenolic constituents and served as a promising source of carbohydrates that could be converted into a type of fruit wine, one that possessed a pleasant alcoholic flavor and attractive appearance (Minh 2022). Thus, wine production could be developed. Flavor compounds have been isolated by Bicas *et al.* (2011).

The wood of *A. glabra* is used to make bottle caps, oars, and as a substitute for cork in fishing nets. The wood is used for fuel (Zotz *et al.* 1997). The roots are pretty long and thick, numerous, very light in weight, and spongy. They can be used as a substitute for corks in various applications, such as lifesavers, buoys on nets, shoe insoles, and knife sharpeners (Correa 1926, Thang *et al.* 2012). Stems were used by the Seminoles in Florida to make bows (Bennett 1997).

Annona muricata grafted on *A. glabra* rootstock receives a dwarfing effect (Thang *et al.* 2012). It is used for seedling rootstocks and can serve as an excellent source of nutrients or fulfill the cultural needs of a good rootstock (Longar-Blanco *et al.* 2004). Seedlings are helpful as a rootstock for other *Annona* species in wet soils. (Mansfeld's World Database of Agricultural and Horticultural Crops 2025).

Conservation in the face of climate change. Due to its wide distribution across tropical and subtropical America, with an estimated extent of occurrence of 22,854,895 km² and an area of occupancy of 3,320 km², *A. glabra* is classified as Least Concern by the IUCN (Verspagen & Erkens 2020). However, at the regional scale along the Gulf of Mexico coast, freshwater swamps dominated by *A. glabra* have declined dramatically, primarily due to the expansion of livestock (Sánchez-García 2020). These swamps, characterized by organic, fertile soils and short annual flooding

periods, are frequently cleared for timber and converted into cattle pastures with the introduction of exotic grasses (Infante-Mata 2011, Moreno-Casasola *et al.* 2012, 2018). Consequently, they have nearly disappeared, leaving only flooded pastures with scattered remnant trees (Moreno-Casasola & Infante-Mata 2010, Infante-Mata 2011).

In addition, climate change could jeopardize the remaining populations of *A. glabra* and disrupt the structure and functioning of floodplain forests. In the Gulf of Mexico, one of the primary projected impacts is an increase in the intensity and frequency of hurricanes (Radfar *et al.* 2024). Hurricanes have been documented to topple dominant trees in freshwater swamps, such as *P. aquatica* (Vázquez-Benavides 2019), leading to gap formation and grass encroachment, which hinder seedling establishment. Altered rainfall patterns and rising temperatures (Biasutti *et al.* 2012) may modify the hydroperiod of these swamps, disrupting key ecological processes such as seed dispersal, germination, and seedling recruitment. Perhaps, the most critical climate-related threat to these ecosystems is sea-level rise (Sánchez-García *et al.* 2023b), which can trigger freshwater wetland salinization and prolonged hydroperiods. Greenhouse experiments demonstrate that salinity severely reduces *A. glabra* seedling survival, with observed mortality at concentrations as low as 5 ppt and 15 ppt (Sánchez-García *et al.* 2022a). Increased salinity and permanent flooding also suppress growth, leaf production, and biomass accumulation (Sánchez-García *et al.* 2022a). These findings underscore the heightened vulnerability of *A. glabra* during early life stages to sea-level rise. Adult individuals are similarly susceptible: sustained salinity levels of 31.87 ppt can have negative repercussions and even lead to mortality (López-Rosas *et al.* 2023). Further research is needed in several ecological and physiological aspects of the different life stages of *A. glabra*.

Behavior as an invader.—*Annona glabra* is considered a highly invasive woody species that threatens wetland and riparian ecosystems of tropical regions in Australia and parts of Asia, and is regarded as one of the worst invaders of the wet tropics. In Australia, where it is considered a pest, it was introduced in 1912 as a grafting stock for custard apple. Its tolerance of salt and flooding in fresh water enables it to invade Melaleuca (*Melaleuca* spp.) wetlands, forming a dense understory that prevents young native Melaleucas from establishing and developing (Global Invasive Species Database 2025). Dense monotypic stands that displace native vegetation have formed in north Queensland, Australia (PIER 2003). Despite its restoration potential, the species is invasive in Australia, affecting native wetlands, underscoring the need for biogeographic contextualization.

Mechanical and chemical control measures can be effective, but control is very site-specific. Fire helps control trees and seeds, as they are readily destroyed by fire. Pulling and dozing have also been successful, mainly in ditches and drainages. There are no chemicals registered for its control (Global Invasive Species Database 2025).

Ecological restoration strategies. Globally, wetlands have lost approximately 50 % of their original coverage, with even higher losses in countries such as the United States, Australia, China, and New Zealand (Mitsch & Gosselink 2015). In Mexico, wetland loss reaches 62 %, while in the states along the Gulf of Mexico, this figure stands at approximately 58 % (Landgrave & Moreno-Casasola 2012). Livestock farming development has been the primary driver of degradation in the region's freshwater swamps (Moreno-Casasola *et al.* 2018). This leads to ecosystem destruction, the spread of exotic grasses (often of African origin), and livestock encroachment (López-Rosas *et al.* 2019). This situation underscores the pressing need for ecological restoration studies and projects that focus on *A. glabra*-dominated freshwater swamps.

Although the principles of ecological restoration in wetlands and terrestrial ecosystems are similar, wetland restoration involves more complex environmental and social dynamics, particularly due to hydrological considerations (Zedler 2000). Restoring these ecosystems is critical not only for their ecological and biological significance but also for the economic value of their ecosystem services (Costanza *et al.* 1997, Vázquez-González *et al.* 2019). However, ecological restoration studies in wetlands remain scarce and are often limited to short-term assessments (Zedler 2000, López-Barrera *et al.* 2017).

On the central Gulf of Mexico coast, pilot ecological restoration experiments have been conducted in degraded *A. glabra*-dominated freshwater swamps converted to flooded pastures and invaded by the African grass *Echinochloa*

pyramidalis (Lam.) Hitchc. & Chase, called Antelope grass. Sánchez-García *et al.* (2023a) found high restoration potential when adult tree remnants persist, ensuring continuous seed production. Notably, *E. pyramidalis* does not inhibit *A. glabra* seed germination: experiments even showed higher germination rates in grass-present treatments where it provides shade and possibly conserves soil humidity (Sánchez-García *et al.* 2023a). However, exotic grasses like *E. pyramidalis* may hinder seedling establishment through competition. Exotic grasses can have a negative impact on the survival and growth of tree seedlings (Williams-Linera *et al.* 2015). Specifically, *E. pyramidalis* forms a dense organic mat, up to 10 cm thick (López-Rosas *et al.* 2019), which could be a barrier to the establishment of *A. glabra* seedlings (Sánchez-García *et al.* 2023a) as shown for *P. aquatica* seedlings. In another study, Sánchez-García *et al.* (2022b) observed that the greatest success in the survival and height growth of *A. glabra* saplings occurs using elevated mounds in wetlands as ground-level elevation restoration techniques. These findings align with research from the Florida Everglades, where elevated soil conditions similarly promoted the highest survival of *A. glabra* seedlings (van der Valk *et al.* 2008). Saplings collected directly from freshwater swamps near the degraded site showed higher survival rates, and the cost of these plants was lower compared to nursery-grown seedlings (Sánchez-García *et al.* 2022b). The cost per hectare of applying the soil elevation restoration technique, including planting wild *A. glabra* saplings, was estimated at \$3,782 USD/2020 (\$1 USD = \$19.24 MXN). Therefore, evaluating ecological processes such as seed germination and seedling establishment is essential for environmental restoration projects. Despite these advances, critical knowledge gaps persist, particularly regarding the compounded pressures from climate change and sea-level rise, which are yet to be integrated into restoration projects for *A. glabra* ecosystems.

Discussion

This research demonstrates that *Annona glabra* represents a fundamental ecological component in tropical wetlands, particularly in freshwater swamps where it can form monodominant stands or exist as part of diverse tree communities. Its ability to tolerate extreme flooding conditions and moderate salinity positions make it a keystone species for ecosystem resilience in the face of climate change.

The productivity data obtained from La Mancha-Diada (12.4 t/ha/year) are comparable to those reported for other tropical forested wetlands and rival the productivity of mangroves (Cejudo *et al.* 2022). This high productivity, combined with documented decomposition rates (89 % in 390 days), indicates that *A. glabra*-dominated swamps play a crucial role in nutrient cycling and carbon sequestration in coastal ecosystems.

The documented morphological and physiological adaptations, including aerenchyma development, adventitious roots, and hypertrophied lenticels, explain the species' remarkable tolerance to prolonged flooding. However, our findings on seedling vulnerability to salinities as low as 5 ppt suggest that sea-level rise represents a significant threat to natural regeneration of these ecosystems.

The ethnopharmacological potential of *A. glabra*, supported by the identification of annonaceous acetogenins and other bioactive compounds, underscores the importance of conserving these populations as reservoirs of chemical diversity. The documented antimicrobial, anti-inflammatory, and larvicidal properties have particular relevance in the context of emerging diseases and vector control.

The ecological paradox of *A. glabra* -a keystone species in its native habitat but invasive in Australia- highlights the importance of biogeographic context in management strategies. This duality requires differentiated approaches that promote its conservation in the Neotropics while controlling its expansion in non-native ecosystems.

Ecological restoration experiments in Veracruz demonstrate that recovery of degraded swamps is viable when remnant adult trees persist. The soil elevation technique, with an estimated cost of \$3,782 USD/ha/2020, offers a cost-effective strategy for restoration. However, competition with exotic grasses such as *Echinochloa pyramidalis* remains a significant challenge.

Key research gaps include population dynamics, pollination, long-term demography, interactions with fauna, and roles in carbon and nutrient cycles. Standardized monitoring and integrative studies are necessary to assess the ecosystem services and resilience of this system under sea-level rise.

Despite the limited studies on *A. glabra*, this work highlights its ecological and cultural significance in Mexico. Its functional traits, productivity, and restoration potential justify its inclusion in conservation and restoration agendas. Given its vulnerability to salinity and flooding extremes, it is an indicator species for wetland integrity under climate change. Therefore, the main conclusions are as follows:

Annona glabra functions as a “freshwater mangrove” with unique adaptations that allow it to dominate wetlands subject to prolonged flooding and moderate salinity, playing fundamental ecological roles in productivity and nutrient cycling.

The species exhibits significant potential for ecological restoration of degraded wetlands, though it requires careful management due to its invasive behavior in non-native regions.

Climate change, particularly sea-level rise and resulting salinization, poses the most critical threat to *A. glabra* populations, with a significant impact on early life stages.

The wealth of identified bioactive compounds justifies the conservation of *A. glabra* not only for its ecological value, but also for its pharmacological and ethnobotanical potential.

Knowledge gaps regarding population dynamics, ecological interactions, and responses to climate change require urgent research to develop effective conservation strategies.

The integration of traditional knowledge, ecological research, and restoration techniques presents a promising framework for conserving *A. glabra*-dominated swamps in the Gulf of Mexico.

Perspectives and further necessary studies

This review highlights the ecological importance and restoration potential of *Annona glabra*, while also underscoring the need for critical knowledge that demands immediate research. Priorities extend across disciplines, from understanding its molecular traits to designing management strategies at the ecosystem scale. Long-term demographic studies, climate change vulnerability assessments, and improved restoration techniques are identified as key areas where evidence is urgently needed. These efforts must not only track population trajectories and resilience but also explore physiological limits and practical restoration methodologies.

Equally pressing are studies on pollination ecology, seed dispersal, and physiological adaptations. While beetle pollination and hydrochory are known, detailed analyses of pollinator networks, dispersal distances, and genetic connectivity are lacking. Investigations into *A. glabra*'s flood tolerance (such as root adaptations and hormonal regulation) could have wider applications for breeding programs in flood-prone environments. Alongside these ecological insights, applied research should quantify ecosystem services, test the pharmacological potential of bioactive compounds, and address the paradox of the species functioning as a keystone in its native range yet acting invasively elsewhere.

Technological advances and broader collaboration are essential to move this agenda forward. Remote sensing, genomics, and citizen science provide opportunities to expand monitoring and conservation capacity. At the same time, adaptive management frameworks and enhanced policy analysis can facilitate the translation of research into practical applications. International comparative studies are particularly valuable given the species' wide distribution and transboundary threats. The urgency is clear: with freshwater forested wetlands vanishing rapidly and climate pressures intensifying, scientific knowledge must advance in parallel with conservation action to ensure *A. glabra* continues to sustain ecosystems and communities in the future.

Acknowledgements

We thank R. Monroy Ibarra for his support in designing the figures and maps C. Madero-Vega for the field experiments on leaf litter degradation, and J.R. Torres Velázquez for his collaboration analyzing *A. glabra* litter degradation. The authors express their gratitude to the reviewers and editor who revised the manuscript and whose comments and suggestions helped improve it.

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Associate editor: Andrés Ernesto Ortiz Rodríguez

Author contributions: EASG, Conceptualization, Literature review, Validation, Writing - original draft, Writing - review and editing; HLR, Conceptualization, Literature review, Fieldwork, Validation, Writing - original draft, Writing - review and editing; DIM Conceptualization, Literature review, Validation, Writing - original draft, Writing - review and editing; PMC Conceptualization, Literature review, Validation, Writing - original draft, Writing - review and editing.

Supporting agencies: Instituto de Ecología AC, International Tropical Timber Organization, and scholarships provided by SECIHTI and WWF (Russell E. Train scholarship).

Conflict of interests: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data, and results of this article.