

STUDIES ON THE SEED GERMINATION OF ANNONACEAE SPECIES FROM MEXICO: A SYSTEMATIC REVIEW

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Abstract

Annonaceae is a family of approximately 2,430 species of angiosperms, about 70 of which contribute to the diversity of Mexico's tropical forests. Some species produce pleasant fruits, others generate essences used in perfumery or food flavoring, and others biosynthesize secondary metabolites of pharmaceutical and agronomic interest. However, information on seed germination in these species is still scarce. Several species produce dormant seeds as a protective mechanism for the perpetuation of the species. This review highlights the state-of-the-art, with emphasis on seed formation and the dormancy and germination mechanisms of Annonaceae species from Mexico. Systematic research was conducted in Scielo, Web of Science, Scopus, PubMed, and Embase databases. The PRISMA strategy was used with keywords related to seed formation, germination and dormancy of Annonaceae species from Mexico combined by Boolean operators. The search yielded 1,185 articles, of which 59 provided relevant information and were included in this review, which identified studies involving seeds of 15 species. The most investigated species are from the genus *Annona*. The research includes the mechanisms involved in seed formation, germination process, and the establishment and overcoming of dormancy. Factors such as hormonal balance, temperature, and light are considered. The main prospects for further studies lie in expanding the number of species to be studied, from seed formation, establishment and classification of dormancy to methods for overcoming dormancy, as well as the ecophysiology of germination, in order to assist in agronomics projects involving seedling production and ensuring the conservation and biodiversity of Mexican Annonaceae.

Keywords: *Annona*, *Cymbopetalum*, *Desmopsis*, Dormancy, *Oxandra*, *Stenanona*

Resumen

Annonaceae es una familia con aproximadamente 2,430 especies de angiospermas, ~ 70 de ellas contribuyen a la diversidad de bosques y selvas de México. Algunas especies tienen frutos agradables, otras generan esencias utilizadas en perfumería o en la aromatización de alimentos y otras biosintetizan metabolitos secundarios de interés farmacéutico y agronómico. Sin embargo, la información sobre la germinación de las semillas de estas especies es escasa. Varias anonáceas producen semillas con dormancia como un mecanismo de protección para la perpetuación de la especie. Esta revisión se realizó con búsquedas sistemáticas en las bases de datos Scielo, Web of Science, Scopus, PubMed y Embase mediante la estrategia PRISMA con palabras clave relacionadas con la formación, latencia y germinación y de semillas de anonáceas de México. La búsqueda arrojó 1,185 artículos, de ellos 59 proporcionaron información relevante para la elaboración de este escrito. Se identificaron estudios en semillas de 15 especies, las más investigadas pertenecen al género *Annona*. Se discuten los mecanismos involucrados en la formación de semillas, el proceso de germinación y el establecimiento y el rompimiento de la latencia considerando factores como el equilibrio hormonal, la temperatura y la luz. Las perspectivas radican en ampliar el número de especies para conocer los aspectos de la formación de semillas, el establecimiento, la clasificación y métodos para superar la latencia; así como la ecofisiología de la germinación, con el fin de coadyuvar en la producción de plántulas para proyectos agronómicos y para la conservación de la biodiversidad de las anonáceas mexicanas.

Palabras clave: *Annona*, *Cymbopetalum*, *Desmopsis*, Latencia, *Oxandra*, *Stenanona*

The Annonaceae family is one of the oldest angiosperms, with history dating back approximately 112 million years (Pirie & Doyle 2012). It has pantropical distribution and includes approximately 106 genera and 2,430 species (Chatrou *et al.* 2018), significantly contributing to forest diversity, both due to its abundance and its phenological characteristics that allow the survival of other organisms (Gottsberger 2014, González-Esquinca *et al.* 2016). Furthermore, they biosynthesize bioactive molecules of interest to the pharmaceutical and agrochemical industries (Lúcio *et al.* 2015, Lima *et al.* 2022, Durán-Ruiz *et al.* 2024), and some species produce edible fruits of high nutritional and organoleptic quality (Anaya-Esparza *et al.* 2020).

Knowledge of the seed propagation strategies of the Annonaceae family is important as a way to ensure the perpetuation of species and due to its economic importance for the production of seedlings of commercial species. Some species produce seeds that germinate soon after dispersal, if the basic germination requirements are met (Ferreira *et al.* 2019). Other species, however, have seeds that exhibit dormancy (González-Esquinca *et al.* 2015, Ferreira *et al.* 2016), which is the inability of viable seeds to germinate within a specific period of time under ideal environmental conditions (Bewley *et al.* 2013a, Baskin & Baskin 2014). Reports of dormancy in the family mainly involve morphological and physiological characteristics of the embryo, with some factors related to the seed coat (Ferreira *et al.* 2019, Vidal-Lezama *et al.* 2024).

Based on the above, this review aims to present an overview of the seeds of Annonaceae species from Mexico, in order to obtain a study state-of-the-art. The analysis includes the mechanisms involved in seed formation, dormancy establishment and overcoming, and germination. Factors such as hormonal balance, temperature, and light are considered, as they are important for ensuring germination and the establishment of new plants in the environment. This knowledge may be valuable in strategies for maintaining diversity and perpetuation of the family, and in addition to being a compilation of advances, this review also aims to indicate perspectives for further studies.

Material and methods

The study considered Annonaceae species from Mexico presented in the list by De-la-Cruz-Chacón *et al.* (2016) and Villaseñor (2016). This review was conducted using a database search strategy, where articles and data retrieved were submitted to inclusion and exclusion criteria according to the study objectives (adapted from Chan *et al.* 2020, Kazman *et al.* 2020, Cascaes *et al.* 2021).

Search strategy. Two systematic searches were conducted in the Scielo, Web of Science, Scopus, PubMed, and Embase databases. Both strategies searched for articles published up to December 2024, using keywords (Spanish, Portuguese, and English) combined with Boolean operators. The first search strategy focused on keywords related to seed germination and dormancy of seeds of Annonaceae species from Mexico, resulting in 78 articles in Scielo, 296 articles in Web of Science, 332 articles in Scopus, 43 articles in PubMed, and 46 articles in Embase databases. The second search strategy focused on keywords related to the structure and formation of seeds of Annonaceae species from Mexico, resulting in 35 articles in Scielo, 21 in Web of Science, 17 in Scopus, and 317 in Embase databases.

After the initial search, the results were filtered, and the study selection process was meticulously outlined according to the PRISMA flowchart (Figure 1). Duplicate articles, those not involving Annonaceae species from Mexico, and those lacking data related to seed formation, dormancy, and germination were excluded.

Inclusion and exclusion criteria. Studies mentioning seed formation, germination, and dormancy of seeds of Annonaceae species from Mexico were included in this review, while those that did not meet the aforementioned criteria were excluded.

Data extracted from studies. Data extracted from studies included seed structure and formation, seed dormancy, seed germination of Annonaceae species from Mexico, as well as author and year of publication.

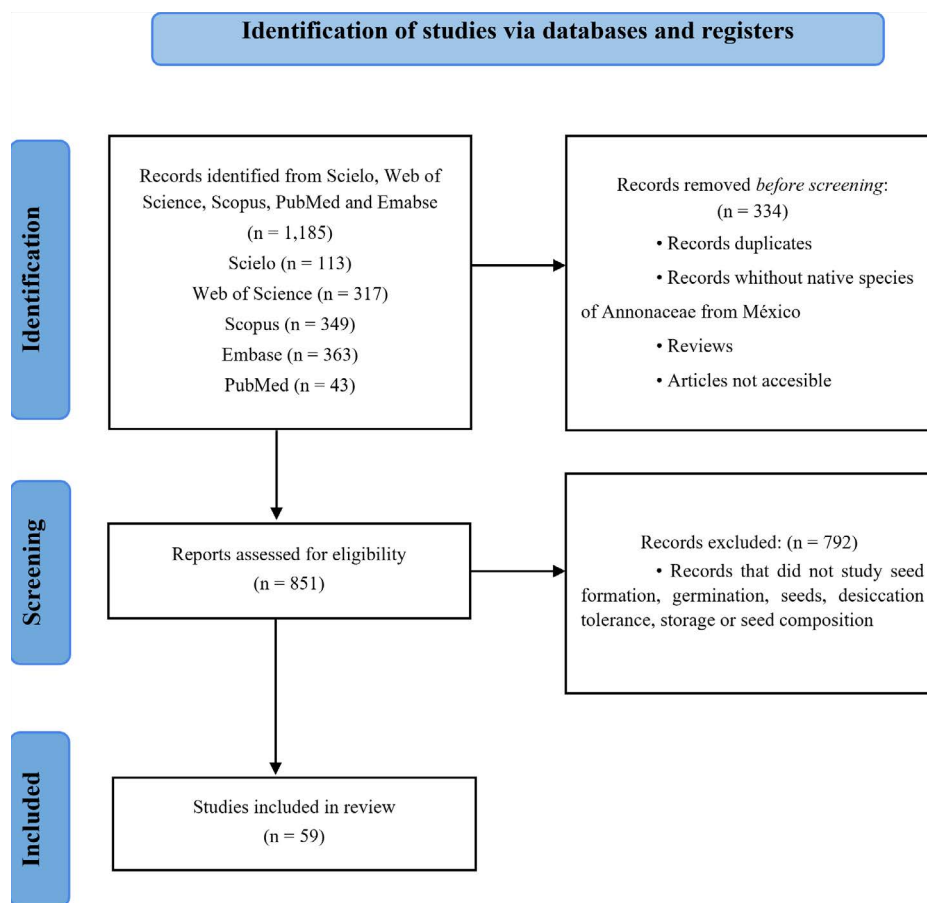


Figure 1. PRISMA Flow diagram of the systematic review, encompassing the two search strategies used for Annonaceae species from Mexico (Page & McKenzie 2021).

Results and discussion

The studies included (59) in this review were conducted in 10 countries, with Mexico, Brazil, and Spain standing out, with 20, 18, and 9 studies, respectively. Other countries with more than one publication include Colombia and India, with 4 and 3 studies. Austria, Cuba, Ecuador, the Philippines, and Indonesia had only one publication each. These data highlight the predominance (93 % of studies) of Latin American countries in the production of research focused on seeds of the Annonaceae family (Figure 2).

Among the fifty-nine articles included in this review, studies involving seeds of only fifteen species were identified, out of a total of 70 species. The most investigated species were *Annona squamosa*, with 22 %, followed by *Annona cherimola*, with 20 %, and *Annona mucosa*, with 10 % (Figure 3).

Among the topics covered in the review, 29 (49 %) studies specifically address seed formation, ranging from floral biology to seed coat, 18 (31 %) focus on germination, and 3 (5 %) on dormancy. Furthermore, 9 (15 %) articles were classified as multithematic, as they simultaneously address more than one topic.

Among studies, the following overlap was observed: eight studies addressed germination and dormancy, and one associated dormancy with aspects related to seed structure and formation.

Thirty articles addressed the seed formation and structure of Annonaceae species from Mexico, taking this overlap into account. Of the species under study, 25 belong to the genus *Annona*, two to the genus *Cymbopetalum*, one to the genus *Desmopsis*, one to the genus *Oxandra*, and one to the genus *Stenanona*. *Annona cherimola* stands out, accounting for 31 % of studies (Figure 4).

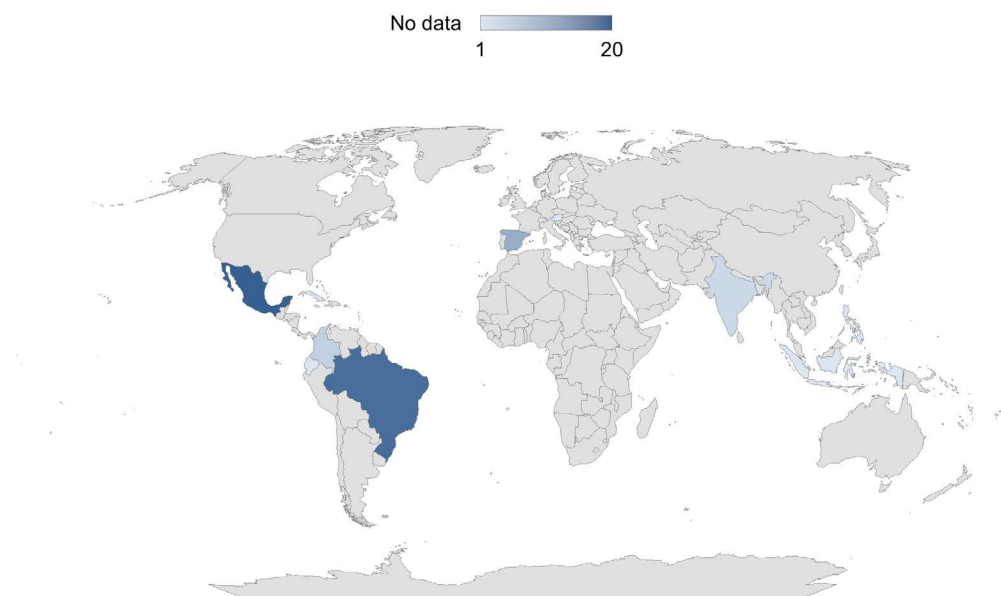


Figure 2. Distribution of studies conducted on seeds of Annonaceae species from Mexico.

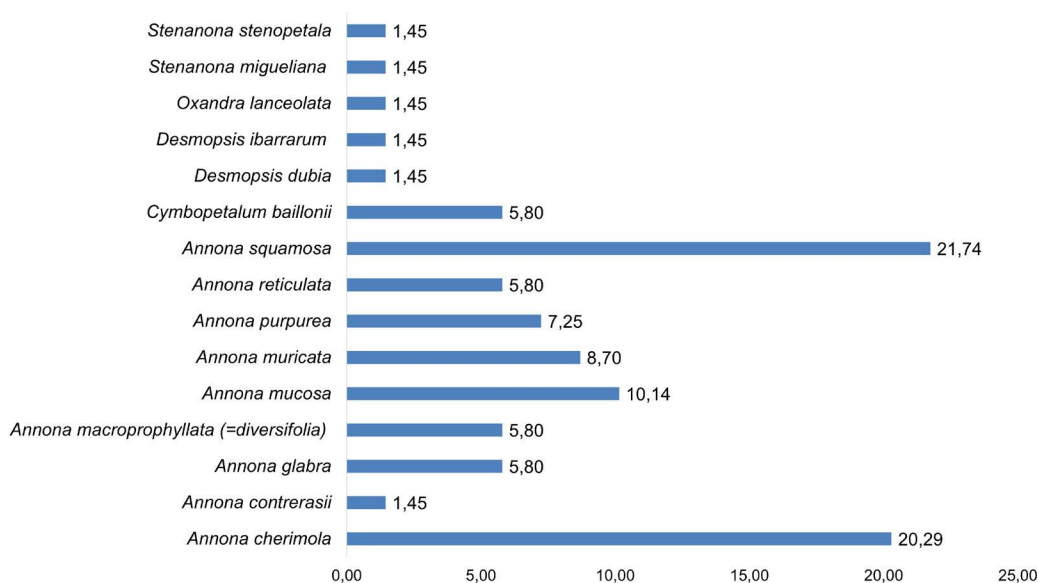


Figure 3. Percentage of studies that address the germination of Annonaceae species from Mexico, identified in the systematic review.

Six species were studied in articles addressing dormancy, distributed across 12 articles. *A. purpurea* was the most investigated, representing 27 % of articles, followed by *A. macrophyllata* (syn. *Annona diversifolia*), *A. mucosa*, and *A. squamosa*, with 20 % of articles each. *A. cherimola* and *A. muricata* accounted for 6 % and 7 %, respectively.

A total of 25 articles addressed the germination process of Annonaceae species from Mexico. Eight belong to the genus *Annona* and one to the genus *Cymbopetalum*, with *Annona squamosa* standing out, accounting for 25 % of articles ([Figure 5](#)).

The results and discussion of each topic are presented below, including topics such as seed formation and methods for overcoming dormancy used to enhance the germination process.

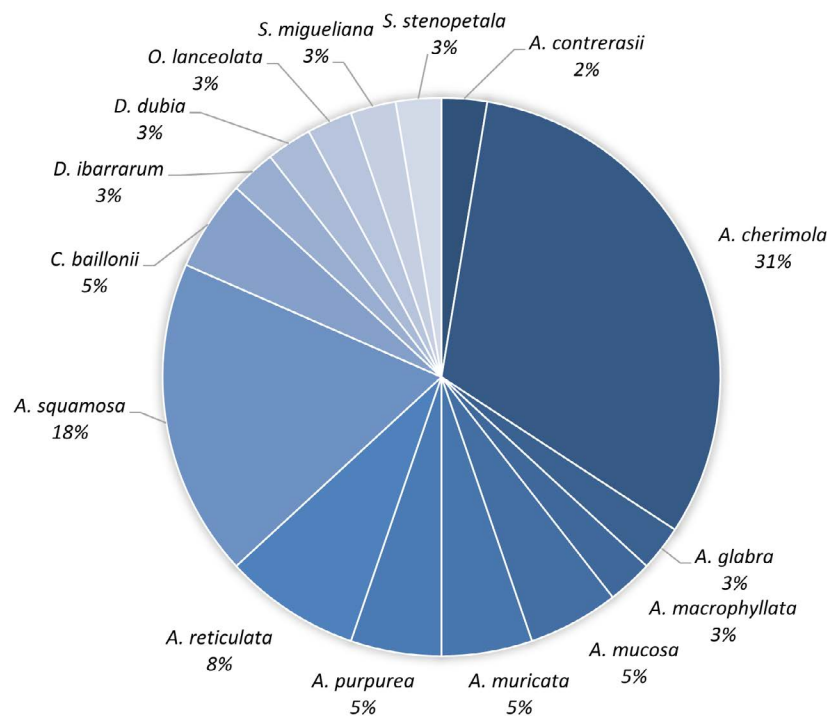


Figure 4. Percentage distribution of the most studied Annonaceae species from Mexico regarding seed structure and formation.

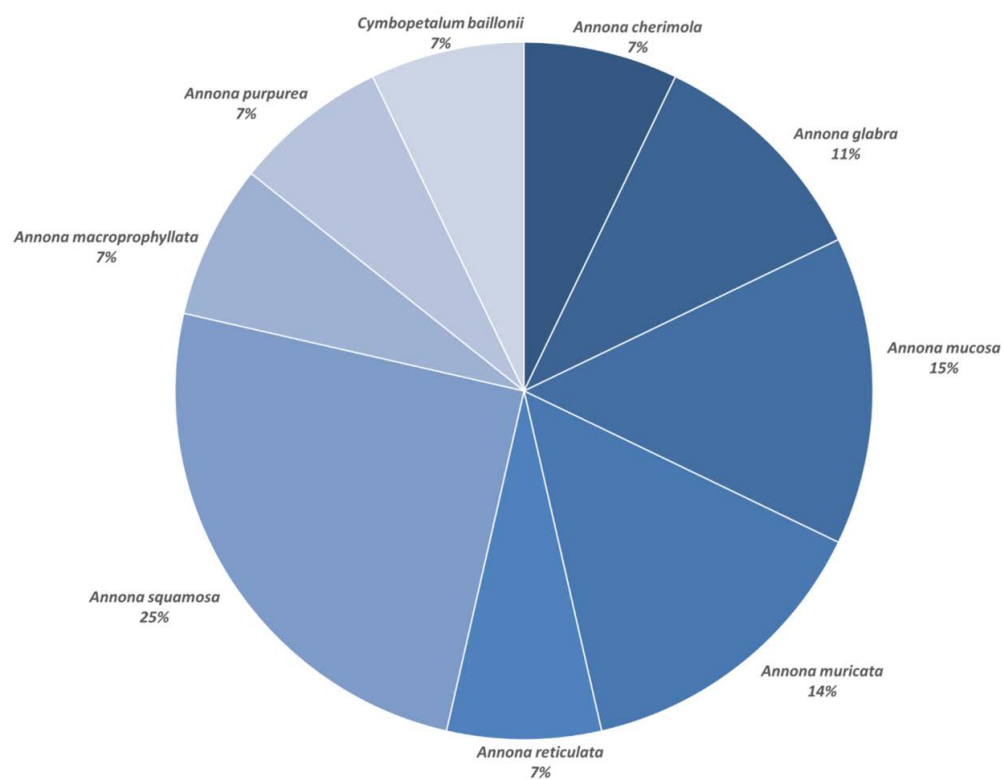


Figure 5. Percentage of species evaluated in articles on the germination process of Annonaceae species from Mexico.

Seed formation. Seed formation in angiosperms is a complex process that begins with ovule fertilization, an event intrinsically linked to floral biology. A widely observed characteristic among Annonaceae is the presence of protogynous dichogamy, a mechanism in which the gynoecium matures before the androecium. This reproductive strategy is crucial to reduce self-fertilization rates, which favors the genetic and adaptive diversity of populations (Gottsberger 1999, Pinto *et al.* 2005).

Several species of the genus *Annona* analyzed in this review, such as *A. squamosa* (Araújo *et al.* 2021), *A. reticulata*, *A. purpurea*, *A. macrophyllata* (González-Esquinca *et al.* 2016), and *A. cherimola* (Lora *et al.* 2009a, b, Maita *et al.* 2022) exhibit protogynous dichogamy.

In *A. squamosa*, the sexual transition from the female to the male phase occurs in less than 24 hours (Ribeiro *et al.* 2007, Araújo *et al.* 2021), after meeting the need for 22 days and 360.8 accumulated degree-days in the dry season, and 34 days and 622.2 degree-days in the rainy season, demonstrating its sensitivity to climate variations (Rodrigues *et al.* 2018), while in *A. cherimola*, the floral cycle lasts two days, with the male stage marked by synchronized anther dehiscence (Lora *et al.* 2009b).

In *A. macrophyllata*, *A. purpurea*, and *A. reticulata*, dichogamy manifests itself in three distinct stages. In the pre-female stage, petals remain closed or half-open for 24-48 hours. The female phase begins with the partial opening of petals, revealing a bright, fragrant stigma, and is receptive to pollen for up to three days. Finally, in the male phase, petals reach full opening, stamens become visible and separate, releasing pollen (González-Esquinca *et al.* 2016). Flowering in these species can last about two months, and in *A. macrophyllata* and *A. purpurea*, flowering is marked by the transition between the dry season and the onset of the rainy season of dry tropical forest, while *A. reticulata* produces sporadic flowers throughout the year, but only the dry season flowering is effectively productive (González-Esquinca *et al.* 2016).

Another strategy to prevent self-pollination is observed in *A. cherimola*, whose syncarpous gynoecium, composed of approximately 100 carpels and up to 200 stamens, presents non-functional carpels that act as a physical barrier, even in hermaphrodite flowers (Lora *et al.* 2011). On the other hand, there is the possibility of prolongation of the female phase and anticipation of the male phase in *A. cherimola* due to environmental variations, such as increased humidity and reduction of light and heat, which increases the overlap between compatible sexual stages and favors self-fertilization (Cautín *et al.* 2010).

Several studies mention the floral biology of species, but without reports of dichogamy, such as *Annona contrerasii* (Jiménez-Ramírez & Soto-Núñez 2015), and species of the genera *Stenanona* (*Stenanona migueliana* and *S. stenopetala*) (Ortiz-Rodríguez *et al.* 2014) and *Desmopsis* (*D. ibarrarum* and *D. dubia*) (Ortiz-Rodríguez 2022), which address floral anatomy, and studies related to pollen (Rodrigues *et al.* 2016, 2018, Bettiol Neto *et al.* 2009).

Embryo development. - After the fusion of gametes, the zygote initiates a series of cell divisions that culminate in the formation of a multicellular embryo. Most Annonaceae species have small, rudimentary, or underdeveloped embryos at the time of dispersal, ranging in size from 3 to 4 mm, as observed in *A. reticulata* (Vargas-Simón *et al.* 2022), *A. purpurea* (Vidal-Lezama *et al.* 2023), and *A. cherimola* (De Smet *et al.* 1999), whose radicle extends toward the micropyle (De Smet *et al.* 1999). *A. purpurea* has underdeveloped embryos at dispersal (approximately 17 % of the seed volume), which continue to expand during storage, characterizing active morphological dormancy (Vidal-Lezama *et al.* 2023), while in *A. reticulata*, the embryo is basal and occupies approximately ¼ of the seed (Vargas-Simón *et al.* 2022).

The small size and developmental stage of the embryo of most Annonaceae species at the time of dispersal have led to discussions regarding the morphological and morphophysiological dormancy of *A. cherimola* (Lora *et al.* 2010, De Smet *et al.* 1999), *A. purpurea* (Vidal-Lezama *et al.* 2023), *A. reticulata* (Vargas-Simón *et al.* 2022) and *O. lanceolata* seeds (Montejo-Valdés *et al.* 2014), and even physiological dormancy in *A. purpurea* and *A. macrophyllata* seeds (Ferreira *et al.* 2016, 2020).

In *A. purpurea*, embryonic development continues after a few months of warm, dry storage, which reinforces morphological dormancy and indicates the need for specific pre-germination treatments (Vidal-Lezama *et al.* 2023).

Endosperm formation.- The endosperm, a generally triploid tissue, results from the fusion of two polar nuclei with the second pollen grain and functions as the main nutritional reserve of the seed. In Annonaceae seeds, the endosperm has a ruminated pattern, characterized by internal laminae and folds that increase the surface area in contact with the embryo, optimizing nutrient transfer, as observed in *A. cherimola* (De Smet *et al.* 1999, Lora *et al.* 2010), *A. reticulata* (Vargas-Simón *et al.* 2022), *A. mucosa* (Cunha *et al.* 2018), and *Desmopsis ibarrarum* (Ortiz-Rodriguez 2022).

In *A. cherimola* a bipolar pattern of initial endosperm division is observed, generating a larger cell near the zygote and a smaller one in the chalazal region (Lora *et al.* 2010). Furthermore, the endosperm is divided into two regions: an internal and non-lobed one, and an external and lobed one, with tegmen lamellae visible between lobes (De Smet *et al.* 1999), as observed in *A. muricata*, which has a finely toothed surface, with reticulations and transversal ruminative marks that penetrate the endosperm (Mohaddesi & Dudhrejiya 2015). Similarly, *A. reticulata* has ruminated endosperm formed from folds of the mesotesta and endotesta (Vargas-Simón *et al.* 2022).

There is variation in the shape of the endosperm, while *Desmopsis ibarrarum* has a ruminated endosperm with a spine or pin shape (Ortiz-Rodriguez 2022). In *Stenanona migueliana*, the internal rumination has an irregular, hook-shaped appearance (Ortiz-Rodriguez *et al.* 2014). On the other hand, the white or yellowish-white color of the endosperm has been standard for several species, such as *A. cherimola* (De Smet *et al.* 1999) and *A. purpurea* (Vidal-Lezama *et al.* 2023).

The reserves present in Annonaceae seeds consist primarily of lipids, proteins, and carbohydrates (starch), as documented in *Annona cherimola* (Lora *et al.* 2010), *A. mucosa* (Soares *et al.* 2014), *A. macrophyllata*, and *A. purpurea* (Ferreira *et al.* 2016).

Seed coat.- Derived from the ovule integuments, the seed coat is differentiated into protective layers that envelop the entire seed, constituting the main physical barrier.

In *Oxandra lanceolata*, the thick and grooved testa prevents water loss and imposes physical dormancy, requiring the micropyle to be the primary water entry route at the beginning of germination (Montejo-Valdés *et al.* 2014). In *A. cherimola*, the woody sclerenchymatous testa is almost completely impermeable, conferring high mechanical strength and selectivity during imbibition (De Smet *et al.* 1999). In *A. glabra*, the testa is rigid and considered impermeable (Zamora-Cornelio *et al.* 2010).

In *Cymbopetalum baillonii*, seeds have a hard seed coat (Rodríguez *et al.* 2000), endosperm is rich in protein, a slippery texture seed coat, and with the presence of a reddish-orange aril, highly nutritious and lipidic, which favors dispersal by animals (Coates-Estrada & Estrada 1988). In *A. purpurea*, the seed coat is woody, rigid, and fibrous (Vidal-Lezama *et al.* 2023). In *A. mucosa*, seeds are bitegmic (Cunha *et al.* 2018).

In *Annona cherimola*, *A. muricata*, and *A. squamosa*, the micropylar seed plug is formed by an endotesta composed of multiple cell layers. This structure extends along both sides of the perichalazum, forming small “internal walls” that reach the base of the seed. The cells of the multiple endotesta have all their cell walls thickened and lignified, while in the single-layer endotesta, present in the seed coat, only the outer and radial walls are thickened and lignified. At the micropylar end, a sticky mass of parenchyma tissue gives rise to an initial stage of the operculum, which partially contributes to the closure of the opening in the fibrous testa (Svoma 1998).

Morphological and dimensional characteristics of seeds.- The morphological diversity of seeds of Mexican Annonaceae is given in [Table 1](#), which summarizes their dimensions and internal structures.

The smallest Annonaceae seeds are found in the *Desmopsis ibarrarum* species and measure around 5 to 7 mm in diameter, about 3 mm in thickness (Ortiz-Rodriguez 2022); in contrast, the largest seeds are those of *Annona purpurea*, which are about 2 cm in length, 1 to cm in width and 0.7 mm in thickness (Vidal-Lezama *et al.* 2023). *Stenanona migueliana* and *A. reticulata* seeds are intermediate in size, ranging from 14 to 22 mm in length, 12 to 15 mm in width, and 9 to 12 mm in thickness for *S. migueliana* (Ortiz-Rodriguez *et al.* 2014) and approximately 14 mm in length, 7 mm in width, and 4 to 5 mm in thickness for *A. reticulata*, with average volume of 229 mm³ (Pontes *et al.* 2018).

Table 1. Morphology and characteristics of seeds of Annonaceae species from Mexico.

Species	Seed shape and Size	Ruminated Endosperm	Embryo	Seed coat/Testa	Observations	Reference
<i>Annona cherimola</i>	3-4 mm (embryo)	Yes (bipartite)	Small and rudimentary (3-4 mm)	Dark brown, lignified, and rigid	Tegmen lamellae between endosperm lobes	De Smet <i>et al.</i> (1999)
<i>Annona glabra</i>	No precise data	Not specified	Not specified	Rigid and impermeable testa	No internal morphological details	Zamora-Cornelio <i>et al.</i> (2010)
<i>Annona macrophyllata</i>	Oblong. Length 2.3 cm. Feret diameter 1.7 cm	Yes	Small and rudimentary	Hard and waxy coating	No internal morphological details	González-Esquinca <i>et al.</i> 2015
<i>Annona mucosa</i>	Elongated; Ob-ovoid; 82.7 seeds/fruit; 1,000 seeds = 333 g	Yes	Small	Brown; bitegmic	Endosperm with high lipid content	Cunha <i>et al.</i> (2018), Soares <i>et al.</i> (2014)
<i>Annona muricata</i>	Hard. ovoid-oblong to elliptical. flattened 1.5–2 × 1–1.3 cm; 0.2–0.6 mm in thickness	Yes	Very small	Dark brown, hard, reticulate, and shiny	Teeth and ruminative marks where they penetrate the endosperm	Mohaddesi & Dudhrejiya (2015)
<i>Annona purpurea</i>	Obovate, 1.91 cm long × 0.95 cm wide. Woody and heavy husk	Yes	Rudimentary, small (3.4 mm long × 0.58 cm wide); underdeveloped (17% seed volume)	Dull dark brown; fibrous and rigid	Embryo continues growing in storage.	Vidal-Lezama <i>et al.</i> (2023)
<i>Annona reticulata</i>	14.1–14.2 × 6.8–7.2 × 4.24–4.9 mm; 229.64 mm ³	Yes; occupies about ¼ of the seed	Basal reduced and rudimentary (3-4 mm)	Smooth, shiny, dark brown, laterally compressed	116 seeds/fruit;	Pontes <i>et al.</i> (2018); Vargas-Simón <i>et al.</i> (2022)
<i>Cymbopetalum baillonii</i>	Large	Slightly ruminated, rich in protein	Not specified	Woody, slippery, shiny brown husk	Red-orange lipid aril; High tolerance to dehydration	Coates-Estrada & Estrada (1988); Rodríguez <i>et al.</i> (2000)
<i>Desmopsis ibarrarum</i>	Discoid/hemispherical; 5-7 mm in diameter; 3 mm in thickness	Yes	Not specified	Smooth, light reddish brown	4–6 seeds/fruit; spine- or pin-shaped rumination	Ortiz-Rodríguez (2022)
<i>Oxandra lanceolata</i>	Elliptical, grooved surface	Yes	Linear; underdeveloped; small	Absence of arils; thick and furrowed testa	Absence of arils or mucilage	Montejo-Valdés <i>et al.</i> (2014)
<i>Stenanona migueliana</i>	14–22 × 12–15 × 9–12 mm	Yes	Not specified	Not specified	3 -10 seeds/fruit; Hook-shaped internal rumination	Ortiz-Rodríguez <i>et al.</i> (2014)

Regarding shape, most seeds of Annonaceae species from Mexico are ellipsoidal, as observed in *Oxandra lanceolata* seeds (Montejo-Valdés *et al.* 2014), and obovoid, as observed in *A. purpurea* (Vidal-Lezama *et al.* 2023) and *A. mucosa* seeds (Cunha *et al.* 2018). On the other hand, there are other shapes for seeds of this family, such as discoid or hemispherical in *D. ibarrarum* species (Ortiz-Rodríguez 2022), ellipsoidal to lenticular for *S. migueliana* (Ortiz-Rodríguez *et al.* 2014) and ovoid-oblong to elliptical and flattened for *A. muricata* seeds (Mohaddesi & Dudhrejiya 2015).

The largest number of seeds per fruit was observed in *Annona reticulata*, which has approximately 116 seeds, with average individual weight of 0.3 g (Vargas-Simón *et al.* 2022), followed by *A. mucosa*, with intermediate number of 82.7 seeds per fruit and 1,000-seed mass of 333 g (Cunha *et al.* 2018). The smallest number varies between *S. migueliana*, with approximately 3 to 10 seeds per fruit (Ortiz-Rodríguez *et al.* 2014), and *D. ibarrarum*, with 4 to 6 seeds per fruit (Ortiz-Rodríguez 2022).

Most seeds of Annonaceae species from Mexico are brown in color, as observed in *Cymbopetalum baillonii* (Coates-Estrada & Estrada 1988) and *Annona mucosa* (Cunha *et al.* 2018), ranging from dark brown for *A. reticulata* (Vargas-Simón *et al.* 2022), dark brown for *A. purpurea* (Vidal-Lezama *et al.* 2023), and light reddish brown for *D. ibarrarum* (Ortiz-Rodríguez 2022). It has also been observed that some seeds have a shiny appearance, as observed in *A. muricata* (Mohaddesi & Dudhrejiya 2015), *A. reticulata* (Vargas-Simón *et al.* 2022), and *Cymbopetalum baillonii* (Coates-Estrada & Estrada 1988).

Although this systematic review gathered relevant information on the structure and formation of seeds of Annonaceae species from Mexico, significant gaps in the scientific literature were identified. Of the 59 articles evaluated, 30 addressed these aspects, covering only 15 of the ~ 70 recognized Mexican species. This low representativeness reveals a critical shortage of studies on the reproductive biology and seed morphology of most species in the family in the country.

Another critical point is that, of the 30 articles addressing seed structure or formation, only one investigated desiccation tolerance (Figure 6), an essential physiological parameter for classifying seeds as orthodox, recalcitrant, or intermediate. The lack of this type of data compromises not only the understanding of the reproductive ecology but also the development of *ex situ* conservation and germplasm storage protocols. The only study on this topic was that with *Cymbopetalum baillonii*, which revealed high desiccation tolerance, even when submitted to rapid drying (Rodríguez *et al.* 2000).

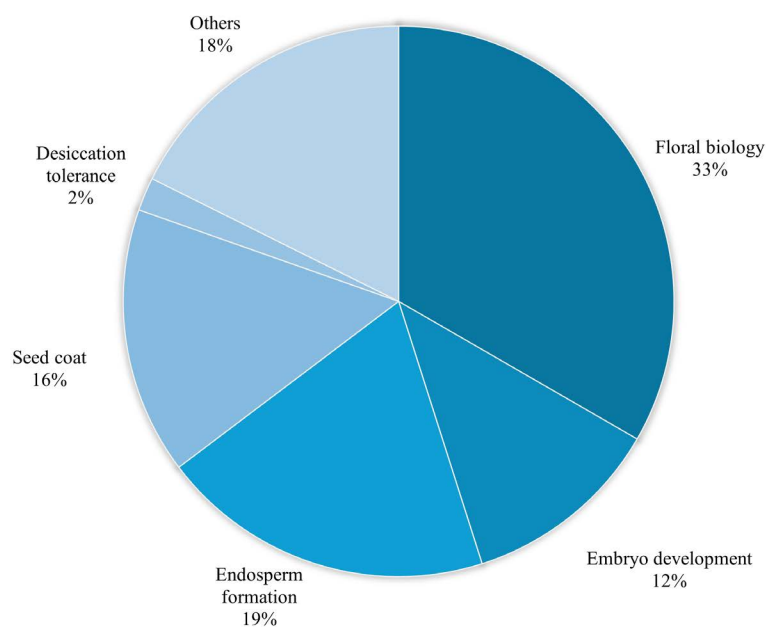


Figure 6. Distribution of topics covered on seed structure and formation, indicating the percentage corresponding to each topic.

In general, the literature reports that Annonaceae seeds have been dispersed with some degree of dormancy, which is overcome for germination to occur.

Seed dormancy in Annonaceae. Seed dormancy is characterized as a physiological state in which viable seeds fail to germinate, even when submitted to seemingly favorable environmental conditions, such as adequate temperature, humidity, presence of light and oxygen, and absence of inhibitory substances (Bewley *et al.* 2013a). This process is recognized as a natural resistance mechanism that allows seeds to withstand adverse environmental conditions until a more favorable time for germination occurs (Alves *et al.* 2000).

Dormant seeds can remain viable in the soil for prolonged periods, with germination being conditioned by overcoming dormancy and the simultaneous presence of environmental factors favorable for seedling growth (Dantas *et al.* 2000, Mašková & Poschlod 2022). In evolutionary and ecological terms, dormancy contributes to the survival of plant species by regulating the timing of germination and preventing it from occurring at unfavorable times. It is common for species belonging to the same family to share similar types of dormancies, even though they are distributed across different geographic regions (Seglias *et al.* 2018). In the Annonaceae family, seed dormancy plays an essential role in the formation of seed banks. This strategy allows for staggered germination, favoring the maintenance and stability of populations over time (Ferreira *et al.* 2022).

Regarding dormancy in Annonaceae species from Mexico, the most frequently addressed species was *Annona purpurea*, with four studies, followed by *Annona macrophyllata*, *A. mucosa*, and *A. squamosa*, with three studies. *A. cherimola* and *A. muricata* were addressed in only one study.

Morphological, morphophysiological, and physiological dormancy have been recorded in Annonaceae (Ferreira *et al.* 2019). Morphological dormancy occurs in seeds that have still-immature embryos at the time of dispersal, which require a period of internal development, conditioned by favorable environmental factors for germination to occur (Baskin & Baskin 2004, 2014). In contrast, morphophysiological dormancy associates the rudimentary embryo with a physiological block that prevents germination (Baskin & Baskin 2004). To overcome it, treatments such as stratification are recommended, although in some cases, the application of gibberellic acid (GA_3) is also effective by acting to remove hormonal inhibition (Finch-Savage & Leubner-Metzger 2006). Physiological dormancy is also observed, as occurs in *A. macrophyllata*, whose embryos are differentiated at the time of dispersal and dormancy is overcome by changes in hormonal balance (González-Esquinca *et al.* 2015, Ferreira *et al.* 2016, 2020).

Among *Annona* of Mexico species evaluated, 34 % are reported to have morphophysiological dormancy, 27 % physiological dormancy, and 13 % morphological dormancy. In another 13 %, no dormancy was observed, and in another equivalent portion, the type of dormancy could not be determined, indicating the need for further studies to characterize it.

The study conducted with *Annona cherimola* and *A. muricata* reveals consistent evidence of the presence of morphophysiological dormancy, classified as simple and not deep dormancy, according to criteria proposed by Baskin & Baskin (2014). In *A. cherimola*, germination reached 91.7 % with the combination of hot stratification and application of gibberellic acid (GA_3 at 800 ppm), in contrast to the 9 % observed in the control treatment (Lobo *et al.* 2007). Similarly, *A. muricata* presented germination rates of up to 62.5 % with the application of GA_3 , alone or combined with scarification, being decisive in overcoming dormancy, while controls showed no germination (Table 2).

In *A. squamosa*, dormancy is also characterized as morphophysiological, involving both embryonic development and overcoming physiological inhibition. The application of gibberellic acid (GA_3) has been shown to be effective in overcoming dormancy, indicating the importance of the physiological component (Stenzel *et al.* 2003, Vidal-Lezama *et al.* 2011, Nietsche *et al.* 2005). Seed storage favors embryonic development (morphological component), while GA_3 acts to remove physiological inhibition, both essential for germination. On the other hand, treatments such as immersion in acetic acid (commercial vinegar), mechanical scarification, seed coat cutting, and immersion in cold or warm water were not effective in overcoming dormancy (Nietsche *et al.* 2005, Stenzel *et al.* 2003).

Regarding *Annona mucosa* (syn. *Rollinia mucosa*), both Ferreira *et al.* (2009) and Campos *et al.* (2015) observed that scarification significantly increased seedling emergence, demonstrating the effectiveness of the treatment in

Table 2. Types of dormancy in Annonaceae Mexican species, germination percentage of treatment with the highest yield (%GT), emergence percentage of treatment with the highest yield (%ET), germination percentage of the control group (%GC), emergence percentage of the control group (%GE), and methods used to overcome dormancy.

Species	Dormancy	%GT / %ET	%GC / %ET	Overcoming	Reference
<i>Annona cherimola</i>	Morphophysiological	91.70	9	Hot heat treatment + GA ₃ 800 ppm	Lobo <i>et al.</i> (2007)
<i>Annona macrophyllata</i>	Physiological ¹	77 ¹	0 ¹	200 ppm GA4+7+ BA (benzyladenine) ¹	Ferreira <i>et al.</i> (2016) ¹ , Ferreira <i>et al.</i> (2020) ² ,
	Physiological ²	- ²	- ²	Through hormonal changes (GA/ABA) ²	González-Esquinca <i>et al.</i> (2015) ³
	- ³	71.1 ³	0 ³	Storage for 8 months, intact seeds in basal portion ³	
<i>Annona mucosa</i>	Physical ¹	88 ¹	5 ¹	Scarification 43 days after sowing ¹	Campos <i>et al.</i> (2015) ¹ ; Cunha & Braga (2018) ² ;
	Morphological ²	87 ²	10 ²	Hydration for 48 hours followed by storage with stratification for 25 days ²	Ferreira <i>et al.</i> (2009) ³
	Physical ³	76 ³	58 ³	Scarified with 80-grit sandpaper on both sides + soaking with distilled water for 24 hours ³	
<i>Annona muricata</i>	Morphophysiological	62.5	0	GA ₃ 800ppm	Lobo <i>et al.</i> (2007)
<i>Annona purpurea</i>	Physiological or Morphophysiological ¹	30 ¹	1 ¹	200 ppm GA4+7 + BA (benzyladenine) ¹	Ferreira <i>et al.</i> (2016) ¹ ; Ferreira <i>et al.</i> (2020) ² ;
	Physiological ²	- ²	- ²	Through hormonal changes (GA/ABA) ²	Vidal-Lezama <i>et al.</i> (2023) ³ ;
	Morphological ³	- ³	- ³	Dry storage at 25 ± 3°C favored embryo growth ³	Vidal-Lezama <i>et al.</i> (2024) ⁴
	Physiological ⁴	43 ⁴	5.7 ⁴	GA ₃ (Merk®) 350 ppm ⁴	
<i>Annona squamosa</i>	Morphological ^{1,2,3}	~70 ¹	- ¹	Storage for 180 days ¹	Nietsche <i>et al.</i> (2005) ¹ ;
				GA ₃ 50ppm ²	Stenzel <i>et al.</i> (2003) ² ;
		75 ²	3.75 ²	GA ₃ 400ppm + storage for 2.5 months (24 ± 5°C) ³	Vidal-Lezama <i>et al.</i> (2011) ³
		83.68 ³	16.55 ³		

Values indicated with “~” correspond to approximate estimates extracted from graphs, with no exact value determined by the authors. In cases where data were not reported by the authors, the symbol “-” was used.

overcoming dormancy. In Ferreira *et al.* (2009), scarification was performed on both sides of the seed followed by 24 hours of imbibition in distilled water. In Campos *et al.* (2015), scarification consisted of a cut in the seed coat using pruning scissors on the side opposite the hilum. Dormancy is attributed to the impermeability of the seed coat which limits water uptake and prevents germination and is therefore considered physical dormancy (Baskin *et al.* 2000, Weitbrecht *et al.* 2011, Radchuk & Borisjuk 2014). However, the germination behavior of *A. mucosa* also indicates the existence of embryonic dormancy. Hydration for 48 hours followed by stratification for 25 days resulted in significantly higher germination, suggesting that dormancy may be related to embryo underdevelopment at the time of dispersal (Cunha & Braga 2018).

In *Annona purpurea*, the application of 200 mg L⁻¹ of GA₄+₇+ BA resulted in 30 % germination, while control showed only 1 % (Table 2), which suggests further studies to determine whether dormancy is physiological or morphophysiological (Ferreira *et al.* 2016). Vidal-Lezama *et al.* (2023) identified underdeveloped embryos in *A. purpurea*, which developed during dry and heated storage for up to six months, indicating morphological dormancy. In a later study, the application of 350 mg L⁻¹ of gibberellic acid (GA₃) promoted 43 % germination, compared to 6 % in the control, evidencing physiological dormancy. (Vidal-Lezama *et al.* 2024). Therefore, data indicates the possible coexistence of different types of dormancy in the species, highlighting the importance of further investigations.

Annona macrophyllata (syn. *Annona diversifolia*) seeds showed 77 % germination with the application of 200 mg L⁻¹ of GA₄+₇ and N-(phenylmethyl)-aminopurine, while control showed no germination (Table 2). It is noteworthy that GA₄+₇ promoted higher germination at all concentrations tested, compared to the isolated application of GA₃ (Ferreira *et al.* 2016). A higher germination percentage was also observed in *A. macrophyllata* (71 %) after eight months of storage, despite a reduction in seed viability throughout this period (Table 2) (González-Esquinca *et al.* 2015). The effect of storage was associated with the synchronization of germination with the onset of the rainy season, favoring seedling survival. However, it was unclear whether the storage time was related to embryo development, nor was the type of dormancy explicitly defined. However, this study served as the basis for later studies that confirmed that the embryo is dispersed when fully developed and that the dormancy is physiological (Ferreira *et al.* 2016, 2020).

It is noteworthy that *A. purpurea* and *A. macrophyllata* seeds are dispersed with high ABA levels, which inhibits gibberellin synthesis and contributes to maintaining dormancy during the dry season. The application of gibberellin combined with cytokinin reduced ABA levels, activated the degradation of reserves, and stimulated germination, reinforcing the hypothesis of physiological dormancy (Ferreira *et al.* 2020).

Gibberellins act to overcome dormancy by blocking the expression of germination repressor genes (RGL2, SPY) and/or promoting the degradation of their respective products (mRNAs and proteins), leading to increased embryo germination potential (Peng & Harberd 2002), as reported in the Annonaceae in this review. These studies demonstrate, therefore, that germination occurs after overcoming dormancy, similar to quiescent seeds dispersed without dormancy (Considine & Considine 2016, Ferreira *et al.* 2019, 2020).

Germination of Annonaceae seeds. Understanding the physiology of seed germination is essential to aid in the perpetuation of species (Albrecht & Penagos 2012). Annonaceae species generally exhibit slow and uneven germination (Costa *et al.* 2011), leading to the search for pre-germination treatments that promote standardization and increase the germinability of these species.

Germination is characterized by a cascade of events that include the resumption of embryo growth, which is halted in the final maturation stages of orthodox seeds, whether dormant or quiescent. This process begins with the entry of water into the dry seed and ends with the emergence of the primary root (Nonogaki *et al.* 2010, Bewley *et al.* 2013b).

Water acquisition by the seed is associated with the initial water content and is characterized by a three-phase pattern that demarcates the metabolic processes of germination (Hoekstra *et al.* 2001, Soriano *et al.* 2011, Bewley *et al.* 2013b). In *Annona macrophyllata* (*A. diversifolia*) seeds, imbibition (Phase I) lasts approximately 50 hours, and in *A. purpurea*, 70 hours, reaching 31 % moisture content at the end of Phase I (Ferreira *et al.* 2013). The timing of imbibition is important for determining, for example, treatments with plant growth regulators in seeds.

Studies with Annonaceae species from Mexico demonstrate a correlation between time of seed immersion in aqueous solutions and differences in germination rates ([Appendix Table 1](#)). One example is *A. squamosa*, which presents variability in germination rates using different seed immersion times, with 3.70 % germination reported for the control group after 24 hours of immersion in water (Stenzel *et al.* 2003), 24 % after 48 hours (Moreno *et al.* 2013a), and 54 % after 5 hours of immersion (Ferreira *et al.* 2002). In *A. muricata*, there is also evidence of a correlation between immersion time and seed germination rate, where seeds immersed in water for 24, 48, and 72 hours resulted in different germination rates (66, 88, and 91 %, respectively) (Singh & Maheswari 2017).

At the end of Phase I, the seed's water potential stabilizes, and then Phase II begins, when water slowly returns due to the degradation of reserves. The reserve substances transported in Phase II are reorganized into complex substances in Phase III, forming protoplasm and cell walls. This promotes the growth of the embryonic axis, accompanied by a further increase in water content (Borghetti & Ferreira 2004). The emergence of the primary root marks the end of germination and beginning of seedling development (Hadas 1976).

The time for the seed to pass through the three phases and for the emergence of the primary root varies on the anatomical and physiological characteristics of the seminal covering and embryo and the germination conditions of the seeds of each species. Species of the Annonaceae family exhibit slow and uneven germination, as demonstrated in a study with Mexican species ([Appendix Table 1](#)), which reports germination times ranging from 13 to 39 days for *Annona squamosa* (Ferreira *et al.* 2002, Moreno *et al.* 2013a), 29 to 60 days for *A. reticulata* (Kudikala *et al.* 2018, Vargas-Simón *et al.* 2022), and 19 to 35 days for *Cymbopetalum baillonii* (Becerra-Vázquez *et al.* 2020).

Various factors can influence germination rates, as can be seen in the articles included in this review ([Figure 7](#)), among which hormonal balance plays a key role. Gibberellins, cytokinins, and ethylene promote germination, while abscisic acid induces dormancy (Bewley *et al.* 2013b, Ferreira *et al.* 2013). For Annonaceae, the use of plant growth regulators has proven effective both in overcoming seed dormancy and in increasing germination speed and uniformity in non-dormant seeds (Ferreira *et al.* 2013).

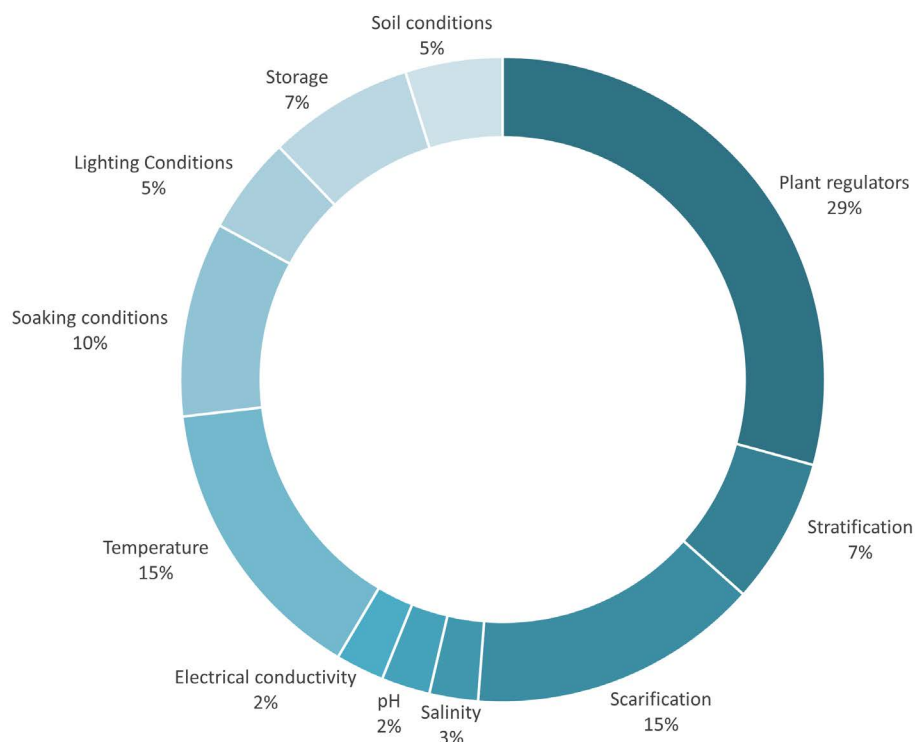


Figure 7. Percentage of treatments used in the cited studies on the germination process of Annonaceae species from Mexico.

Of the 25 germination studies with Annonaceae species from Mexico, ten evaluated the effect of gibberellin, one study with two species used only gibberellin and the combination of gibberellin and cytokinin, and one study used only cytokinins as a pre-germination treatment, totaling 12 studies (29 %) using plant growth regulators ([Appendix Table 1](#) and [Figure 7](#)). Among these, 11 studies with regulators showed similar results, where the use of regulators as a pre-germination treatment resulted in increase in the germination rate compared to control, which can be exemplified by the study with *A. macroprophyllata*, where the control group did not germinate, and the group treated with GA₄₊₇+BA 200 mg L⁻¹ showed significant germination rate, reaching 77 % (Ferreira *et al.* 2016).

In addition to the direct supply of gibberellins, environmental factors such as temperature and light induce the synthesis of GAs in natural environments, signaling the overcoming of dormancy and promoting germination. In studies addressing different environmental conditions in seeds of Annonaceae species from Mexico, it was observed that factors such as temperature variations can influence germination. This temperature response is demonstrated in *Annona squamosa*, where germination at constant temperature of 35 °C resulted in germination rate of 58 %, while at temperature of approximately 18 °C, the seeds of this species did not germinate (Martínez *et al.* 2012). In *A. macroprophyllata* and *A. purpurea* seeds, studies have been carried out in germinators with temperatures between 20 and 30 °C in the dark (Ferreira *et al.* 2016).

This review suggests that, although there is great diversity of Annonaceae species from Mexico, few species have been studied regarding seed formation, dormancy, and germination. The most numerous studies are on the genus *Annona*, with emphasis on species of fruit importance. In particular, articles specifically addressing the classification and overcoming of dormancy are limited, which should be carried out with a specific analytical focus.

Prospects for further studies. This review revealed the need for studies related to seed formation of Annonaceae species from Mexico, especially studies characterizing desiccation tolerance. Studies evaluating the accumulation of sugars and late embryogenesis proteins (LEA) would be interesting to characterize their orthodox or recalcitrant nature, as well as the enzymes involved in metabolic repair during imbibition. During seed formation, it is important to evaluate the accumulation of germination inhibitors such as ABA (abscisic acid), which characterizes physiological dormancy in the family, which reports have only been found in *Annona macroprophyllata* and *A. purpurea*. Another aspect to be explored is the structure and composition of the seed coat, which is often permeable to water but not to gases, indicating another dormancy mechanism. The embryo also represents an important reason for further studies, since its differentiation during seed formation may be related to morphological dormancy.

Therefore, the main prospects for further studies lie in expanding the number of species to be studied, from seed formation, dormancy establishment and classification to methods for overcoming dormancy, in order to assist in projects involving seedling production aimed at the conservation and biodiversity of Mexican Annonaceae.

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Appendix

Table 1. Germination data and factors affecting germination (treatments) obtained from the systematic search carried out for Annonaceae species from Mexico.

Immersion time	Germination rate control group	Treatments	Best result	Beginning of germination (days)	Average germination time (days)	Reference
<i>Annona cherimola</i>						
0, 24 and 48h	Experiments: 1 – 65 %; 2 – 62.5 to 77.5 %; 5 – 60 %	Salinity; GA ₃ concentrations; Imbibition time; Light/dark; With/without seed coat; Temperature.	1 – 8.67 µM GA ₃ in distilled water: 85 %; 2 – 48 h of imbibition: 80 %; 3 – Dark: 80 %; 4 – Without removing the seed coat: 85 %; 5 – 30°C: 85 %.	-*	-	Padilla & Encina (2003)
-	9-12 %	Warm/cold stratification and GA ₃	Hot scarification 90 days + GA ₃ 800 ppm: 91.7 %	-	-	Lobo <i>et al.</i> (2007)
<i>Annona glabra</i>						
-	-	Mechanical scarification	Mechanical scarification: 86 %	8	40	Zamora-Cornelio <i>et al.</i> (2010)
-	-	Seeds ingested/ Seeds not ingested	Seeds ingested without feces: 46.0 %	24-46	-	Burgos-Rodríguez <i>et al.</i> (2016)
-	-	Soil composition and water condition	Soil field capacity (grass with grazing): 91 %; flooded soil (without grass): 20 %	Soil field capacity: 12-16 Flooded soil: 18-22	-	Sánchez-García <i>et al.</i> (2023)
<i>Annona macrophyllata</i>						
96 hours	0 %	Plant regulators: GA ₃ and GA ₄₊₇ + BA	GA ₄₊₇ + BA 200 mg L ⁻¹ : 77 %	-	13.16	Ferreira <i>et al.</i> (2016)
-	0 %	Storage time and presence/absence of micropilar buffer	Intact seeds after 7 and 8 months of storage: 53 - 71.1 %	-	-	González-Esquinca <i>et al.</i> (2015)
<i>Annona mucosa</i>						
48 hours	-	Imbibition, stratification and storage.	1 – Imbibition + 25-day stratification: 80 %; 2 – 60-day storage + 25-day stratification: 87 %	Fixed evaluation periods	Fixed evaluation periods	Cunha & Braga (2018)
20 hours	-	Scarification and GA ₃	GA ₃ 1000 mg/L + scarification: 87 %	-	-	Campos <i>et al.</i> (2015)
24 hours	0.2025	GA ₃ and Scarification in Concentrated H ₂ SO ₄	GA ₃ 250 mg/L: 49 %	-	-	Santos <i>et al.</i> (2009)

Immersion time	Germination rate control group	Treatments	Best result	Beginning of germination (days)	Average germination time (days)	Reference
-	-	<i>In situ</i> (field) conditions	<i>In situ</i> (field): Bt (75 %)	<i>In situ</i> : 20 days	-	Pérez-Hernández <i>et al.</i> (2011)
			<i>Ex situ</i> (nursery): shade 40 % (98 %)	<i>Ex situ</i> : 18 days		
<i>Annona muricata</i>						
Various	50 %	Scarification, immersion in water, immersion in concentrated H ₂ SO ₄ , and immersion in GA ₃	GA ₃ 500 ppm/24h: 100 %	24-31	-	Singh & Maheswari (2017)
24 hours	16.66 %	GA ₃	GA ₃ 200 ppm: 27.77 %	-	-	Ummah & Rahayu (2019)
-	0 %	Warm/cold stratification and GA ₃	GA ₃ 800 ppm: 62.5 %	-	-	Lobo <i>et al.</i> (2007)
15 minutes	-	Electrical conductivity	Conductivity 1.5 dS m ⁻¹ : 79.02 %	-	-	Nobre <i>et al.</i> (2003)
<i>Annona reticulata</i>						
3, 6 and 24 hours	43.3 %	Mechanical scarification and immersion in GA ₃ .	Mechanical scarification: 76.6 %	17-19	29-37	Vargas-Simón <i>et al.</i> (2022)
24 hours	0-5 %	In vitro germination in different culture media, Mechanical scarification; hot water immersion and GA ₃ immersion	GA ₃ 8.67 µM <i>in vitro</i> (MS medium): 60 %	-	40-60	Kudikala <i>et al.</i> (2018)
<i>Annona squamosa</i>						
24 hours	3.70 %	Immersion in GA ₄ and Temperature	GA ₄ 50 ppm: 75.00 %	14	14-28	Stenzel <i>et al.</i> (2003)
-	Room temperature (~18.7°C): 0 %	Temperature variations in two locations	Constant 35°C (Apulo): 58 %	5-10	17.09-18.41	Martínez <i>et al.</i> (2012)
48 hours	24 %	Zeatin	Zeatin 1.0 mg L ⁻¹ : 69.6 %	9	13	Moreno <i>et al.</i> (2013a)
-	20 and 23.2 %	Temperature and stratification	Cold moist stratification 45 days at 35°C: 65.6 %	-	-	Moreno <i>et al.</i> (2013b)
5 hours	54 %	GA ₃	GA ₃ 250 mg.L ⁻¹ : 77 %	-	Up to 33	Ferreira <i>et al.</i> (2002)

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Immersion time	Germination rate control group	Treatments	Best result	Beginning of germination (days)	Average germination time (days)	Reference
24 hours	Experiments: 1- 70,37 %; 2 - 18,99; 3 - 16,55 e 21,48	Storage, Temperature and GA ₃ Concentrations	1 - Room temperature: 70.37 %; 2 - 600 ppm GA ₃ : 78.87 %; 3 - storage at room temperature + 400 ppm GA ₃ : 83.68 %	-	-	Vidal-Lezama <i>et al.</i> (2011)
120 hours (treatment)	53.14 %	Prolonged immersion (120 h)	Immersion 120h: 80.67 %	-	2.82 – 3.38	Pompelli <i>et al.</i> (2023)
<i>Annona purpurea</i>						
96 hours	1-4 %	GA ₃ and GA ₄₊₇ + BA	GA ₄₊₇ + BA 200 mg L ⁻¹ : 30 %	-	14.54	Ferreira <i>et al.</i> (2016)
84 hours	5,79 %	pH and gibberellic acid 350 mg L ⁻¹	Gibberellic acid: 43.16 %	17	-	Vidal-Lezama <i>et al.</i> (2024)
<i>Cymbopetalum baillonii</i>						
-	84 %	Dehydration 30 %	Dehydration 30 %: ~95 %	-	-	Rodríguez <i>et al.</i> (2000)
15 days (treatment)	83.3 %	Hydroconditioning (15 days); Natural conditions (clearing)	Natural conditions (clearing): 90.6 %	-	19.0-35.4	Becerra-Vázquez <i>et al.</i> (2020)

* (-) Data not reported by the authors.