

Physiology of the recalcitrant seed of chayote (*Sechium edule* [Jacq.] Sw.) and its role in postharvest fruit deterioration

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ABSTRACT

Objective: To integrate existing knowledge on the physiology of recalcitrant chayote seeds and their interaction with fruit tissues, highlighting their impact on conservation alternatives and postharvest life.

Methodology: A systematic review of the scientific literature related to the recalcitrant seed of *Sechium edule* was conducted, focusing on studies published over the last 25 years. The review addressed fruit and seed biology and physiology, conservation practices in germplasm banks, and postharvest management alternatives for reducing premature seed germination.

Results: Chayote has a recalcitrant seed characterized by high sensitivity to dehydration and low temperatures, which hinders conventional storage. This characteristic represents a major challenge for conservation programs, making the maintenance of living plant collections essential for preserving the biodiversity of the genus *Sechium*. Moreover, this same trait reduces the postharvest life of the fruit. Therefore, postharvest treatments such as wax coatings, 1-MCP application, and cold storage are viable alternatives for extending shelf life. The knowledge generated also provides valuable information for designing more efficient and sustainable postharvest strategies and contributes to the conservation and appropriate use of species with recalcitrant seeds, which cannot be preserved using conventional seed storage methods.

Implications: The physiology of recalcitrant chayote seeds has direct implications for postharvest fruit deterioration because their high metabolic activity promotes premature germination and vivipary, while also hindering long-term conservation.

Conclusions: The recalcitrant seed is not only a challenge for long-term conservation but also the main physiological determinant of postharvest deterioration in chayote fruit. Despite these limitations, viable conservation alternatives are available, including *in vivo*, *in situ*, and *in vitro* approaches.

Keywords: recalcitrant seed, germplasm conservation, germplasm banks, postharvest management, fruit-seed coupling.

Citation: Ramírez-Rodas, Y. C., Gayosso-Rosales, L. Y., Arévalo-Galarza, Ma. de L., Cadena-Iñiguez, J. & Riviello-Flores, M. de la L. (2026). Physiology of the recalcitrant seed of chayote (*Sechium edule* [Jacq.] Sw.) and its role in postharvest fruit deterioration. *Agro Productividad*. <https://doi.org/10.32854/2yth6z73>

Academic Editor: Jorge Cadena Iñiguez

Associate Editor: Lucero del Mar Ruiz Posadas

Guest Editor: Daniel Alejandro Cadena Zamudio

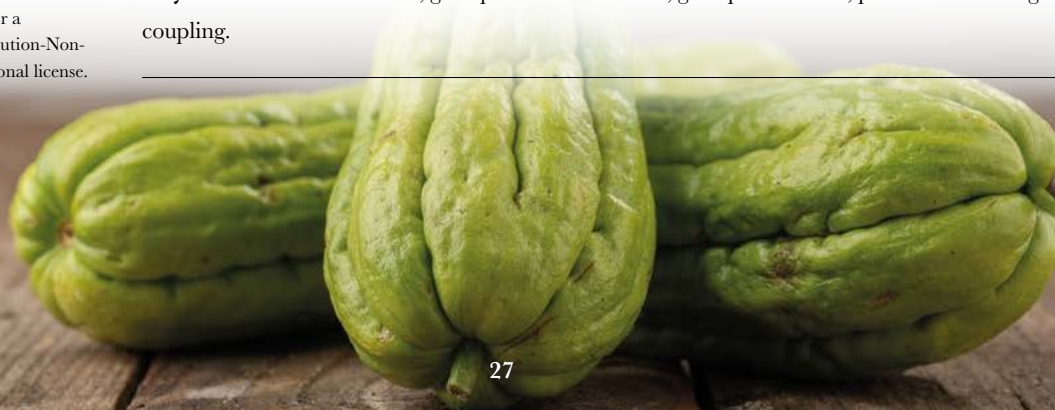
Received: January 23, 2026.

Accepted: April 17, 2026.

Published on-line: June 26, 2026.

Agro Productividad, 19(5). May. 2026. pp: 27-42 .

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INTRODUCTION

Seeds play a fundamental role in plant reproduction and the preservation of biodiversity; moreover, they are essential for food systems. However, not all seeds can be stored in the same way. Some seeds, after reaching physiological maturity and a low moisture content, can be stored for long periods without losing viability. These seeds, known as orthodox seeds, have the ability to enter a state of dormancy, during which they remain viable until favorable conditions for germination such as water, light, and oxygen are present. This period of dormancy involves complex physiological, genetic, and environmental processes.

In contrast, recalcitrant seeds are characterized by their high water content at the time of dispersal and their inability to tolerate desiccation or low temperatures, which prevents long-term storage, unlike orthodox seeds (Bewley *et al.*, 2013; Walters *et al.*, 2013). This type of seed is common in tropical, subtropical, and forest species, such as avocado (*Persea americana*), cacao (*Theobroma cacao*), mango (*Mangifera indica*), and oaks (*Quercus* spp.), among others (Normah *et al.*, 2019; Priyanka *et al.*, 2021). The physiological characteristics of these seeds pose significant challenges for long-term ex situ conservation and postharvest management. In this context, chayote seeds (*Sechium edule*) are recalcitrant, which limits their long-term conservation. For this reason, chayote plants are mostly conserved using in vivo methods, which allow long-term preservation of genetic diversity (Barrera-Guzmán *et al.*, 2021).

In addition, seed type directly influences the postharvest management of the endocarpic fruit because, once the seed reaches physiological maturity, germination begins inside the fruit. This process can occur as early as 13 days after harvest, coinciding with the period when the fruits are being marketed. This phenomenon not only negatively affects the fruit's appearance but also facilitates pathogen entry, increases moisture loss, and significantly reduces shelf life. The objective of this review is to integrate existing knowledge on the physiology of recalcitrant chayote seeds and their interaction with fruit tissue, highlighting their impact on conservation strategies and postharvest life.

MATERIALS AND METHODS

A systematic review of the scientific literature related to *Sechium edule* seeds was conducted, focusing on publications from the last 25 years. The databases consulted were Google Scholar, Scopus, SciELO, and Redalyc. Studies addressing fruit and seed biology and physiology, germplasm conservation methods, conservation practices in germplasm banks, and alternative approaches to postharvest fruit management were prioritized. The exclusion criteria included articles published outside the established timeframe, opinion papers, essays, and theses (Figure 1).

RESULTS

Physiological basis of recalcitrance in chayote seeds

Characteristics of orthodox and recalcitrant seeds

Seeds are the means by which plants ensure their survival; however, successful germination depends on their tolerance to desiccation. The terms *orthodox* and *recalcitrant* began to be used in the 1970s to describe seed tolerance to desiccation and low temperatures

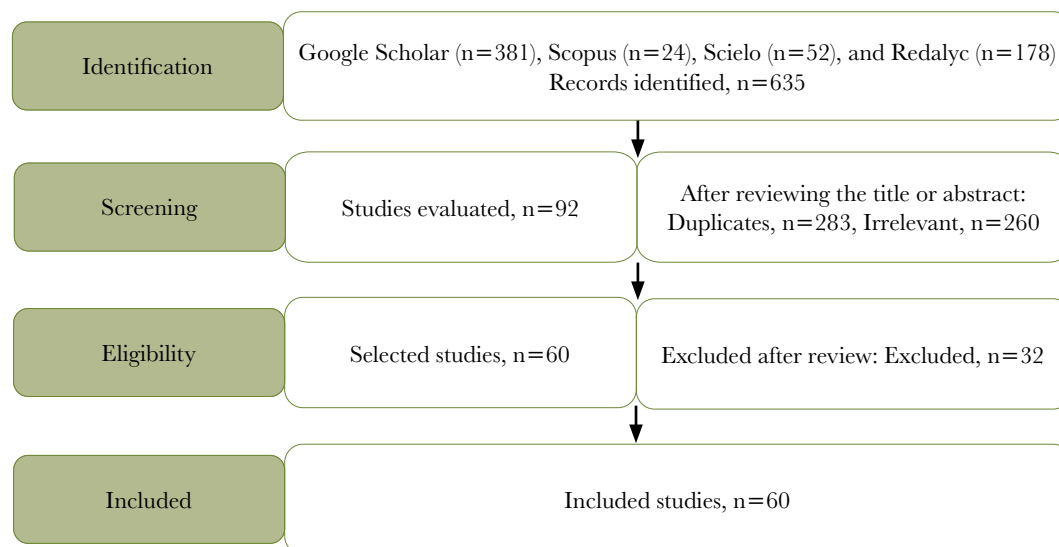


Figure 1. PRISMA flow diagram of the information selection process.

during conservation. Based on these characteristics, seeds are classified into three groups: orthodox, intermediate, and recalcitrant (Barbedo *et al.*, 2013; Bewley *et al.*, 2013; Walters *et al.*, 2013) (Table 1).

Orthodox seeds can reach equilibrium and survive under limited moisture conditions, with moisture contents as low as 5%. Desiccation tolerance is acquired progressively during seed maturation. Once seeds have completed maturation, including embryo morphogenesis and reserve accumulation, they enter a period of dormancy characterized by minimal metabolic activity, which is maintained until favorable conditions allow germination (Berjak and Pammenter, 2013). Intermediate seeds are partially tolerant to desiccation; however, they lose viability when their moisture content ranges between 10% and 12% (Tweddle *et al.*, 2003).

In contrast, recalcitrant seeds are generally found in tropical species, are larger than 1 cm, have high water content, and do not tolerate desiccation at moisture levels of 30%-50%. This sensitivity may be related to low levels of protective proteins involved in preventing damage during desiccation. Because they undergo only partial dehydration, these seeds maintain active metabolism and continue developing by initiating germination after

Table 1. Plant species with orthodox, intermediate, and recalcitrant seeds.

Seed Types	Plant Species	Reference
Orthodox	Maize (<i>Zea mays</i>), oat (<i>Avena sativa</i>), wheat (<i>Triticum aestivum</i>), common bean (<i>Phaseolus vulgaris</i>), cucumber (<i>Cucumis sativus</i>), among others.	Solberg <i>et al.</i> (2020)
Intermediate	Oil palm (<i>Elaeis guineensis</i>), papaya (<i>Carica papaya</i>), coffee (<i>Coffea</i> sp.), citrus (<i>Citrus</i> sp.), among others.	Sharmela <i>et al.</i> (2019); Ballesteros <i>et al.</i> (2021)
Recalcitrant	Cacao (<i>Theobroma cacao</i>), mango (<i>Mangifera indica</i>), rambutan (<i>Nephelium lappaceum</i>), mangosteen (<i>Garcinia mangostana</i>), chayote (<i>Sechium</i> spp.), among others.	Normah <i>et al.</i> (2019); Priyanka <i>et al.</i> (2021)

reaching physiological maturity. This characteristic hinders long-term storage; therefore, these species are maintained as living plants in germplasm banks (Magnitskiy and Plaza, 2007; Kalemba and Pukacka, 2012).

Because recalcitrant seeds are sensitive to desiccation, they are vulnerable to rapid viability loss shortly after harvest (Berjak and Pammenter, 2013). However, in chayote, the seed remains inside the fruit throughout development, which helps maintain embryo viability. When fruits with recalcitrant seeds detach from the mother plant, the seeds have high moisture content, are metabolically active, and lack some mechanisms required to acquire desiccation tolerance. These limitations may include insufficient accumulation of vacuolar proteins that provide mechanical resistance against cellular collapse, as well as limited starch and lipid reserves, molecules commonly reported in orthodox seeds (Delahaie *et al.*, 2013; Berjak and Pammenter, 2013).

Biology and physiology of chayote seeds

Botanically, the chayote fruit is a fleshy berry that grows on a peduncle and is typically fleshy or fleshy with fibers surrounding the single seed located in the central-basal cavity of the fruit. The seed is flattened and large (3.47 cm) and consists of two cotyledons and a soft testa, 1.5 mm thick, that surrounds the embryo (Figure 2). At harvest, corresponding to horticultural maturity, the seed has not yet reached morphophysiological maturity because the cotyledons are only 25% developed and other embryonic components are not yet evident (Ramirez-Rodas *et al.*, 2023).

Chayote seeds are among the 10%-20% of angiosperms that produce recalcitrant seeds (Walters *et al.*, 2013). Because of their recalcitrant nature, these seeds do not undergo developmental interruption. Therefore, when the fruit reaches physiological maturity and the seed has completed its development, germination begins, particularly if the fruit experiences preharvest or postharvest stress. As a reproductive strategy, germination may

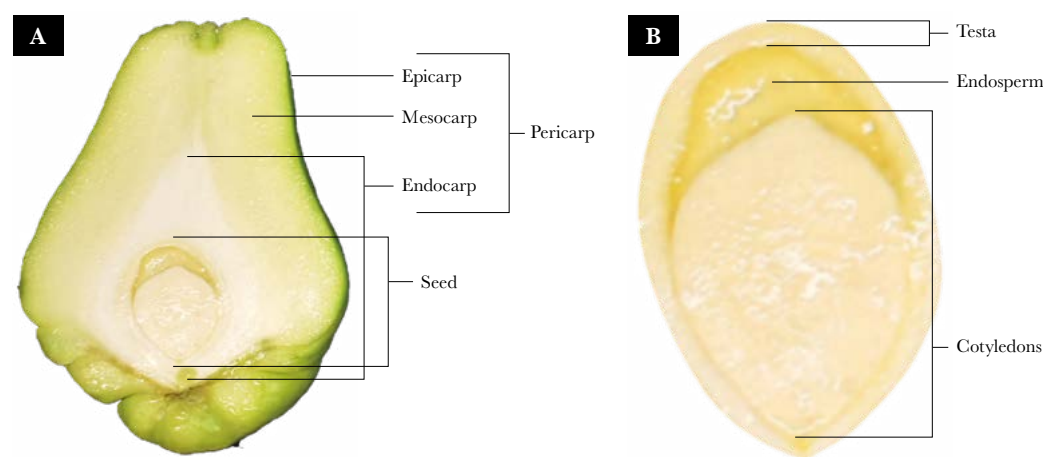


Figure 2. Morphology of the fruit and seed of chayote var. *virens levis*. Morphological structure of the fruit, composed of the pericarp epicarp, mesocarp, and endocarp and the seed located in the central-basal region of the fruit (A). Morphological structure of the seed, consisting of the testa, gelatinous endosperm, and two cotyledons, from the outermost to the innermost layer, respectively (Ramirez-Rodas *et al.*, 2023).

occur even while the fruit remains attached to the plant (Chauhan *et al.*, 2018). It has been observed that when chayote vines bearing fruits are damaged or wilted, germination is induced in the attached fruits (Figure 3).

Morphophysiological changes associated with chayote seed development occur both before and after fruit harvest (Figure 4). Following pollination and fertilization, chayote fruit development begins from an inferior ovary. From this stage, fruit growth follows a simple sigmoidal curve, similar to the developmental patterns observed in squash (*Cucurbita pepo* L.), cucumber (*Cucumis sativus*), and pineapple (*Ananas comosus* L. Merr. cv. Sarawak) (Oloyede *et al.*, 2013; Soloman *et al.*, 2016; Liu *et al.*, 2020).

The cell division stage (0-9 days after anthesis, DAA) is characterized by slow seed growth and the initial accumulation of gelatinous endosperm. During the cell elongation stage (9-18 DAA), endosperm presence increases, along with evident cotyledon growth. In the final stage of seed development prior to harvest, the growth rate declines, and the fruit reaches horticultural maturity, making it ready for harvest. At this point, the seed remains immature, with cotyledons developed to approximately 25%.

After harvest, the seed continues its development and reaches physiological maturity around 10 days later, at which point the cotyledons fill the seed cavity. Subsequently, germination begins, leading to testa rupture and the basal opening of the fruit, a phenomenon known as vivipary. This process is evidenced by the growth of a new seedling within the fruit and ultimately results in a loss of fruit quality during the postharvest stage (Figure 4).

Vivipary and hormonal regulation during germination

Chayote fruits lose commercial quality, causing consumers to perceive them as less attractive. This quality loss is associated with factors such as dehydration, pathogen presence, physiological maturity, and, primarily, vivipary (Romero-Velázquez *et al.*, 2015; Ramirez-Rodas *et al.*, 2023; Rivera-Ponce *et al.*, 2024). Vivipary is observed during the first week after harvest at room temperature (24 °C). However, when fruits are stored

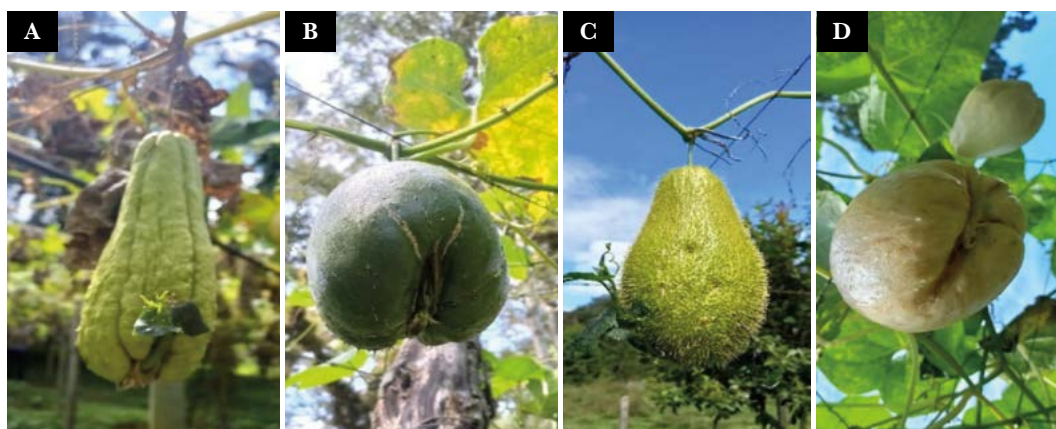


Figure 3. Vivipary in different varieties of chayote fruits at physiological maturity. Vivipary in *nigrum maxima* (A), *nigrum xalapensis* (B), *nigrum spinosum* (C), and *virens levis* (D), showing visible shoot emergence in fruits attached to the mother plant.

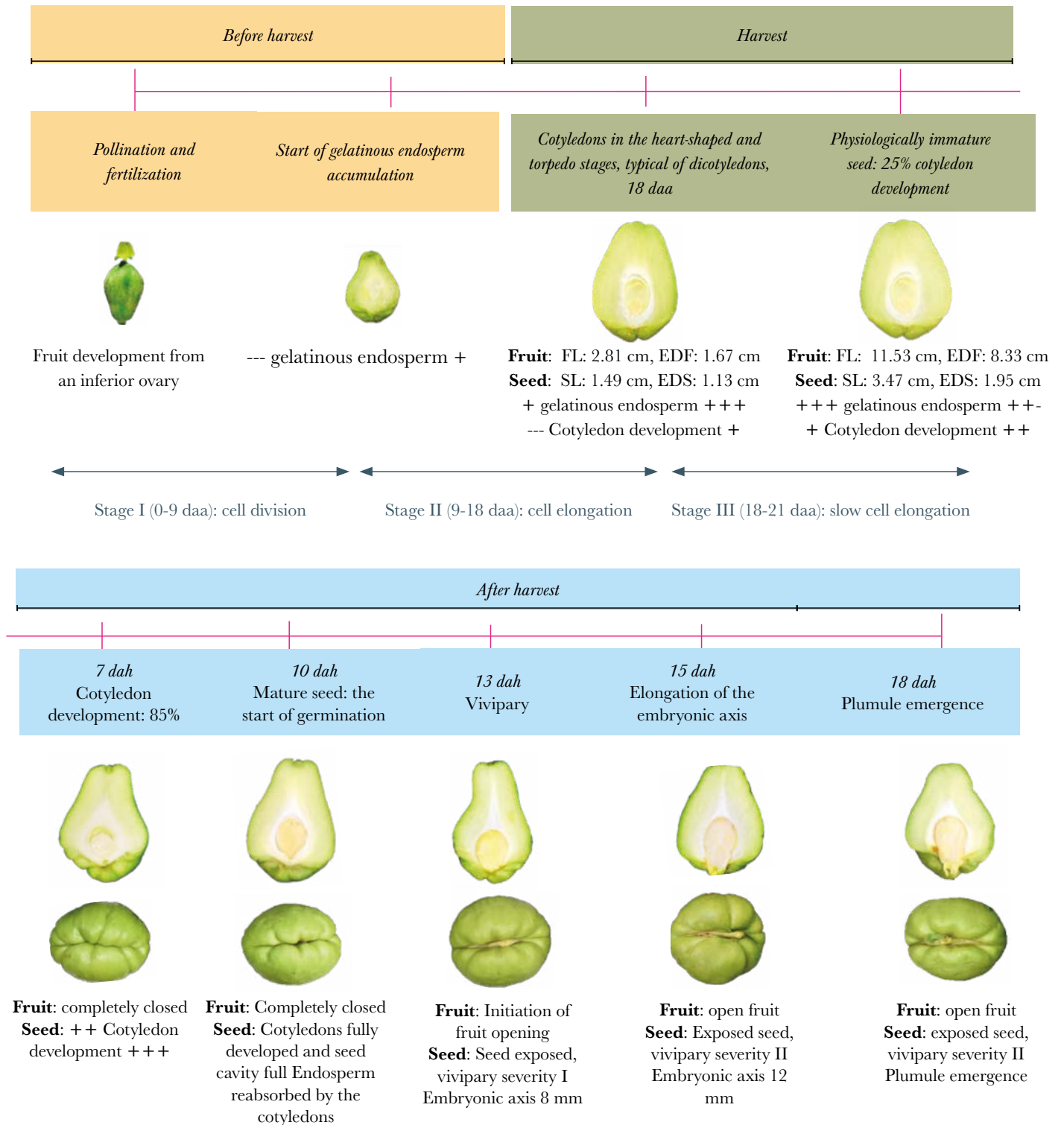


Figure 4. Morphophysiological changes in chayote seeds var. *virens levis* during development, from anthesis to vivipary. Before harvest, fruit and seed development consists of three stages: cell division, cell elongation, and slow cell growth. At harvest, the fruit is at horticultural maturity, whereas the seed remains physiologically immature. During postharvest, the seed reaches physiological maturity at 10 days, and vivipary is observed at 13 days, with basal opening of the fruit. daa=days after anthesis, dah=days after harvest, FL=fruit length, EDF=equatorial diameter of the fruit, SL=Seed length, EDS=equatorial diameter of the seed.

at 13 °C, it is observed at 13 days after harvest, whereas at 7 °C, it appears more rapidly. As an endocarpic fruit with a recalcitrant seed, chayote continues its development after reaching physiological maturity, allowing germination, fruit opening, and visible growth of the new seedling (Ramírez-Rodas *et al.*, 2021; Ramírez-Rodas *et al.*, 2023).

Vivipary and hormonal regulation during germination

Chayote fruits lose commercial quality as consumers perceive them as less attractive due to dehydration, pathogen presence, physiological maturity, and, primarily, vivipary (Romero-Velázquez *et al.*, 2015; Ramírez-Rodas *et al.*, 2023; Rivera-Ponce *et al.*, 2024). Vivipary is observed during the first week after harvest at room temperature (24 °C). However, when fruits are stored at 13 °C, it is observed at 13 days after harvest, whereas at 7 °C, it appears earlier. As an endocarpic fruit with a recalcitrant seed, chayote continues developing after reaching physiological maturity, allowing germination, fruit opening, and visible growth of the new seedling (Ramírez-Rodas *et al.*, 2021; Ramírez-Rodas *et al.*, 2023).

This phenomenon also occurs in papaya, mamey sapote (*Pouteria sapota*), tomato (*Solanum lycopersicum*), maize, *Arabidopsis thaliana*, pecan (*Carya illinoensis*), coconut (*Cocos nucifera*), chili pepper (*Capsicum annuum*), mango, and other species (Cruz and Deras, 2000; Farnsworth, 2000; Shareefa *et al.*, 2014; Wood, 2015; Cota-Sánchez, 2018; Krishna *et al.*, 2020; Garg and Garg, 2021). However, in these fruits, vivipary does not necessarily affect appearance, whereas in chayote it causes fruit deterioration by facilitating pathogen entry, altering appearance, and ultimately reducing shelf life (Figures 5A-5C).

Protection against desiccation in seeds, particularly orthodox seeds, is considered to arise from the production of molecular antioxidants and carbohydrates, as well as metabolically inert proteins that are highly soluble in water. The production of these potential protective compounds is induced in both orthodox and recalcitrant seeds during late embryogenesis; however, this response appears to be more pronounced in orthodox seeds (Walters *et al.*, 2008).

In orthodox seeds, embryo viability during dormancy has been associated with a reduction in water volume within the vacuoles (Magnitskiy and Plaza, 2007; Méndez-Ferreira *et al.*, 2013). During desiccation, these seeds acquire adaptive mechanisms that prevent cellular deterioration. These mechanisms may be related to the accumulation

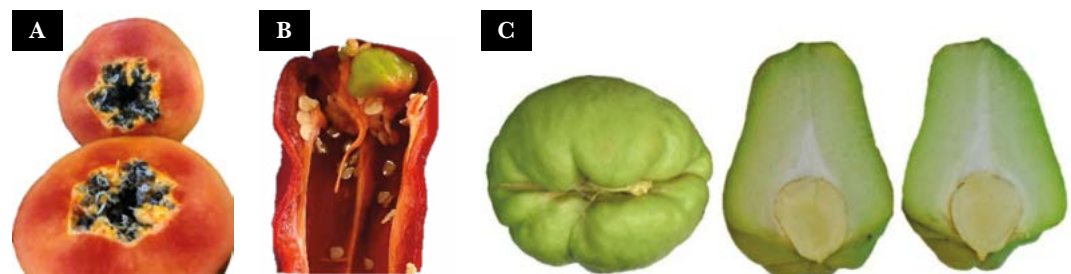


Figure 5. Vivipary in fruits of different species. Postharvest vivipary in papaya (A) and chili pepper (B), species in which fruit appearance is not affected because the fruit remains completely closed. Vivipary in chayote (C), showing the basal opening of the fruit.

of disaccharides, such as trehalose and sucrose, and oligosaccharides, such as raffinose, which help stabilize membranes through hydrogen bonding and cellular vitrification. In addition, during this period, orthodox seeds accumulate antioxidant compounds, heat shock proteins (HSPs), and late embryogenesis abundant (LEA) proteins. These LEA proteins are small, hydrophilic, intrinsically disordered, and thermostable, and they exhibit antioxidant activity, help remove reactive oxygen species, prevent the degradation of other proteins, and form hydrogen bonds that stabilize membranes (Berjak and Pammenter, 2013; Méndez-Ferreira *et al.*, 2013; Farooq *et al.*, 2022).

Dormancy and germination processes are closely related to phytohormones, including gibberellins, ethylene, and abscisic acid, as well as their synergistic and antagonistic interactions (Kucera *et al.*, 2005). During dormancy in orthodox seeds, abscisic acid (ABA) regulates the accumulation of storage reserves, including proteins, lipids, and carbohydrates; inhibits embryo growth; and induces the production of late embryogenesis abundant (LEA) proteins and heat shock proteins (HSPs), which provide protective functions to other proteins during seed desiccation (Kermode, 2005).

Plants accumulate ABA through phloem transport or through synthesis within the seed itself, which occurs during the intermediate stage of seed development. Among the transcription factors that regulate seed development are *abscisic acid insensitive 3 (ABI3)*, a central ABA-related transcription factor, and *FUSCA 3 (FUS3)*, a gene involved in seed development. These factors promote reciprocal activation, and ABA accumulation inhibits gibberellin (GA) biosynthesis, thereby maintaining dormancy (Sano and Marion-Poll, 2021).

When seeds encounter the conditions required to break dormancy, the levels of certain phytohormones change: ABA decreases, whereas GA levels increase and promote germination. In addition, GAs activate genes involved in the biosynthesis of enzymes such as endo- β -1,4-mannanase, endo- β -1,3-glucanase, and expansins in the endosperm. They also stimulate embryonic cell expansion, regulate the activity of *replication protein A1 (RPA1)*, which is found in actively dividing tissues, and activate hydrolytic enzymes that degrade starch (Kucera *et al.*, 2005; Corbineau *et al.*, 2014; Miransari and Smith, 2014). Other phytohormones, including ethylene, auxins, jasmonic acid (JA), brassinosteroids (BRs), and cytokinins (CKs), also participate in promoting germination. In addition to GAs, ethylene interacts antagonistically with ABA and synergistically with GAs, contributing to dormancy release (Farooq *et al.*, 2022).

Unlike orthodox seeds, in which LEA proteins accumulate more abundantly and are considered important protective molecules during desiccation, recalcitrant seeds show reduced abundance of these proteins. In this regard, Delahaie *et al.* (2013) characterized the cotyledon proteomes of *Castanospermum australe* (recalcitrant) and *Medicago truncatula* (orthodox). They identified transcripts for 16 homologs of 17 LEA genes for which polypeptides were detected in *M. truncatula* seeds. For 12 LEA genes, the corresponding polypeptides were absent or strongly reduced in *C. australe* cotyledons compared with *M. truncatula* seeds.

Recalcitrant seeds generally contain limited amounts of ABA during development and higher levels of GAs during germination, accompanied by other phytohormones that act

synergistically or antagonistically (Romero-Rodríguez *et al.*, 2018). In the specific case of chayote, Ramirez-Rodas *et al.* (2024) described the complex hormonal relationship in the seed before and during germination, at 7 and 10 days after harvest, using metabolomic data. They highlighted that ethylene, gibberellins, and their precursors synergistically accelerate seed germination.

Delayed seed germination is attributed to the differential accumulation of indole-3-acetic acid, indole-3-butyric acid, abscisic acid, and their precursors, which stimulate their own biosynthesis. Therefore, the antagonistic behavior of these two phytohormonal groups gibberellin ethylene and auxin abscisic acid accelerates or delays chayote seed germination, respectively, by mutually restricting their biosynthesis.

Physiology and postharvest response of chayote as a non-climacteric fruit

Harvested agricultural products are living plant organs with high water content and active metabolism. Therefore, when metabolic processes accelerate, postharvest life becomes shorter. Physiological changes, such as respiration, transpiration, ripening, and senescence, may occur slowly or rapidly and are influenced by environmental conditions, including temperature, humidity, and physical damage stress, as well as genetic factors, phytohormones, diseases caused by phytopathogens, and whether the fruit is climacteric or non-climacteric (Fukano and Tachiki, 2021). Climacteric fruits show a characteristic increase in respiration and ethylene production, accompanied by postharvest ripening. Examples include tomato, avocado (*Persea americana*), apple (*Malus domestica*), peach (*Prunus persica*), mango, pear (*Pyrus communis*), and banana (*Musa paradisiaca*). In contrast, non-climacteric fruits do not show a relevant increase in respiration or ethylene production. However, after harvest, at consumption maturity, they begin senescence. Examples include cucumber, strawberry (*Fragaria* spp.), blackberry (*Rubus ulmifolius*), watermelon (*Citrullus lanatus*), pineapple (*Ananas comosus*), grape (*Vitis vinifera*), citrus fruits, and chayote (Chen *et al.*, 2018; Kou *et al.*, 2021).

Chayote fruit is classified as non-climacteric, with a low respiration rate ($0.86\text{-}1.3 \text{ kg}^{-1} \text{ s}^{-1} \text{ CO}_2$) and minimal ethylene production after harvest, approximately $3.5\text{-}5 \text{ ng kg}^{-1} \text{ s}^{-1}$ (Cadena-Iñiguez *et al.*, 2006). In addition, a dependence between the fruit and the seed has been observed. Therefore, once the fruit is harvested, it enters senescence, making it necessary to develop preharvest and postharvest strategies to extend fruit shelf life. To counteract senescence caused by dehydration, chilling injury, blistering, and other phytosanitary disorders, and especially to delay vivipary, several studies have been conducted in different chayote varieties (Figure 6). Vivipary in chayote cannot be attributed solely to fruit deterioration; rather, it results from a physiological interaction between the seed and the fruit. Unlike most fleshy fruits, chayote contains a large, recalcitrant, nondormant seed that remains metabolically active. The fruit supplies water, gases, and hormonal signals to the seed, highlighting the importance of postharvest treatments for controlling vivipary. Although these treatments are not applied directly to the seed, they modify the physiological environment of the fruit.

To counteract vivipary, low-temperature storage and modified atmospheres have been used to slow fruit and seed metabolism. Edible coatings have also been applied to

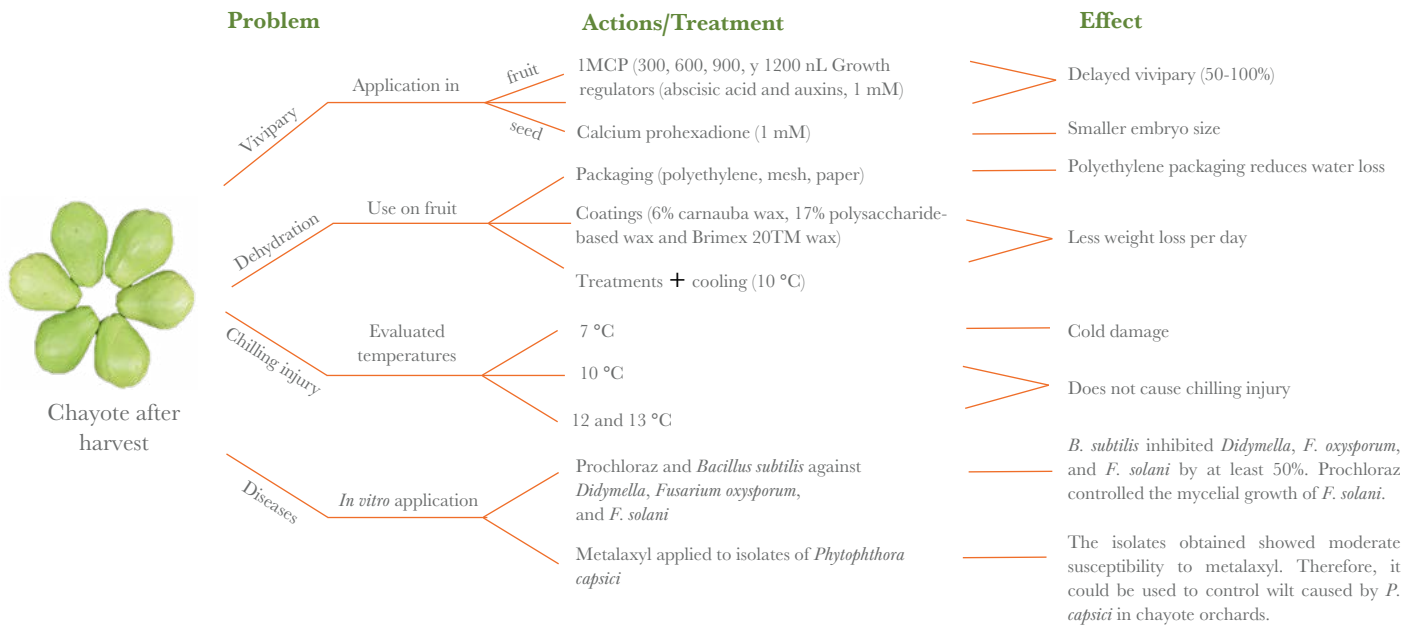


Figure 6. Postharvest management of chayote fruits. The four main problems affecting postharvest fruit quality are shown: vivipary, dehydration, chilling injury, and diseases, along with their respective management actions or treatments and effects.

regulate gas exchange within the fruit. Because vivipary is influenced by modulation of the hormonal balance, treatments such as 1-methylcyclopropane (1-MCP) have been evaluated. Due to its structural similarity to 1-aminocyclopropane-1-carboxylic acid (ACC), the ethylene precursor, 1-MCP competes for ethylene-related action sites and has a high affinity for ethylene receptors (ETRs), making it a direct competitor for ethylene perception (Balaguera-López *et al.*, 2021). Cadena-Iñiguez *et al.* (2006) applied 1-MCP at 300, 600, 900, and 1,200 nL L⁻¹ to chayote fruits var. *virens levis*. The treatments delayed vivipary in more than 90% of fruits after 31 days after harvest, consisting of 28 days at 10 °C followed by 3 days without refrigeration. Similarly, Ramírez-Rodas *et al.* (2021) applied 600 nL L⁻¹ 1-MCP to fruits of the varieties *virens levis*, *nigrum spinosum*, and *nigrum xalapensis*. After 21 days after harvest, consisting of 14 days at 13 °C followed by 7 days at 24 °C, vivipary was delayed by 50%, 87%, and 100%, respectively. Calcium prohexadione (1 mM) has also been injected directly into chayote seeds to inhibit gibberellin (GA) synthesis, resulting in smaller embryos (~80 mm) after 35 days of fruit storage at 25 °C (Aung *et al.*, 2004).

The application of abscisic acid and auxins also delays vivipary in chayote fruits var. *virens levis* by affecting the biosynthesis of ethylene, gibberellins, and their precursors. Ramirez-Rodas *et al.* (2024) applied 2-chloroethylphosphonic acid, an ethylene-releasing compound, at 1.4 mM; GA₃ at 0.6 mM; ABA at 1 mM; and auxins, including indole-3-acetic acid and indole-3-butyric acid, at 1 mM to *S. edule* var. *virens levis* fruits. A control group treated with distilled water was also included. Fruits were evaluated at 0, 7, 10, 13, and 18 days at 21 ± 1 °C and 65% relative humidity. Exogenous application of 2-chloroethylphosphonic acid and GA₃ accelerated germination and vivipary, whereas auxins and abscisic acid delayed both processes.

Implications for germplasm conservation

Conservation of orthodox and recalcitrant seeds

The conservation of plant species depends on the type of seeds they produce. Accessions are stored as different types of collections. Orthodox seeds can be conserved in germplasm banks in the short and medium term, between 10 and 20 years, as active collections stored under controlled refrigeration conditions of 0-5 °C and 10%-30% relative humidity. They can also be conserved long term, for more than 20 years, as base collections under controlled freezing conditions of –18 to –20 °C and 10%-30% relative humidity (Rao *et al.*, 2007). These conditions allow collections to remain metabolically slow but viable over time. In Mexico, several germplasm banks store orthodox seeds from different species, such as maize, chili pepper, common bean, squash, rice, wheat, roselle, and sesame. These include the National Genetic Resources Center (CNRG), the Southern Orthodox Seed Germplasm Bank of the National Institute for Forestry, Agricultural, and Livestock Research (INIFAP), the Seed Germplasm Bank of the International Maize and Wheat Improvement Center (CIMMYT), and the National Plant Germplasm Bank of Chapingo Autonomous University, among others. Once seeds reach physiological maturity, they are dehydrated to ensure storage and enter a period of dormancy until conditions become favorable for germination.

In contrast, because recalcitrant seeds do not tolerate desiccation, alternative *ex situ* conservation methods are used, including the following:

- **Cryopreservation of embryonic axes.** This technique requires partial drying to prevent damage caused by ice crystal formation, allowing the vitrification of the remaining intracellular water when cooling rates are sufficiently rapid. Recalcitrant seeds are generally too large to allow the drying and cooling rates required for vitrification; therefore, excised embryonic axes are used (Pammenter and Berjak, 2014; Berjak and Pammenter, 2014). However, this storage method is not widely used because of seed complexity, maintenance costs, and short-term viability limitations.
- ***In vitro* conservation.** Plant tissue culture techniques allow plant material to be preserved under controlled conditions. These methods maintain plantlets in *in vitro* germplasm banks, free of pathogens, in reduced space, at low cost, and under controlled conditions that facilitate short- and long-term management of plant material (Morales, 2015).
- ***In vivo* conservation.** This approach involves maintaining collections in germplasm banks, botanical gardens, nurseries, or even in the cultivation area itself, including *in situ* conservation with cooperating producers (Fernández *et al.*, 2023).

Conservation of chayote diversity in México

Conservation techniques

Techniques for conserving chayote diversity include a set of *in situ* and *ex situ* strategies focused on preservation, management, and use. Common crop varieties are generally maintained *in situ* as living plants by producers within traditional agricultural systems and are part of conservation practices (Priyanka *et al.*, 2021). Different cultivated species

and varieties of *Sechium* have been conserved in family backyard gardens because they contribute to food supply and income generation. To date, this has been the most effective approach for conserving chayote diversity *in situ* in Mexico (Cadena-Iñiguez *et al.*, 2010).

Common crop varieties are generally maintained *in situ* as living plants by producers within traditional agricultural systems, making this an important conservation practice (Priyanka *et al.*, 2021). Different cultivated species and varieties of *Sechium* have been conserved in family backyard gardens because they contribute to food supply and income generation. To date, this approach remains the most effective method for conserving chayote diversity *in situ* in Mexico (Cadena-Iñiguez *et al.*, 2010).

For *ex situ* conservation, *in vitro* conservation represents a strategic alternative for safeguarding chayote genetic diversity. Several studies have reported *in vitro* protocols for the regeneration of *S. edule* plant material through organogenesis (Alvarenga-Venutolo *et al.*, 2007; Cruz-Martínez *et al.*, 2017; Soto-Contreras *et al.*, 2022), as well as shoot regeneration and callusogenesis in *S. compositum*, a wild chayote species (Riviello-Flores *et al.*, 2024). These approaches support the conservation of plant material and provide an important source of natural products, such as phenolic compounds and cucurbitacins (Cadena-Iñiguez *et al.*, 2024). In addition, techniques such as clonal micropropagation, axillary bud culture, and conservation under slow-growth conditions have been widely used for *in vitro* conservation of other species. These methods allow genotypes to be maintained in reduced spaces and under controlled conditions, thereby decreasing risks associated with environmental and phytosanitary factors (Engelmann, 2011). However, the application of these methodologies in *Sechium* still faces challenges, including the optimization of genotype-specific protocols, evaluation of the genetic stability of regenerated material, and possible occurrence of somaclonal variation (Benson, 2008).

Regarding institutional actions for chayote conservation, the Interdisciplinary Research Group on *Sechium edule* in Mexico (GISEM) has designed a national program for the rescue, conservation, and research of infraspecific variation in *S. edule*, including wild species, cultivated varieties, and hybrids. Most of the morphological, structural, biochemical, and genetic characterization has been carried out, enabling the identification of varietal descriptors and the establishment of the *Sechium edule* Germplasm Bank (BANGESE) in 2005-2007, located in Huatusco, Veracruz. BANGESE currently contains more than 100 accessions from 10 Mexican states, as well as accessions from Guatemala and Costa Rica (Cadena-Iñiguez *et al.*, 2010).

At BANGESE, accessions of domesticated chayote belonging to *S. edule* are arranged according to varietal groups. Wild accessions of *S. edule*, *S. compositum*, and *S. chinantlense* are located in understory areas, which provide greater protection from excessive irradiation, drought, and herbivore attack. In addition, BANGESE includes an area for improved germplasm, such as bitter varieties and hybrids. Currently, the GISEM interdisciplinary group is working to achieve *in vitro* conservation of this plant germplasm. This effort aims to provide a backup of chayote diversity and preserve it for long periods in the *in vitro* germplasm banks of the National Center for Genetic Resources and Productivity (CNRG-INIFAP).

CONCLUSIONS

Chayote is a vegetable crop with distinctive characteristics due to its recalcitrant seed, which creates specific challenges for crop conservation and postharvest management. The physiological characteristics of its seed require high humidity and controlled temperature conditions to maintain viability, making long-term storage difficult. Therefore, its diversity is conserved mainly through methods used in producers' backyard systems, *in vivo* germplasm banks, and some *in vitro* collections. Another important area of opportunity is postharvest fruit management, as strategies are needed to minimize physical damage, prevent pathogen proliferation, and delay dehydration and vivipary. Given that chayote is a commercially important vegetable crop for both national markets and export, developing technologies that help maintain fruit quality for longer periods is essential.

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