International Journal of Innovation and Applied Studies
ISSN 2028-9324 Vol. 48 No. 2 Apr. 2026, pp. 633-641
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http://www.ijias.issr-journals.org/

Fruit dehiscence: Mechanisms, genetic determinism, and evolutionary implications

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ABSTRACT: Fruit dehiscence is a complex process that leads to seed dispersal and affects the completion of the reproduction cycle of many plant species. This process has a negative impact on crop yields at harvest, regardless of the harvesting method used, and when dehiscence is complete, mechanized harvesting becomes almost impossible. Environmental factors such as temperature and humidity certainly play a crucial role, but structural factors and fruit anatomy also contribute significantly. The aim of this review was to summarize fruit dehiscence in general, including its causes, mechanisms, and genetic determinism. The intrinsic causes inherent in the fruit itself, which determine the type of dehiscence, and tissue desiccation as an extrinsic cause were reviewed. This literature review also provided an understanding that fruit dehiscence, its mechanisms, and its development are determined within the fruit and regulated by specific genes in the pericarp and the dehiscence zone.

KEYWORDS: shattering, genetic, determinism, crop improvement.

1 INTRODUCTION

The fruit is a set of parts resulting from fertilization that forms a complete whole after ripening, in which the main parts (seeds, placentas, carpels, and cavities) and accessory parts (calyx, receptacles, cell partitions) play a crucial role. Reference [1] report that fruits are a major evolutionary innovation of angiosperms, whose purpose is to develop seeds and facilitate offspring. The latter function is of great ecological importance and explains the high adaptive forces that have led to the great diversity of fruit morphology and function. [2] and [1] add that a fruit is a dispersal unit that can either result from abscission or dehiscence, and that these have elements in common: a layer of small cells held together by the extracellular matrix formed at the point of rupture, and the lignification of cells in the surrounding tissues.

Fruit dehiscence is a complex process whereby ripe fruits open spontaneously to release their seeds. This mechanism, the result of millions of years of evolution, is a particularly sophisticated seed dispersal strategy in many flowering plants [3]. It occurs at maturity in follicles and capsules and causes the release of the seed (s) due to the rupture of the fruit wall as a result of internal tension ([4], [5]) in the area (s) of dehiscence and the action of the dehiscence mechanism [6]. It leads to seed dispersal, and although this is an adaptation strategy in wild habitats [2], seed retention allows maximum yield to be harvested while mitigating seed deterioration [7]. However, in cultivated species, it is a critical process that affects the completion of the propagation cycle of many plant species and leads to yield losses ([8], [9]). It is a trait that has been counter-selected since the beginning of agriculture. For example, in sesame, capsule dehiscence can cause seed yield losses of up to approximately 80%, making mechanized harvesting almost impossible ([8], [10]) and highlight that resistance to dehiscence is an interesting trait in cultivated species [11]. Various studies have been conducted on fruit dehiscence, but most have been conducted on *Arabidopsis thaliana,* a Brassicaceae. Understanding this phenomenon is of considerable importance from both a fundamental and applied perspective, particularly for crop improvement, where premature dehiscence can lead to substantial agronomic losses of up to 25-80% of yield in some crops ([12], [13]).

This review presents some general concepts on fruit dehiscence, mechanisms, and genetic determinism in order to better understand fruit dehiscence and the various factors and phenomena involved. In addition, perspectives are outlined to contribute to genetic improvement for resistance/tolerance to dehiscence.

2 DEFINITION AND CLASSIFICATION

Dehiscence refers to the natural opening of a ripe fruit along predetermined lines of least resistance [14]. There are several types of dehiscence, depending on how the fruit opens. Dehiscent fruits are opposed to indehiscent fruits, which remain closed when ripe and whose seeds are dispersed with the fruit envelope [15]. The main types of dehiscence (Fig. 1 & 2) include loculicidal dehiscence, where the opening occurs at the back of each carpel; septicidal dehiscence, characterized by an opening along the partitions separating the locules; septifrage dehiscence, which combines the two previous modes; and pyxidial (or transverse) dehiscence ([16], [17], [18]). Legumes have a particular type of dehiscence along two sutures, dorsal and ventral, allowing the fruit to separate into two valves [19]. Reference [18] adds that dehiscence itself (loculicidal and septifrage) is a rupture of the walls of the chambers, either irregularly so that they fall apart (genus *Linaria*), either by perforation (*Antirrhinum*, *Campanula*), or by a transverse slit (*Anagallis*), but most often as a result of one or more longitudinal slits running from top to bottom or bottom to top on the fruit, covering all or part of its length. Finally, pyxidial dehiscence occurs through the transverse rupture of the pericarp (whether this pericarp is composed of a single or several carpels, or whether it comes from a free ovary or an adherent ovary).

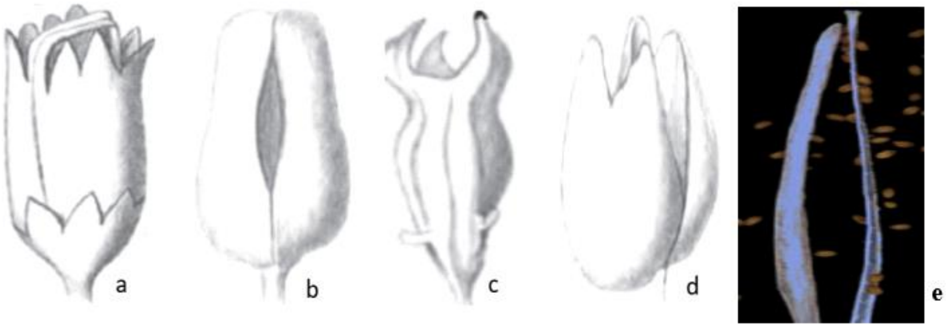

Fig. 1. Some types of fruit dehiscence.
(a): loculicidal dehiscence in Linaria; (b): septicidal dehiscence in Digitalis; (c): poricidal dehiscence in Campanula; (d): pyxidial dehiscence in Hyoscyamus; (e): septifrage dehiscence in Arabidopsis.

Sources: a, b, c, and d [17], e [2]

Fig. 2. Different degrees of dehiscence in sesame
(a) Super dehiscent, (b) semi-dehiscent, (c) indehiscent

3 ANATOMICAL AND DEVELOPMENTAL BASES

Dehiscence results from anatomical and histological changes that occur in the early stages of fruit development [20]. The areas of dehiscence (Fig. 3), often referred to as abscission zones or suture lines, are characterized by specialized cells with thinner and less lignified walls than the surrounding tissue [21]. These cells form a region of predetermined structural weakness. During fruit development, these zones undergo progressive changes. Cells in these zones accumulate hydrolytic enzymes, particularly cellulases and pectinases, which degrade cell wall components ([22], [23]). At the same time, adjacent tissues may develop mechanical elements that create internal stresses. The combination of localized weakening and mechanical stresses results in the controlled rupture of the fruit.

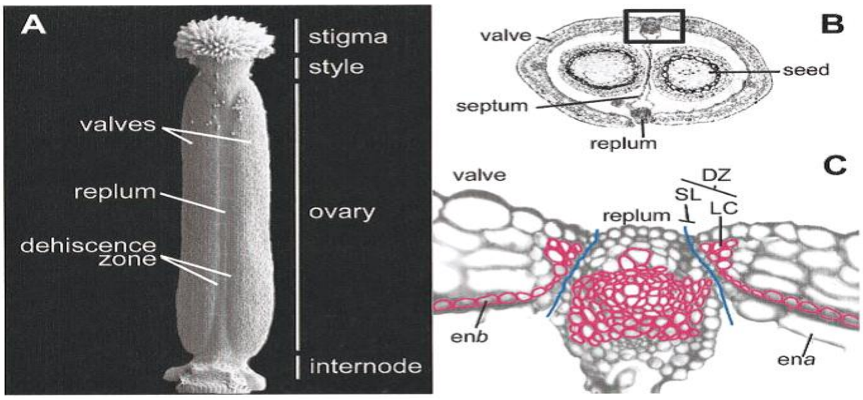

Fig. 3. The Arabidopsis fruit. Scanning micrograph of a silique shortly after pollination (stage 14, according to Smyth et al., 1990). The different parts of the fruit are indicated. Transverse section of the ovary of a mature silique (stage 17B). A close-up of the boxed area is shown in (C). Section of the dehiscence zone of a stage 17B silique. Lignified cell walls have been traced in pink for clarity, and the fracture surface in the separation layer is noted by a blue line. DZ, dehiscence zone; SL, separation layer; LC, lignified cells at the valve margin mesocarp; ena, endocarpa, already disintegrating in the left valve; enb, endocarpb

Source: [24]

4 CAUSES AND FACTORS INVOLVED IN FRUIT DEHISCENCE

Reference [25] report that structural factors and anatomical mechanisms are also involved There are many causes of fruit dehiscence, including intrinsic and extrinsic causes. [17] reports tissue desiccation as the sole and main extrinsic cause considered by botanists to be capable of causing dry fruit dehiscence, whether produced by an increase in temperature or a decrease in atmospheric humidity. According to the same author, intrinsic causes are inherent in the fruit itself and must be sought in its structure; for these causes, the fruit has a particular mode of dehiscence. A combination of mechanical forces on the pericarp and the development of a mechanically weak region in the pericarp may cause fruit dehiscence ([26], [5]).

5 MECHANISMS OF FRUIT DEHISCENCE

Dehiscence occurs in an area called the dehiscence zone, often consisting of specialized cells where separation occurs ([27], [24], [26], [5]). There is diversity in the shape, texture, and maturity of fruits. However, the cytological processes of lignification and separation in the dehiscence zone determine fruit dehiscence [9]. After a fruit opens due to desiccation, some of its parts curl and contract to produce the slits and openings through which the seeds escape [17]. Lignified fibers contract less in the direction of their length than in a perpendicular direction, and lignified cellular elements of any shape contract even more. Non-lignified tissues, on the other hand, contain much more water and contract much more during desiccation. In the other hand, [28] and [29] report that hygroscopic deformations (Fig. 4) are often used by plants to activate dehiscence mechanisms.

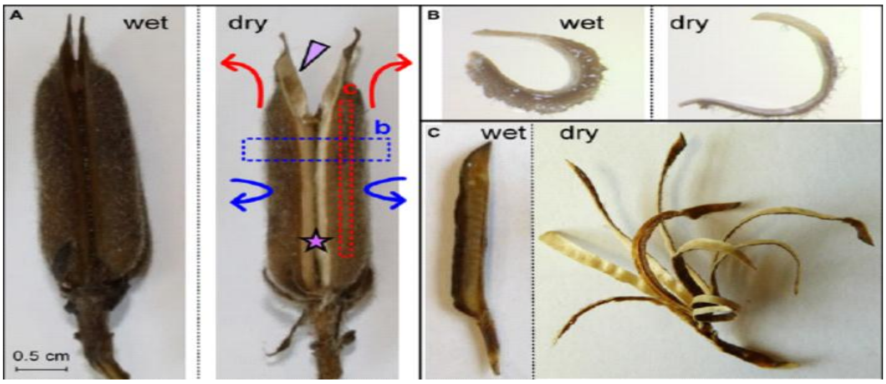

Fig. 4. Hygroscopic movement of the sesame capsule. (A): Movement of the entire capsule. The dry capsule opens along a slit marked by a star. An arrow points to one of the four seed compartments. The arrows represent circumferential (blue) and longitudinal (red) movements. (B): The cross section, marked by a blue frame in (A), straightens as it dries. (C): The longitudinal segments are marked by a red frame in (A). Note the gradient of curvature along the circumference of the locule. The scale bars represent 5 mm.

Source: ([28], [29])

In sesame (*Sesamum indicum* L.), when the capsule dries, the mesocarp cells dry out, but not those of the endocarp (Fig. 5). This phenomenon creates tension that causes the ends to open along the false membranes inside the carpels, causing the placental membranes to separate and forcing the capsule to split open. Dehiscence in sesame is thought to be influenced by additional cell layers of parenchyma in the mesocarp, in the middle and at the end of the capsule [29]. Five (5) characteristics of the sesame capsule that affect the degree of dehiscence have been described, namely: its opening (the degree of opening of the carpels), capsule division, capsule constriction (narrowing of the capsule wall around the seed), completeness of the capsule membrane (in some cultivars, the false membranes are partially missing), and seed attachment to the capsule placenta [30].

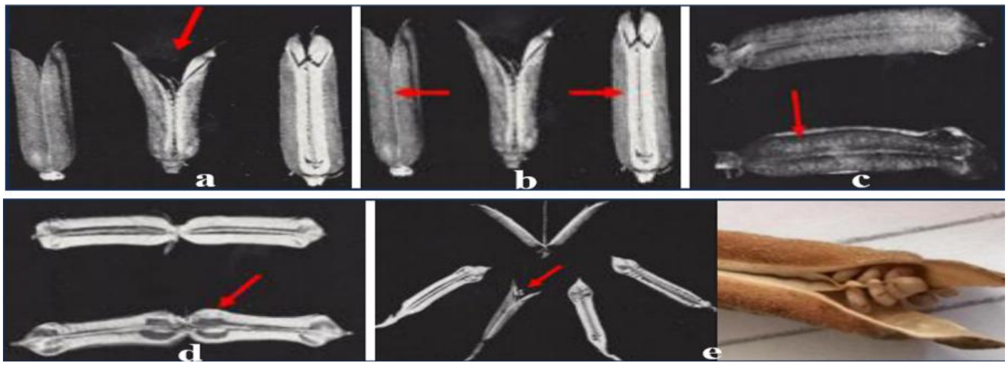

Fig. 5. Capsule characteristics affecting the degree of dehiscence. (a): degree of capsule opening; (b): capsule division; (c): capsule constriction; (d): completeness of the capsule membrane; (e): attachment of seeds to the placenta.

Source: [29]

5.1 MOLECULAR MECHANISM OF DEHISCENCE

Advances in molecular biology have revealed a complex genetic architecture governing dehiscence. The best-characterized model is that *of Arabidopsis thaliana,* whose fruit (silique) has four distinct tissue zones: the valves, the dehiscence zone (valve margin), the replum (central tissue), and the septum (partition) [20].

Fruit dehiscence is controlled by molecular mechanisms that have been well characterized in *Arabidopsis thaliana*: The fruit elongates, then the valve margins differentiate after fertilization ([3], [24], [1]). The dehiscence of *Arabidopsis thaliana* siliques is mainly related to the lignification of the endocarp and the valve edge [31]. Reference [6] report that the behavior of cells in different areas of the fruit wall, namely swelling, shrinking, and the production of osmotic turgor pressure, provides the basic mechanism for the dehiscence of the fruiting carpel. According to the same author, in Brassicaceae species, fruit dehiscence begins when the fruit valves tear due to mechanical tension developing on the inner area of the pericarp; then the drying cells of the sclerenchyma orient themselves where lower static tension is exerted. As for the dehiscence of *Camellia oleifera,* it begins at the apex of the fruit, which appears to be the weakest point, and continues along the suture [9].

The dehiscence of soybean pods (*Glycine max*) is correlated with various stresses that develop within the cells of the inner layer of the sclerenchyma following dehydration due to the difference in physical strength between the pericarp and endocarp [32]. The moisture content of the pods and the relative humidity of the environment are also correlated and constitute the physical forces underlying pod dehiscence.

5.2 GENETIC DETERMINISM OF FRUIT DEHISCENCE

Several authors ([27], [24], [33], [34]), have shown that fruit dehiscence, its mechanism, and its development are genetically determined in the capsule and regulated by the expression of specific genes in the pericarp and dehiscence zone. These two decades have also been decisive in determining the genes and mutations involved in fruit dehiscence in general ([35], [36], [7], [37]). Various genes have been described as having key regulatory roles in the formation of valve margins and the differentiation of the dehiscence zone *in Arabidopsis thaliana* ([38], [34], [2]). According to [39] and [9], the cellulose gene (CEL6) and the hemicellulose gene (MAN7) promote dehiscence in *Arabidopsis thaliana,* and the pectinase genes (ADPG1 and ADPG2) encoding polygalacturonase (PG) are also essential.

The MADS-box SHATTERPROOF (SHP1/SHP2) genes repeatedly control the identity of the valva margin and are essential for the formation of the dehiscence zone ([24], [2]). In *shp1 shp2* mutants, the fruits become completely indehiscent because the dehiscence zone does not differentiate properly [21]. SHP1 and SHP2 activate the expression of genes encoding cell wall degradation enzymes, including polygalacturonases and cellulases. According to ([24], [40], [34], [1], [41]), in addition to SHP1 and SHP2, the ALCATRAZ (ALC) and INDEHISCENT (IND) helix-loop-helix genes, the FRUITFULL (FUL) gene, NAC (NST1 and NST2), and SPATULA (SPT) genes are also known to be involved in the formation of the dehiscence zone. ALC controls final cell separation in the dehiscence zone. It activates the expression of genes involved in the degradation of the middle lamella between cells [27]. *Alc* mutants show delayed or absent dehiscence. SHP1 and SHP2 regulate the expression of IND and ALC genes. They therefore contribute to the establishment and differentiation of the valve margin tissue, leading to the opening of the valve through lignification, which plays a key role in fruit dehiscence ([42], [3]). In addition, some authors ([21], [27], [43]) report that the IND gene is necessary for lignification and separation of the valve margin. IND codes for a bHLH transcription factor that spatially delimits the dehiscence zone. It is expressed in a narrow band of cells along the valve margin and restricts SHP activity to this specific region [40]. *IND* mutants exhibit abnormal expansion of the valve margin tissues. The FUL gene negatively regulates the ALC, IND, SHP1, and SHP2 genes to ensure the differentiation of the valve margins at the edge of the valve ([44], [40]). Mutants (shp1, shp2, alc, nst1, and nst2) show no lignin deposition, corresponding to an indehiscent phenotype. The SPATULA (SPT) gene participates in the regulation of valve margin differentiation by interacting with IND and ALC [43]. These genes therefore form a complex hierarchical network. FUL and SHP act antagonistically to delimit tissue domains: FUL defines the valves, while SHP specifies the margin valve. IND refines this delimitation by spatially restricting the activity of SHP. ALC acts downstream to execute the cell separation program [40].

A study conducted on peaches (*Prunus persica*) showed that the PPERFUL and PPERSHP genes are involved in the very early formation of the dehiscence zone in a susceptible variety [33]. The same authors report that higher expression of the FUL gene and low suppression of SHPs gene expression compared to the resistant variety are responsible for the rapid formation and lignification of the dehiscence zone, leading to the separation of the endocarp under the pressure of the growing fruit. The sh1 and sh2 genes control sesame dehiscence and function differently from Shp1, SHP1b, and BnSHP1, which control the dehiscence of *Lepidium campestre, Capsella bursa-pastoris,* and *Brassica napus,* respectively [41]. In fact, sh1 and sh2 act together in a recessive state to confer resistance to dehiscence in sesame, while total indehiscence (completely closed capsule) (Fig. 6c) is a pleiotropic recessive monogenic trait (id). This id gene also governs the shape of the leaves (Fig. 6a) and floral organs (corolla and style) (Fig. 6b).

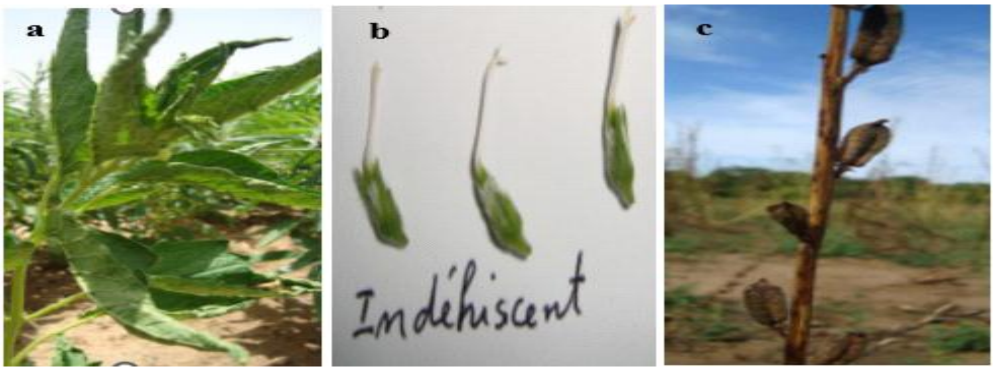

Fig. 6. Some expressions of the id gene that governs indehiscent seeds in sesame
(a) flared leaves; (b): curved style; (c): indehiscent capsule

Source: [45]

5.3 EFFECTOR GENES: DEGRADATION ENZYMES

Downstream of the regulatory network, genes encoding hydrolytic enzymes are activated in the dehiscence zone: the Polygalacturonases **(**PG) degrade pectins in the middle lamella [23] while the Cellulases depolymerize cellulose in cell walls and the Pectate lyases cleave pectate chains. The Expansins facilitate the relaxation of the cell wall [46].

The coordinated expression of these enzymes gradually weakens the cell walls in the dehiscence zone, allowing the fruit to open.

5.4 HORMONAL REGULATION OF DEHISCENCE

Fruit dehiscence is not regulated solely by gene expression. Reference [24] reports that the action of certain hormones could play a role both in the differentiation of the dehiscence zone and in the coordination of physiological events leading to cell separation:

AUXINS

In rapeseed, auxin activity is regulated by the activity of hydrolytic enzymes that act on the dehiscence zone [47]. Even at low doses, auxin is necessary for dehiscence to occur [48]. Auxin transport genes, particularly PIN transporters, create this hormonal gradient. Disruption of auxin transport leads to dehiscence defects.

GIBBERELLIC ACID (GA)

Gibberellins control fruit ripening and the timing of dehiscence. They regulate the expansion of fruit valves and modulate the expression of dehiscence genes [49]. GA-deficient mutants show delayed dehiscence, while exogenous treatments accelerate the process.

ETHYLENE

Ethylene is involved in the final stages of ripening and can trigger the expression of hydrolytic enzymes necessary for cell separation [50]. Its role varies depending on the species, being particularly important in legumes.

JASMONIC ACID (JA)

Recent studies suggest that jasmonic acid also participates in the regulation of dehiscence, particularly by modulating the expression of margin valve genes and coordinating the response to environmental stresses [26].

6 CONSERVATION AND EVOLUTIONARY DIVERGENCE

The genetic network of dehiscence shows remarkable conservation within Brassicaceae, but exhibits significant variation in other families. In legumes, orthologs of SHP and IND have been identified, but their regulation may differ [51]. In rice, the *qSH1* gene controls resistance to dehiscence through a distinct mechanism involving the formation of an abscission layer [52]. These evolutionary variations reflect independent adaptations to similar ecological constraints, illustrating the phenomenon of evolutionary convergence in seed dispersal mechanisms.

7 IMPLICATIONS FOR SYNTHETIC BIOLOGY

A detailed understanding of this genetic network paves the way for rational engineering of dehiscence. Overexpression of FUL or mutation of SHP can produce completely indehiscent fruits, an approach used to improve rapeseed [53]. Conversely, fine manipulation of these genes could allow precise control of the timing of dehiscence to optimize harvesting.

8 BIOMECHANICAL ASPECTS

Dehiscence also involves remarkable biomechanical considerations. Some fruits generate explosive movements when they open, propelling seeds several meters away from the parent plant [54]. These mechanisms are based on the accumulation of internal stresses resulting from differential tissue dehydration or the expansion of certain cell layers. The fruit of the touch-me-not (Impatiens), for example, ejects its seeds by suddenly and violently curling its valves when touched [5]. Other fruits exhibit hygroscopic movements in which the opening and closing of the valves responds to variations in humidity, promoting seed dispersal under favorable conditions [55]. These adaptations illustrate the sophistication of the evolutionary solutions developed to optimize seed dispersal.

9 EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE

Dehiscence is a major adaptation that profoundly influences the reproductive success of plants. By allowing for active and often directed seed release, it optimizes the chances of colonizing new habitats [56]. The timing of dehiscence is finely tuned to environmental conditions and plant phenology, maximizing the chances of seed survival.

The evolution of dehiscence has followed different trajectories depending on the plant lineage. In some groups, secondary loss of dehiscence has occurred, particularly when other modes of dispersal (by animals, wind, or water) have proven more advantageous [57]. This evolutionary plasticity demonstrates the selective importance of dispersal strategies.

10 AGRONOMIC APPLICATIONS

In agriculture, premature dehiscence is a major problem for many crops, particularly cereals and oilseeds [58]. The loss of seeds before or during harvest can result in considerable economic losses. Rapeseed (*Brassica napus*), for example, can lose up to 25% of its potential yield due to natural dehiscence of the siliques [12].

The selection of varieties resistant to dehiscence has been a crucial challenge in the domestication of many crop species. In sesame, rice, wheat, and other cereals, modern varieties show a marked reduction in dehiscence compared to their wild ancestors ([59], [52]). Identifying the genetic basis of this trait opens up prospects for varietal improvement through marker-assisted selection or genome editing approaches [60].

11 PROSPECTS FOR IMPROVING DEHISCENCE IN SPECIES OF AGRONOMIC INTEREST

Current research is moving towards an integrated understanding of dehiscence, combining genomics, physiology, and biomechanics [1]. The identification of new genes and regulatory networks will enable more precise control of this process in crops of interest. Furthermore, comparative studies of dehiscence in different species will shed light on the evolutionary convergences and divergences of this mechanism [61].

Modern biotechnologies, notably CRISPR-Cas9 and mutagenesis, offer precise tools for modulating dehiscence without affecting other important agronomic traits [62]. Furthermore, crossing varieties with complementary dehiscent-limiting traits, coupled with conventional selection, remains another way to create genetic variability and promote the development of lines with dehiscent-limiting characteristics.

These approaches promise to resolve the dilemma between maintaining characteristics that are advantageous for natural dispersal and the requirements of modern agriculture.

12 CONCLUSION

Fruit dehiscence beautifully illustrates the ingenuity of the evolutionary solutions developed by plants to ensure their reproduction. From the developmental specification of opening zones to the molecular mechanisms that orchestrate the process, to the biomechanical prowess of certain explosive fruits, this phenomenon reveals the complexity and sophistication of the plant world.

Dehiscence is regulated by the expression of specific genes, and various hormones play an important role in the differentiation of the so-called dehiscence zone. Efforts have certainly been made to understand the causes and mechanisms, identify the genetic basis, and produce fruits that limit their dehiscence at maturity. A deeper understanding of dehiscence continues to enrich our fundamental knowledge while offering concrete applications for sustainable agriculture and global food security.

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