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Chapter 29

The Trials and Tribulations of the Plant Male Gametophyte — Understanding Reproductive Stage Stress Tolerance

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Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/61671

Abstract

Yield and productivity of many crop species depend on successful reproductive development to produce seeds or fruits for human nutrition. Plants determine the right time to flower based on environmental cues (day length, temperature) and angiosperms have evolved a plethora of mechanisms to adapt flowering to specific environmental conditions. Despite these adaptation mechanisms, fertilisation and seed production remain subject to the reigning weather conditions before and during flowering. To fertilise the immobile female gametes inside the ovule, the male gametophytes need to be dispersed in a hostile environment. In crop plants, unexpected inclement weather conditions during male gametophyte development and pollen dispersal are often associated with dramatic yield losses. Molecular and physiological studies are gradually making progress in identifying genes and processes that control various aspects of pollen development, but the many intricacies involved in environmental control of pollen development and – in particular – regulation of male fertility remain poorly understood. The aim of this paper is to draw attention to the enormous amount of complexity and biodiversity that exist in angiosperm male gametophyte development. A better understanding of the strategies that exist in adapting pollen production and fertility to environmental challenges may ultimately benefit improvement of abiotic stress tolerance in major food crops.

Keywords: Male gametophyte, pollen, development, abiotic stress, angiosperms, fertility

1. Introduction

The reproductive cycle in plants alternates between a haploid gametophytic and a diploid sporophytic generation. During the evolution from green algae (Charophytes) to land plants, the dominance of the gametophytic generation has gradually decreased in favour of the

sporophytic generation. Originally, the gametophyte and sporophyte were separate independent organisms with very different appearances. In the first non-vascular land plants (liverworts, mosses) the gametophyte was still dominant, but in the first vascular land plants (ferns) the sporophyte prevailed. In ferns, the gametophyte is still an independent organism but with vastly reduced size. In seed-producing higher plants (Spermatophyta: angiosperms, gymnosperms), the gametophyte reduction became extreme (only a few cells) and both male and female gametophytes became physically part of the sporophyte [1, 2]. The emergence of the sporophyte as the dominant phase of the life cycle in seed plants has been attributed to genetic complementation and the capacity of the diploid stage to mask deleterious DNA mutations, an idea that was supported by the fact that land plants had to adapt to a more hostile environment. This argument has been disputed and the exact reason why the diploid sporophyte stage became dominant in land plants is still being debated [1, 3–5].

The ecological pressure to adapt to a dry environment with exposure to many new environmental stresses (water stress, UV light and heat) required a lot of morphological and developmental changes during the evolution from mosses and ferns (Archegoniatae) to Spermatophyta [6]. The generation of the vascular system, roots, stomata and the hormonal system that regulates these developmental features in Spermatophytes evolved along with adaptation to new environmental challenges [7–9]. The next step in the evolution of land plants was the establishment of sexual reproduction in a land environment and the development of gametophytes with different sizes and sexes (heterospory). Sexual reproduction offers an opportunity to recombine combinations of genetic traits and spread genetic variability between populations. This new-found capacity played a major role during evolution in the adaptation of plants to the terrestrial environment [10–12]. Sexual reproduction became therefore the prevalent reproduction system in both plants and animals [13]. The immobility of the sporophyte in land plants makes pollen and seeds the only vector systems to exchange genetic information between plant populations. Pollen production and pollination are critical in the breeding system of land plants, and the large biodiversity that evolved in plant pollination mechanisms illustrates the tight linkage with environmental adaptation [11, 14].

The origin of pollen can be traced back to heterosporous Pteridophyta (vascular plants) [15–17], which have microspores with features that are reminiscent of pollen: similar cell wall (intine and exine), storage reserves for the first stages of growth, reduction or absence of watery vacuoles at maturity [18]. In seed plants, the female gametophyte is immobile and develops totally inside the ovule of the ovary [19]. This makes pollen grains a crucial mobile vector for exchanging genetic information between different plant populations. The male gametophytes form inside the pollen sac in gymnosperms and in the anthers of angiosperm flowers (Figure 1) [2, 20, 21]. Pollen grains need to be dispersed from the anther and travel to the stigma to fertilise the immobile egg cell inside the ovule(s) of the ovary. This ovary can be located in the same flower, another flower of the same plant, a neighbouring plant or a more remote plant. The tough multi-layered pollen wall is an adaptation to protect the male gametes against environmental stresses during presentation and dispersal, while it is at the same time adapted for different pollen dispersal methods [22, 23]. The pollen dispersal methods and breeding systems in plants are amazingly diverse [14, 24]. Following domestication, many crop species

http://dx.doi.org/10.5772/61671

are grown in environments that are vastly different from their original growth habitat. The breeding system of many crop species may therefore not be optimal for their current growth habitat, let alone whether it will be adapted to a future world with a different climate. In many staple crops (e.g. rice and wheat) male reproductive development is considered the 'Achilles tendon' of reproductive development, with massive yield losses under unexpected adverse weather conditions (heat, drought, cold) becoming increasingly common occurrences [25–28]. Although the generation of haploid male gametes in angiosperms occurs via a conserved pathway, there are many variations present in different plant species in the way this process proceeds. In many cases, this biodiversity can be associated with adaptations to particular environmental restraints. This paper will explore the complexity in angiosperm pollen development and investigate how it can contribute to a better understanding of abiotic stress tolerance of male reproductive development. The focus of this review paper will be on the interaction between environment and pollen developmental processes and not on the diversity that exists in pollen–stigma compatibility and plant breeding systems. A supplementary glossary of commonly used terms and definitions related to male gametophyte development is supplied for those readers who are less familiar with this subject (See Appendix).

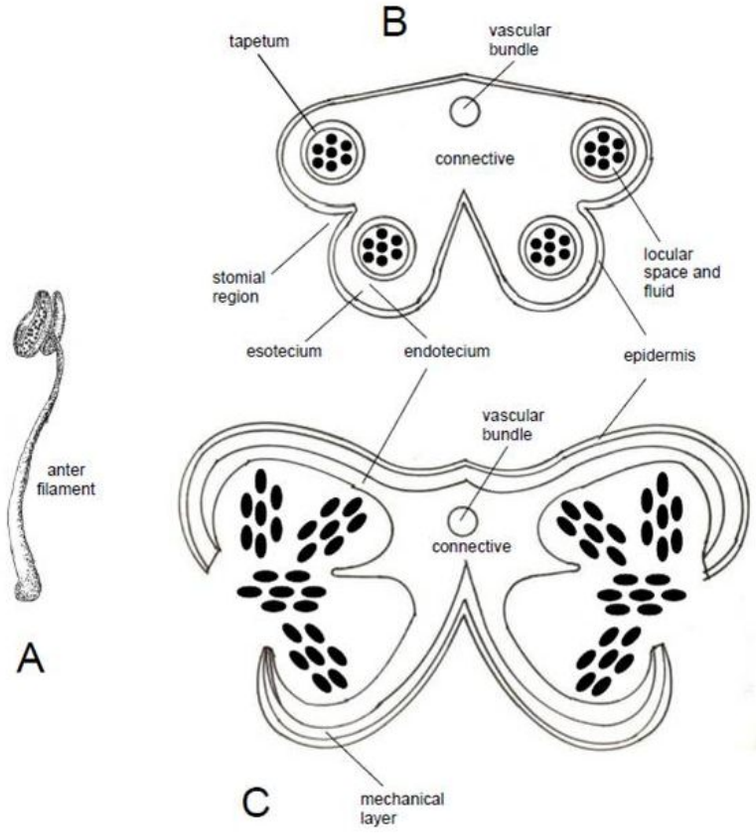

Figure 1. Schematic drawing of an ideal stamen (A), anther at microspore stage (B) and just after anther opening (C) with their components and functions. Water and some nutrients are transported by the vascular bundle from the mother plant via the filament towards the anther. Nutrients move to the tapetum via the connective tissue and components synthesised by the tapetum are then released into the loculus, where they are absorbed by the developing grains, and they are either utilised immediately or stored temporarily in the locular fluid, vacuole or amyloplasts.

2. Male gametophyte development and its biodiversity

In angiosperms, male gametophytes develop in the anther. Each anther consists of two thecae, each consisting of two adjacent microsporangia that are separated by the connective tissue (Figure 1). The first phase in pollen development, the meiotic division of the sporophytic meiocytes of the four microsporangia to form haploid tetrads and young microspores, is called microsporogenesis (Figure 2). During the second phase, microgametogenesis, the microspores enlarge and become vacuolated. Vacuolisation and the cytoskeleton force the nucleus to migrate to a peripheral position. The first mitotic division is asymmetric and produces a germ cell that is engulfed by the cytoplasm of the vegetative cell to become physically isolated from the vegetative cell (bi-cellular pollen; cell-within-a-cell). The germ cell then undergoes a second mitotic division to produce the two sperm cells (Figure 2). During fertilisation, one male gamete fuses with the egg cell and the other with the two polar nuclei of the central cell to form the zygote and endosperm, respectively. The male sperm cells are very diminutive in size, but transcriptome analysis has recently revealed that their gene expression pattern is unlike any other plant tissue, suggesting that they are functionally very specialised [29].

Pollen type	**Starch content**	*Two-celled*	*Three-celled*
Orthodox (>20% water)	Starchy	· *Olea europaea* (Oleaceae) PK · *Erica arborea* (Ericaceae)	· *Wolfia arrhiza* (Araceae) (PK) · *Lilium bienne* (Liliaceae) (PK) · *Nelumbo nucifera* (Nelumbonaceae) (PK)
	Starchless	· Solanaceae (PK presence depends on pollination syndrome) · Lamiaceae (PK) · Myrtaceae (PK) · Scrophulariaceae (PK) · *Acanthus mollis* (Acanthaceae) (PK) · *Bryonia dioica* (Cucurbitaceae) (PK) · *Cucumis melo* (Cucurbitaceae) (PK) · Liliaceae (some species) (PK)	· *Hedera helix* (Araliaceae) (PK) · *Borago officinalis* (Boraginaceae) (PK) · Caprifoliaceae (PK) · Asteraceae (PK) · *Canna indica* (Cannaceae) (PK) · *Tulipa gesneriana* (Liliaceae) (PK)
Recalcitrant (<20% water)	Starchy	· *Cucurbita pepo* (Cucurbitaceae) (PK) · *Plantago* sp. (PK) · *Portulaca tuberosa* (PK)	· Amaranthaceae (PK) · Alismataceae (PK) · Poaceae
	Starchless	· *Laurus nobilis* PK · Malvaceae PK	· *Cereus* sp. (Cactaceae) (PK) · Caryophillaceae (PK)

Table 1. Classification of pollen diversity according to cytological events during pollen development, and examples of some representative plant species. Pollenkitt (PK) is typically present in zoophilous and entomophilous species and is generally absent in anemophilous species, with the exception of *Olea europaea*, a secondary anemophilous species. Some plant families (e.g. Liliaceae) have a majority of members with two-celled starchless grains and some species with three-celled starchless pollen grains [30, 185] (E. Pacini, personal observations).

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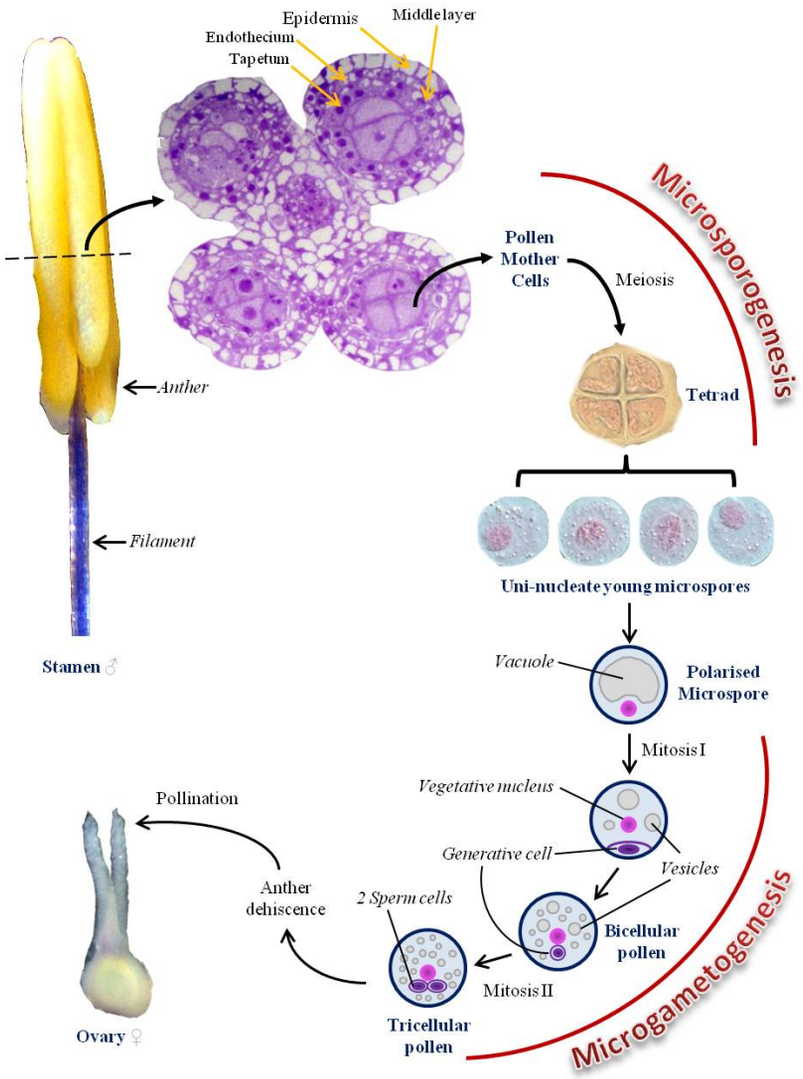

Figure 2. Male gametophyte development in angiosperms. Pollen grains develop in the stamen, which consists of a filament supporting the anther. The vascular bundles in the filament conduct nutrients from the mother plant to the anther. The cross-section of the anther (rice) before the onset of meiosis shows the four microsporangia where the male gametophytes develop. From outside to inside, the anther wall consists of the epidermis, the endothecium, the middle layer and the tapetum. Both the middle layer and the tapetum degenerate towards pollen maturity, leaving only the epidermis and the endothecium to protect the pollen grains in the loculus before anther opening. The central cells of the anther, the pollen mother cells (meiocytes), differentiate and become selectively isolated from the mother plant through callose secretion by the meiocyte cytoplasm. The pollen mother cells undergo meiosis to form tetrads. The uni-nucleate young microspores are released from the tetrad with the help of enzymes secreted by the tapetum [313]. Exine is completed with the intervention of polymers secreted by the tapetum in the loculus [35]. Young microspores have a central nucleus and in Poaceae they are with the pore attached to tapetum until anther opening. The germination pore becomes visible and a large vacuole forms, pushing, with the intervention of the cytoskeleton, the nucleus in a peripheral position (polarised microspore stage) [176, 314]. At the vacuolated stage, the microspores undergo an asymmetric division (pollen mitosis I) to produce the vegetative and generative nucleus. The generative nucleus is then isolated in a separate compartment within the vegetative cell to form a bi-cellular pollen grain (cell-within-a-cell). During pollen maturation, the vacuole of the vegetative cell gradually decreases in size and accumulation of starch granules is observed (engorgement). In plants with tri-cellular pollen, a second mitotic division of the germ cell takes place before anthesis (pollen mitosis II) to produce the two sperm cells. At this stage, the two germ cells are found in close proximity of the vegetative nucleus (male germ unit).

Nuclei number (meiosis, tetrad, microspores), pollen grain cell number (bi-cellular and tri-cellular pollen) and other cytological events (vacuolisation, starch accumulation/hydrolysis, water content) are used to determine pollen developmental stages (Figure 2). These parameters can differ between plant species and differences in pollen development can be used for systematic classifications (Table 1). At dispersal, angiosperm pollen grains can be bi-cellular or tri-cellular (Table 2) [30]. In tri-cellular pollen, the second mitotic division occurs prior to dispersal and pollen is dispersed with the two sperm cells already formed (Figure 2). In bicellular pollen, the second mitotic division occurs during pollen tube growth inside the style-stigma. The term male germ unit describes the relative position and cytological connections between the generative cell, the sperm cells and the vegetative cell nucleus in the mature pollen and pollen tube [2, 31]. Very few species release bi- and tri-cellular pollen grains at the same time. When this occurs (e.g. *Annona cherimola*), the ratio between bi-cellular and tri-cellular pollen grains was shown to depend on environmental factors such as temperature regime and relative humidity during the last phases of maturation [32]. Tri-cellular pollen grains have completed their development before dispersal and are typical for plant families that include important dicot and monocot crop species such as Asteraceae, Lamiaceae, Brassicaceae and Poaceae (Table 1). In some plants, pollen is dispersed as aggregates containing a high number of pollen grains (e.g. massulate orchids) [33]. Orchids are monocots that produce bicellular pollen; the generative cell is spherical at dispersal but changes to the normal spindle shape prior to the second mitotic division when pollen lands on the stigma and starts emitting the pollen tube [34]. Pollen development is further subdivided in early, middle and late stages according to cytological and morphological features such as the presence of a vacuole (Table 1; Figure 2) [35–37]. Vacuolisation occurs only once in some species, but twice in others (once during the early microspore to bi-cellular stage and once during early bicellular to late microspore stage) [18]. Stages of pollen vacuolisation alternate with stages of starch accumulation in plastids (engorgement) and starch accumulation can therefore also occur once or twice. Mature pollen grains can be starchy or starch-less depending on whether starch is present in mature exposed pollen grains (Table 1). Another classification is based on water content of pollen at dispersal: orthodox and recalcitrant pollen is dispersed in partially desiccated or partially hydrated form, respectively. Other differences concern the presence or absence of pollenkitt that distinguish animal/ insect from wind pollinators, respectively (with rare exceptions; Table 1). The diversity in pollen development between different plant species is complex and is functionally important. Different mechanisms have evolved under a variety of environmental constraints to secure pollination success and survival of the species.

3. Meiosis: The start of reproductive development

The decision to flower in higher plants is carefully controlled by environmental stimuli such as temperature and photoperiod [38–42]. After floral meristem initiation and formation of flower buds, meiosis is the committed step for sexual reproduction and formation of the gametophytes. The onset of meiosis is regulated by signals coming from the mother plant. Sugar availability plays an important role in driving cell division by inducing expression of

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Locular space availability	*Pollen number*	*Pollen density and dispersal unit*
Abundant, space between pollen	Few pollen/locule	6–12 per loculus cross section (Poaceae)
	Many pollen/locule	15–30 per loculus cross section (Solanaceae, Fabaceae, Liliaceae)
Reduced, closely packed pollen	Septate anthers	Compound pollen in each septum, polyad type (8–32 pollen) (Mimosaceae, some Annonaceae)
	Aseptate anthers	Monad pollen, tightly packed, tetrahedral shape (Myrtaceae)
		Compound pollen, very high pollen number, reduced size (Orchidaceae, Asclepiadaceae)

Table 2. Table showing the presence and abundance of locular space and fluid and relationship to pollen dispersal units in angiosperms. The locular fluid volume is extremely reduced when the pollen dispersal unit is of the compound type. Locular space and fluid are present from meiotic prophase until anther desiccation and opening.

the cell cycle regulatory protein cyclin that induces meiosis [43–46]. The initiation of meiosis to form the male and female gametophytes in the anther and ovary is normally a synchronised process [47–52]. However, this is not always the case in some plants and abiotic stresses can cause asynchrony between male and female meiosis [47, 51]. Most commonly, in aseptate anthers all sporogenous initials will proceed to undergo meiosis, while in septate anthers only some initials will undergo meiotic division [53]. This difference will affect locular space and liquid volume available to pollen, pollen number per locule and ultimately the dispersal unit (Table 2). After meiosis, male and female gametophytes follow a very different path of development. While ovule development and maturation is a gradual process, formation of large amounts of pollen grains in the anthers is energetically more demanding. At the time of meiosis, the anthers represent the highest sink strength in the flower and anthers are known to have the highest soluble sugar content of any plant tissue [54, 55]. Synchrony of male meiosis can also be affected in interspecific hybrids [50]. Pollen sterility caused by meiotic asynchrony is a major problem in interspecific rice hybrids where productivity is affected [56]. Mutagenesis approaches in model plants are gradually revealing genes that are involved in initiating meiosis and its progression through the different phases [57–61]. Silencing of the anther-specific zinc finger transcription factor *MEZ1* causes abnormal meiosis and pollen abortion in petunia [62]. The Arabidopsis *STUD*, *TAM, DUET, MALE MEIOCYTE DEATH1, AtKIN14a, b* and *TETRASPORE* genes are responsible for different aspects of male meiosis, such as maintaining pace, synchrony, chromosome organisation and transition between different stages [63–68].

Pollen biotechnology is a potentially powerful tool for crop breeding. Genes that regulate progression and synchrony of pollen meiosis and their regulation (e.g. effect of abiotic stresses) can be exploited for establishing hybrid breeding technologies, for instance, using mutant lines that are conditionally arrested at pollen meiosis [69, 70]. Progress in understanding pollen meiosis will be accelerated by more refined technologies that make it possible to study the meiotic transcriptome in detail [71]. Transcriptome profiling has been used to investigate the

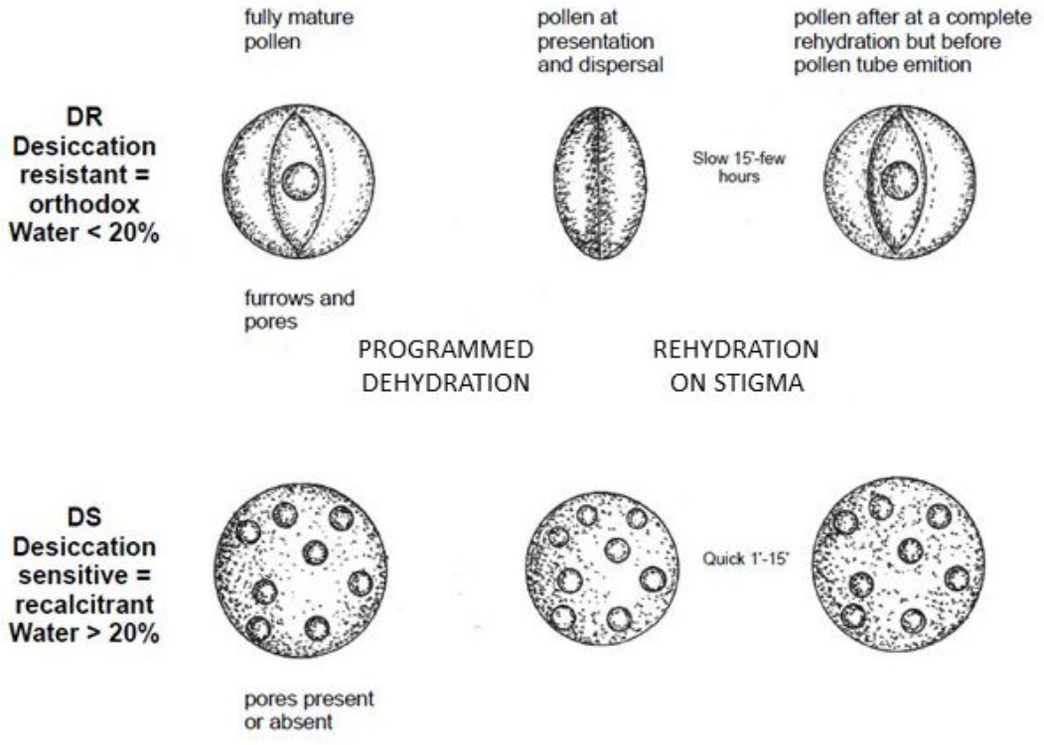

Figure 4. Change of shape and size of pollen according to their water content during the more critical phases of dehydration, presentation, dispersal and rehydration. High temperature and low relative humidity affect desiccation-sensitive pollen (DS) more than desiccation-resistant pollen (DR).

effect of abiotic stresses on pollen meiosis and pollen development [72, 73]. Abiotic stresses such as cold during meiosis can lead to formation of diploid gametes [74]. Polyploidisation and manipulation of chromosome number during meiosis can be used to increase diversity in breeding of crop plants [75, 76]. Some Arabidopsis mutants (*DIF1*, *TETRASPORE*, *PARALLEL SPINDLE1* and *Jason*) that affect ploidy levels can improve our understanding of pollen meiosis and how it is affected by the environment [66, 77–80].

4. The importance of the anther tapetum

The tapetum surrounds the pollen mother cells before meiosis and is the inner cell layer of the anther wall (Figure 2). The tapetum plays an important role in pollen development: it secretes the locular fluid containing nutrients for pollen development and deposits components of the pollen cell wall. When these functions are fulfilled, the tapetum undergoes a natural programmed cell death response (PCD) [81–83]. This process is essential to sustain pollen development: PCD generates nutrients for the locular fluid to feed the native pollen grains [81, 83–88]. Tapetum cells are generally polyploid and/or multinucleate and are metabolically very active. Tapetal-specific gene transcripts are the most prevalent fraction of total anther transcripts [89]. Polyploidisation and genome endoduplication are commonly observed in plant tissues with high metabolic activity [90]. High

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Pollen size	**Water content** **Shape (dehydrated)** **Examples**	*Time for pollen rehydration and tube emission* [1]	*Consequences*
15–30 μm	[H_2O]<20% (Orthodox)  Boraginaceae, e.g. Forget-me-not	30 min to 1 hour	· Rehydration and pollen tube emission in extra-stigmatic sites of the flower or other plant parts may occur when air relative humidity rises
	[H_2O] <20% (Recalcitrant)  Spinach, Parietaria, Urtica	From a few seconds to a few minutes	· Time for rehydration and germination is less for recalcitrant pollen and depends on water percentage during stigma adhesion · Due to their small size they lose water quickly and die
30–100 μm (most common)	[H_2O]<20% (Orthodox)  Fabaceae, Solanaceae, Liliaceae	More than 1 hour	· Orthodox grains of this size resist thermal stress better during presentation and dispersal than smaller orthodox pollen · The time for rehydration and germination is also higher compared to smaller orthodox pollen
100–200 μm	[H_2O]<20% (Recalcitrant)  Pumpkin, maize	A few minutes	· This category resists thermal and low relative humidity stresses better because of their larger size

[1]: Time depends on the status of pollen at stigma adhesion.

Table 6. Table showing the main categories of monad pollen, their size, shape at dispersal, time for rehydration and germination of orthodox (oval) and recalcitrant (spherical) pollen grains, including representative examples and some ecological consequences. The average pollen diameter is 30–100 micrometers with low water content. Orthodox and recalcitrant grains have ecological devices to reduce water loss during presentation and dispersal, e.g. pollen presentation by anthers that are enclosed by the flower corolla and exposing anthers outside the flower as for poricidal anthers.

metabolic activity of tapetum cells is required during meiosis for production of callose, a temporary cell wall that separates the microspores from the tetrad, and for biosynthesis and secretion of sporopollenin for the exine pollen cell wall [91–93]. Mutations that affect callose deposition and dissolution affect microspore development and fertility [94, 95]. The main tapetum nutritional activity occurs during the microspore stage and the first signs of

degeneration do not occur at the same stage in different species [96] but degeneration normally reaches completion near the end of the uni-nucleate microspore stage [97].

The secretory tapetum is the most common type [97]. The tapetum cells form the inner lining of the loculus and remain in place until they degenerate. In some plant species (e.g. Poaceae), the young microspores are found to attach themselves to the tapetum inner wall [35, 98]. In the secretory tapetum, the inner cell wall directed towards the loculus and the radial walls dissolve using a natural protoplasting event to facilitate the secretory function. Orbicules or Ubisch bodies are secreted towards the loculus by the tapetum cytoplasm; their function is not yet elucidated and only unproven hypotheses as to their role have been put forward [99–101]. During development, microspores are dispersed in the locular fluid, the volume of which can vary widely according to anther morphology (aseptate or septate) and the type of pollen dispersal units: more locular fluid is generally present in aseptate anthers and/or when pollen are dispersed as single units, while less fluid is present when pollen are dispersed as aggregates (Table 2) [82]. When released from the tetrad, pollen grains are in direct contact with the secretory tapetum [82]. The substances that are secreted in the locular fluid are neutral polysaccharides, pectins, proteins and lipids, and their relative proportion varies during pollen development [102]. The amount of locular fluid secreted depends also on the number, size and shape of the pollen grains and the dispersal unit (monads *vs*. polyads; Table 2).

Another form of tapetum is the amoeboid or periplasmodial tapetum which is, for example, found in the Asteraceae family [82]. In this case, the tapetum cell layer undergoes a reorganisation rather than degeneration during its early development. During meiosis, the tapetal cells form long extensions that engulf individual pollen mother cells. At the tetrad stage, the tapetum reorganises to form a periplasmodium which separates the individual young microspores and encloses them within a vacuole in the tapetal cytoplasm [103]. The amoeboid tapetum, better than the more common secretory type, illustrates the nurturing function of the tapetum.

The tapetum forms the interface between the sporophyte and the male gametophyte and is therefore in a strategic position to control reproductive development. Some of the substances entering the tapetum come from the external cell layers of the anther and other parts of the mother plant [104]. The mother plant supplies nutrients via the vascular bundle of the anther filament [84, 105]. Downloading occurs in the anther connective tissue cells and transport to the middle layer occurs symplastically [83]. The outer anther wall cells are connected via plasmodesmata, but the tapetum layer is symplastically isolated from other anther wall cells. Delivery of sugars into the tapetum requires apoplastic transport [55, 106, 107]. The apoplastic cell wall invertase gene is expressed in the tapetum and is responsible for mobilising sucrose into the tapetum cells [108, 109]. Repression of tapetal cell wall invertase activity and gene expression by different abiotic stresses blocks sugar transport to the pollen grains [108–112]. At least in some species nutritive substances are stored temporarily in the tapetum and are then absorbed by the developing pollen grains [102, 113].

The meiotic stage of pollen development is very sensitive to cold, heat and drought stress (Table 3) [25, 28, 109, 110, 114, 115]. It is likely that abiotic stresses at the time when the tapetum is metabolically most active interfere with the synthesis of pollen cell wall components and

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the secretion of the locular fluid. This may cause abortion of the young microspores. The formation of the locular fluid is associated with an increase in pollen volume and increased vacuolisation, a process that is affected by water stress (Table 3) [28]. The presence of abundant locular fluid (e.g. Solanaceae and Poaceae) or its extreme reduction (e.g. some orchids, Fabaceae and Myrtaceae; Table 2) has so far not been correlated with higher or lower tolerance to drought stress. Plant species with a periplasmodial tapetum have a reduced volume of locular fluid. In this case, each microspore is engulfed in the tapetum cytoplasm, so pollen nutrition is direct and does not require an abundant locular fluid [82]. Abiotic stresses may interfere with tapetal PCD and affect its functionality [87]. Both premature and retarded degeneration of the tapetum cause pollen sterility [83, 87, 116–119]. Production of reactive oxygen species (ROS) has recently been implicated in the regulation of PCD timing in the tapetum [120]. ROS are produced in response to many abiotic stresses [121]. Premature tapetum degeneration is a major cause of pollen sterility and yield loss under abiotic stress conditions [118, 122–125]. Carbohydrate mobilisation to the tapetum and its genetic control may play an important role in guaranteeing pollen development under stress conditions. Anther sink strength is reduced in stress-sensitive species [108–110, 126]. At the same time, sugars appear to be redirected to other tissues, e.g. leading to starch accumulation in the endothecium layer of the anther wall [106, 107, 127]. The tapetum is a sporophytic tissue and its function is controlled by signals from the sporophyte (sugars, hormones). Improvement of stress tolerance in crop species will therefore require a better understanding of the effect of stress on the sporophyte, as well as on sporophyte–gametophyte communication.

Stages	*Stress type*	*Targeted stage and/or compartment*	*Defence mechanisms*
Pollen meiosis & further development	· Water stress	· Tapetum, locular fluid formation	· Locular volume reduction
	· Water stress	· Microspore or bicellular pollen vacuolisation	· Anthers protected inside thick flower whorls
	· Low temperatures >0°C	· Cytoplasm activity and cyclosis	· Programmed developmental arrest
	· Heat stress >30°C	· Cytoplasm activity and cyclosis	· Programmed developmental arrest
Anther desiccation	· Rain	· Locular fluid fails to evaporate, anthers fail to dehisce	· Anthers are protected inside the corolla where pollen is exposed
	· Heat stress	· Carbohydrate metabolism	· Synthesis of heat shock proteins
	· Low temperatures	· Carbohydrate metabolism, cyclosis	· Presence of high amounts of LMW carbohydrate reserves
Pollen presentation	· Heat stress	· Pollen water content	· Pollen is presented inside the corolla
	· High/low relative humidity	· Pollen water content	· Pollen is presented inside the corolla and for a short time lapse
Pollen dispersal	· Heat stress	· Number of viable, dispersed grains	· Social plants with shorter pollen flight

Stages	*Stress type*	*Targeted stage and/or compartment*	*Defence mechanisms*
	· High/low relative humidity	· Number of viable, dispersed grains	· Anthers can delay pollen dispersal

Table 3. Effect of abiotic stresses on different stages of pollen development, and possible evolutionary defence mechanisms of the male gametophyte.

5. The pollen cell wall

5.1. Exine

The synthesis of the pollen cell wall starts during meiosis and depends on the activity of the tapetum. The composition of the pollen wall is unique compared to other plant cell walls and shows species-specific diversity. The biodiversity in pollen cell walls is functionally important for the plant to distinguish its own pollen from that of other plants [128–131]. The pollen cell wall can vary physically and chemically to match environmental aspects of pollination. Pollen wall diversity serves a taxonomical value, forming the basis of palynology [132]. The extremely resistant and elastic outer exine wall has evolved to protect pollen during dispersal. Exine is deposited first to provide pollen grains with their distinctive and characteristic features (Figure 3A). Pollen cell wall organisation starts just before meiosis when meiocytes become surrounded by callose secreted by the tapetum [92, 93, 133]. The callose special cell wall (SCW) is formed during prophase and interphase and closes the cytomictic channels that synchronise the first meiotic division. Exine is patterned under the callose layer and the microspore plasma membrane (primexine or exine presursor) at the end of meiosis (late tetrad stage) and is completed after the release of the microspores from the SCW at the end of the tetrad stage. The tapetum then produces callase, a β-1,3-D-glucanase enzyme responsible for dissolution of the callose wall, as well as sporopollenin precursors, a complex polymer of fatty acids and phenolic compounds. These are released in the loculus and polimerise on the primexine of the microspore following its release from the tetrad [132, 134, 135]. Mutant screens for impaired pollen walls in Arabidopsis revealed several genes involved in sporopollenin biosynthesis and most of these mutants are male sterile [92, 136–140]. Sporopollenin precursors are deposited by ABC transporters that are expressed in the tapetum at the early vacuolated microspore stage [134, 141]. Sporopollenin biosynthetic enzymes form a complex (‘metabolon’) in the endoplasmatic reticulum of the tapetum [142]. Recent ultrastructural studies reveal the involvement of specialised tapetum organelles, elaioplasts or tapetosomes, in exine wall deposition [140, 143]. Exine deposition is reduced, interrupted and can even be absent altogether in aquatic plants or plants living and pollinating in extremely wet environments [144]. The absence of exine in species having underwater pollination (e.g., seagrasses) is correlated with the fact that in water pollen grains do not undergo desiccation and have to remain hydrophilic; there is no developmental arrest and changes in shape and volume do not occur [145].

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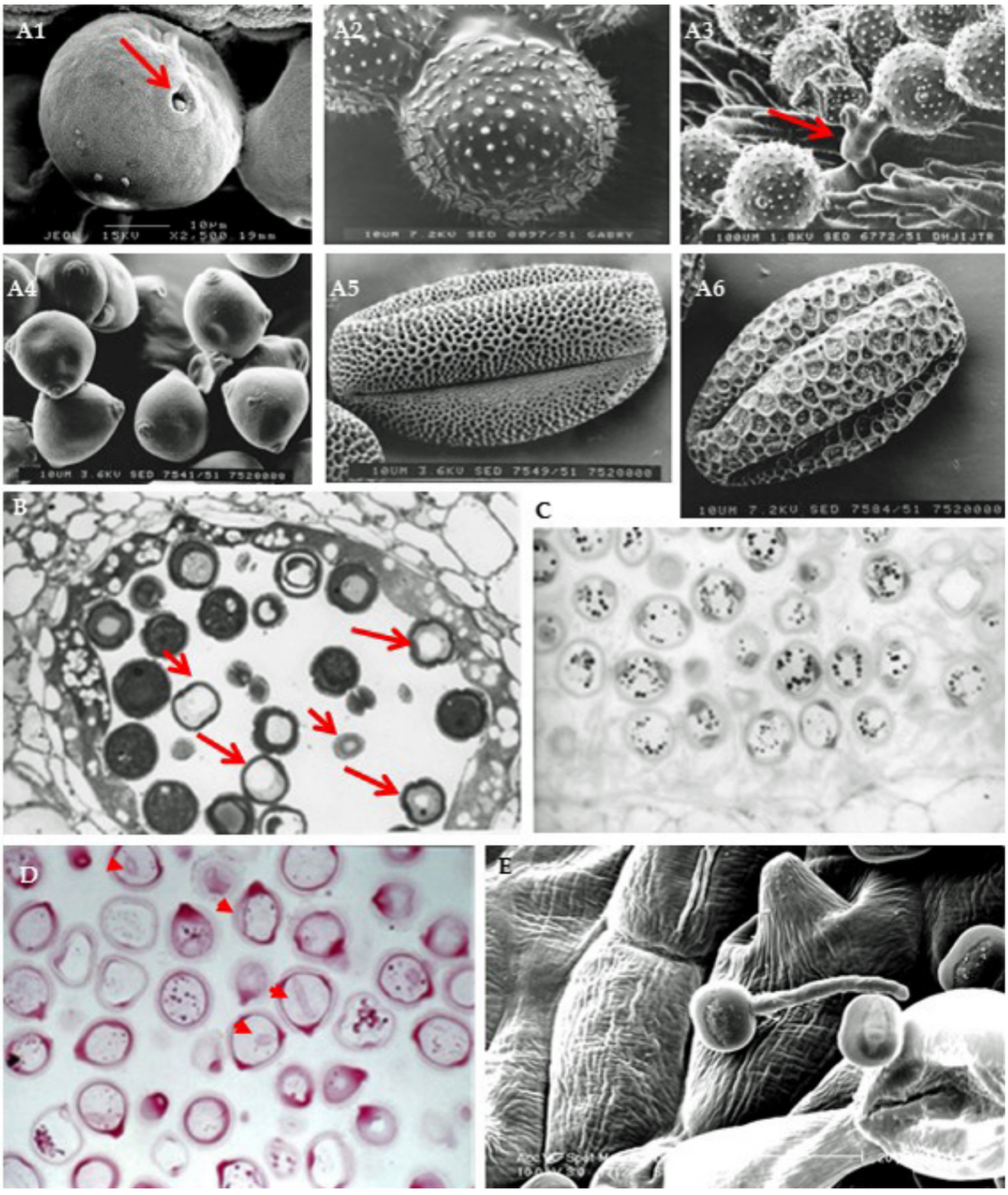

Figure 3. Different stages of pollen development in angiosperms.

A1-4: Scanning electron micrographs of mature desiccation-sensitive recalcitrant grains which are devoid of furrows.

A1: A rice pollen grain close to anthesis, showing the cell wall surface and the germination pore (arrow). A2: three pollen grains of *Lavatera arborea* (Malvaceae) kept together by pollenkitt, a viscous fluid covering the pores of the grains. A3-6: Pollen grains of different members of

the Cucurbitaceae family with recalcitrant pollen grains. A3: *Cucurbita pepo*, with a germinating pollen grain (arrow) taken 10′ after pollination. A4: *Cucumis sativus*, a species with recalcitrant pollen grains. A5 and A6: *Bryonia dioica* and *Cytrullus lanatus* orthodox pollen grains with furrows.

B-E: Asynchrony in vacuolisation and starch storage in olive (*Olea europaea*) pollen grains. B: A section of anther at mid-bi-cellular stage during the second vacuolisation, with degenerating tapetum (toluidine blue O staining). The asynchrony of development of pollen is evident: grains have vacuoles of different sizes and some grains are degenerating (arrows). C: A section of an anther at mid-microspore stage at the first starch engorgement (stained with Periodic Acid Schiff). Starch grains have different sizes because of the asynchrony of starch storage. D: Section of an anther at the early bi-cellular stage and second starch engorgement (PAS stained). Grains have an asynchronous development with respect to starch engorgement and in some grains the generative cell (arrow heads) can be discerned because of the thin polysaccharide wall. E: Pollen grains of *Cerinthe major* (Boraginaceae) displaced by flower visitors on the corolla (SEM). Only one has emitted a pollen tube because of precocious rehydration due to high humidity during the night – probably indicating asynchronic development of the grains.

5.2. Intine

The exine wall is completed by the mid-microspore stage before the internal intine layer is deposited. Intine is less elastic and consists of a pecto-cellulose mixture. Intine synthesis also starts before the first mitotic division and is always completed by the time the vegetative and generative cells are formed [132, 146]. Mutagenesis approaches have identified genes involved in the biosynthesis of pectins for the intine cell wall [147–152]. Some of these genes are expressed in the tapetum and ABC transporters transfer intine components to the pollen grains [153]. Mutations affect pollen shape and fertility, as well as growth of the pollen tube. Pectin is the main component of intine and is secreted by the tapetum into the locular fluid. Accumulation is highest at the vacuolated microspore stage [146]. The *Brassica campestris Male Fertility2* and *9* (*BcMF2, 9*) genes encode novel polygalacturonase enzymes that play a role in pectin metabolism, intine formation and tapetum degradation [151, 152]. At pollen germination, the intine wall forms a continuum with the the pollen tube pectocellulose wall.

5.3. The role of the cell wall in regulating pollen size and shape

The pollen wall controls homeostasis of the cytoplasm and reduces fluctuations in pollen volume due to variations in water content. This is important during dispersal, when pollen is exposed to air. The characteristic exine wall furrows and surface pattern are crucial for the harmomegathic functions that regulate pollen shape during dehydration [154] (Figure 3 A5–6). After landing on the stigma, the pollen wall controls the rehydration process with water coming from the stigma in angiosperms or from the ovule in gymnosperms (pollination drop) [155].

The exine layer has generally one or more pores through which the pollen tube is emitted (Figure 3 A1, 3). When pollen pores are absent, the pollen tube is emitted at the site where the

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pollen grain contacts the stigma surface. The pattern and distribution of the apertures are determined by the tetrad shape and callose deposition at the intersporal walls [156, 157]. The Arabidopsis *tam* mutant (*t*ardy *a*synchronous *m*eiosis) shows an altered cytoplasmic partitioning (cytokinesis) during tetrad formation and altered aperture patterning, suggesting that the last contact points between the cytoplasms of the future microspores during cytokinesis are the place where apertures are formed [158]. The number of pores per pollen grain can vary within one species and germination speed is positively correlated with pore number [159] and pollen water content at dispersal [160]. The intine wall is a continuous layer but is generally thicker and more elaborate at the pores and/or furrows to support the harmomegathic process [161]. Exine and intine have a similar thickness but in some cases intine, especially in the poral region, is much thicker and very pectin-rich, which may help in keeping pollen cytoplasm hydrated during dispersal [162–164].

5.4. Pollenkitt

In some plant species, the surface of the pollen wall contains various amounts of pollenkitt, a viscous hydrophobic substance. The sticky nature of pollenkitt is thought to play a role in pollen adhesion to pollinators during dispersal [165, 166], but several other functions have been suggested [167]. Plants with zoophilous or entomophilous pollination, some of which having secondary anemophylous pollination, have exine cavities or ornamenations containing pollenkitt [168]. A simple and effective method was developed to reveal its presence or absence [169, 170]. The synthesis of pollenkitt is linked to tapetal degeneration [171] and plastids are implicated in its formation [104, 167]. In anemophilous plants, the plastids develop into elaioplasts which are resorbed by other tapetum cell components during degeneration. In entomophilous plants, the elaioplasts or tapetosomes (plastids accumulating lipids) are the more abundant organelles in the degenerating tapetum cytoplasm [167]. Tapetosomes are oil and flavonoid containing organelles in the tapetum that contribute to pollenkitt formation [172–174]. Pollenkitt is formed by the fusion of elaioplasts and spherosomes of tapetal cells during the late microspore stage [167]. After release in the locule, pollenkitt is deposited on the exine surface of the pollen grains, covering the exine ornamentations at the onset of anther dehydration [171]. In the entomophilous Brassicaceae family, elaioplasts are involved in forming tryphine, which plays a role in adhesion of pollen to the stigma [104] (Table 1). A conditionally male sterile mutant that affects tryphine production in Arabidopsis is affected in pollen-stigma recognition [69]. Pollenkitt consists mainly of saturated and unsaturated lipids, carotenoids, flavonoids, low molecular weight proteins and carbohydrates [167, 175]. An additional role of pollenkitt in biotic pollination could be in preventing water loss and other damage [167].

6. Pollen metabolism and development: role of vacuoles and plastids

6.1. Role of vacuoles

Vacuoles appearing at several stages of pollen development are correlated with metabolic activity. Pollen mother cells, like undifferentiated meristematic cells, are originally devoid of vacuoles but at telophase II small roundish vacuoles start to develop. Vacuolisation can occur once or twice (depending on species) during further stages of development [18]. Cyclic vacuolisation is always followed by storage of starch in amyloplasts (Figure 3 B–D), which then leads to disappearance of vacuoles and formation of new cytoplasm. Vacuolisation plays a role in increasing the volume of the pollen grain with the formation of new cytoplasmic components such as mitochondria, amyloplasts, other cell components and cytoplasmic reserves. Vacuolisation therefore reflects metabolic activity in the developing microspores. Vacuolisation is also associated with the storage of pectins during intine cell wall synthesis [146]. In Arabidopsis a large vacuole is formed by fusion of smaller vacuoles; this large vacuole is converted to smaller vacuoles again after the first mitotic division [176]. Lytic vacuoles (lysosomes) are formed to degrade mitochondria, ribosomes and plastids [18]. Mature pollen has only small vesicles filled with carbohydrates, but in species producing pollinia rather than single pollen (e.g. massulate orchids) small vacuoles with watery content are present. Reduced vacuolisation at maturity may be required to reduce pollen size during presentation and dispersal [33]. Pollen vacuolisation is also affected by abiotic stresses such as drought and temperature stresses (Table 3). Heat stress was shown to reduce pollen release from anthers [177]. Vacuoles also store metabolites such as sugars and play a role in regulating sugar homeostasis, metabolic activity and growth processes [178]. Sucrose cleavage into hexoses by vacuolar invertases can regulate osmotic potential of cells [179] and this can be used as a defence mechanism against stresses such as drought (Table 3). Abiotic stresses in Arabidopsis induce vacuolar invertase, as well as a tonoplast-associated monosaccharide transporter (*ESL1*) in vascular parenchyma cells [180]. Regulation of cellular sugar fluxes between cytoplasm and vacuoles is important to regulate osmotic potential and pollen hydration and this could play a role under environmental stress conditions. Vacuolar invertases that are expressed in pollen grains have been identified [108, 109], but their role in regulating pollen metabolism under stress conditions requires further investigation.

6.2. Role of plastids

Plastids are commonly present as undifferentiated pro-plastids at the end of meiosis. They divide later to differentiate and accumulate starch [181, 182]. Plastid division occurs in the vegetative cell of pollen before starch engorgement. Usually, there are one or two waves of starch accumulation in amyloplasts during pollen grain development in gymnosperms and angiosperms [162, 181]. In some plant species, pro-plastids in the generative cells are degraded by lysosomes immediately after the first haploid mitosis [183]. Plastids also store fatty acids and alcohol intermediates for pollen wall synthesis, as evidenced by the male sterile mutant *defective pollen wall* (*dpw*) [184]. Starch stored in the amyloplasts of the vegetative cell is in most plants hydrolysed before anther opening and pollen dispersal (Figure 3C). Physico-chemical

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properties of starch in plants with two cycles of starch synthesis vary between and within species [185]. Mature pollen can be starchy or starchless, depending on the presence or absence of starch grains in the vegetative cell amyloplasts (Table 1). This can be characteristic for plant families [185]. In some plants that flower throughout the year in the same environment pollen grains are always starchless (e.g., *Mercurialis annua*) [186]. Vice versa, in the case of *Parietaria judaica* which flowers from springtime to autumn, the proportion of starchy and starchless grains varies according to the season [187].

6.3. Adjustment of osmotic pressure and water balance in pollen

Like soluble sugars, starch stored in plastids can play a role in adjusting osmotic pressure, particularly during presentation and dispersal (Table 3). Stored carbohydrates in plastids or in the cytoplasm, soluble or insoluble, can be used to adjust turgor pressure and protect grains against desiccation [188]. Many genes are involved in starch biosynthesis throughout pollen development [189]. Drought and temperature stresses can severely affect starch accumulation, and absence of starch in mature pollen can be an indicator of pollen sterility [109, 110, 115, 190–192]. Endogenous starch is consumed during the first phases of pollen tube emission when pollen tube growth is at the expense of pollen reserves [193, 194]. After this autotrophous phase, pollen grains obtain carbohydrates and other substances from the stigma and style. Starch presence is not a direct indication of carbohydrate reserves present in pollen; hydrolysis of starch from amyloplasts increases soluble sugar levels in the cytoplasm and sugars are stored in the vacuole [188, 193]. Carbohydrates derived from starch hydrolysis in starch-less pollen grains alleviates the effect of heat and humidity stress during presentation and dispersal [193]. Starch in plants is normally phosphorylated. A tomato mutant lacking starch phosphorylation activity (*Legwd*) fails to degrade starch for pollen germination, resulting in sterile pollen [182]. Hydrolysis of starch supplies soluble osmotically active sugars which, together with amino acids such as proline, provide osmotic adjustment [195] (Tables 3 and 4). Regulation of turgor pressure is an essential aspect of pollen tube growth and elongation [196]. Osmo-regulation during the late maturation phase may function in the dehydration of pollen. Pollen dehydration is associated with the induction of proteins that play a role in drought response: dehydrins, aquaporins, heat shock and LEA proteins [197]. High levels of osmotin expression in mature tobacco pollen is another indicator of osmotic stress response [198]. Potassium ions [199, 200] and phospholipids can also regulate osmotic pressure and cell swelling in pollen [201]. Regulation of pollen osmotic potential and water content and the role carbohydrates play in this process are clearly important in pollen development. Abiotic stresses (cold, heat and drought) during meiosis affect sink strength of the tapetum [109, 110, 126, 191, 202], but the dynamics of carbohydrate metabolism at the gametophyte level remain poorly understood.

Stage of development	*Metabolic activity*	*Physiological effect*
Ripening*	· Hydrolysis of starch · Synthesis soluble carbohydrates, amino acids, peptides	· Molecules increase pollen turgor pressure

Stage of development	*Metabolic activity*	*Physiological effect*
Desiccation*	· Resorption of water by phloem of filament · Water redistributed to other flower parts · Evaporation through anther cuticle · Synthesis of protective molecules, proteins (LEA, dehydrins)	· Desiccation leads to higher pollen osmotic pressure · Size of pollen grains affects desiccation
Presentation and dispersal	· Pollen water content is affected by humidity, temperature, content in osmotic molecules and their biosynthetic enzymes, levels of protective molecules	· High relative humidity causes precocious rehydration and extra-stigmatic pollen tube emission (especially in recalcitrant pollen)
Rehydration and pollen tube emission	· Time for rehydration/pollen tube emission depends on water content, osmotic molecules, biosynthetic enzymes, stigma adhesion	· The physiological state of the stigmatic surface plays an important role in pollen rehydration

(*): The ripening and desiccation stages can – at least in some species – be totally or partially overlapping.

Table 4. Synthesis of osmotically active components in pollen, and their effect at different stages of development. Orthodox and recalcitrant grains could have a similar physiological behaviour until the onset of desiccation, but the amount and quality of the osmotic molecules and the activity of their biosynthetic enzymes distinguish the two categories in the later stages of pollen development.

7. Consequences of synchrony and asynchrony in pollen development: Pollen competition

The synchrony of the first meiotic division is likely due to the presence of cytomictic channels that unite the cytoplasm of all the meiocytes present at meiosis within a loculus [203, 204]. These channels close during the meiotic inter-phase and synchrony can be lost from the second meiotic division onwards; the two nuclei within one meiocyte can divide independently, but a certain proportion (30–40% in *Lycopersicum peruvianum*) can still divide synchronously [205]. Nevertheless, the dissolution of the callose wall that keeps the tetrad cells together is synchronous and is controlled by callase, which is produced and released by the surrounding tapetal cells [95]. Meiotic asynchrony can cause the second haploid mitosis and other cellular processes (vacuolisation, starch hydrolysis storage in plastids, intine formation) to be asynchronous [206]. In orchids, the process of microspore development is synchronous because of the persistence of cytomictic channels throughout meiosis, uniting all the microspores of a loculus until pollen mitosis [33]. Pollen maturation is not a synchronous event from the first mitotic division onwards. Because a large amount of ovules needs pollinating in the ovary, the staggered pollen maturation in orchids may offer an advantage in that overcrowding and competition of germinating pollen on the stigma can be avoided [33].

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At anthesis, the release of microspores is controlled by the sporophyte; all pollen grains from a loculus are dehydrated and released irrespective of their developmental stage. In addition, pollen desiccation at the end of pollen development affects all pollen grains of the anther at the same time. The mix of asynchronic and synchronic events during pollen development results in a mixture of pollen grains at slightly different stages of maturity; the difference in physiological stage means that different pollen grains may contain different amount of reserves when they are released together during anthesis. Asynchrony in pollen development is obvious from differences in starch engorgement, vacuolation and pollen size at different stages of development (Figure 3 B–D). Asynchrony can also explain why in vitro pollen germination tests show variable efficiency, particularly for some plant species and for plants grown under stressful circumstances. In vitro pollen germination issues may reflect the in vivo situation; the higher the asynchrony of microspore development, the higher is the percentage of unviable and immature pollen grains at maturity. Environmental stresses such as drought, frost, heat, high humidity (rain and mist) exacerbate the degree of developmental asynchrony [114, 207], causing a further reduction in viable pollen count. Application of heat stress is a common technique used for improving yield of haploid embryos during microspore embryogenesis [208, 209]. Through induction of asynchrony in pollen development, abiotic stresses can affect the production of viable pollen at the gametophytic level. Very little is known about this process and its molecular and physiological basis.

Asynchronous development is responsible for pollen competition. Competition between grains occurs at different stages: during development, after rehydration on the stigma and during pollen tube growth. Asynchronous development, combined with the fact that the haploid pollen grains have a different genetic composition due to recombination of the sporophyte genome during meiosis, leads to differences in ability to compete during pollen development and this presents a continuous selective force throughout male gametophyte development. The tapetum cells secrete nutritive substances synchronously, but the asynchronous pollen grains have a different capacity to use these substances for development, causing competition. Asynchrony in development and differences in genetic composition then lead to competition during rehydration and pollen tube growth and the speed of pollen rehydration depends on the orientation of the pore(s) with respect to the stigma surface. The competition to be the first to fertilise the ovule(s) is an important selective force in plant sexual reproduction and played an important role in both plant and animal evolution [210].

8. Duration and continuity of pollen development

Pollen development is normally a continuous process that is interrupted only by pollen presentation and dispersal. Pollen meiosis takes only a few hours, but the duration of pollen development after meiosis can vary widely and depends on the plant species. As a rule, annuals develop pollen faster than perennials and woody species: pollen development takes 8 days for the herbaceous perennial *Lycopersicum peruvianum* [211] and approximately 7 days for geophytic *Lilium* species [212], while 18 days are required for the grass *Phalaris tuberosa* [213]. However, in some plants the process can be interrupted at various stages before presentation and dispersal. In some woody plants from temperate environments, the process

can be paused once or twice at the microspore or bicellular stages. The ability of pollen development to be interrupted is an adaptation mechanism to protect pollen against extreme environmental conditions during summer or winter. Interruptions are more likely to occur in plants where pollen development takes longer, especially in temperate climates where unexpected harsh weather conditions can occur. Some gymnosperms (e.g. *Juniperus communis*) and woody perennial angiosperms (e.g. birch, elder and hazelnut) that disperse their pollen at the end of winter differentiate their flower buds in autumn when environmental conditions are favourable [214, 215]. Under severe winter conditions, flower development is arrested and resumed in early spring. In hazelnuts, this interruption occurs at the bi-cellular stage [215]. The developing pollen grains appear dormant and anther metabolism is repressed. The influx of substances from the mother plant and the activity of anther wall chloroplasts are also reduced, suggesting that developmental arrest may be regulated by the mother plant. In some species, developmental arrest occurs prior to pollen meiosis. In some Mediterranean plants, flower buds develop during late spring but stay dormant during the hot and dry summer and development resumes in autumn [216]. The dioecious bay laurel (*Laurus nobilis*) flower buds of both sexes develop in early autumn, they pause development in winter and flower ripening and pollination occurs during early springtime [163]. It is not known how this developmental arrest of pollen development is controlled at the molecular and physiological level, but it provides a powerful defence mechanism to protect pollen and maintain fertility under sub-optimal climatic conditions.

9. Pollen dehydration, presentation and anther dehiscence

9.1. Orthodox pollen and cross-pollination

In cross-pollinating plants, the flower opens at anthesis and the pollen is dispersed to reach other plants (chasmogamy). To survive dispersal in the environment, pollen needs to be in a dehydrated state with low metabolic activity (Figure 4) [217, 218]. This is the case for orthodox pollen which is dehydration-tolerant and is dispersed with low water content (<20%). Orthodox pollen can travel over larger distances without losing viability [160, 219]. Near anthesis, rapid extension of the anther filament seals the xylem, interrupting sap flow to the anther. The phloem redistributes the locular content to other plant parts [160, 220, 221]. The epidermis and endothecium layers of the anther wall dehydrate and pollen grain hydration levels reach an equilibrium with the environment [222]. Environmental parameters such as temperature and relative air humidity influence pollen water content [186] and osmotic adjustment is used to balance water content in function of environmental conditions (Table 4) [27]. Orthodox pollen also has low metabolic homeostasis to prevent cellular damage during dispersal [160]. The duration of developmental arrest and viability of pollen depends on environmental conditions at dispersal and the type of reserve substances present in the pollen (Table 4) [27, 188]. These defence mechanisms protecting pollen grains during presentation, dispersal and pollination vary depending on the degree and duration of dehydration during dispersal and depend on whether plants are anemo- or zoophilous pollinators (Table 5) [27, 160, 223]. Relative air humidity can adversely affect pollination efficiency because absorption of water from the

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environment can lead to precocious pollen tube emission when the correct hydrated state is reached (Figure 3E) [160]. Entomophilous pollen is also affected by compounds that are secreted by the insect carrier (e.g. bees) [224–226]. Plants producing orthodox pollen are potentially out-crossing; both out-crossing and self-pollination can occur in these plant species, unless there is a self-incompatibility system in place to prevent self-pollination [227].

Type of defence	*Defence mechanism*	*Stage affected*	
		Presentation	**Dispersal**
Structural, species-specific	· Close proximity of small herbaceous (social) plants		X
	· Grains protected inside anther until dispersal:		
	◦ Pollinia of massulate orchids	X	
	◦ Gradual dispersal, e.g. poricidal anthers of Ericaceae, Solanaceae		
	· Anthers exposing and protecting pollen inside the corolla	X	X
Ecological	· Pollen is presented during short periods with more favourable conditions		
	◦ Night pollination in dry habitats, e.g. Cactaceae	X	
	◦ During dry and sunny periods of the day, e.g. Gymnosperms		
Cytological	· Synthesis of molecules that protect pollen under stress conditions: carbohydrates, proteins and enzymes	X	X
	· Intine is thick and stores water, regulating the water content of the cytoplasm	X	X

Table 5. Common types of modalities present in different angiosperms in order to reduce and/or avoid the harmful effects of the environment during pollen presentation and dispersal.

9.2. Recalcitrant pollen and self-pollination

In self-pollinating plants, pollen does not have to travel far to pollinate and therefore does not need to undergo severe dehydration at maturity. These plants produce recalcitrant pollen grains which are dispersed with high relative water content (30–70%); pollen remains metabolically active at dispersal and continues to develop to the point of germination (reduced developmental arrest). Recalcitrant pollen grains are dehydration-sensitive and are typically very short-lived and highly sensitive to variation in relative air humidity [160] (Figure 3 A1 and A2; Figure 4). However, cross-pollination with recalcitrant pollen is possible but is restricted to proximate flowers only [228]. Some plant species produce both chasmogamic and cleistogamic flowers, thereby increasing the chance of reproductive success [227]. In crop

species (e.g. wheat, barley, rice), cleistogamic breeding systems may have been selected during domestication to limit gene flow and preserve preferred gene combinations [229–233]. The absence of pollen presentation in cleistogamic self-pollinating plants is thought to be a protection against abiotic stresses such as drought and heat, as pollen number is considered less of a constraint for pollination in cleistogamic compared to chasmogamic species [227, 234]. Some crop species still have both cleistogamic and chasmogamic varieties [232, 235, 236]. Cleistogamic rice varieties were shown to be more tolerant to heat stress at flowering compared to non-cleistogamic lines [237]. However, recalcitrant pollen (e.g. maize) can lose water quickly, especially at low air humidity [238] and many cleistogamic crop species (e.g. cereals, legumes, Solanaceae) have well-documented pollen sterility problems. These problems occur when plants experience stress at the young microspore stage or anthesis [25, 115, 191, 239–241]. Sterility in these cases may be inflicted earlier in development and may not be due to interference with pollen presentation and dispersal [242, 243]. This may indicate that cleistogamy *per se* may help avoiding pollen dispersal, but it may not offer protection against abiotic stresses that occur at other periods of flowering. Genetic manipulations and hybrid breeding in crop species have sparked renewed interest in controlling the breeding system of some crop species [231, 244–246]. Some progress has been made in recent years to identify the genes associated with the cleistogamy trait and flower opening in rice, wheat and barley [246–249]. This research will lead to a better understanding of the genetic basis of cleistogamy and chasmogamy and the implications for abiotic stress tolerance in crop plants.

9.3. Pollen size, shape and anther dehiscence

The size of mature pollen grains at dispersal varies from less than 15 to 200 μm in diameter, with an average size of 70–100 μm in the desiccated state. The variation in pollen size has been related to the stigma size [250] and does not always correlate with water content (Table 1) [160]. Pollen grain volume increases progressively from the young microspore stage to maturity but is generally restricted by available locular space and the type of pollen dispersal unit in different species [168, 251]. The dehydration process in orthodox pollen leads to a change in shape and size of pollen grains and the harmomegathic properties of the cell wall play an important role in this process (Figure 4; Table 6) [154]. Recalcitrant pollen do not have furrows to facilitate mechanical folding of the cell wall in response to dehydration and pollen remain spherical (Figure 4; Table 6).

Pollen release from the anther requires thickening of the secondary wall of the endothecial layer (= mechanical layer) and dehydration of the epidermis [163, 252–254] (Figure 1). Dehiscence mutants in Arabidopsis affect secondary wall thickening and cause male sterility; these mutants were shown to affect transcription factor genes *MYB26, NST1* and *NST2* [255–257]. Secondary cell wall thickening can also control temporary re-closure of the anther during rainy or misty weather [258, 259]. Dehydration of the epidermis is associated with increased abscisic acid (ABA) levels [260] and induction of dehydrin-like proteins [261]. Aquaporins regulate the movement of water during anther opening [262, 263]. Cells of the inter-locular septum are ruptured as a result of PCD, causing the joining of both locules of one theca – see Figures in Keijzer CJ [171] and Bonner LJ and Dickinson HG [264]. The locule volume increases and

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absorption of the locular fluid is accelerated [220, 265–268]. The locular content is re-distributed to other plant parts via the elongating anther filament [160, 221] and aquaporins may facilitate the movement of water through the anther wall membranes [262]. A cell death response in the stomium then causes the anther to open and pollen grains dehisce with the help of tension caused by secondary wall thickening [253]. Depending on the plant species, the stomium can rupture completely (from the top of the anther to the base), partially, or form pores for pollen dispersal [266, 267, 269]. Plant hormones regulating senescence and cell death such as auxin, jasmonic acid and ethylene play a role in anther opening and pollen dehiscence [252, 270–273]. The elongation of the anther filament in some plant species is required to expose the anthers from the flower to facilitate dispersal (Table 5) [274].

Pollination in plants requires favourable interactions between pollen morphological factors and environmental conditions (Tables 6 and 7) [275]. The size and shape of pollen grains, together with the events in the anther wall regulating dehiscence all collaborate to determine desiccation time, pollen viability and pollination success (Tables 6 and 7). Variation in relative air humidity, together with abiotic stresses that affect relative humidity (heat, drought, cold stress), cause problems with pollen presentation, anther opening, dehiscence [276, 277] and pollen tube growth [32]. Precocious germination while still in the anther [278, 279], or while waiting for a pollinator to disperse the pollen (Figure 3E) [280, 281], is due to inappropriate levels of humidity. Plants have evolved clever species-specific adaptation mechanisms such as dehiscence at particular times of the day [282], dispersal as single pollen or aggregates [168, 283], active dispersal by explosive forces rupturing the anther (e.g. *Ricinus communis*) and interaction with grooming insects [284, 285].

Pollen stages	*Processes affected by abiotic stress*
Pollen development · Meiosis · Tetrad stage · Microspore stage · First haploid mitosis (asynchronous) · Bi-cellular/tri-cellular stage	· Drought prevents secretion of the locular fluid · Drought during pollen development influences volume increase of the different floral parts · High/low temperatures and drought lead to consumption of starch reserves and carbohydrate starvation in anthers, affecting sugar delivery to pollen
Anther and pollen desiccation	· Drought during anther and pollen desiccation prevents transport of locular fluid water to other floral parts · High air relative humidity prevents anther and pollen desiccation · Too low relative humidity of the air accelerates anther and pollen desiccation
Pollen presentation (*)	· Too low air relative humidity affects pollen viability, especially in recalcitrant species

Pollen stages	*Processes affected by abiotic stress*
	· High air relative humidity induces precocious rehydration of pollen grains and pollen tube emission · Low or high temperature extends or reduces pollen presentation · Drought reduces flower longevity
Pollen dispersal	· Low air relative humidity affects pollen viability · High air relative humidity induces precocious pollen rehydration and can prevent anther dehiscence · Some volatile compounds emitted by bees affect pollen viability
Pollen rehydration	· Low air relative humidity prevents pollen rehydration and affects water availability from the stigma

(*): This phase is absent when pollen leaves the anther when it opens (e.g. Poaceae) or is launched from the anther (e.g. castor bean)

Table 7. Stages of male gametophyte development in angiosperms and processes affected by abiotic stresses.

9.4. Breeding systems and pollen:ovule ratio

The pollen:ovule ratio (P/O) has traditionally been used as a rough estimator of plant breeding systems (Cruden 2000), but little is known about the effect of environmental stresses on this ratio. When pollen is dispersed in aggregates of hundreds of grains (e.g. massulate orchids), the locular space is restricted and limited locular fluid limits nutrition and volume increase [34]. Changes in pollen volume can be measured under optimal or stressed conditions [28, 286]. Pollen dispersed as aggregates provides greater pollination success when the ovary contains multiple ovules [168, 287] and water loss during presentation and dispersal under heat and drought conditions affects only the externally exposed pollen grains and not the internal ones. To improve pollination success, some plants produce different types of pollen (different size, shape, colour, carbohydrate and water content) in one flower. One type, fecundative pollen, is fertile and able to emit the pollen tube and fertilise, while the other type is sterile nutritive pollen that serves as a reward for pollinators who – at the same time – get dusted with fecundative pollen [288]. The flower morphology can affect accessibility of pollen by different pollinators. Self-incompatible dimorphic *Primula* species have two different flower types with reciprocal anther and style length, producing pollen with different water content depending on the position and exposure of the anthers with respect to the corolla tube [289, 290]. Three flower types, producing three types of pollen grains, occur in trimorphic species (e.g. *Lythrum salicaria*) [289, 291]. The differences in flower morphology result in non-random mating patterns in plant populations and may play an important role in pollinator selection and adapatation to different environments [292, 293].

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10. Conclusions

The diversity in adaptation mechanisms available in nature to secure reproductive success in angiosperms is considerable (Tables 6 and 7). This diversity can serve as a valuable resource to advance our insights into stress adaptation mechanisms that will benefit breeding strategies for crop species. Cytological and morphological studies, combined with other science disciplines (physiology, genetics and genomics) will continue to improve our understanding of pollen development and its adaptation to the environment. The number of genes and mutants involved in male reproduction is steadily increasing [294], but several research areas require further attention:

- Two crucial stages of anther development are strongly affected by environmental conditions. Until dehiscence, anthers are protected by the calix and corolla, but for pollen dispersal, anthers need to be exposed. Both flower opening and anther dehiscence are strongly influenced by the environment [171, 184]. Secondly, the secretion functions of the anther tapetum are strongly affected by abiotic stresses. Tapetum cells are highly specialised secretion cells that loose their inner cell walls, effectively turning them into natural protoplasts and making them very vulnerable to water stress [82]. Drought stress at meiosis reduces locular fluid secretion [115], causing malnutrition and asynchrony of the developing pollen grains. Interestingly, some plant species are adapted to growth in very arid environments and expose pollen during the hot season, yet always have a very reduced volume of locular fluid (e.g. *Eucalyptus* and *Acacia* species in Australia). *Eucalyptus rhodanta* can resist temperatures higher than 50°C for several days without significant reduction in pollen viability [295]. It is important to understand how the tapetum of these plants manages to provide sufficient nutrients to sustain pollen development. The available locular space and the capacity to store locular fluid are abundant in plants dispersing solitary pollen, but very reduced when grains are dispersed as polyads (e.g. pollinia) [82]. Abundant locular fluid is considered a 'primitive' character in land plants and is a characteristic shared by all gymnosperms [160]. During evolution, locular volume has been gradually reduced and/or replaced by polyad dispersal, possibly as an adaptation to drier environments or to allow pollen presentation over longer periods of time (e.g. massulate orchids) [33, 105]. Orchid species can have monad or pollinia dispersal units [296]; the more primitive species have monad and tetrad pollen with abundant locular fluid, while the more evolved species disperse pollinia and produce very little locular fluid [33]. It remains to be established whether/how reduced locular fluid volume and compound pollen dispersed over longer periods of time could benefit sexual reproduction in arid environments and orchid species could be used for this research. Various other adaptation mechanisms could alleviate the effect of abiotic stresses, including shorter duration of pollen development, night – rather than day – pollination, deposition of a thicker protective intine wall, dispersal of compound rather than single pollen can all reduce the negative effect of stresses [160, 279].

- The control of pollen number, size and shape is another poorly understood aspect of pollen development. Pollen development is started (meiosis) and terminated (anther dehiscence) at a fixed moment. When environmental conditions induce various degrees of asynchrony

throughout pollen development, this leads to decreased numbers of viable pollen at anthesis. Larger pollen numbers could be obtained in plants with larger anthers. Anther size is a trait that has been used for selection of cold tolerance in rice [297] and the growth hormone gibberellic acid plays an important role in controlling stamen development [298]. Elucidating the mechanism of interrupting or pausing pollen development under unfavourable conditions may also provide useful information about avoiding stress damage. Understanding these mechanisms will require a better understanding of the signals driving gametophyte development *per se*. The haploid genome of the male gametophyte is derived from the sporophyte, but very little is known about its functionality in regulating pollen-specific development and metabolism. Achieving this challenge is now within reach, thanks to sensitive new-generation transciptome analysis techniques [29, 71, 299].

- It is important to understand the signalling mechanisms between mother plant and male gametophyte. Some crucial steps in pollen development (meiosis, tapetal activity and anther dehiscence) are clearly under sporophytic control. The high sensitivity to abiotic stresses of the meiotic, young microspore and anthesis stages indicates that sporophytic signals are critical in controlling male gametophyte development. Stress-proofing crop plants may therefore have to start by understanding the sporophyte signals (sink-source relationships, carbohydrate and hormone signalling, control of PCD during tapetum degeneration and anther dehiscence). It has been known for some time that treatments with one stress or with the stress hormone abscisic acid (ABA) can improve tolerance to another stress – a process called stress 'hardening' or 'priming' [300–305]. More recent studies in rice have shown that stress treatments at the vegetative stage can affect abiotic stress tolerance during flowering and reactive oxygen species (ROS) signalling could play a role in this sporophytic signalling event [306]. But evidence for involvement of genomic imprinting and epigenetic mechanisms in sporophyte-gametophyte signalling is also mounting [307–309].

- The importance of air relative humidity in pollen development has so far been grossly underestimated. The growing area of staple crops such as cereals is increasingly extending into environments that require different adaptations of pollen development. For instance, tropical rice is grown in temperate climate zones and temperate climate wheat is grown in humid tropical environments [310–312]. Air humidity and climatic conditions modifying atmospheric humidity (rain, fog, cold, heat and drought) have a dramatic effect on plant species producing orthodox and recalcitrant pollen, causing asynchrony and reducing pollen number and fertility. The dynamics of water relations and osmotic regulation in pollen grains and their interactions with the environment are research topics that need urgent attention. Adapting the breeding system of crop species (self- versus cross-pollination) may offer opportunities for improved protection of pollen during dispersal, but the trade-offs between chasmogamy and cleistogamy in terms of abiotic stress tolerance require more detailed investigations.

http://dx.doi.org/10.5772/61671

11. Appendix

Term	Definition
• Meiocyte, pollen mother cell	Sporophytic cell in the centre of the anther that is destined to undergo meiosis and generate haploid pollen grains.
• Microspore	Alternative term used to refer to a pollen grain, but mainly used for the earlier uni-nucleate stages of pollen development. Young microspores refer to the first stage of pollen development, i.e. the cells released from the tetrad after meiosis. Microspores develop into the male gametophyte.
• Tapetum	Inner layer of the anther wall surrounding the meiocytes and loculus of the anther. Consists of secretory apoptotic cells that nourish and regulate pollen development. The tapetum degenerates, producing pollenkitt and other substances that cause pollen grains to aggregate.
• Cleistogamy/chasmogamy	Cleistogamy refers to automatic self-pollinating plants that do not open their flowers before pollen dispersal. In contrast, chasmogamy refers to plants that do open their flowers to release pollen in the environment for dispersal by animals or wind (potential cross-pollinators).
• Pollen Dispersal Unit	Pollen grains can be dispersed as single grains (monads) or as aggregates of several pollen grains kept together by viscous fluids or filaments (polyads). Tetrads derived from a single meiocyte can stay together in groups of four, united by common walls. In orchids, many packed tetrads can be arranged in different ways to form pollinia containing hundreds or thousands of pollen grains.
• Monads, polyads, pollinia	See pollen dispersal unit.
• Orthodox/recalcitrant pollen	Based on water content at dispersal, pollen grains can be classified as orthodox or recalcitrant. Orthodox pollen is desiccation-resistant and has a low water content (2–20%). Recalcitrant pollen is desiccation-sensitive, with water content between 20% and 50%. Orthodox and recalcitrant pollen grains both have advantages and disadvantages at pollination.
• Male germ unit	Is the association of a vegetative nucleus with a generative cell or two sperm cells to form a functional male reproductive unit in angiosperms. The term 'unit' reflects the close connection between the sperm cells and the vegetative nucleus.
• Septate/aseptate anthers	In septate anthers, in contrast to aseptate anthers, the meiocytes are separated by a wall (septum), dividing the locule in smaller compartments filled with pollen grains.
• Pollen presentation	Is the process of pollen exposure for dispersal to reach the stigma for pollination. Pollen presentation involves interaction between the anther and other floral parts. Primary presentation occurs when pollen grains are

Term	Definition
	exposed in the anther. Secondary presentation involves developmental relocation of pollen from the anther to another floral organ. Pollen grains are not presented by the anther when they are launched using different mechanisms.
• Zoophilous, entomophilous and anemophilous pollen	Pollen dispersal by animals, insects and wind, respectively.
• Pollen engorgement	Pollen maturation is associated with accumulation of starch granules in the cytoplasm. This process is called engorgement.
• Harmomegathy	The capacity of pollen grains to change shape in response to a decrease in volume during dehydration and prior to the development arrest state. This dynamic process is controlled by the mechanical properties of the cell wall (furrows) and can be reversed by rehydration on the stigma. When pores are absent, this increase and decrease in volume is due to the elasticity of exine and intine.
• Furrow	A fold region where the exine cell wall has reduced thickness, whilst intine is thicker. Furrows allow the cell wall to collapse to comply with the decrease in pollen volume during dehydration and increase volume during rehydration.
• Development arrest state	Term used to indicate the state of physiological and metabolic arrest when pollen grains reduce water content before dispersal.
• Of the locular fluid changes	Central cavity in the anther where pollen grains develop. The loculus is filled with the locular fluid which is secreted by the tapetum and serves to nurture pollen. In cross-section, anthers show four locules. The composition of the locule fluid changes during pollen development, and before anther dehiscence the fluid is reabsorbed by the filament or other floral parts to allow pollen presentation. The locular fluid is abundant in anthers with monad and tetrad pollen, but is reduced in species with pollinia or where grains are tightly packed.
• Mechanical layer	External cell layer of the anther wall where, after tapetum degeneration, cells develop lignified wall thickenings. The mechanical layer is responsible for anther opening and pollen exposure
• Pollenkitt	Hydrophobic glue derived from the degeneration of the tapetum, composed of saturated and unsaturated lipids, carotenoids, flavonoids, proteins and carbohydrates. Pollenkitt makes grains stick to the anther, to the pollinator body and to the stigma surface.
• Pollen viability	Term used to indicate the percentage of viable pollen (i.e., able to emit pollen tubes and fertilise). Pollen viability can be assessed by hand pollination, in vitro germination and several methods evaluating physico-

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Term	Definition
	chemical parameters of pollen (e.g., plasma membrane intactness, the presence/abundance of some molecules or enzymes).
• Sporopollenin	Chemically and biologically resistant and elastic substance forming the building block of the exine cell wall. Sporopollenin consists of a mixture of carotene and carotenoid esters.
• Exine	External discontinuous cell wall of pollen grains. Exine is elastic, is composed of sporopollenin and has an opening called the pollen germination pore or aperture.
• Intine	Inner continuous pecto-cellulosic wall of pollen grains. The intine structure is more complex at the apertures and furrows where pollen tubes will be emitted. The intine wall becomes continuous with the pecto-cellulosic wall of the pollen tube during germination.
• Callose	Polymer of glucose residues linked together through β-1,3-linkages. Callose is deposited during meiosis to separate the meiocytes and tetrad cells during meiosis. Callose represents a molecular filter to separate cells and is degraded by callase separated by the tapetum (β-1,3-glucanase).
• Pollen desiccation and water content	Pollen grains desiccate before dispersal to reach equilibrium with environmental conditions. Metabolism is slowed down to better resist the negative effects of the environment (high or low temperature and relative humidity). Orthodox and recalcitrant pollen have different water contents at dispersal.
• Secreted by the gymnosperm ovule	Liquid secreted by the ovule and exposed outside the stigma. When pollen grains land in the pollination drop, they rehydrate and germinate.
• Pollination syndrome	Term to describe the pollination traits that plants use in their natural environment to move from one flower to another, using different vectors. Plant can use abiotic (wind, water), as well as biotic (bees, birds) vectors to transfer pollen grains.
• Pollen competition	Haploid pollen grains differ in their genomic composition (recombination during meiosis) and therefore behave differently during development, pollen tube germination and in response to environmental challenges. This leads to competition between pollen grains. Pollen competition is an example of rapid Darwinian selection.

Acknowledgements

Special thanks to Drs C. Carrizzo, G.G. Franchi and M. Nepi who helped with the development of some of the arguments reported in this review, Dr D. Nocentini for providing pictures shown in Figure 3 Claudia Faleri and Massimo Guarnieri for technical assistance. RD is indebted to

the Australian Grains Research and Development Corporation for financial support (GRDC, grants CSP00175 and CSP00143).

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