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(REVIEW ARTICLE)



A review in pollen grains for plants

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Abstract

Ripe pollen's primary morphological, cytological, and physiological characteristics are explained, contrasted, examined, and explored alone, in various combinations, and in relation to the female counterpart as well as the biotic and abiotic environmental factors. The goal is to attempt and figure out why pollen grains have the same reproductive function yet differ greatly in morphology and physiology during dispersal. One or more grain types per species, size and shape, number of cells, pollen dispersal unit types, sporoderm stratification, furrows, colpori, and other apertures, pollen presentation and array, water content percentage, mature pollen reserves, and osmotics are among the characteristics taken into consideration. Some pollen characteristics are related to each other, while others are tied to the female counterpart or competition between males and females, and still others are related to the many elements of the species' habitat, flowering season, and pollen presentation time.

Keywords: Osmotics; Pollen dispersal units; Exine; Intine; Number of pollen cells; Size; Shape; Walls; Water content; Reserves of soluble and insoluble carbohydrates

1. Introduction

In the anther, also known as the pollen sac, where grains are fed by the tapetum—a transient, sporophytic, apoptotic tissue that acts as a bridge between the mother plant tissues and the gametophytic generation—pollen, the male gametophyte of Spermatophyta (gymno- and angiosperms), develops. Every grain is made up of several cells (the genuine gametophyte), which include exine that has been accumulated with the help of the sporophyte, intine that is of gametophytic origin, and inside common walls (Pacini, Franchi & Hesse, 1985). There are two forms of tapetum, which differ in how nutrients are transferred from the tapetum protoplast to growing grains (Pacini & Franchi, 1991). Beginning at the beginning of meiosis, the tapetum secretes a fluid that fills the loculus, the anther cavity where grains are submerged and grow. This fluid carries substances made by the tapetum and the maternal sporophyte to the developing grains submerged in it (Firon, Nepi & Pacini, 2012). The links between the tapetum and the type of pollen dispersal unit are linked to the fluid's volume, which varies based on taxonomic groups (Pacini, 2010). Pollen exhibits four following developmental phases, all of which happen irrespective of the mother plant's growth environment, cytological events that take place throughout development, and taxonomic group. When grains adhere to the stigma, rehydrate, and begin interacting with the female counterpart prior to and/or during pollen tube emission, the fourth phase takes place. The first and second phases take place inside the anther, before and after the first meiotic division; the third phase, known as pollination, takes place in the environment where grains are presented for dispersal and during dispersal, i.e., when grains are exposed to environmental conditions (Carrizo García, Nepi & Paci, 2017). A developmental arrest may occur at various stages of development depending on the species, ranging from meiotic prophase to the early bicellular stage. In most cases, pollen development is a continuous process that lasts a few days to a few months (Pacini & Dolferus, 2016). Due to crucial environmental times, such a hot summer or a harsh winter, this arrest lasts for no more than a few months (Mirgorodskaya et al., 2015).

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In order to prevent potential damage during dispersal, the more common developmental arrest caused by partial programmed desiccation occurs when pollen is mature. This phenomenon is also present in land plant spores and seeds, i.e., in all reproductively dispersed structures of plants (Footitt & Cohn, 2001).

Grain development in the various species results in morphological, cytological, and physiological differences. While some of the described characteristics examined in this work occur during the two-celled phase or the latter stage of maturity and dehydration, others form earlier, during the tetrad stage, when pollen walls are patterning and certain types of pollen dispersal units (PDU) are present.

2. Shapes of polar and equatorial views

Anther-produced grains typically have comparable morphologies (number of pores and furrows, same exine ornamentations), which makes it possible to identify the variety among farmed species (Pacini & Vosa, 1979). Because of the crossing over, asynchronous development, and simultaneous drying of all the grains of a single anther, grains of the same anther differ genetically and physiologically despite their outward similarity (Carrizo García et al., 2017). When pollen is simultaneously placed on the stigma, this becomes evident. Even when rehydration is simultaneous, pollen tube discharge is dispersed over time, and this also happens during in vitro germination. Despite this broad perception, most species only generate one kind of grain in each of a flower's anthers, however some have anthers with grains that vary greatly in morphological, cytological, and ecological aspects. The same anther, the anthers of the same flower, the inflorescences of the same plant, or the blossoms of different people can all exhibit these variations. The case of hybrid corn (Zea mays L.) provides an illustration of distinct pollen grains in the same anther. Due to gene segregation, 50% of the mature pollen in an anther includes starch granules, whereas the remaining pollen is starchless (Hixon & Brimhall, 1968). When developing anthers are cultured to create haploid plants, another example is apparent; two grain types (pollen dimorphism) that differ in their cytological characteristics and subsequent developmental pattern were occasionally found, with embryos only being produced in grains with particular traits (Sunderland & Huang, 1987). A second instance concerns distinct anthers within a single bloom, each containing a different pollen grain. Only fertile pollen can form a pollen tube and fertilize the female counterpart. The flowers of Lagerstroemia indica L. (Lythraceae) bear two types of anther: the inner ones produce yellow nutritive pollen to reward pollinators, while the outer ones produce blue-green fertile pollen to be dispersed for pollination (Nepi, Guarnieri & Pacini, 2008). Couroupita guianensis Aubl. of the Lecythidaceae exhibits the similar behavior (Ormond, Pinheiro, & De Castells, 1981). Because Lagerstroemia indica and Couroupita guianensis flowers don't produce nectar, pollinators are rewarded with nutritious pollen. Male flowers in certain Apiaceae have smaller grains than hermaphrodite flowers (McKone & Webb, 1988). A third instance is when a single individual produces distinct pollen grains from multiple blooms. The andromonoecious Capparisspinosa L. (Capparaceae), for example, has larger grains from male flowers than from perfect flowers. Hand pollination experiments showed a higher seed set with pollen from male flowers, despite pollinators not being able to distinguish between flower morphs (Zhang & Tan, 2009). The lychee (Litchi chinensis Sonn., Sapindaceae) is an exception, as each plant produces three different kinds of flowers: a female and two males (M1 and M2), all of which are found in the same inflorescence, however M1 blooms before the females and M2 blooms after them. While there are no physical differences between grains, M2 pollen consistently and noticeably outperforms other pollen in terms of germination rate and pollen tube length. Additionally, M2 flowers produce larger amounts of nectar than M1 flowers; this is because M2 pollen is more viable and M2 blooms are more appealing to pollinators, which increases the effectiveness of M2 flowers for pollination (Stern & Gazit, 1996, 1998).

Monadous grains are typically spherical in shape during development (Franchi et al., 2002, fig. 1), but they become more oval in shape and have a lower volume when the anther opens and the grains are visible (Firon et al., 2012, fig. 2). After the stigma is rehydrated, the volume rises and the shape takes on a spherical form. These changes in grain form and volume caused by water loss or income related to anther opening and pollen rehydration after landing on the stigma are referred to as harmomegathy (Wodehouse, 1935; Katifori et al., 2010). The stigma, furrows, pores, walls, and protoplast all undergo these volume changes during anther desiccation and rehydration (Katifori et al., 2010). Pollen viability is only preserved at a high level if these changes are compatible with the pollen machinery, regardless of environmental variations (Franchi et al., 2011; Firon et al., 2012). There is currently insufficient discussion on this subject from a broad perspective. When a species' grain size is reported, it is important to specify whether the grains were treated, the medium in which they were submerged during measurement (since shape and volume vary depending on the medium), the condition of the cytoplasm, and the grain's viability. When measured in water, ripe oval grains with furrows or colpori rapidly rehydrate and take on a spherical shape. While grains that are hydrated must be measured in water or following a full rehydration on the stigma, the actual size of exposed grains must be measured when they are submerged in a substance that prevents water absorption or elimination, such as immersion oil (Nepi & Franchi, 2000). The shape of single grains is not spherical but rather polyhedral when they are distributed as tedrads, which are derived from the same pollen mother cell or multiples of tetrads, grouped together, as in compound pollen, with

common walls (as in Orchidaceae, asclepiad Apocynaceae, and Acacia Mill.). In these situations, tetrad grains are grouped in various ways, with tetrads of various kinds and forms; that is, the four grains are packed closely together with little space between them (Pacini & Franchi, 1998, Pacini, 2009). Certain seagrasses produce filiform pollen, which is 3-mm long and 10- μ m wide (Pettitt et al., 1980). Due to their size and structure, they form a tangle at the orifice, and water currents cause them to separate during dispersal (Ducker & Knox, 1976, Larkum & den Harttog, 1989). By measuring the polar and equatorial axes, the pertinent research of pollen grains began by observing the form of the two perspectives' external boundaries. The equatorial axis was the one that runs along the equator, and the polar axis was the one that links the pollen's poles to the equatorial perspective. By calculating the polar axis to equatorial P/E ratio (Table1), as reported by (Erdtman, 1971).

Table 1 Pollen forms according to the P/E value

Shape classes	P/E
Per oblate	< 4/8
Oblate	4/8-6/8
Sub spheroidal	6/8-8/6
Sub oblate	6/8-7/8
Oblate spheroidal	7/8-8/8
Spheroidal	8/8
Prolate spheroidal	8/8 - 8/7
Sub prolate	8/7 - 8/6
Prolate	8/6 - 8/4
Per prolate	> 8/2

Table 2 Pollen particle sizes of several plant species

NO	Size of pollen grain	Measurement
1	Very small	<10 µm
2	Small	10 – 25 μm
3	Medium size	25 – 50 μm
4	Large	50 – 100 μm
5	Very large	100 – 200 μm
6	Gigantic	> 200 µm
7	Very small	<10 µm

3. The numbers, position and characters of apertures

The complex walls of gymno- and angiosperm pollen, which are often made up of exine (external) and intine (internal), are referred to as sporoderms (Erdtman, 1952). Exine is made of a biopolymer termed sporopollenin, is elastic, generally waterproof, and typically features perforations and apertures for pollen tube emission. It is created initially, following meiosis, during the late tetrad stage (Blackmore et al., 2007). Under EM, exine is frequently separated into layers with varying chemical compositions and appearances (Hesse, 2000). Numerous academics have been interested in exine ornamentation, mostly due to its taxonomic significance and connections to different kinds of pollen vectors. Compared to zoophilous species, anemophilous species' grains have a less decorated exine (Hesse, 2000). According to Heslop-Harrison & Heslop-Harrison (1982), intine is fibrillary, laid down prior to the first haploid mitosis, and shares a composition with the pectocellulosic walls of vegetative cells. It contains various forms of pectin and related arabinan, which enable volume growth during development as well as the flexibility and elasticity required to withstand stress,

particularly during dehydration and rehydration (Vieira & Feijó, 2016). Additionally, Intine is frequently zonate, with distinct components, like in certain gymnosperms (Chichiriccò & Pacini, 2008), where the outermost one is more gelatinized (Nepi et al., 2005). Jiang et al. (2015) found that plants exposed to maximum temperature regimes of up to 36 °C have thicker intine. Additionally, intine is thicker in the porous areas where its composition and structure are more intricate (Heslop-Harrison & Heslop-Harrison, 1982). Because it is exterior, exine, an elastic passive wall, promotes the volumetric changes in cytoplasm and intine brought on by pollen rehydration and dehydration. Conversely, intine plays a key role in grain metabolism, particularly during development, as it sieves the locular fluid substances in conjunction with the plasma membrane. Additionally, when thick, uniform, or only in accordance with the pores, it serves as a water reserve for the protoplast of the vegetative cell below (Pacini, Sciannandrone & Nepi, 2014). Together, exine, intine, and the pollen protoplast also contribute to the slight volume changes that happen during presentation as a result of changes in the environment's relative humidity (Bassani, Pacini & Franchi, 1994; Lisci, Tanda & Pacini, 1994). The observed changes in turgor pressure brought on by the polymerization and depolymerization of mature pollen osmotics or the absorption or release of trace amounts of water (as a result of adaptations to relative humidity) can both cause variations in pollen volume during presentation (Carrizo García, Guarnieri & Pacini, 2010). It is difficult to comprehend the impacts of pollen's abiotic stress tolerance because surprisingly little is known about the physicochemical modifications of these cell walls in response to changes in the various environmental conditions (Nepi et al., 2010). As observed in Juniperus communis L. by Nepi et al. (2005), intine and exine function independently in gymnosperms with taxoid type pollen, with exine breaking as a result of protoplast and intine rapidly increasing in volume due to the rapid rehydration of grains in the pollination drop (Mugnaini et al., 2007). A few angiosperms, such as Montrichardia arborescens (L.) Schott (Araceae), also experience this exine burst for the same reason (Weber & Halbritter, 2007). It has been hypothesized that the water stored in the thick intine keeps the vegetative cell cytoplasm wet and viable during presentation and dispersal. In contrast, pollen of Laurus nobilis L. (which lacks pores) has a thick intine and a spinous discontinuous exine, and the volume of the intine and protoplast varies according to the relative humidity of the surrounding environment (Pacini et al., 2014). According to Heslop-Harrison, Heslop-Harrison, and Heslop-Harrison (1986), the same appears to happen in species with Zwischenkörper, meaning that a poral intine makes up a significant amount of the pollen volume, such as about 25% in Corylus avellana L. Gametophytic proteins from the cytoplasm of vegetative cells are deposited during intine buildup in tubular plasmamembrane evaginations that bridge the poral intine of porate grains and the intine of poreless grains. These evaginations can occasionally be branched (Heslop-Harrison & Heslop-Harrison, 1991). During the last stage of pollen maturation, a thin intine neoformed layer closes up the entrance of these tubules (Heslop-Harrison, 1987). Sometimes found in the poral intine are sporophytic proteins that are produced from anther tapetum activity (Pacini, Franchi, & Sarfatti, 1981): Although it hasn't been proven yet, the theory that this mix of gametophytic and sporophytic proteins plays a role in pollen-stigma recognition has been proposed (Pacini & Juniper, 1979). As previously mentioned, the word "harmomegathy" refers to changes in the shape and volume of pollen grains that take place during pollen dehydration and rehydration during presentation and throughout atmospheric passage. Exine only serves to favor constant volume variations because it is an external factor (Pacini, 1990). Plants in the same genus (Callitriche L., for example) that live in conditions with rising relative humidity percentages experience a gradient of exine reduction with a final disappearance (Osborn, El-Ghazaly & Cooper, 2001). of contrast, pollen of the Nymphaeaceae family, which frequently floats on the water, has exine and colpi. Only in Barclaya Wall. is pollen inaperturate and devoid of colpi; it is visible in flowers that bloom at the water's surface, and self-pollination and cleistogamy are frequent (Williamson & Schneller, 1994). Because of the ideal climatic circumstances during pollination, which include a high relative humidity percentage, exine is reduced without compromising pollen viability. Due to the existence of several layers and types of pectin, intine often becomes specialized to store water, keeping the protoplasm wet, when the thickness of the exine decreases and this wall becomes discontinuous or even nonexistent (Pacini et al., 2014). Exine is discontinuous or almost absent in some terrestrial tropical species (Kress, 1986) or in those that are submerged and have underwater pollination (Pettitt et al., 1980), and it is also changed or even absent in the inner grains of massulate compound pollen, as in orchids (Pacini, 2009). This is because the process of dehydration and rehydration involves fewer interior grains. The perforations from which the pollen tube will be released interrupt the exine. The inner tetrad of the massulate essentially lacks these openings. omniaperturate-grained angiosperms (Erdtman, 1952). Certain species that are disseminated with a high water content, such grasses (Heslop-Harrison & Heslop-Harrison, 1980a, b) and Cucurbita pepo (Nepi, Ciampolini & Paccini, 1995), have been found to have three walls: exine, intine, and a thin callosic wall adjacent to the plasma membrane. This most likely happens because the pollen tube is released in a matter of seconds, and within 15 minutes of touching the stigma, the grains' thin calosic wall merges with the expanding pollen tube (Drábková & Honys, 2017). Exine, particularly in zoophilous species, can be decorated in a variety of ways. However, in certain Araceae, polysaccharides, occasionally in combination with proteins, form an ornamental layer outside the exine (Pacini & Juniper, 1983; Weber, Halbritter & Hesse, 1999). It is currently unknown what this layer does and why it is related to exine ornamentations (Pacini & Hesse, 2012). Only exine forms the aerial sacs in the pollen of Pinus L. and other gymnosperms; either these sacs or the exine's surface are coated in epicuticular waxes (Niester, Gülz & Wiermann, 1987), which prevent water loss and ingress during dispersal, maintain the pollen's shape, and enable the female counterpart's stereological recognition,

enabling species-specific pollination (Niklas, 1984; Paccini & Hesse, 2012). This waterproof covering, which is likely made of wax because xylol may remove it (Pacini et al., 1999), appears to show that, at least in Pinus, only the pollen aperture, which is located between the two wings, permits water to get through for rehydration. The furrow, also known as the colpus or sulcus (Punt et al., 1994), is a specific area of intine and exine that is designed to facilitate the volume drop that occurs during pollen dehydration and the volume rise that occurs during rehydration and pollen tube emission. The pectocellulosic portion is concealed by a furrow connected to a pore (colporus) that folds during dehydration and extends during rehydration. The furrow and the colporus were only taken into consideration from a morpho-taxonomic perspective by classical palynologists, but they also have physiological significance because they are in charge of the steady variation in pollen volume that occurs during pollen dehydration and rehydration (Halbritter & Hesse, 1993; Punt et al., 1994; Blackmore et al., 2007; Katifori et al., 2010).



Figure 1 The numbers of apertures (NPC)



Figure 2 The position of apertures (NPC)

4. Presentation and variety of pollen

The locular fluid, in which pollen has been submerged since meiotic prophase, vanishes when pollen grains have finished developing, the anther mechanical layer is fully differentiated, and the anther opening and pollen exposure are determined by the further dehydration of certain anther layers and the decrease in cell connection in the stomium (Carrizo García, Nepi & Pacini, 2006; Nelson et al., 2012). According to Culley and Kloster (2007), cleistogamous anthers skip the pollen presentation phase, which describes how grains are presented for dispersal in the open anther. The mechanical layer, filament structure, PDU type, and pollen vector alterations all affect the ways that pollen is presented

(Pacini & Hesse, 2004). Since pollen is not constrained by pollenkitt or other linking modalities, or is released by other mechanisms, it can exit the anther as soon as it opens. In Ricinus communis L. (castor bean), an unusual alteration of the anther mechanical layer permits explosive anther dehiscence (Bianchini & Pacini, 1996). Both the time of an anther explosion as well as the distance that grains travel are influenced by the relative humidity level of the surrounding environment. The anther wall of Urticaceae is reduced to a single layer of cells at maturity, without wall thickenings. The anther filament, which contains cells with U-thickened walls, suddenly moves like a lever, launching pollen (Franchi et al., 2007). Usually, pollen, particularly if it is ingested by pollenkitt, remains in the anther until it is either actively or passively expelled by animals that visit the flower or dislodged by air currents (Castellanos et al., 2006). Pollinia are offered for dispersal and protection inside the pollinarium for varying lengths of time in massulae-bearing orchids. The longest periods are one to three months in Paphiopedilum Pfitzer and five minutes in Dendrobium appendiculatum (Blume) Lindl., during which self-pollination frequently takes place if the pollinarium is not picked up by a pollinator (Endress, 1994). Due to the corolla closing up (Franchi, Nepi & Pacini, 2014), pollen presentation with grains exposed in the anther can persist anywhere from a few hours, as in the case of Cucurbita pepo (Nepi & Pacini, 1993), to several days, as in some bulbous species (Primack, 1985). In the cases of Lilium philadelphicum L. (Edwards & Jordan, 1992) and Laurus nobilis (Pacini et al., 2014), presentation may be sporadic when the anther closes due to unfavorable circumstances but reopens to reveal pollen when conditions are ideal. Even when the corolla of the same flower opens and closes a few times, certain tropical species also do this in reaction to sudden changes in their surroundings (Franchi et al., 2014).

5. Osmotics and mature pollen stores

The presence or lack of starch grains in the plastids of the angiosperm vegetative cell was the subject of some of the earliest comprehensive cyto-physiological investigations on pollen; lipidic reserves are also present as sphaerosomes, which are common in entomophilous species and particularly in starchless species (Baker & Baker, 1979). Only undifferentiated plastids, not amyloplasts, are found in generative cells and sperm cells; this is unique to animals whose plastid inheritance is biparental (Clément & Pacini, 2001). Grayum (1985) asserts that at least in Araceae, there occurs the trend with increasing diameter from starchless to starchy pollen, although this trend is also reversible when insect Pollinators consume pollen for sustenance. In commelinid monocots, Zona (2001) discovered that the starchy pollen grains were noticeably bigger than the starchless ones. With the exception of species where pollinators ingest the pollen, a considerable portion of big pollen in the Araceae family is starchy (Grayum 1985). Bees prefer to gather starchless pollen with pollenkitt (Franchi et al., 1996; Pacini & Hesse, 2005); they only gather other types of grain from plants that do not have pollenkitt nearby the hive, such as corn (Wille & Wille, 1983; Malerbo-Souza, 2011) or hemp (Franchi, personal observation). Both of these crops contain starchy grains, which the bees combine with saliva to create pollen balls and fill corbiculae. Pacini & Franchi (1988) detailed the physicochemical variations of the starch deposited during the various developmental stages of some chosen species, while Franchi & Pacini (1988) and Franchi et al. (1996) described the physicochemical characteristics of the starch of ripe grains in representatives of some angiosperm families. The amyloplasts may contain one or more starch grains, which would speed up accumulation, hydrolysis, and consumption in accordance with needs (Pacini, 1996b; Clément & Pacini, 2001).

6. Conclusion

A single species or homogeneous set of grains are used in nearly all current research on pollen, taking into account morphological, cytological, ecological, or evolutionary (adaptative) characteristics. Our goal was to identify any potential relationships between a species' environment, female counterpart, and different characteristics. In an effort to uncover more pollen biodiversity, we present a few additional generic relationships here. We are confident that this strategy will help clarify the intricacies of pollination and associated issues. Pollen from many plant species has a similar shape; the most frequent orthodox pollen in eudicots has three colpori. However, within this group, two- or three-celled grains and starchy or starchless grains can be distinguished (Table 1). The quantity of ovules per ovary and the kind of pollination are linked to the presence of pollenkitt occurrence (Pacini & Franchi, 1998; Pacini & Hesse, 2005). Poaceae pollen has a uniform morphology but varies in size; starch is always present but physicochemical characteristics, like the amount of soluble sugar and resistance to desiccation, differ greatly (Chaudhuri & Shivanna, 1987; Hoekstra, Crowe & Crowe, 1989; Franchi et al., 1996). On the other hand, male competition is fierce and female competition is nonexistent when pollen is distributed in monads, as in Poaceae, which contain just one ovule per ovary (Ottaviano & Mulcahy, 1989; Pacini & Franchi, 1998). As shown at least in Mercurialis annua, the presence or absence of pollenkitt affects male competitiveness because pollen grains that have been linked together may splash when they land on the stigma and be scattered on the stigmatic surface, lowering male competition. There is more competition when there are more donors because pollen from herbaceous species that are spread in monads without pollenkitt can mix in the air and land on the stigma. Pollen dispersal and survival are generally influenced by the biological form: herbaceous plants, particularly

those with many individuals living close to one another, may disperse grains quickly and reproduce successfully, especially in self-compatible species; in contrast, a self-incompatible tree with few individuals per unit area, that is, with individuals living far apart, needs effective pollination (i.e., orthodox pollen surviving longer in hostile environments) to ensure successful reproduction (Franchi et al., 2002, 2011). The same is true for dioecious trees, which have no compatibility issues but whose reproductive success is determined by the pollination type and the ratio of male to female plants. Some of the eight traits mentioned are influenced by the amount of people per unit area. A lengthy flowering period, pollen presented in pollinia, and a comparable number of grains and ovules overcome the low probability of pollination in the case of tropical orchids (low number of individuals per unit area and scarcity of suitable, frequently even species-specific, pollinators). The date palm (Phoenix dactylifera L.), an anemophilous dioecious species with individuals of different sexes often separated by kilometers in the natural environment (Soliman, Al-Saif & Al-Obeed, 2016), is relatively resistant to the stress of the harsh desert environment because of the high concentration of sucrose in the pollen cytoplasm. In summary, two groups of similar features can be distinguished from one another. The habitat of the plant, sexual expression, relative distance between individuals, environmental conditions during pollination, and self-compatibility or incompatibility are some of the variables that affect the duration, length, and success of pollen flights. Whether a species is zoophilous or anemophilous has no bearing on this. On the other hand, the female counterpart, the biological form, and the male gametophyte competition are the water percentage in pollen at the beginning of presentation and the existence of physiological homoeostatic processes that enable the maintenance of a consistent turgor pressure. Some species reproduce at low cost through cleistogamy due to the changeable environment and the resulting metabolic adaptability (Culley & Klooster, 2007); this happens in species with both orthodox and recalcitrant pollen (our observations). This indicates that all of the morpho-physiological processes that result in flower opening and the dehydration of anther and pollen are deactivated by the environment.

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