POLLEN GRAIN SPORODERM AND TYPES OF DISPERSAL UNITS

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ABSTRACT

The pollen of gymnosperms and angiosperms may be dispersed in monads, tetrads, polyads, massulae or compact pollinia. The monads and tetrads may form larger clumps of pollen because filiform pollen is tangled while other kinds of pollen can be glued by means of different devices. Exine and intine modify their structure to adapt to pollen dispersing units, exine in some cases can be absent. An additional layer, a thin callosic wall, can be present in some species beneath the intine; this occurs when pollen grains are slightly dehydrated before dispersal.

KEY WORDS: sporoderm, exine, intine, furrows, pores, harmomegathy, pollen dispersal units, pollination.

INTRODUCTION

The sporoderm is the outermost part of walls of pollen and spores (Heslop-Harrison 1963). It consists in most cases of an outer layer of exine and an inner layer of intine, neither of which are homogeneous in structure because of layering and modifications near apertures (Knox 1984). The intine is continuous, thicker near the apertures and always present, whereas the exine is interrupted by the apertures and may be discontinuous, extremely reduced or absent (Pacini 1997). Exine is made of sporopollenin and intine of polysaccharides such as pectocellulose and pectin (Southworth 1990, Heslop-Harrison and Heslop-Harrison 1991).

The exine and intine are joined in the interface zone. This enables the pollen to undergo partial or slight dehydration, which causes slowing of metabolism, and a decrease in volume, before exposure to dispersing agents, and to take up water again and increase in volume on the stigma. This process, called harmomegathy by Wodehouse (1935), enables the pollen to survive its passage in the atmosphere. Pollen morphology such as furrows and other wall features are necessary for water loss and uptake and subsequent changes in volume (Pacini 1990a).

Exine and intine contain proteins of different origin. Those of the intine are derived from the pollen cytoplasm, whereas those of the exine are derived from the tapetal cytoplasm. After nourishing the developing pollen, especially in species with zoophilous pollination, at degeneration time the tapetum gives rise to viscous fluids which are deposited on the exine surface. These fluids include pollenkitt (the most common), tryphine (in Cruciferae) and elastoviscin (only in Orchidaceae) (Pacini and Franchi 1998). The way in which they are deposited on the surface is peculiar to each type of fluid.

Many evolutionary convergences are found among pollen dispersal units, even in quite distant taxa. The mucilage produced by anther connective tissue in *Tylosema esculentum* (Caesalpinaceae) is similar to pollenkitt and tryphine and has the same function (De Frey et al. 1992). The free filaments produced by anther of certain Heliconiaceae and Strelitziaceae are similar to viscin threads (Rose and Barthlott 1995).

It is worth recalling that the most primitive angiosperms were entomophilous and that anemophilous plants are secondary. However, strict anemophiles (which do not have pollenkitt, e.g. Fagaceae and Poaceae) should be distinguished from anemophiles, such as *Olea europaea* (Pacini and Casadoro 1981) and *Mercurialis annua* (Lisci et al. 1994) which have pollenkitt and belong to families which are almost exclusively entomophilous.

During sporoderm ontogeny, the exine forms before the intine. The exine begins to form during tetrad stage when it is called primexine (Heslop-Harrison 1971). When the callosic component dissolves, it becomes mature exine. Depending on the type of tetrads, the sites of the pores become detectable in tetrad stage. The intine begins to form when the exine is complete, that is, about middle microspore stage. The intine is not usually complete until after the first haploid mitosis, when the evaginations of the plasma membrane containing the gametophytic proteins are sealed with a pectocellulosic layer (Pacini 1990b).

The present study is concerned with pollen wall modifications in pollen dispersal units, and is part of a research programme in cytology, ecology and evolution of the various types of pollen dispersal units which are described in a previous paper which also examines tapetal cell activity (Pacini 1997). Other aspects of the programme already examined include evolution of the types of dispersal unit of spermatophytes.

phytes (Pacini and Franchi 1996) and pollen dispersal units in relation to type of pollination, number of ovules and gynoecium structure (Pacini and Franchi 1998). A fourth paper deals with pollen dispersal units in relation to male and female competition (Pacini and Franchi 1999).

TYPES OF POLLEN DISPERSING UNIT AND THEIR RAISON D'ÊTRE

With few exceptions, the spores of mosses and ferns are dispersed singly. In the genus *Lecanopteris*, epiphytic myrmecophilous ferns, the 16 spores of the sporangium form massulae held together by exine thin ropes that attach to ant bodies for dispersal (Walker 1985).

The pollen of gymnosperms is dispersed as single grains, although pollen clumping occurs in species with zoophilous dispersal, such as certain Cycadaceae and the genus *Ephedra* (Bino and Meeuse 1981). Angiosperm pollen is dispersed in essentially four ways: 1. as monads; 2. as extremely long, fine grains in tangled masses; 3. in massulae held together by viscous materials (pollenkitt, tryphine, elastoviscin); 4. in groups united by common walls (multiple units or tetrads, polyads, massulae and pollinia, Fig. 1). Combinations are also possible (Fig. 1). Polyads, massulae and pollinia are almost exclusively dispersed by animals, usually insects but sometimes birds and winged mammals (Pacini and Franchi 1998). The dispersing units are exposed to pollinators when the anther opens and the pollen is always dispersed to several flowers, except in the case of compact pollinia which are deposited on the stigma of a single flower.

The most common type of pollen dispersal unit is the monad with pollenkitt. It is common in monocots and dicots and is thought to be the most ancient type of dispersing unit in angiosperms (Pacini and Franchi 1996). Besides holding the pollen together, pollenkitt sometimes has other functions, the most common of which are imparting colour and perfume to pollen, sticking the pollen together and to insect bodies, and enabling pollen compaction so that hymenopters can form balls to stick to their third pair of legs (Pacini 1997).

The reason for dispersal of single spores of ferns and gymnosperm pollen and for clumping and compound pollen in angiosperms may be related to one or more of the following factors: 1. the type of dispersal agent; 2. the presence of many ovules and female gametes in the ovary (several thousand in orchids); 3. strong male competition operating selection (obviously this type of competition not only depends on the type of pollen dispersal unit but also on the structure of the gynoecium and the number of ovules per ovary) (Ottaviano and Mulcahy 1989; Pacini and Franchi 1996, Pacini and Franchi 1998).

POLLEN ADAPTATION BY HARMOMEGATHY

Most pollen is partly dehydrated at dispersal. This implies loss of water and a change in shape from roundish to oval before dispersal. During exposure to dispersing agents and dispersal, pollen grains are usually subjected to a further water loss. The pollen then takes up water from the stigma and its metabolism is fully activated again, before it emits pollen tubes. Hence, pollen volume first decreases and then increases. This means that pollen walls are elastic with special modifications in the furrows (thicker intine and thinner exine) which are flexible and allow changes in volume (Wodehouse 1935).

Harmomegathy is a property of monad, tetrad and polyad pollen. Polyads never contain more than 32 pollen grains (Kenrick and Knox 1989) which are disposed in the same plane. Each grain is in contact with the outside and has some linear interruptions in the exine. These breaks are organized so as to permit changes in volume (Fitzgerald et al. 1993, where the breaks are shown in photographs but not described in the text).

As the number of pollen grains increases in compound pollen, that is in the various types of pollinium, harmomegathy becomes impossible because changes in volume of the various adpressed tetrads would break the cohesion between them.

In angiosperms there are, however, species with pollen that dehydrates only slightly (Nepi and Pacini 1993) and in which metabolism does not slow down but cyclosis continues even during dispersal (Heslop-Harrison et al. 1997 and our unpublished data). This pollen is not programmed for harmomegathy; it does not have biochemical defences against excessive water loss and dies in a short time. Slight dehydration has the advantage of leaving the pollen ready to emit pollen tubes promptly (a few seconds to ten minutes) after landing on the stigma. This may be why some pollen already has a thin callosic wall inside the intine at dispersal. This wall has so far been found in pollen of Poaceae and two other unrelated species, *Cucurbita pepo* and *Lavatera arborea*. Irrespective of pollination type, structure and number of pollen cells at maturity and pollen reserves, all these species have partially dehydrated pollen (Heslop-Harrison et al. 1997, Nepi et al. 1995). However, they have very different types of intine and exine. The Poaceae have very thin exine, a very thin intine and a single pore, whereas *C. pepo* and *L. arborea* have thick exine, thin intine and many pores. In all three cases, the pollen germinates a few seconds to 10 minutes after pollination.

The exine and intine are organized to accommodate changes in pollen volume by virtue of their conformation and the fact that they are joined together at their interface. This is not found in certain genera of gymnosperms such as *Calocedrus*, *Cryptomeria*, *Cupressus*, *Sequoia*, *Taxus*, *Torreya* and *Juniperus* in which the exine detaches from the intine on rehydration in the micropylar drop (Pacini 1990a, Pacini et al. 1999).

SPORODERM MODIFICATIONS

Monad pollen

The outer surface of pollen may vary according to the type of dispersing unit and the type of pollination. Anemophiles generally have relatively little exine microsculpture, whereas entomophiles with monad and tetrad pollen have more intricate exine microsculpture, perhaps to aid deposition of viscous fluids that enable clumping. In species belonging to an entomophilous family but which have reverted to anemophily, such as *Mercurialis annua* (Euphorbiaceae), the exine has microsculpture typical of an entomophilous species and there is pollenkitt (Lisci et al. 1994). Similarly, the exine of *Erica arborea* which initially has entomophilous and there later anemophilous pollination (Franchi and Pacini 1996), has elaborate microsculpture.

In pollen with viscin threads, pollenkitt is devoid of any function and therefore is extremely reduced or absent (Pacini and Franchi 1998); the filaments are made of sporopollenin and are appendages of the exine.

Dispersing units consisting of many grains of pollen (polyads and various types of pollinia) generally have relatively little microsculpture. This is evidently so that dispersing insects do not attach to the pollen but to a special long appendage: the viscidium in orchids and the corpusculum in Asclepiadaceae (Pacini and Franchi 1998).

Marine monocot pollen has exceptional adaptations to water, which is the dispersing vehicle. One of the main adaptations is the total loss of exine, because the pollen does not

dehydrate before it is released or during dispersal (Pettitt 1981). Another adaptation is the extremely long form of the pollen grains, which enables them to tangle at the start of dispersal and to adhere to the stigma as a massula.

Compound pollen: tetrad versatility

The tetrad is the basic element for compound pollen. Some or all species of about 50 families have pollen in tetrads or multiples of tetrads (Knox and McConchie 1986). Families

	Types of pollen dispersal units		Examples
A	monad pollen		Betulaceae, Urticaceae, Poaceae
B	a tangle of elongated monad pollen		Zosteraceae (McConchie and Knox 1989)
C	monad pollen grouped by pollenkitt or tryphine		pollenkitt: Euphorbiaceae, Oleaceae Labiatae, Compositae, tryphine: Cruciferae
D	monad pollen grouped by viscin threads		<i>Oenothera</i> (Oenotheraceae), <i>Fuchsia</i> (Onograceae)
E	monad pollen grouped by elastoviscin		<i>Apostasia wallachii</i> (Orchidaceae; Schill and Wolter 1986)
F	tetrad pollen		Typhaceae and Juncaceae
G	tetrads grouped by pollenkitt		many Ericaceae
H	tetrads grouped by viscin threads		<i>Rhododendron</i> species (Ericaceae)
I	polyads (16-32 grains)		<i>Acacia</i> (Leguminosae: Mimosaceae)
J	groups of tetrads united together by a thin external layer of callose (soft pollinium A)		<i>Polystachia pubescens</i> (Orchidaceae; Schlag and Hesse 1993)
K	tetrads grouped by elastoviscin (soft pollinium B)		some members of the tribes Orchideae and Neottieae (Yeung 1987b)
L	tetrads grouped by common walls forming a massula; exine is present on exterior of each massula: massulae kept together by the stipe or other devices consisting of elastoviscin (dotted) which also sticks the pollinarium to pollinator body, by means of the viscidium (soft pollinium C)		<i>Loroglossum hircinum</i> (Orchidaceae) (Pandolfi and Pacini 1995)
M	tetrads grouped in a compact flat pollinium with exine on the outside (hard or compact pollinium)		some orchids (Yeung and Law 1987b), the pollinarium adheres to the body of the pollinator by means of a viscidium; some Asclepiadaceae (Dannenbaum and Schill 1991), the pollinarium adheres to the body of the pollinator by means of a corpusculum

Fig. 1. Different types of pollen dispersal units with examples. Pollen grains are not drawn to scale. Types of pollen dispersal units as A. and F. are dispersed by air currents; B. by sea water currents; D., E., H., I., J., K., L., M., by animals, mainly insects; C. and G. by animals and/or air currents.

such as the Asclepiadaceae, Mimosaceae and Orchidaceae have more complex pollen dispersing units consisting of multiple tetrads (Walker and Doyle 1975). Although the latter family has most of the types of pollen dispersing units, the relation between number of ovules per ovary and number of pollen grains per dispersal unit has never been studied.

It is widely agreed that large pollen dispersing units are a way of ensuring the fertilization of most, if not all, the ovules in an ovary. When the pollen grains are derived from the same microspore mother cell and are dispersed together, the pollen dispersing unit is a tetrad and the pollen is held together by exine. The four grains of the tetrad may be disposed with a large or a small surface of contact. In the first case, the pollen is often held together by many bridges between the tectum and the bacula and each grain is like a tetrahedron with three planar faces and one convex face, and has therefore the shape of a quarter of a sphere. Examples of this type are in *Typha latifolia* (Takahashi and Sohma 1984), certain Velloziaceae (Ayensu and Skvarla 1974) and *Calluna vulgaris* (Dahl and Rowley 1991). When the contact region is small, the pollen grains are usually spherical in shape and connected by a few large exine bridges. Examples of this type are in certain Droseraceae (Takahashi and Sohma 1982) and Onagraceae (Skvarla et al. 1975).

The Caesalpiniaceae family has monad and tetrad pollen which is disposed, according to subfamily, in ways that reflect the phylogeny of this group (Ferguson and Banks 1994).

When the pollen dispersal unit consists of multiple tetrads, the pollen is usually held together by one of the following substances: a) viscous substances (Pacini and Franchi 1998); b) exine, as in the polyads of the genus *Acacia* (Fitzgerald et al. 1993); c) the intine of internal grains of the unit (soft pollinia) because the tetrads or peripheral grains have individual exine which has breaks between adjacent tetrads (Zavada 1990); d) exine for the peripheral grains of the unit and intine for the internal grains, as in compact pollinia of orchids and pollinia of Asclepiadaceae, in which the exine is uninterrupted (Yeung 1987a; Dannenbaum and Schill 1991). In this case the intine of the inner grains has many layers and is continuous between adjacent tetrads (Yeung 1987; Pandolfi and Pacini 1995).

The evolution of the various types of pollen dispersal units in the orchids is reflected by exine structure (Burns-Balogh 1983). In the pollinia, the exine evolved discontinuities and breaks up into small flakes on acetolysis (Wolter and Schill 1985). This is why it is so rare to find fossil orchid pollen (Wolter and Schill 1985).

From Fig. 1 it is evident that some of the pollen dispersal units are the arrival point of an evolutive trend, while other dispersal units are steps towards more evolved forms. This is the case of Fig. 1j, k which represent a prelude to pollinia. Quite recently, a new intermediate form was described by Verhoeven and Venter (1998) in many genera of Periplocoideae (Apocynaceae) where a few tetrads, all with exine and intine, are held together by exine bridges to form a sort of small pollinium.

Ontogeny of compound pollen

Compound pollen has mostly been studied at maturity; there have been fewer studies of its development and how the connections between pollen grains form. The grains become connected very early, namely at tetrad stage. The callosic wall forms a mould for the exine (Longly and Waterkeyn 1979). In species without exine, such as marine monocots, there is no callosic wall (Ducker et al. 1978, Pettitt 1981).

The callosic wall is also absent in internal tetrads of compact pollinia (Wolter and Schill 1986). In Asclepiadaceae with pollinia, it is found only between tetrads, which in this case are disposed in a line (Dannenbaum and Schill 1991). In tetrad pollen and multiple tetrads the callosic wall only forms on the outside (Fitzgerald et al. 1993).

Cytomictic channels and compound pollen

Cytomictic channels are connections between contiguous meiocytes derived from widening of a plasmodesma. They form during prophase and generally close between the first and second meiotic division. In compound pollen, they close later. In massulate orchids they close after the first mitosis (Pacini, unpublished data) which is synchronous throughout the anther (Heslop-Harrison 1968).

Apertures and furrows

Monad pollen has one or many pores, very often three, or none. In pollen with no pores or more than one pore, the site of pollen tube emission is determined once the pollen has interacted with the female part. This does not exclude the possibility that the emission site depends on the polarization of the generative cell.

There is no exine in the poral area of the sporoderm but the intine is rarely exposed during dispersal because the edges of the exine fold to form a furrow. Particularly in pollen with many pores, the apertures are closed by opercula which are removed by the pollen tube at germination (Nepi and Pacini 1993). The intine is thicker in the pore and has transverse zoning. It is penetrated radially by plasma membrane evaginations which contain sporophytic proteins (Pacini 1994).

Pollinia with tetrads and polyads also have apertures, but they are completely absent in orchid pollinia.

ALONE OR TOGETHER —ADVANTAGES AND DISADVANTAGES

Two aspects, which may be influenced by the number of pollen grains in each clump, are important for reproductive efficiency: 1. fertilization of as many ovules as possible to ensure many descendants; 2. multiple paternity to ensure genetic diversity and environmental adaptation. Clearly, for a given number of ovules per ovary, the more pollen grains per clump, the fewer the male individuals contributing to the gene pool, and vice versa (Pacini and Franchi 1998). In most cases, the two aspects balance: the number of pollen grains in each clump is high enough to ensure an adequate pollen load for fertilization, but on its own is not sufficient, so that several clumps are needed and genetic diversity is ensured.

The two extreme cases are exceptions to this rule. When the ovary contains only one ovule and the pollen is dispersed in monads (e.g. Poaceae), only one pollination could be necessary, and male gametophyte competition occurs when more than one pollen grain reaches the stigma at the same time. When the ovary contains many ovules but pollen is dispersed in compact pollinia (e.g. some orchids), all ovules are fertilized at once, but the seeds have single paternity (Pacini and Franchi 1998).

Some unusual cases obey this general rule. For example, in orchids with soft pollinia, the number of pollen grains left by an insect is very high, but not enough to ensure fertilization of all the ovules. More than one insect visit is therefore necessary, ensuring some degree of paternal diversity. On the other hand, pumpkin pollen has pollenkitt but travels as mon-

ads because of its large size (Nepi and Pacini 1993). The fact that the ovary contains several hundred ovules favours multiple paternity and fertilization of most of the ovules is ensured by very fast and efficient pollination (the pollen is transported in an almost fully hydrated state and quickly loses viability) by bees and other hymenopters. The plant invests heavily in nectar. The pollen must arrive and germinate at different times because the pollen tubes have to pass a constriction in the style (Nepi and Pacini 1993). The last example is *Typha*, in which the ovary has only one ovule but the pollen is dispersed in tetrads. This seems a needless waste, however the female flowers are so close to each other that when a tetrad adheres to a stigma, the pollen grains on top germinate too and their tubes can successfully reach an adjacent unpollinated stigma (Nicholls and Cook 1986). This is slightly disadvantageous for multiple paternity, but ensures abundant seed production in a plant with anemophilous and hence somewhat aleatory pollination.

POLLEN PORES AND POLLEN DISPERSAL UNITS

Some monad pollen has no pores, other has one or more pores. The presence of viscous fluids that favour cohesion, does not seem to be correlated with the presence of pores. Tetrad and polyad pollen always has pores which are obviously on the external surfaces. Although pollinia do not have pores, there is a difference between the Asclepiadaceae, in which the tubes all emerge in a given area, and the Orchidaceae. For example, in *Loroglossum hircinum*, which produces compound pollinia consisting of massulae, the tubes are emitted after the tetrads move away from one another (Pandolfi and Pacini 1995).

In pollen with pores and furrows, the pectocellulosic wall of the pore protrudes during pollen development, retracts before anther opening and protrudes again at hydration on the stigma or in culture medium (Pacini 1990a). This is possible because of the flexibility of the endexine of the furrow zone.

The pores are covered by opercula made of exine with the same microsculpture as the rest of the exine. In *Urtica dubia*, the operculum fits perfectly into the aperture at dispersal (Pacini et al. 1980; Fig. 1c). In *Cucurbita pepo*, the pore resembles a nipple with the operculum on top, exposing 9.5% of the surface area of intine to the atmosphere. This, and the limited dehydration of the pollen at dispersal, explain why viability decreases dramatically during exposure (Nepi and Pacini 1993).

Since the Mesozoic, there has been an evolutionary trend towards a greater number of pores (Walker and Doyle 1975). However this increase leads to a decrease in the mean pollen life, especially in plants with exposed poral intine such as *Cucurbita*. Pollen with only one pore is subject to competition (Ottaviano and Mulcahy 1989). When an anther produces pollen with different numbers of pores, as in some species of the genus *Viola*, pollen with more pores germinates faster but also loses viability faster (Dajoz et al. 1993).

CONCLUSIONS

Spores and pollen always have two walls that vary according to systematic group and the manner in which the gametophyte or pollen tube is emitted. In the angiosperms, they also vary in relation to the type and number of apertures, the type of pollination and the female counterpart. Pollen dispersing units with up to several hundred pollen grains presumably

form because the ovary contains multiple ovules (Pacini and Franchi 1998). Wall structure reflects the type and manner of dispersal of these units.

Wall morphology, not only external morphology but also that of the various layers including the intine, and the distribution and form of the apertures, is responsible for the flexibility or adaptability of the walls to changes in volume and shape (harmomegathy) occurring when the pollen dehydrates before dispersal (Pacini 1990a). In very large clumps in which the intine and exine are fused together, harmomegathy is not possible. In situations in which harmomegathy does occur, it is significant; this is because partially dehydrated pollen is relatively quiescent and remains viable for a longer time in the atmosphere. It can therefore exploit less specific (and hence less efficient) vectors. On the other hand, it requires time to rehydrate before it can germinate.

The various substances that promote pollen cohesion also enable pollen to adhere to pollinator bodies (Pacini 1997). The microsculpture of the exine surface and any opposite electrostatic charges (proposed for adhesion of polyads of *Mimosaceae*) also contribute to adhesion (Chaloner 1986).

Unfortunately, many microscopical techniques do not reveal these cohesive substances. For instance, acetolysis destroys all but the exine (e.g. all internal structures of pollinia having internal pollen grains linked only by intine, leaving only a discontinuous shell of exine) and so only the viscin threads can be observed. Most stains requiring the use of organic solvents (including ethanol series for dehydration of specimens) dissolve most of the viscous substances that hold pollen grains or tetrads in clumps. To observe clump structure or count the number of grains or tetrads it contains, it is therefore preferable to use direct water-based stains on fresh material (e.g. lactophenol cotton blue), or fresh unstained material, or fluorescence microscopy techniques that exploit autofluorescence and therefore do not require stains.

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SPORODERMA ZIARNA PYŁKU I TYPY JEGO ROZSIEWANIA

STRESZCZENIE

Pyłek nagonasiennych i okrytonasiennych może być rozsiewany w monadach, tetradach, polyadach, masulach lub zwartych polliniach. monady i tetrazy tworzyć mogą większe bryłki pyłku, gdyż pyłek nitkowaty jest splątany, podczas gdy inne rodzaje pyłku mogą być zlepione w inny sposób. Budowa egzyny i intyny decyduje o różnych sposobach rozsiewu pyłku, przy czym w niektórych przypadkach egzyna może nie występować. Dodatkowa warstwa, cienka ściana kalozowa, może u niektórych gatunków występować pod intyną; zdarza się to, gdy ziarna pyłku są lekko odwodnione przed rozsiewem.

SŁOWA KLUCZOWE: sporoderma, egzyna, intyna, bruzdy, pory, harmomegati, typy rozsiewu pyłku, pollinacja.