SOME CYTOLOGICAL, ECOLOGICAL AND EVOLUTIONARY ASPECTS OF POLLINATION

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ABSTRACT

Different types of pollen dispersing units are described. The pollen of angiosperms may be dispersed in monads, tetrads, polyads, massulae or compact pollinia. The monads and tetrads may form larger clumps of pollen with the aid of the following substances: a) pollenkitt, a product of *in situ* degeneration of the tapetum; b) tryphine, a product of tapetal *extra situm* degeneration, found only in *Cruciferae*; c) elastoviscin, a highly viscous product of the degeneration of a limited number of tapetal cells, found only in certain *Orchidaceae*; d) viscin threads or sporopollenin filaments arising from the pollen exine. The number of pollen grains composing the clumps depends on pollen diameter and the cohesive forces holding the pollen grains together. The various types of pollen dispersing unit are discussed in relation to the type of pollination and number of ovules per ovary.

KEY WORDS: pollen dispersing units, pollination, tapetum.

INTRODUCTION

The spores of land plants and the pollen of gymnosperms are always dispersed singly by wind. Angiosperm pollen may be dispersed singly or in clumps held together in different ways, by wind, water, insects or other animals (Fig. 1) (Pacini and Franchi 1993). Dispersal of pollen in clumps is associated with plants having ovaries with many ovules, up to several thousand in tobacco and orchids (Benzing 1987). In the evolutionary process between gymnosperms and angiosperms, there is also an increase in the distance from the pollen landing site to the female gamete. In gymnosperms this distance is usually slightly less than a millimetre, whereas in angiosperms it is generally greater and may exceed ten centimetres, as in the genus *Lilium* and in *Zea mays*. Ottaviano and Mulcahy (1989) observed that the greater the distance between the stigma surface and the female gametophyte, the stronger the gametophytic competition. They also proposed that the differentiation, success and spread of angiosperms has been due to the selective effect of gametophytic competition.

Pollen grains may clump together in three different ways: **a.** by means of fluids of different viscosity: pollenkitt, tryphine and elastoviscin; **b.** by means of viscin consisting in a tangled mass of sporopollenin filaments arising from the exine (Hesse 1981); **c.** by means of common walls as in tetrads, polyads, massulae and pollinia (Pacini and Franchi 1993).

The aim of this paper is to identify the cytological features that permit pollen dispersal *en masse* and to discuss their ecological, genetic and evolutionary repercussions.

POLLENKITT

Pollenkitt is typical of plants with entomophilous pollination, but without orbicles (Fig. 1). It is also found in anemophilous plants like *Mercurialis annua* which have orbicles (Pacini and Franchi 1993, Lisci and Pacini 1994). Pollenkitt is derived from tapetal cell degeneration and usually consists of two components: elaioplasts and spherosomes. The plastids of the tapetal cells divide actively during early microspore stage (Ciampolini et al. 1993). They later begin to store lipids and become elaioplasts (Pacini and Casadoro 1981). In *Rosmarinus officinalis*, pollenkitt is derived solely from spherosomes (Hesse et al. 1994). Spherosomes normally appear when the plastids have already differentiated into elaioplasts (Pacini and Casadoro 1981, Pacini and Keijzer 1989, Ciampolini et al. 1993). During binucleate stage, when the rest of the protoplast has almost disappeared, the content of the elaioplasts and spherosomes fuses to form pollenkitt. Pollenkitt is found in plants with parietal and amoeboid tapetum (Pacini and Franchi 1991). In plants with parietal tapetum in which the cells remain separate at the end of degeneration the pollenkitt forms spherical structures, one for each cell, until just before anthesis, when they fuse. The pollenkitt is deposited on the pollen only when the two contiguous locules fuse, or in any case before the anther opens (Weber 1991, Nepi and Pacini 1993). In plants with amoeboid tapetum, since there is a syncytium, the pollenkitt is deposited on the pollen grains as soon as degeneration is complete.

According to Pacini and Franchi (1993), the functions of pollenkitt are: **1.** to keep the pollen in the anther; **1.1.** until

Fig. 1. Diagram showing a hypothetical phylogeny of pollen dispersing units with the main pollination types.

Pollenkitt occurs only in the angiosperms. Orbicles are usually associated with anemophilous pollination; polyads dispersal is mostly carried out by birds. Pollenkitt, tryphine, viscin threads and elastoviscin stick pollen together in clumps or enable pollen to stick to pollinator bodies. When these devices are lacking, as in pollinia, other structures are provided to stick pollen to insect bodies.

collected by insects; **1.2.** until a sufficiently strong wind blows it away; **2.** to keep the pollen grains that form clumps together in the air so that they land on the stigma together; **3.** to stick the pollen to the bodies of pollinators; **4.** to protect the pollen from sunlight; **5.** to prevent further water loss from the pollen; **6.** to colour the pollen and make it visible or invisible to insects (Pacini and Bellani 1986); **7.** to keep the sporophytic proteins in the exine cavities; **8.** to perfume the pollen so as to attract pollinators; **9.** to permit secondary presentation of pollen.

In many plants, such as the *Compositae*, the flowers are small and the anthers open towards the interior of the flower. The pollenkitt sticks the pollen to the style which grows, carrying the pollen outside the flower where it remains until removed by insects or wind. This process is known as secondary presentation of pollen (Yeung 1993) as opposed to primary presentation which occurs on the anther. The number and relative importance of pollenkitt functions vary from species to species.

The number of pollen grains held together by pollenkitt varies in relation to pollen volume and the viscosity of the

various components. In most species, pollen is dispersed in clumps even of tens of grains; in *Cucurbita pepo*, probably because of its enormous pollen size, the grains are dispersed singly (Nepi and Pacini 1993). In this case the function of pollenkitt is therefore to stick the pollen to pollinator bodies rather than to form clumps.

In primitive angiosperms, pollenkitt and orbicles probably coexisted. As pollination became more specialized, the orbicles remained in anemophilous species and the pollenkitt remained in zoophilous species that rely on adhesion to animal bodies for dispersal (Fig. 1). For example, in *Olea europaea*, an anemophilous species, they coexist, being however the *Oleaceae* a prevalently entomophilous family (Pacini and Juniper 1979). The same occurs also in the entomophilous *Prunus avium* (Pacini et al. 1986). On the other hand, in predominantly anemophilous families such as *Graminaceae*, *Urticaceae*, *Cupuliferae*, there are orbicles but no pollenkitt (Fig. 1). Pacini and Franchi (1993) list a large number of angiosperms with pollenkitt and/or orbicles.

TRYPHINE

Tryphine has so far been found only in *Cruciferae* and is derived from early degeneration of tapetal cells, or rather rupture of the walls and/or plasma membrane at a stage when the organelles are still recognizable, so that the organelles are emptied into the loculus. The plasmalemma ruptures at late microspore stage in *Raphanus sativus* (Dickinson and Lewis 1973 a, b) and at early trinucleate stage in *Arabidopsis thaliana* (unpublished data). Intact organelles such as mitochondria and elaioplasts are temporarily situated at the surface of the pollen grains, but later are no longer recognizable. Tryphine always seems to be composed of various components, which may be hydrophilic and hydrophobic, whereas pollenkitt is more homogeneous (Pacini and Franchi 1993). Because the tapetum cells rupture and their contents enter the locule and later cover the pollen grains, this type of degeneration has been called *extra situ*, as opposed to that of pollenkitt which is defined as *in situ* (Pacini and Franchi 1991).

The functions of pollenkitt and tryphine seem to be substantially the same, however tryphine never coexists with orbicles. Proteins that permit pollen-stigma recognition have been identified in tryphine. In fact, *Cruciferae* have sporophytic self-incompatibility (Elleman and Dickinson 1994).

ELASTOVISCIN

Elastoviscin is a highly viscous product of tapetal degeneration found only in *Orchidaceae*. It is derived from the degeneration of the whole cytoplasm but its main components are spherosomes (Wolter et al. 1988). In the anther of orchids, elastoviscin may have various locations and functions: **a.** to hold monad pollen together as in *Apostasia wallachii* (Schill and Wolter 1986) or to hold massulae together (Hesse and Burns-Balogh 1984) and stick them to pollinator bodies; **b.** to hold massulae of a pollinium to the caudicle as in *Epidendrum ibaguense* (Blackman and Yeung 1983 a, b).

VISCIN

Viscin consists of flexible filaments of sporopollenin attached to the exine (Hesse 1981). They form on the microspore when it is released from the callosic wall (Takahashi and Skvarla 1990). Pollen grains covered by viscin filaments are found in certain species of the *Ericaceae*, *Caesalpiniaceae*, *Mimosaceae* and *Onagraceae* (Waha 1984).

TETRADS

Some or all the species of the following families have pollen which is dispersed in tetrads rather than monads: *Agavaceae*, *Annonaceae*, *Apocynaceae*, *Araceae*, *Asclepiadaceae*, *Begoniaceae*, *Berberidaceae*, *Bignoniaceae*, *Bromeliaceae*, *Caesalpiniaceae*, *Clethraceae*, *Cornaceae*, *Cucurbitaceae*, *Cynomoriaceae*, *Datisceae*, *Droseraceae*, *Empetraceae*, *Ericaceae*, *Gentianaceae*, *Goodeniaceae*, *Guttiferae*, *Hydrocharitaceae*, *Juncaceae*, *Lactoriaceae*, *Marcgraviaceae*, *Mimosaceae*, *Monimiaceae*, *Myrothamnaceae*, *Nepenthaceae*, *Nymphaeaceae*, *Oenotheraceae*, *Orchidaceae*, *Pedaliaceae*, *Periplocaceae*, *Phyllidraceae*, *Proteaceae*, *Pyrolaceae*, *Rubiaceae*, *Sapindaceae*, *Saxifragaceae*, *Solanaceae*, *Tiliaceae*, *Typhaceae*, *Velloziaceae*,

Winteraceae (Davis 1966, Erdtman 1969, Werhoveen and Venter 1994).

In anemophilous species, the tetrads are dispersed singly (Fig. 1) as in the *Typhaceae*. In entomophilous species they may be united in clumps by pollenkitt, viscin or elastoviscin (Fig. 1). The four pollen grains of a tetrad are all derived by meiosis from the same mother cell. They may have common walls, or be more or less independent but held together by bridges of sporopollenin joined to the roof, as in certain *Onagraceae* (Skvarla et al. 1975). In the tetrads of some *Asclepiadaceae*, cytotoxic channels may persist in mature pollen, in which case the cytoplasm of the four vegetative cells form a syncytium while the generative cells remain independent (Dannenbaum and Schill 1991).

POLYADS

Polyads are characteristic of the *Mimosaceae*. They originate from clustering of pollen grains derived from one to eight microspore mother cells (Kenrick and Knox 1989). If the polyad is derived from a single mother cell, it is a tetrad; if it is derived from four cells, it consists of 16 pollen grains; if it is derived from eight cells, it consists of 32 pollen grains. The most common polyad is composed of 16 pollen grains (Kenrick and Knox 1989). Polyads form in anthers with longitudinal septa and each cavity contains a polyad. Tapetum cells with persistent walls adhere to the surface of the polyad and nutrition is direct, without the locule and locular fluid as intermediary. Orbicles may be present but not pollenkitt (Fig. 1) (Kenrick and Knox 1979).

MASSULAE

The massula is a group of tetrads, typical of the orchids; many massulae clumped together form a pollinium. Pollinia are said to be soft (or mealy), as distinct from compact (or hard), when they are made up of massulae (Fitzgerald et al. 1994). The pollinator takes the whole pollinium, but at subsequent flowers massulae may be left on different stigmas. Massula structure may vary in that the tetrads composing it may have their own exine, or the exine may only coat the massula as a whole.

The tetrads are packed together with little space between them (Pandolfi and Pacini 1995). They are of different types, and therefore have microspores disposed in different ways, in order to reduce spaces to a minimum. In the mature massula, spaces account for only 15-20% of a section. They increase between pollination and germination, as pollen volume increases, reaching 50-60% (Pandolfi and Pacini 1995). Once adequate intercellular spaces have been created, pollen tubes can be emitted (Fig. 2) (Pandolfi and Pacini 1995).

COMPACT POLLINIA

In this case there are no massulae but a number of pollen grains disposed in tetrads packed together. The number may range from 40,000 to 4,000,000 (Schill et al. 1992). Compact pollinia are characteristic of orchids and the *Asclepiadaceae*. The exine is prevalently external and in orchids consists of the externally orientated surfaces of the tetrads in the outer layer, which is why it is not continuous (Dannenbaum and

Fig. 2. Changes in male and female gametophytes of orchids as a consequence of the formation of massulae or compact pollinia, and reasons for delay in pollen tube emission. Features refer to flowers having a long life span.

Schill 1991, Zavada 1990). Since the pollinium is compact and does not consist of massulae, the pollen grains composing it are deposited on a single stigma. This means that the seeds that develop are not genetically very different, originating as they do from the same parent sporophytes. The stigmas of anemophilous and entomophilous plants normally receive pollen of the same species but from many different plants. The fact that many pollen grains are united in a pollinium, whether soft or compact, determines a series of modifications of both the pollen and the female part. The transformations of the male and female gametophytes of orchids are shown in Fig. 2.

Except in rare cases such as some *Araceae* and the *Musaceae* (Zavada 1983) the monads have apertures in the form of pores and/or furrows. Grains grouped in tetrads and polyads always have apertures. Pollen grouped in pollinia does not have apertures and the site of pollen tube emission cannot be identified until at least 24 hours after pollination and after the tetrads break up (Fig. 2) (Pandolfi and Pacini 1995).

Irrespective of the type of pollen dispersing unit, the microspore and gametophyte of orchids do not increase greatly in volume during development (Pandolfi et al. 1993). If the grains of the massulae and pollinia increased much in volume they could not stay together. The pollen grains develop synchronously and are joined by cytotoxic channels up to a certain stage. Mature pollen grains do not dehydrate and have a very slow metabolism. Germination is preceded by the formation of many vacuoles which cause an increase in volume and intercellular spaces through which gradually emitted pollen tubes can pass (Fig. 2) (Pandolfi and Pacini 1995). In most orchids pollination and/or pollen germination stimulate the

ovule to continue development, which was suspended when the female gametophyte formed (Benzing 1987).

CONCLUSIONS

There is substantial agreement to the effect that primitive angiosperms were essentially entomophilous and probably lacked specialized structures for this type of pollination. The pollen, however, must have been coated with pollenkit (Frees and Crepet 1988, Meeuse 1990). At different stages of evolution, even very early, some groups of angiosperms went back to being anemophilous, perhaps to avoid competition for pollinators within and between species, and also to avoid the loss of pollen viability associated with dispersal by insects (Mesquida and Renard 1989). Moreover, in typically entomophilous families like the *Ranunculaceae*, *Euphorbiaceae* and *Compositae*, there are anemophilous members such as *Thalictrum*, *Mercurialis*, *Ricinus*, *Ambrosia* and *Artemisia*, which have pollenkit. Unlike other members of these entomophilous families, anemophilous species do not have floral nectaries. Nectar is a very costly secretion and when it is produced the plant consumes up to 33% of the substances it derives from photosynthesis (Pyke 1991).

In strictly anemophilous plants, there is no pollenkit and the plastids of the tapetum cells follow the same model of differentiation as entomophilous species up to a certain stage, that is, they differentiate as elaioplasts. However they are subsequently reabsorbed with the rest of the tapetum, without leaving any residues (Pacini et al. 1992). Pollen clumps may also be formed by methods less usual than the above: a. by

filaments derived from anther epidermal cells (Kronstedt and Bystedt 1981) as in *Strelitzia reginae*; **b.** by a viscous liquid produced by the anther connective tissue as in *Tylosema esculentum* (*Caesalpinaceae*) (De Frey et al. 1992); **c.** in marine monocotyledons, by the pollen grains themselves which are long and thin (up to several mm $\times$ tens of microns) and become tangled (Fig. 1) (Cox and Knox 1989).

The number of pollen grains only remains constant during transport of the pollen dispersing unit in the case of tetrads, polyads and compact pollinia. A few species are known in which the pollen, held together by common walls, is dispersed in a variable number of grains: Takahashi (1986) describes polyads consisting of a variable number of tetrads in certain species of the genus *Chimaphila* (*Pyrolaceae*).

The number of grains stuck together in clumps by pollenkit varies in entomophilous pollination (Nepi and Pacini 1993) and especially in anemophilous pollination in which wind speed and pollenkit viscosity are responsible for breaking up the clumps (Lisci et al. 1996). Similarly, in hydrophilous pollination of marine monocots, the pollen grains are tangled together when released by the anther but separate at a rate proportional to the speed of the current (Cox and Knox 1989).

It is interesting that certain mechanisms aimed at mass transport of pollen for zoophilous pollination do not exclude the possibility of anemophilous pollination if necessary: this is true when there is pollenkit, tryphine or polyads. In other cases wind dispersal is prevented by the size of the pollen clumps (massulae and pollinia) or the strength of the material that holds the clumps together (very viscous elastoviscin, viscin threads of sporopollenin).

The trend to disperse pollen in clumps in the angiosperms may be related to the fact that the pistil contains many ovules and dispersal en masse leads to high pollination efficiency and a low ratio of pollen to ovules. This has principally been observed in certain *Onagraceae* which have viscin threads (Cruden and Jensen; 1979), in the genus *Acacia* that has pollen in polyads (Kenrick and Knox 1989) and in the *Orchidaceae* that disperse pollen in pollinia (Benzing 1987). On the other hand, in most cases of strictly anemophilous pollination, the ovary contains only one ovule, e.g. in *Urticaceae*, *Cupuliferae*, *Salicaceae* and *Graminaceae*.

The orchid family has the largest variety of pollen dispersing units (Fig. 1), as well as a wide range in life span of flower and female receptivity, from 30-60 days down to only five minutes (Endress 1994). Anyway there does not seem to be any data on how the number of ovules varies in relation to type of pollen dispersing unit. Orbicles have never been described in orchids, even in those that have pollen dispersed in monads (Pandolfi et al. 1998). From some viewpoints, the orchids represent a peak of angiosperm evolution. In their specialization, they "return" to very "ancient" methods. The fact that the female gametophyte of orchids only develops after pollination is a feature they have in common with most gymnosperms. In both cases the purpose is the same, namely to make a safe investment by allowing only fertilized ovules to develop. In gymnosperms, pollination is anemophilous and the pollen grains travel separate; the gametophyte of each ovule begins to develop only when the pollen reaches it; in any cone, some ovules may develop and others may not. In the orchids, dispersal in pollinia ensures that a number of pollen grains fairly similar to the number of ovules in the ovary, and therefore sufficient to fertilize them all, is received with a single pollination. Once pollination has occurred, the gametophytes of all the ovules can begin to develop.

ACKNOWLEDGEMENTS

This research was supported by a grant from CNR, program "Reproductive Ecology".

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CYTOLOGICZNE, EKOLOGICZNE I EWOLUCYJNE ASPEKTY ZAPYLANIA

STRESZCZENIE

W pracy opisano różne typy rozprzestrzeniania się pyłku. Pyłek okrytonasiennych rozprzestrzeniany jest jako pojedyncze ziarna, tetrady, polyady, massulae lub zwarte pollinia. Pojedyncze ziarna lub tetrady mogą być połączone w większe skupienia za pomocą następujących substancji: **a)** kitu pyłkowego, substancji, która powstaje podczas degradacji tapetum i powleka ziarna pyłku; **b)** tryfyny – produktu degeneracji tapetum *extra situm*, który występuje tylko u *Cruciferae*; **c)** elastowiscyny – bardzo lepkiej substancji powstającej w wyniku degeneracji ograniczonej liczby komórek tapetum, występuje tylko u *Orchidaceae*; **d)** nici wiscynowych lub włókien sporopoleninowych wyrastających z egzyny ziaren pyłku. Liczba ziaren pyłku tworzących skupienia zależy od średnicy pyłku i sił przylegania utrzymujących ziarna w skupieniu. Różne typy rozprzestrzeniania jednostek pyłkowych zostały przedyskutowane w stosunku do typu zapylania oraz liczby załączków w załączni.

SŁOWA KLUCZOWE: typy rozprzestrzeniania się pyłku, zapylanie, tapetum.