PLASTIDS AND MITOCHONDRIA COMPORTMENT IN DIVIDING MEIOCYTES OF *PSILOTUM NUDUM*

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ABSTRACT

In prophase I meicyte plastids and mitochondria were situated at random. By telophase I plastids and mitochondria were aggregated in an equatorial plane. The aggregation was differentiated into three layers, the middle layer formed mostly by mitochondria, the outer layers consisted largely of plastids. By telophase II the mitochondria layers separated the cell into four domains, while plastid layers were disaggregated. Inside the mitochondrial layer the cell plates were formed. During this process mitochondria layers gradually disintegrated. During prophase I to telophase I numerous plastids seem to undergo divisions. The telophase I layer mitochondria seemed to give rise to small electron-lucent vesicles.

KEY WORDS: *Psilotum*, sporogenesis, aggregation of organelles, organelles apportionment.

INTRODUCTION

Rearrangements of plastids and mitochondria during sporogenesis were described in several pteridophytes (ref. Gabarayeva 1985, Sheffield and Bell 1987, Rodkiewicz and Duda 1988).

The most prominent features of these rearrangements are equatorial plates of plastids and mitochondria arranged between telophase I nuclei. In *Psilotum nudum* the plate consists of a middle layer mostly formed by mitochondria sandwiched between layers of plastids. In *Equisetum* a similar layer occurring in telophase I, persists until telophase II and after reshaping divides the cell into four parts, separated later by the cell plates.

These telophase II organelle layers consist of mitochondria which are topographically associated with the forming cell plates (Bednara et al 1986). A similar course of events in *Psilotum nudum* sporocytes is presented in this paper.

MATERIAL AND METHODS

Synangia of *Psilotum nudum* L. (*Psilotaceae*) (Fig. 1) were fixed in 2.5% glutaraldehyde and 2.5% paraformaldehyde in 0.05M cacodylate buffer pH 7.0 and embedded in Spurr 69 and Epon 318 mixture 1:1 resin. Semithin sections were stained with 2% toluidine blue. Ultrathin sections were stained with uranyl acetate and lead citrate, to some sections the Thierry reaction for polysaccharides was applied. Preparations were examined with an electron microscope JEM 100B or Tesla BS 500.

RESULTS

Prophase I and metaphase I (Figs 2, 3). Cytoplasm of these stages contained proplastids, mitochondria and other normal cell constituents (Fig. 4). Proplastids with homogenous stroma contained small single starch grains, a small number of plastoglobules and lammelar structures. Some proplastids were constricted, being apparently in the division stage (Figs 5, 6). Mitochondria had circular or elongated profiles (Figs 4, 5, 6).

Telophase I (Fig. 7). At this stage all plastids and mitochondria were aggregated in an equatorial plate. The plate consisted of three distinct layers: the central layer contained mitochondria, while plastids were arranged in the outside layers. Optically empty vesicles were present between the organelles gathered in the plate (Figs 9, 10).

Plastids contained starch grains manifested by Thierry reaction (Fig. 9). The internal structure of the plastids appeared simpler than in prophase I. There were almost no membranous structures and plastoglobules (Fig. 12). Fig. 11 shows a diagonal, and therefore wide, section of the middle layer. Almost all mitochondria in this layer were optically dense and circular, some however, displayed small translucent outgrowths.

Fig. 8 – metaphase II. The equatorial layer more compact than in telophase I, it separates two metaphase chromosome plates.

Figs 13, 14 show simultaneous cytokinesis after telophase II. At early posttelophase II the cell is divided into four parts by rows of mitochondria, while plastids are loosely situated in the space between the mitochondrial layer and the cell nucleus, positioned close to the forming sporoderm (Fig. 15). At first an incipient cell plate lays between the mitochondria. La-

Fig. 1. Three sporangia of synangium in *Psilotum nudum* L.
 Figs 2 and 3. Prophase I and metaphase I sporocytes.
 Figs 4, 5, 6. Prophase sporocyte of *Psilotum*:
 4. Circular and elongated mitochondria and proplastids in cytoplasm.
 5, 6. Constricting plastids with starch grains.

Fig. 7. Telophase I. Organelle in equatorial plate – middle layer of dark mitochondria.

Fig. 8. Metaphase II. Chromosome plates separated by a dense organelle aggregation.

Fig. 9. A region between telophase I nuclei, aggregation of circular mitochondria among plastids with starch stained black after Thierry reaction.

Fig. 10. Telophase I organelle plate, some mitochondria with electron translucent outgrowths (arrows).

Fig. 11. Mitochondria layer of the organelle equatorial region, some mitochondria with translucent outgrowths, numerous translucent vesicles among the mitochondria (arrows).

Fig. 12. Plastids in the outer layer of equatorial organelles aggregation.

Figs 13, 14. Simultaneous cytokinesis after telophase II:

13. Spores of the tetrad separated only by mitochondrial layers.

14. Posttelophase II tetrad of the spores separated by cell walls or cell plates.

Figs 15, 16, 17. Late telophase II and posttelophase II:

15. Mitochondrial layer among differentiating spores.

16. Mitochondria associated with a discontinuous cell plate.

17. More advanced stage of cell plate formation, mitochondria are absent in the peripheral region.

ter the mitochondria begin to disassociate from the cell plate. Figs 14, 16 and 17 show that the mitochondria are not present by the peripheral part of the cell plate, but are still associated with the middle and central regions of the cell plates.

DISCUSSION

Plastids and mitochondria during sporogenesis in *Psilotum nudum* formed a regular aggregation in telophase I. By telophase II this aggregation was reshaped and restructured.

In these processes plastids abandoned the aggregation. Mitochondria remained aggregated and become associated with forming cell plates which separate spores into a tetrad.

Basically similar events were described in telophase I of sporogenesis and microsporogenesis of simultaneous type in various species of Pteridophyta, Gymnosperms and Angiosperms (Birky 1983, Rodkiewicz 1992). The aggregation of plastids and mitochondria in the telophase I cell equator may facilitate their equal apportionment among the postmeiotic cells (ref. Bednara et al. 1986). Now we propose another, but not alternative interpretation.

Plastids and mitochondria are aggregated in meiocytes which have no active mechanism of cytokinesis I (like in *Equisetum* and *Psilotum*) (Lehman et al 1984, Bednara et al. 1986, Gabarayeva 1984, 1985). Consequently after telophase I two nuclei remain in a common cytoplasm. The organelle aggregation in such cells is playing the role of a cell plate preventing fusion of the nuclei and the meiotic spindles. Meiosis may therefore proceed without aberrations.

The mitochondrial layer separates two domains in the telophase II cells, and later it seems to be associated with forming cell plates. The role of this association remains unexplicable. The mitochondria of prophase cell seem to be of two shapes: slightly elongated or circular. Later in the equatorial aggregation, they are circular and optically dense. These mitochondria form translucent bulges or outgrowths which are, as we assume, separated in a form of small vesicles remaining in the aggregation.

Plastid division during sporogenesis was observed thoroughly only in some mosses with one large plastid in the meiospore mother cell. Two divisions of this plastid are restricted to prophase I (Brown and Lemmon 1982). In microsporocytes of *Stangeria* and *Larix* some dividing plastids were observed in prophase I (Rodkiewicz et al 1985, Rodkiewicz and Duda 1988). However, in microsporogenesis of *Nymphaea* a fairly large proportion of plastids is in the course of division in metaphase I and telophase I (Rodkiewicz et al 1988). We may assume that division of plastids occurs mainly in meiosis I of cells.

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ROZDZIAŁ PLASTYDÓW I MITOCHONDRIÓW W MEJOCYTACH *PSILOTUM NUDUM*

STRESZCZENIE

W profazie I mejocytów *Psilotum nudum*, plastydy i mitochondria są rozmieszczone równomiernie. W telofazie I organella te skupiają się w płytkę w równikowej płaszczyźnie komórek. Skupienie jest trójwarstwowe: warstwa środkowa składająca się głównie z mitochondriów otoczona jest dwoma warstwami zawierającymi głównie plastydy. W telofazie II plastydy rozpraszają się, ale płytka mitochondrialna dzieli komórki na cztery przestrzenie. Wewnątrz płytki zakłada się przegroda i wówczas mitochondria rozpraszają się. W czasie profazy I i telofazy I duża część plastydów podlega podziałom. Wydaje się zaś, że w telofazie I od mitochondriów oddzielają się elektronoprzejrzyste pęcherzyki.

SŁOWA KLUCZOWE: sporogeneza, agregacje organelli, rozdział organelli, *Psilotum*.

CHANGES OF ELECTRIC POTENTIAL IN WHEAT PISTILS INDUCED BY POLLINATION

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ABSTRACT

We investigated changes of electric potential induced in wheat (*Triticum aestivum* L.) pistils by pollination with wheat or maize (*Zea mays* L.) pollen. Electric measurements were made in a monophasic system with Ag/AgCl/0.1 M KCl microelectrodes ended with glass capillaries (ϕ 1.5-3 μ m). The reference electrode was implanted into the embryo sac while the measurement electrode was in a surface contact with one stigmatic stylodium. We pollinated 15 min after the implantation of electrodes. Control experiment showed that maize pollen tubes grew much slower than wheat ones. The potential was recorded for 20 min after pollination in 10 selfpollinated wheat pistils and for 70 min in 16 wheat pistils pollinated with maize. After measurements pollen tube growth was examined with aniline blue under fluorescent microscope.

In selfpollinated pistils of wheat the potential decreased quickly and stabilized at $-10 \text{ mV} \pm 3 \text{ mV}$ to the initial level. The fastest rate of changes accompanied the penetration of the stigmatic hair and the growth of pollen tubes in stylodia. In wheat $\times$ maize crosses the potential decreased in every pistil before emergence of pollen tubes. When germination was successful, the potential remained negative. Its minimal value ranged from -3 to -84 mV and was correlated with the number of pollen tubes found in the stylodia. When grains fail to germinate the potential increased. All the recorded changes of potential were long lasting waves with slowly growing amplitudes.

KEY WORDS: electric potential – maize – pollination – wheat.

INTRODUCTION

Action potentials found in animals were suggested to be the universal way of the information transition in the living world. Similar signals were detected in plant tissues (Pickard 1973, Davies 1991). We can assume that electric impulses could inform the ovule about the pollination long before the pollen tube reaches the micropyle. This possibility was investigated by some authors (Lysikov and Dukhovnyi 1966, Sinyukhin and Britikov 1967, Linskens and Spanjers 1973, Spanjers 1981, Spanjers and Pierson 1982). They have found voltage changes of various kinds in pollinated flowers, however, the data were inconsistent and further experiments of this kind were abandoned. It has been found recently that ion distribution and fluxes play an important role in pollen tube growth (Miller et al. 1992, Capkova et al. 1994, Feijo et al. 1995). Ion displacements are always connected with electrical events. In support to the latter it was shown *in vitro* that external electric field influences pollen-tube orientation (Malho et al. 1992). Further studies revealed that growing pollen tubes generate their own electric fields which can interfere with the external ones (Feijo et al. 1994, 1995). Those findings stimulated us to investigate electric current accompanying *in vivo* germination of pollen.

We present here the changes of electric potential in wheat pistils induced by pollination with wheat or maize pollen. Both kinds of pollen germinate easily *in planta* on wheat pistils. The germination of maize pollen on a wheat stigma was studied recently in details (Wędzony and Lammeren in press). Electric potentials have not been yet investigated in wheat. We tried to correlate electric records with the number and the

growth rate of pollen tubes, which was never done in previous studies.

MATERIAL AND METHODS

Emasculated wheat pistils (*Triticum aestivum* L. cv. 'Grana') were placed in Faraday's cage and protected against drying. We pollinated by shaking stamen heads of wheat or maize (*Zea mays* L. line MK286) over the wheat stigma without touching it. For 2 h after pollination (AP) 3 pollinated pistils of each cross were fixed every 15 min to examine the speed of pollen tube growth in the experimental conditions. Electric measurements were made in a monophasic system with Ag/AgCl/0.1M KCl microelectrodes ended with a glass capillary (ϕ 1.5-3 μ m). The reference electrode was implanted into the embryo sac while the measurement electrode was in a surface contact with one stigmatic stylodium (Fig. 1). To control the electric stability of the system, records were taken in 10 unpollinated pistils for 2 h after the electrodes implantation.

Pistils were pollinated when electric potential was stabilized (about 15 min after the implantation of the electrodes). The potential was recorded for 20 min AP in 10 selfpollinated wheat pistils and for 70 min AP in 16 wheat pistils pollinated with maize. After measurements the pistils were fixed for further examination.

The material was fixed in ethanol: acetic acid (3:1). Pollen tubes were investigated under a fluorescent microscope on squashed preparations stained with aniline blue. After electric measurements only stylodia were examined with the above method. The ovaries were embedded in paraplast, sectioned

Fig. 1. A diagram showing the set-up of an equipment for recordings of the electric potential. The measurement electrode (A) in a surface contact with one stigmatic stylodium and the reference electrode (B) implanted into the embryo sac.

10 μ m thick and double stained with safranin and fast green. The precision of implantation of the reference electrode was checked on serial sections. The examination confirmed placement of the reference electrode tip in the embryo sac, mainly in the central cell.

RESULTS AND DISCUSSION

Control of potential stabilization.

Rapid and irregular changes of potential lasted for 7-10 min after implantation of the microelectrodes (not shown on the graph), then the potential became stable for 2 h (Fig. 2 B). The value of the stabilized potential at the moment of pollination was used as "zero" level for further calculations. About 2 h after implantation the measurement electrode usually lost its contact with stylodium because of pistil fading. Short lasting electric instability found here after the electrodes implantation is usual for wounded tissue (Picard 1973, Frachisse and Desbiez 1989).

Wheat selfpollination.

The wheat pollen tubes germinated, grew fast and reached the micropyles within 30 min (Table 1). These observations

are in agreement with data collected *in planta* (Vishnyakova and Willemse 1994, Wędzony and Lammeren in press). Within half a minute AP the potential started to decrease with the fastest rate during the first 5 min AP (Fig. 2 C). Later the potential stabilized at $-10 \text{ mV} \pm 3 \text{ mV}$. Cytological examination showed that pollen tubes were present in the ovarian cavities at the time of fixation.

Based on the above observations we can say that the fastest drop of the potential accompanied the penetration and the growth of tubes in the stylodia. The growth of pollen tubes in the ovarian cavity did not cause further changes in electric polarity of the pistil in our experiment.

Wheat x maize crosses.

Maize pollen on a wheat stigma germinated slower than wheat pollen. (Table 1). The data presented in Table 1 agree with those collected *in planta* (Wędzony and Lammeren, in press). For the first 10 min AP in the wheat x maize cross the potential decreased in every pistil, in spite of further success in germination (Fig. 2 A, D, E). Comparison of the data in Table 1 and Figure 2 A, D and E show that electric changes started before emergence of pollen tubes from grains. When pollen tube growth was successful the potential in the wheat x maize cross

TABLE 1. Wheat (*Triticum aestivum* L.) x wheat and wheat x maize (*Zea mays* L.) crosses. Pollen tubes germination and growth in relation to time after pollination (AP). Data collected in the Faradays' cage in the conditions designed for electric recordings.

TYPE OF CROSS	TIME AP (min)	POSITION OF POLLEN TUBES IN WHEAT PISTILS
wheat x wheat	15	most pollen grains germinated: pollen tubes in stylodia, some in the ovary
	30	10-20 pollen tubes in the ovary, usually one at the micropyle
	45-120	similar as 30 min AP
wheat x maize	15	pollen not germinated yet
	30	some pollen germinated
	45	more pollen germinated, first pollen tubes penetrated the stigmatic hair
	60-75	many pollen tubes penetrated the stigmatic hair, various number of pollen tubes in stylodia
	90-120	pollen tubes in stigmatic hair and stylodia, some reached the ovary

Fig. 2. Examples of records showing changes of electric potential after pollination. A, D, E – wheat x maize, B – control without pollination, C – wheat selfpollination. Bar shows values of amplitudes.

remained negative to the initial level, however shapes of the individual electric waves were variable (Fig. 2 D, E).

Pollen tubes growth within the style in the present experiment resulted in long lasting drops of potential regardless the cross combination. Similar records were obtained in maize styles after selfpollination (Lysikov and Dukhovnyi 1966) and

in styles of *Lilium* and *Incarvillea* (Sinyukhin and Britikov 1967). We can conclude that the decrease of electric potential is the usual reaction of styles to pollen tubes growth. Data of Linskens and Spanjers (1973) in *Petunia* and Spanjers (1981) in *Lilium* do not support this conclusion. All comparisons,

Fig. 3. The minimal potential in wheat pistils pollinated with maize against corresponding numbers of pollen-tubes in stylodia. The trend line shown on the plot. Correlation coefficient = -0.92.

however, should be made with caution, since the schemes of all above experiments vastly differ.

In the present experiment the minimal values of potential in the wheat x maize cross were strongly correlated to the number of pollen tubes found in the stylodia (Fig. 3). It might be possible that the cumulative electric fields generated by pollen tube tips bypassing the measurement electrode had big impact on the recorded results. The exact biological meaning of the quantitative relation of electric potential to pollen tubes number needs further studies.

Viable pollen of maize did not germinate in 6 wheat flowers collected 2 and 3 days after anthesis. Wheat pistils were not receptive for maize pollen then. Electric records showed here the increase of the potential 10 min AP (Fig. 2 A). The reaction to the germination failure is distinctly different from the reaction to the successful pollen tube growth.

All the changes of potential recorded in the present experiment have character of long lasting waves with the slowly growing amplitude. Such waves are usually connected with passive and active transport of ions and small organic molecules (Davies et al.'s 1991). They might be a sign of changing the developmental pathway.

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ZMIANY POTENCJAŁU ELEKTRYCZNEGO W SŁUPKACH PSZENICY POD WPŁYWEM ZAPYLENIA

STRESZCZENIE

Badano zmiany potencjału elektrycznego zachodzące w słupkach pszenicy (*Triticum aestivum* L.) pod wpływem zapylenia pyłkiem własnym i pochodzącym od kukurydzy (*Zea mays* L.). Pomiarów elektrycznych wykonywano w systemie monofazowym przy użyciu mikroelektrod Ag/AgCl/0,1 M KCl zakończonych kapilarą szklaną (ϕ 1,5-3 μ m). Elektroda odniesienia wkluwana była do woreczka zalążkowego, a elektroda pomiarowa znajdowała się w kontakcie powierzchniowym z jednym ze stylodiów. Łagiewki pyłkowe kukurydzy kiełkują i rosną znacznie wolniej od pszenicznych. Potencjał rejestrowano przez 20 minut w 10 słupkach pszenicy po samozapyleniu i przez 70 minut w 16 zapyłonych kukurydzą. Po zakończeniu pomiarów słupki utrwalono i analizowano w nich wzrost łagiewek pyłkowych z użyciem błękitu aniliny i mikroskopu fluorescencyjnego.

W słupkach pszenicy po samozapyleniu potencjał szybko spadał, a następnie stabilizował się na poziomie $-10 \text{ mV} \pm 3 \text{ mV}$ w stosunku do poziomu początkowego. Potencjał zmieniał się najszybciej w okresie wrastania łagiewek pyłkowych do włosków znamienia i do stylodium. W krzyżowaniach pszenica x kukurydza we wszystkich zapyłonych słupkach następował spadek napięcia bezpośrednio po zapyleniu, zanim pojawiły się łagiewki. Obniżone napięcie utrzymywało się dłużej o ile ziarna pyłku kiełkowały a łagiewki wrastały do stylodium. Minimalne wartości potencjału wynosiły wtedy od -3 do -84 mV i były skorelowane z liczbą łagiewek rosnących w stylodium. Jeżeli ziarna nie kiełkowały to około 10 minut po zapyleniu następował wzrost potencjału. Zmiany potencjału miały charakter długich fal o wolno narastającej amplitudzie.

SŁOWA KLUCZOWE: potencjał elektryczny, kukurydza, zapylenie, pszenica.