ULTRASTRUCTURE OF THE ZYGOTE IN *ARUNDO FORMOSANA* HACK.

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Abstract: The polarity in the zygote of *Arundo formosana* Hack. differs from that in the egg. This report mainly describes the changes and shift of the cytoplasmic contents in the zygote of *Arundo formosana* Hack. as observed by both light and electron microscopies. The nuclear fusion in zygote occurs earlier than that in the primary endosperm. The nucleus of the zygote is centrally located and the majority of cytoplasmic organelles become aggregated on one side of the nucleus at the end of nuclear fusion. The new cytoplasmic organelles are formed in great qunatities at the micropylar half of the zygote. Mitochondria, endoplasmic reticulum and ribosomes increase more rapidly than other organelles. As the development takes place, most organelles as well as the nucleus move towards the chalazal pole resulting in the change of polarity in zygote. When the endosperm undergoes nuclear division, electron dense wall materials deposite between the zygote and young endosperm. Wall formation progresses from the micropylar pole to the chalazal pole discontinously. The wall formation completes before the first division of the zygote. The first division in zygote is transverse forming a large basal cell and a small terminal cell. Vacuoles are distributed at the micropylar half of the basal cell and seldom present in the terminal cell. The basal cell contains more dictyosomes and oil drops, whereas the terminal cell contains denser cytoplasm. The cytoplasm of the two-celled proembryo is rich in organelles which are uniformly distributed. Plasmodesmata are found between two cells of proembryo, but not in the walls associated with the two-celled proembryo and developing endosperm.

INTRODUCTION

In angiosperms, a common feature associated with the zygote is the polarized appearance of this cell, under both light and electron microscopies. However, the polarities is established in the egg before fertilization in most angiosperms in which the nucleus is situated at the chalazal pole and a large vacuole occupies the micropylar pole. In some species, including *Papaver* (Olson and Cass, 1981), and grasses *Zea* (Diboll, 1968; Van Larmmeren, 1981), *Horedum* (Norstog, 1972; Engell, 1988) and *Oryza* (Jones and Rost, 1989; Suzuki, et al., 1992), the nucleus of the unfertilized egg was situated at the micropylar pole and central position respectively. After fertilization the nucleus and cytoplasmic contents moved towards the chalazal pole in *Papaver* and *Zea*, but it was not the case in *Horedum* and *Oryza*.

Previous work on the ultrastructure of the zygote has shown that there were variously dramatic changes in different species. In most angiosperms, the general feature is that ribosomes tend to aggregate into polysomes and endoplasmic reticulum becomes more elaborate. However, with the exception of *Gosspyium hirsutum* (Jensen, 1968), the serial changes of the

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post-fertilized zygote was seldom described in details.

This investigation is the second report on embryology of *Arundo formosana* Hack., an endemic grass in Taiwan. Like Zea (Diboll, 1968; Van Larmmeren, 1981) and *Horedum* (Norstog, 1972; Engell, 1988), the nucleus of the unfertilized egg of *Arundo formosana* Hack. is centrally located (Jane, 1992). This study focuses on the dramatic changes of the zygote following fertilization, including the shift of cytoplasmic polarity, ultrastructural changes, and the first wall formation.

MATERIALS AND METHODS

The post-pollination pistils of *Arundo formosana* Hack. were collected from field. Samples were fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer at 4°C overnight. After three 20 min rinses in phosphate buffer, materials were postfixed in 0.1% OsO_4 in the same buffer for 4 h at room temperature, and then risned three times in the buffer, 20 min each. Dehydration was completed by an acetone series and Spurr's plastic was used for embedding (Spurr, 1969). Sectioning was done with Ultracut E ultramicrotome. 0.7-1 μ m thick sections were stained with 0.5% toluidine blue and 60-90 nm thin sections were stained with 6% uranyl acetate and lead citrate (Reynolds, 1963). A Hitachi-600 TEM or JEM 1200 EX II was used for viewing.

RESULTS

Light microscopic observation of the embryo sac after fertilization:

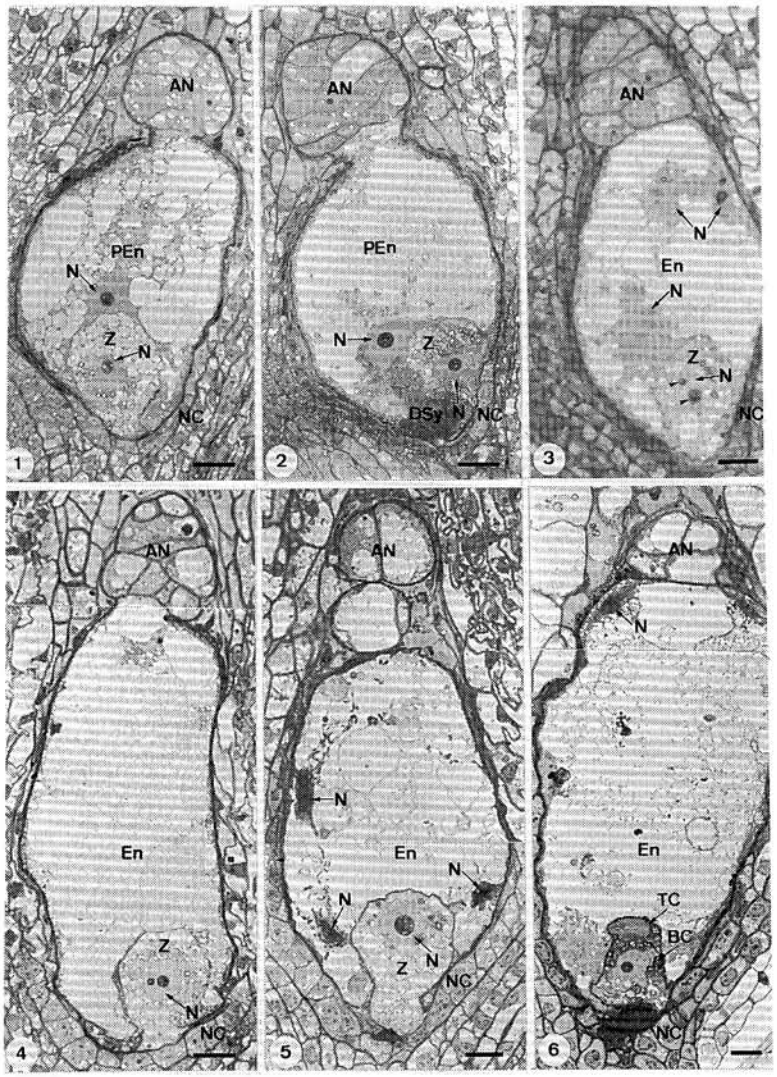
The pollen tube enters the embryo sac through the degenerated synergid after pollination. One of two sperms enters the egg and the other to central cell respectively. Both release their nuclei to undergo double fertilization. During double fertilization, nuclear fusion in the egg takes place earlier than that in the central cell (Fig. 1). The most cytoplasmic contents become concentrated on one side of the zygotic nucleus, and most cell lumen is occupied by numerous vacuoles. While double fertilization completes, the cytoplasmic organelles increase at the micropylar half of the zygote and most cytoplasmic organelles of the primary endosperm are distributed in the perinuclear and peripheral regions (Fig. 2).

The nuclear division occurs in the primary endosperm earlier than that in the zygote (Fig. 3). The nucleus of the primary endosperm undergoes free nuclear divisions. At this time, both the endosperm and the zygote enlarge slightly, and the zygotic nucleus is characterized by the presence of two nucleoli. During growth, the endosperm gradually elongates (Fig. 4).

In prior to the first division of the zygote, its nucleus associated with surrounding cytoplasm shifts towards the chalazal pole, and the cell reaches approximately its final size (Fig. 5). Numerous vacuoles occupy the micropylar half. There are more than twelve nuclei in endosperm at the time of the two-celled proembryo. The first division of the zygote is transverse resulting in the formation of a small terminal cell and a large basal cell (Fig. 6). The basal cell is much more vacuolated than the terminal cell.

The ultrastructure of the zygote:

Immediately after the nuclear fusion in the zygote, the majority of its cytoplasmic organelles appear to aggregate on one side of the nucleus and the rest of cell lummen is almost occupied by numerous vacuoles (Fig. 7). Like the mature egg, the zygote still lacks a continuous wall. The thin cell wall is only present at the micropylar pole. We never find any plasmodesmata in the cell wall of the zygote. The largest amount of organelles in the cyto-



Key to labelling: AN : Antipodal cell; BC : Basal cell; CW : Cell wall; D : Dictyosome; DSy: Degenerated synergid; DV : Dictyosome vesicle; En : Endosperm; ER : Endoplasmic reticulum; M : Mitochondrion; N : Nucleus; NC : Nucellus; Nu : Nucleolus; OD : Oil drop; OG : Osmiophilic globule; P : Plastid; PEn : Primary endosperm; Pl : Plasmodesma; PM : Plasma membrane; PS : Polysome; R : Ribosome; ST : Starch grain; TC : Terminal cell; V : Vacuole; Z : Zygote

Fig. 1-6 : Light micrographs of the longitudinal section of embryo sac, showing the subsequent morphological changes following the fertilization. (bar=15 μ m)

Fig. 1 : The stage after nuclear fusion in zygote and before the nuclear fusion of the primary endosperm.

Fig. 2 : The stage after double fertilization.

Fig. 3 : Showing the slightly enlarged zygote, the endosperm in free nuclear phase, and the nucleus of the zygote containing two nucleoli (←).

Fig. 4 : Showing the enlarging zygote with centrally located nucleus and the elongating endosperm.

Fig. 5 : Pyriform zygote and elongating endosperm, note the relative size of zygote and its nucleus at the chalazal pole.

Fig. 6 : Zygote after first division, note the relative size of two daughter cells.

plasm are mitochondria which contain a few cristae and clear matrix. The starch containing plastids are fewer than the mitochondria. Most endoplasmic reticulum are distributed in the perinuclear and the peripheral regions. Dictyosomes are very scare. Most of oil drops are distributed at the micropylar half.

Following fertilization, the cytoplasmic organelles in zygote conspicuously increase and are distributed at the micropylar half, and most vaculoes occupy the chalazal half (Fig. 11). Plastids with dense matrix are less-differentiated. At the periphery of the zygote, new ER originating from osmiophilic grobules is found and becomes oriented parallel to the plasma membrane (Fig. 12). The ribosomes increases obviously and they are attached to ER or free in the cytoplasm. The amount of oil drops and starch is more than that in its previous stage.

When the endosperm begins to undergo free nuclear division, the zygote slightly enlarges (Fig. 8). Though the nucleus of the zygote is still centrally located, most cytoplasm is re-distributed at chalazal half and some larger vacuoles appear at the micropylar half. Most of free ribosomes tend to be aggregated in clusters forming polysomes (Fig. 13, 15). Most dictyosomes are present at the peripherial region (Fig. 15), but their number is still low. The nucleus contains two equal patent nucleoli (Fig. 14). The amount of ER continues to increase and most ER is distributed at the perinuclear and the peripheral regions of the cell. The amount of starch decreases a little and the matrix of plastids appears lighter.

Before first division, the zygote, whose nucleus shifts towards the chalazal pole, appears pyriform-shaped and nearly reaches as its largest size (Fig. 9). As a consequence, the most evident polarity in zygote is seen by this stage. Polysomes are dominant and mitochondria contain well-developed cristae (Fig.18).

Wall formation in the zygote:

As that in egg, a continuous cell wall is absent from the newly formed zygote. A thin wall is present at the micropolar pole only. As the endosperm undergoes free nuclear division, electron dense wall materials appear in its chalazal pole at the boundary between the zygote and the endosperm (Fig. 15). The deposition of wall materials begins from the micropylar pole and fragmentally extends to the chalazal pole, hence some regions are thicker and some regions are thinner or absent from wall (Fig. 16, 17). Some ER is seen parallel to the thicker cell wall (Fig. 17). Until the polarity of the zygote is evidently established, the cell wall does not appear as a uniformly continuous pattern. The cell wall at the micropylar pole is always thicker than that in the other regions (Fig. 18, 19).

Two-celled proembryo:

The first division of the zygote is transverse forming a small terminal cell and a large basal cell (Fig. 10). The basal cell is much more vacuolated than the terminal one. Most vacuoles are distributed at the micropylar half of the basal cell and seldom in terminal cell. The cytoplasmic contents of the terminal cell appears denser than that of the basal cell (Fig. 10). Both cells are rich in organelles, but the amount and distribution of organelles show variations. The terminal cell contains more mitochondria, plastids and ER than the basal one (Fig. 20, 21). Dictyosomes in the basal cell are more than that in terminal one (Fig. 23, 24). The cytoplasmic organelles are uniformly distributed in the terminal cell, but they are more or less concentrated at the chalazal half of the basal cell. The terminal cell has higher ribosome density, but the basal cell has more amount of lipid bodies. The plastids contain large starch grains (Fig. 20), and mitochondria are with some cristae (Fig. 21, 25).

Many plasmodesmata are found the transversing cell wall between the terminal cell and the basal cell, but not the wall of two-celled proembryo contiguous with the young endosperm (Fig. 20, 22).

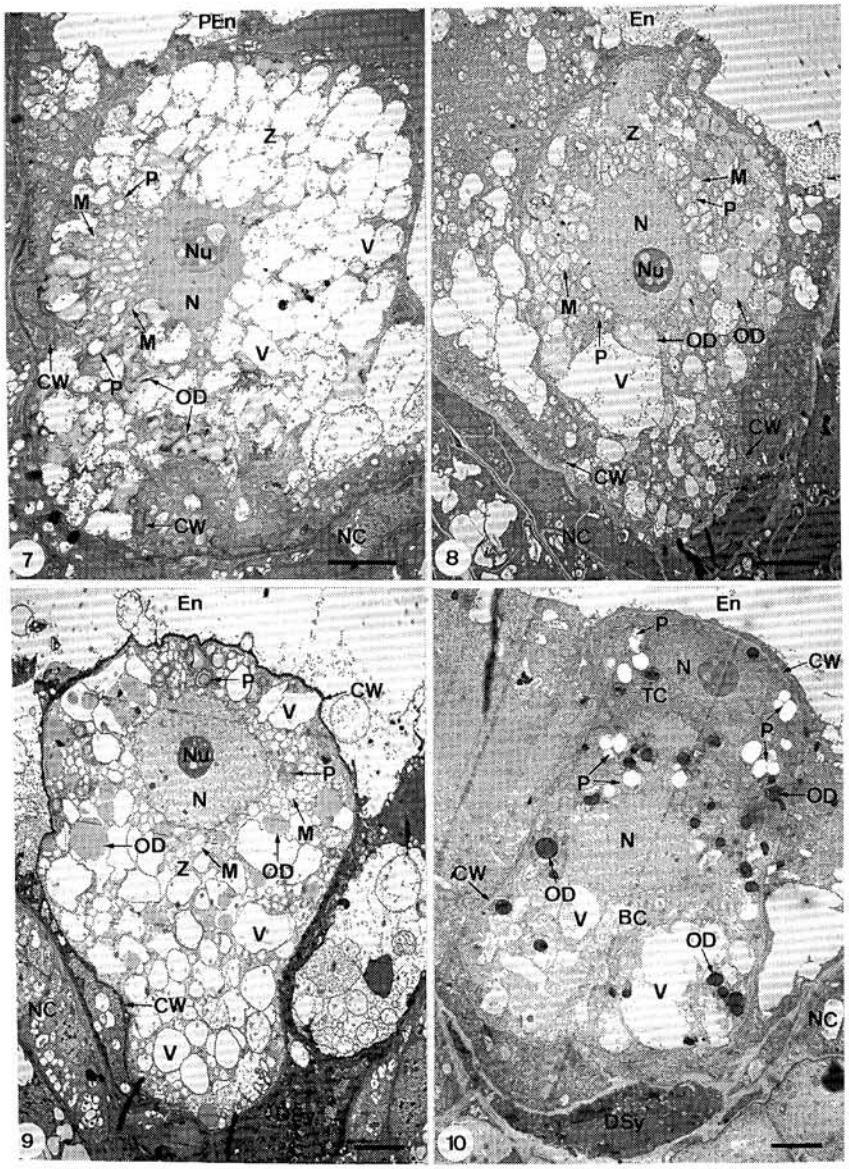


Fig. 7-25 : Electron micrographs showing the subsequent structural changes of the zygote following the fertilization.

Fig. 7: Immediately after the completion of nuclear fusion, note the presence of thin wall at the chalazal pole and centrally located nucleus. (bar=4 μ m)

Fig. 8: Showing the slightly enlarged zygote at the stage which the endosperm undergoes free nuclear division. Note the distribution of vacuoles. (bar=4 μ m)

Fig. 9: Showing the pyriform zygote prior to the first division. Note the conspicuous nucleus, a large cytoplasm at the chalazal half and numerous vacuoles at the micropylar half. (bar=4 μ m)

Fig. 10: Zygote after the first division forming two daughter cells. Note the distribution of vacuoles, plastids and oil drops, and the complete cell wall. (bar=4 μ m)

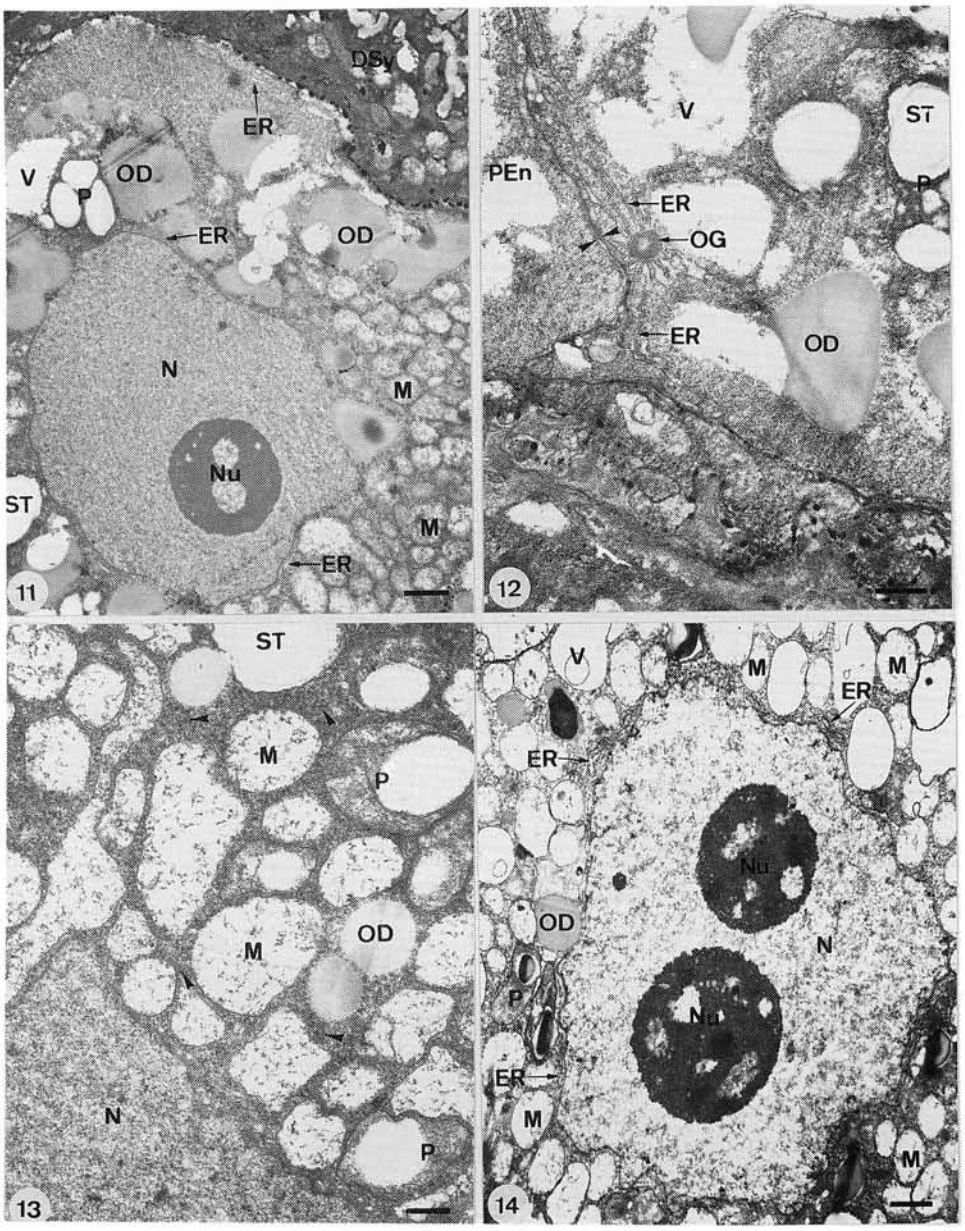


Fig.11 : Portion of the zygote and the degenerated synergid immediately after double fertilization, showing the greatly increasing organelles in the zygote, and the distribution of ER. (bar=l μ m)

Fig.12 : Portion of the zygote and primary endosperm, showing the association of new ER formed and osmiophilic globules, note two closely contacted plasma membranes of two cells (←). (bar=500 nm)

Fig.13 : Portion of the zygote, showing ribosomes tending to aggregate and forming polysomes (←). (bar=500 nm)

Fig.14 : Portion of the zygote, showing the binucleolate nucleus and the distribution of ER. (bar=l μ m)

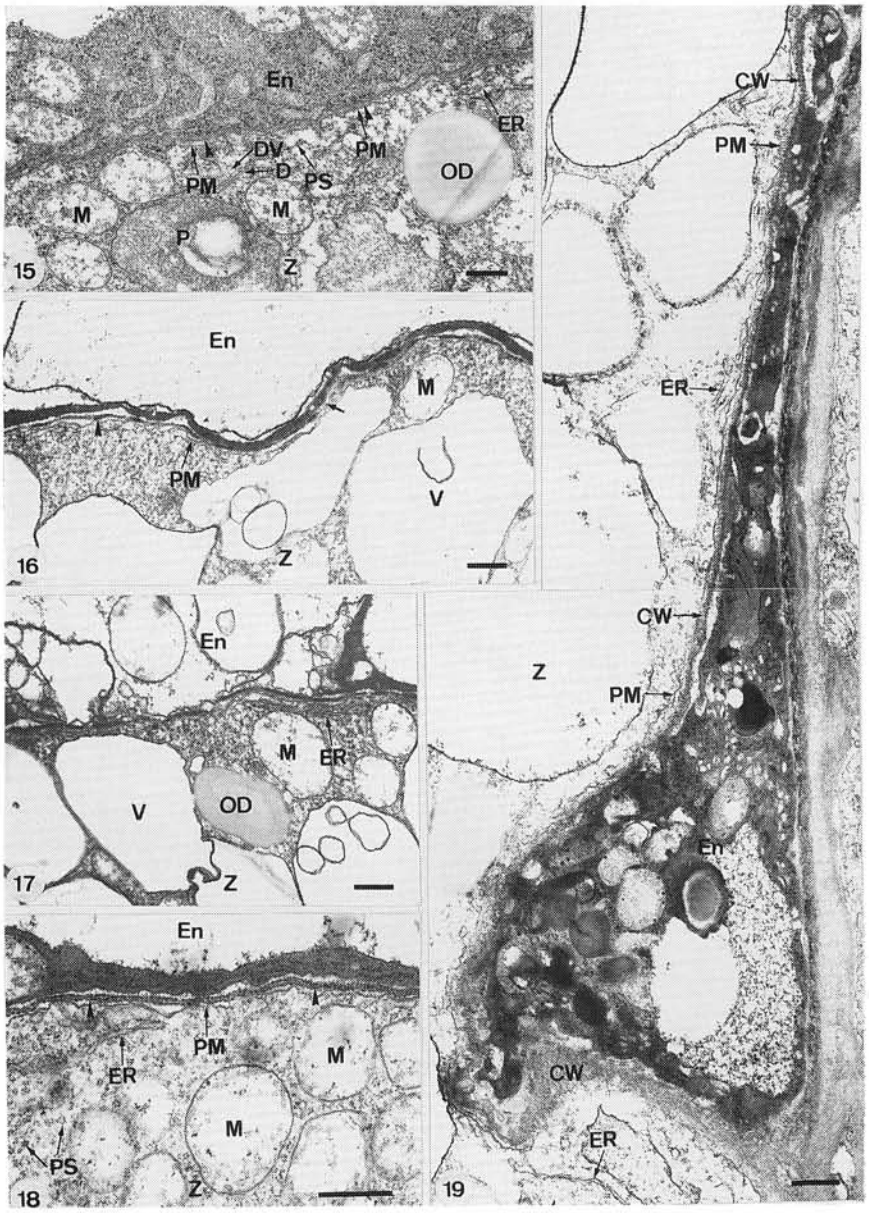


Fig.15-19 : Portion of the zygote and the endosperm, showing the wall formation of the zygote. (bar=500 nm)

Fig.15 : Showing wall materials (←) present between two cells.

Fig.16 : Showing non-uniform deposition of wall materials, some regions are thicker(←) and some thinner (←).

Fig.17 : Showing the following deposition of wall materials. Note the distribution of ER.

Fig.18 : Showing the cell wall (←) in completely uniform stage.

Fig.19 : Showing the stage after the complete formatrion of cell wall at the micropylar pole and middle portion.

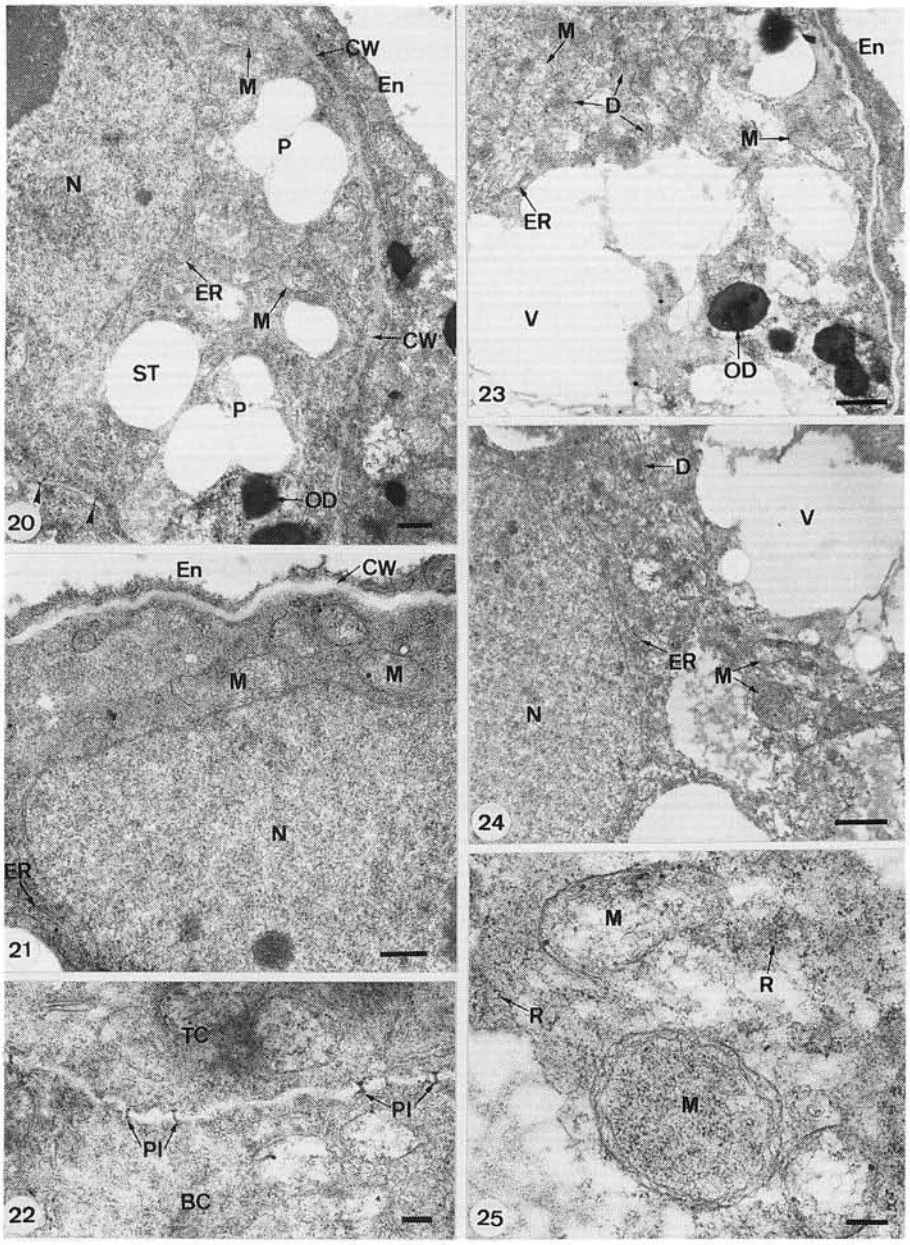


Fig.20 : Part of terminal cell and endosperm, showing the contents of terminal cell. Note the continuous cell wall and plasmodesmata (←). (bar=500 nm)

Fig.21 : Portion of the terminal cell and the endosperm, showing the contents of the terminal cell. (bar=500 nm)

Fig.22 : Portion of the terminal cell and the basal cell, showing some plasmodesmata between two cells. (bar=200 nm)

Fig.23 : Portion of the basal cell and the endosperm, showing the cell contents of the basal cell at the micropylar end. (bar=l μ m)

Fig.24 : Portion of the basal cell, showing the cell contents at the chalazal end. (bar=lμ m)

Fig.25 : Enlargement of Fig.23, showing mitochondria and ribosomes. (bar=200nm)

DISSCUSION

It can be merely seen under LM that the polarity in zygote changes slightly after the fertilization. The EM observation in the present study reveals that the main changes in the cellular contents of zygote are the movement of centrally located nucleus, together with its environmental cytoplasmic inclusions, to the chalazal half. Coordination of the establishment or change of polarity in egg and zygote appears to be a variable feature in the different plants. In many plants, such as *Capsells* (Schulz and Jensen, 1968), *Epidendrum* (Cocucci and Jensen, 1969), *Petunia* (Van Went, 1970), *Hibiscus* (Ashley,1972), *Quercus* (Mogensen, 1972), *Helianthus* (Newcomb, 1973; Yan et al., 1991), *Nicotiana* (Mogensen and Suthar, 1979) and *Arabidopsis* (Mansfield and Briarty, 1991), the polarity that shows the different patterns from the present plants is established before the fertilization in the egg. Their nuclei are found to be situated at the chalazal pole and large vacuoles at the micropylar pole. On the other hand, in some grasses including *Arundo* and *Zea mays* (van Lammeren, 1981), there is a change of cytoplasmic polarity in the zygote after fertilization, but no change in *Hordeum* (Norstog, 1972; Mogensen, 1982; Engell, 1988) and *Oryza* (Jones and Rost, 1989; Suzuki, et al, 1992). A peculiar case has been described in the egg of *Papaver nudicaule* (Olson and Cass, 1981). Its nucleus is situated at the micropylar pole, but there is a reversal of cytoplasmic polarity after fertilization. Its nucleus shifts towards the chalazal pole and the micropylar pole is occupied by a large vacuole. The similar reversal of cytoplasmic polarity also occurs in the zygote of the present plant, *Arundo*, though its nucleus is initially centrally located. The establishment of the zygotic polarity seems to play an important role in the early development of the embryo in angiosperms. This polarity may result in the non-uniform distribution of cytoplasmic contents after the first division of the zygote and lead to its later development.

After fertilization, the zygotic volume of *Arundo* enlarges during the predivision phase. A comparable phenomenon also occurs in *Cypripedium* (Poddubnaya-Arnoldi, 1967), *Capsella* (Schulz and Jensen, 1968), *Oryza* (Jones and Rost, 1989) and *Arabidopsis* (Mansfield and Briarty, 1991). However, the increase of the zygotic volume in *Arundo* is much less than in both *Capsella* and *Arabidopsis*, which become approximately three and half times. In contrast to *Arundo*, a decrease in zygotic volume which occurs immediately after fertilization has been observed in *Gossypium* (Pollock and Jensen,1964; Jensen, 1968), *Hibiscus* (Ashley, 1972) and *Nicotiana* (Mogensen and Suthar, 1979). In *Epidendrum* (Cocucci and Jensen, 1969), *Quercus* (Mogensen, 1972), *Hordeum* (Norstog, 1972; Mogensen, 1982) and *Helianthus* (Yan, et al., 1991), the zygote is approximately the same size as the egg.

According to past studies, a common phenomenon in ultrastructural changes in zygote of most angiosperms is the density of ribosomes, that increases evidently and tends to aggregate into polysomes; and ER becomes more elaborate. Besides, there are a little structural changes occuring in *Capsella* (Schulz and Jensen, 1968), *Epidendrum* (Cocucci and Jensen, 1969), *Petunia* (Van Went, 1970), *Quercus* (Mogensen, 1972; Singh and Mogensen, 1975) and *Hordeum* (Norstog, 1972; Morgensen, 1982; Engell, 1988). However, that in some species still shows a few variations. The number of active dictyosomes increases noticeably in *Zea* (Diboll, 1968; van Lammeren, 1986), *Arabidopsis* (Mansfield and Briarty, 1991) and *Helianthus* (Yan, et al., 1991). In *Arundo*, dictyosomes also increase, but the number remains low. Plastids and mitochondria enlarge in the zygote of *Zea*. This is not the case in *Arundo*, because they increase obviously in number. During zygotic development, the amount of starch and oil drops increases. It is likely that the zygote acts as a sink of carbonhydrates and oil which are derived from the endosperm or synergids and contribute to the further development.

The lack of a complete wall in egg has been described in many plants. The incomplete pattern of the cell wall of these plants still shows some different frames among them. Some of them only have a continuous wall on micropylar half, whereas some others have fragmentary discontinuous ones on the chalazal half. The former situation has been found in most species including *Arundo*. And the later types has been seen in *Capsella* (Schulz and Jensen, 1968), *Ornithogalum* (Tilton, 1981), *Glycine* (Folsom and Peterson, 1984) and *Brassica* (Sumner and van Caeseeles, 1989). However, a complete wall is formed after fertilization in these species. Schulz and Jensen (1968) have interpreted plasmodesmataless condition of zygote as the isolation of young sporophyte from the embryo sac, creating a new environment that enables the zygote to start an independent course of development. In *Rhododendron* and *Ledum* (Williams, et al.,1984), an entire callose wall is produced by the zygote, isolating itself from the surrounding cells. This fact strengthens the concept of Schulz and Jensen (1968). *Helianthus annuus* (Yanet al., 1991), however, is a peculiar case that does not confirm the Schulz and Jensen's suggestion. Its zygote divides before the completion of cell wall.

During the wall formation, the amount of ER close to the plasma membrane increases and becomes parallel to the thicker cell wall. Dictyosomes also increase, but their number is low. This may indicate that ER involves most in the zygotic wall formation of *Arundo*. The involving degree of ER and dictyosomes in the zygotic wall formation shows some variations in different species (Diboll, 1968; Jensen, 1968; Schulz and Jensen, 1968; Cocucci and Jensen, 1969; Mogensen, 1972; Mogensen and Suthar, 1979; Yan et al., 1991).

The size relationship of terminal and basal cell also shows some variations in angiosperms (Sivaramakrishna, 1978). In many species, the terminal cell is approximately equal to or larger than the basal cell. However, in *Arundo, Quercus* (Singh and Mogensen, 1975), *Papaver* (Olson, 1981), *Archis* (Periasamy and Sampoornam, 1984), *Zea mays* (Van Lammeren, 1986), *Arabidopsis* (Mansfield and Briarty, 1991), *Helianthus* (Yan, et al., 1991) and *Oryza* (Jones and Rost, 1989; Suzuki, et al., 1992), the terminal cell is much smaller than the basal cell. Natesh and Rau (1984) suggested that the shape and polarity of zygote, biochemical differences in the microenvironment of the embryo sac, the morphogenetic destination of the two cells, or some others are the main factors that control the specific size relationship between the terminal and the basal cells. However, Gubb (1985) has attained a prevalent suggestion that the genetic control of differentiations is more important than any other factors.

According to the ultrastructural studies in many species including *Arundo, Capsella* (Schulz and Jensen, 1968), *Hordeum* (Norstog, 1972; Morgensen, 1982), *Quercus* (Singh and Mogensen, 1975), *Arabidopsis* (Mansfield and Briarty, 1991), the terminal cell has a denser cytoplasm, full of organelles, than that in the basal cell. The non-uniform distribution of cytoplasmic contents of two cells may be the continuity of the zygotic polarity and important for their furture development. The two-celled proembryo of most species usually contains numerous mitochondria and plastids and well-developed ER system though the distribution and amount of organelles always show some subtle variations in different plants. The relationship of this condition and further development is unknown.

Except for *Helianthus* (Yan, et al., 1991), as in zygote, a complete wall has surrounded the two-celled proembryo and no plasmodesmata are present in the cell walls separating the proembryo from the embryo sac. In *Arundo, Capsella* (Schulz and Jensen, 1968) and *Quercus* (Singh and Mogensen, 1975), the cell wall between the terminal cell and basal cell is traversed by many plasmodesmata. This condition seems to confirm the Schulz and Jensen's suggestion (1968). Indeed, the role and fate of a developing embryo are quite different from its surrounding tissue.

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台灣蘆竹接合子之微細構造

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摘要

台灣蘆竹（*Arundo formosana* Hack.）之卵與接合子於胞器分佈之極性上有所不同。本篇報告主要是利用光學與電子顯微鏡觀察台灣蘆竹接合子之細胞質內含物之變化與移動。接合子內兩性細胞核融合完成時間較初生胚乳細胞早。細胞核融合初完成時，接合子之細胞核位於細胞中央位置，而大部分細胞質胞器則集聚於細胞核的一側。新胞器於近珠孔端大量形成，其中增加最多者爲粒線體，內質網與核醣體。隨著發育，胞器分佈之極性開始變化，先是細胞質胞器而後是細胞核移向近合點端。於胚乳細胞進入自由核分裂期時，接合子與胚乳細胞交接處有細胞壁物質的堆積。細胞壁之形成是從珠孔端以片斷方式往合點端延伸，而於接合子分裂前，細胞壁完全形成。接合子第一次分裂爲橫向，產生一較大之基部細胞和一較小之頂端細胞。液胞多分佈於基部細胞之珠孔端，而頂端細胞則少有液胞。基部細胞有較多之高爾基氏體與油滴，而頂端細胞則有有較濃之細胞質。細胞質內富含胞器，胞器分佈均勻。細胞質連絡絲只存在於頂端細胞與基部細胞之間，而此兩細胞與胚囊之間則無。