ON THE DEVELOPMENT OF THE « SPECIFIC » CELLS DURING MICRO- AND MACROSPORANGIUM FORMATION IN ZEA MAYS

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SUMMARY

In the course of development of stamens and pistils of **Zea mays**, some peculiar cells begin to appear which are similar to the « specific » cells described in other grasses. They possess a number of specific features that testify to their high physiological activity. S-cells lie in the way of the substances moving from the conductive system to the developing sporangia and probably transform them, serving as a peculiar barrier for some of them. Maximal activity of S-cells coincides in time with the differentiation of the archesporium and sporocyte development. S-cells evidently play a certain role at this phase of development of the generative sphere.

RESUME

Quelques données sur le développement des cellules « spécifiques » pendant la formation du sac pollinique et de l'ovule de maïs

Au cours du développement des étamines et des pistils de Maïs, apparaissent des cellules particulières, analogues à des cellules « spécifiques » décrites chez d'autres Graminées. Elles se signalent par une série de caractères qui attestent leur haute activité physiologique. Situées sur le passage des substances provenant du système conducteur alimentant les sporanges en cours de développement, les S-cellules les transforment probablement ou constituent une barrière spécifique pour certaines d'entre elles. Le maximum d'activité des S-cellules coïncide dans le temps avec la différenciation de l'archésporange et le développement des sporocytes. Apparemment, les S-cellules jouent un rôle déterminé au cours de cette étape de développement de la sphère génératrice.

In 1958, Y.-S. MODILEVSKY found, in some grasses, peculiar cells which he called « specific ». According to the author, they differentiated as a cylinder along the periphery of the connectivum initial of a stamen, under the tubercle of a pistil initial. These cells were distinguished by a big and often lobed nucleus and vacuolized cytoplasm, which in some wheat species contained small granules. The author ascrideb the formation of S-cells to the transition of the vegetative apex to the generative mode of development, and pointed out that from the time of the meiosis of sporocytes, activity of S-cells came to nought. S.-S. TATINTZEVA (1967), along with morphology, studied the dynamics of the nucleic acid in S-cells of sorgo stamens. The results of her investigation agree with the conclusions of MODILEVSKY.

Here are reported the data obtained while studying S-cells in a stamen and pistil of **Zea mays.**

At the time when, in a stamen initial, the procambial bundle begins to be formed, the adjacent cells are undergoing divisions oriented perpendicular to the longitudinal axis of the stamen. As a result, a cylinder of isodiametrical cells with strongly chromatic and relatively big nuclei is formed around the bundle (fig. 1). These cells are similar to the « specific » cells of MODILEVSKY. Topographically, they occupy the place similar to that of bundle sheath cells and possibly accomplish the same conductive functions. S-cells come through several developmental stages strictly timed to definite phases of the development of anther.

Simultaneously with the division of hypodermal layer cells in the primordia of sporangia and formation of the archesporium, 30-40 % of S-cells undergo divisions. These end by the formation of two-nuclei cells since no cytokinesis takes place. The next stage of S-cells development, timed to the moment of the separation of endothecium, is their enlargement (fig. 2). Nuclei also become enlarged and considerably less chromatized ; the nucleoli stain less intensively ; cytoplasm becomes vacuolized, some peculiar structures being formed in it, resembling vacuoles by their intensively staining wall. Further, in the cytoplasm of S-cells, in close contact with the nuclei and vacuoles, there appear cytoplasmic lumps slightly staining by haematoxyline after Haidenhein, very well by congo-red and altogether unrevelated by Feulgen reaction. These « lumps » look like balls of entangled threads, some ends of which are often contacting with the cell wall (fig. 3). In the period of mitotic reproduction of the archesporium, along with the growing anther, S-cells become gadually elongated, the nucleus or nuclei place themselves in the centre of the cell, while, at its ends, two very big « lumps » can be seen. At this time, in the « lumps », there appear small

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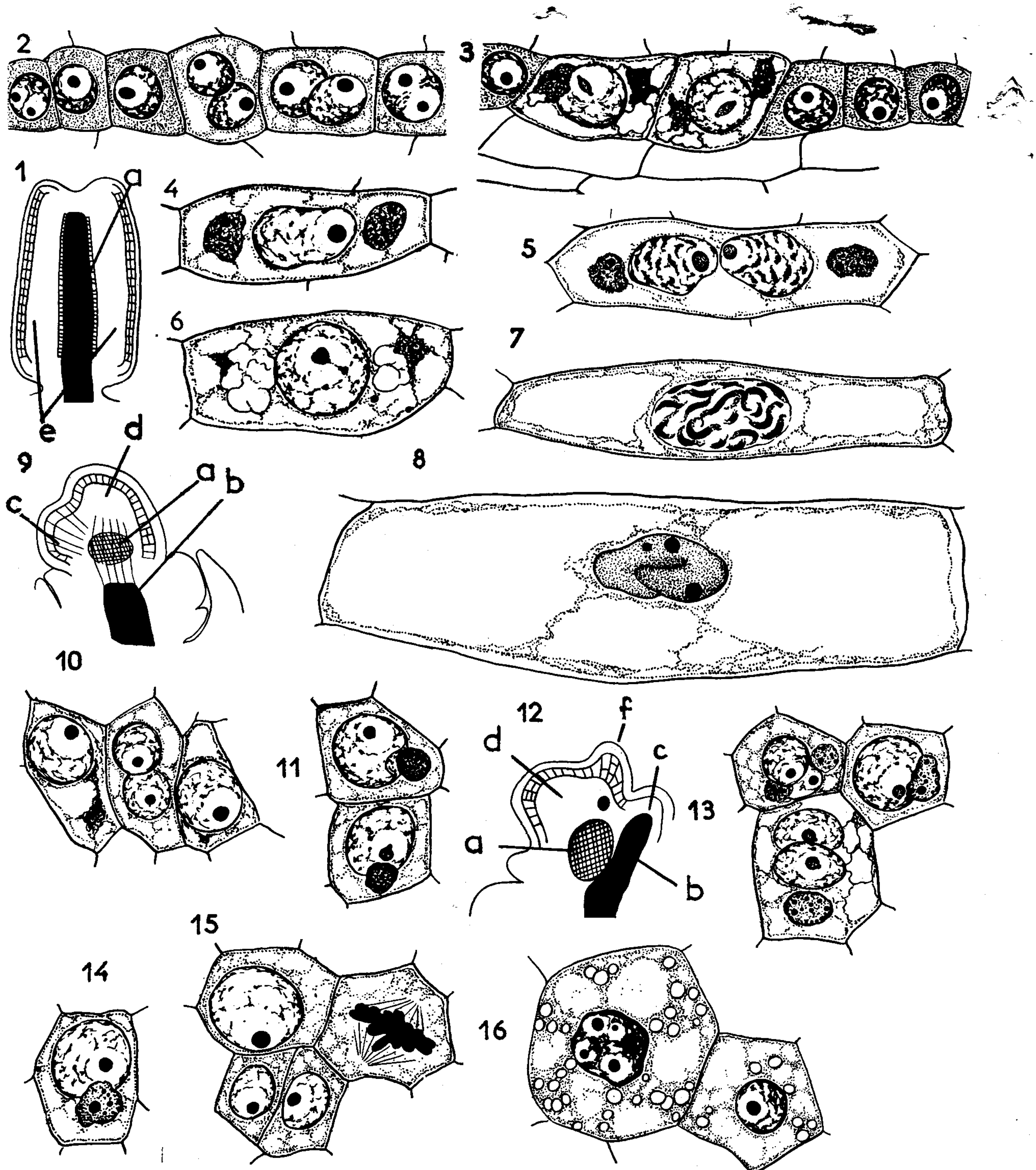

Fig. 1 : A scheme of a longitudinal section through the stamen of **Zea mays.**

Fig. 2-8 : Stages of development of the « specific » cells in the stamen of **Zea mays.**

Fig. 9, 12 : The schemes of longitudinal sections of a female spikelet of **Zea mays** at different stages of development.

Fig. 10, 11, 13-16 : Developmental stages of the « specific » cells in a stamen of **Zea mays.**

a. : « specific » cells ; b. procambial bundle ; c. : stamen initial ; d. : pistil initial ; e. : archesporium ; f. : initial of the ovary wall.

spherical granules intensively stained by haematoxyline and often arranged as a chain (Fig. 4). Later on, these granules increase in size though decrease in number, possibly because of fusion (fig. 5). By the time, mitoses in the archesporium cease to occur, i. e. by the beginning of the microsporocyte formation, a second wave of divisions takes place envolving all the S-cells. The nuclei pass into the state of prophase (fig. 5) fusing in some of the S-cells. However, there is no transition to further phases of mitosis and the nuclei return to the interphase state. It is worth mentioning that, at this time, in the procambial connectivum bundle, phloem is differentiating.

After the mitoses in the archesporium completely cease to occur and during the period of growth and development of microsporocytes, the « lumps » in S-cells begin to disappear. Simultaneously, the peculiar vacuole-like structures begin to appear again giving the impression of being transformed from the « lumps » (fig. 6).

By the time microsporocytes cease to exist, i. e. by the beginning of meiosis, in S-cells the third wave of divisions takes place (fig. 7) which again does not end by cytokinesis. It must be mentioned that nuclei undergo division only in a minor part of cells, mostly in the central region of the anther. Later on, the S-cells become greatly enlarged and, by the end of the existence of the anther, attain gigantic size (fig. 8) ; their least diameter exceeds that of the conductive bundle of the connectivum, though their nuclei are almost not enlarged and cytoplasm content is insignificant, the cell being nearly wholly occupied by a large vacuole. The change in cell morphology obviously testifies to the change in their function.

Principally, similar development of S-cells is observed in the pistil. During the development of a functionally female flower of **Zea mays,** the axial procambial bundle is differentiated only up to the level of the stamens. From the corpus cells of the meristematic ovary initial placed above the procambial bundle, there differentiates a group (an « islet ») of S-cells (Fig. 9).

By the time stamen initials become clearly seen and the ovary wall is still not differentiated (Fig. 9), in S-cells a division wave takes place envolving, as it was in stamens, less than half of all the cells, so that no cytokinesis ensues. Almost simultaneously, S-cells become enlarged, their nuclei increase in size, cytoplasm gets vacuolized, characteristic vacuole-like structures begin to appear, though they are not so pronounced here as in stamens, and, at last, « lumps » begin to form (Fig. 11).

By the time, the vegetative apex gets transformed into the initial of the ovule, which takes place after the beginning of the ovary wall formation (Fig. 12), all the S-cells already contain big « lumps » though still without any granules. The « lumps » are in close contact with nuclei (Fig. 13). After this, the granules start to appear. The « lumps » attain their fullest development by the time of separation of the archesporial cell. By this time, most of S-cells become greatly enlarged. Unlike S-cells of a stamen, which in the process of growth acquire an elongated form owing to the lengthwise growth of the anther, the pistil S-cells remain isodiametrical. Their nuclei almost wholly fill S-cells, often acquiring a slightly lobed form. Granules in the « lumps » attain their maximal size (Fig. 14). As it was mentioned above, the second division wave in the anther takes place at the period of transition from the archesporium to microsporocytes. Meanwhile, in the ovule, the single archesporial cell becomes a macrosporocyte without any divisions. It is possible that this is the cause of the absence of a corresponding division wave in the pistil S-cells.

While the macrosporocyte is preparing for meiosis, in S-cells of the ovule (like in the anther), the « lumps » gradually disappear from centre to periphery of the « islet » so that, by the beginning of the prophase of meiosis, they are altogether absent. During the prophase of meiosis, in most of S-cells, there start to proceed mitoses which correspond to the third division wave of the anther S-cells. But, unlike this process in the anther, divisions end here by cytokinesis (Fig. 15). As a result, the specificity is lost and newly formed cells become similar to the surrounding cells of the ovary base in their size, morphology of nuclei cytoplasm, etc. Those rare cells which do not undergo divisions are obliterated, while the rest persist for a rather long time. They can be seen in the ovary base at the stage of a mature embryo sac. Without differing from the adjacent cells by their cytoplasm, they can be distinguished by their large proportions and big nuclei often of irregular form (Fig. 16).

Thus, in **Zea mays,** the character of development of the specific cells in the stamen and pistil, the sequence of their developmental stages and their simultaneity with certain phases of sporangium development essentially coincide. The differences in the fate of S-cells of the stamen and pistil are evidently connected with the fate of these organs as a whole. The growth of a stamen is known to be limited. The stamen ceases to exist by the time of gametophyte formation. In the ovule, contrarily, the gametophyte formation is an initial stage of its existence, most part of which is occupied by the process of fertilization and seed development. In a stamen, the post-meiotic development of the conductive system is accomplished only by means of multiplication of phloem and xylem elements of the axial connectivum bundle, owing to the differentiation of procambial cells. S-cells in a stamen maintain their position around the conductive bundle in the way of the substances moving towards the primordia of sporangia, evidently accomplishing the functions of sheath cells. Meanwhile, in the pistil in the postmeiotic period, there takes place an active development of the conductive system of placentochalaza. Right above the region of the S-cells, multiple anastomizing conductive bundles are formed. S-cells prove to be isolated from the ovule and come to nought, losing their specificity as a result either of a mitosis or obliteration.

As to the premeiotic period of S-cells, there is a temporal coincidence of an increase in their physiological activity (increase in nuclei material, specific vacuolization, formation of « lumps » with secretion granules) with the archesporium formation and sporocyte development. This allows to suggest a connection between these phenomena. The nature of this connection is as yet unknown. It may be clearly seen that S-cells lie in the way of the substances moving from the conductive bundle to sporangia, but whether they transform these substances and transfer them to sporangia or the S-cells serve as a peculiar barrier for some substances (may be both suggestions are true) will be seen from further investigation. One thing is certain : S-cells stand in the same rank with such structures as tapetum, antipodal tissue, partly endosperm, haustoria, etc with which they have many features in common (a tendency to an increase in nucleic material). The metabolic nature of these structures is of course different. This can be judged from the presence of « lumps » in S-cells which are absent from other structures. It is worthy of note that, when these structures do coexist in time at one or another period, the intensification periods of their physiological activity as a rule do not coincide. Thus, for example, S-cells in the anther of **Zea mays** become particularly active in the period of archesporium differentiation and microsporocyte development. By meiosis, their activity abates ; but, just at this time, there begins to get activated, the tapetum (it becomes two-nuclei) showing maximal activity at the next stage - during microspore development. In the ovule also, a row of physiologically active structures replacing one another can be observed.

One gets an impression that there exists a system of a successive « joining-in » of the activities of different tissues which, so to say, pass the baton to one another, thus providing a successive chain of developmental stages of a stamen and pistil.

It can be thought that this phenomenon is peculiar not only to grasses. The main stages of development of the generative sphere are common for all Angiosperms. These are : archesporium, sporocyte, spore, gametophyte etc. Every next stage differs qualitatively from the previous one and requires certain conditions. These, apparently, include the supply of the developing organs with substances specific for a given stage. One may believe that the above mentioned physiologically active substances in the stamen and pistil present a system of filters and transformers of the substances issuing from the conductive system, the former being worked out in the process of evolution. Replacing one another, they provide an inflow of the substances specific for each stage. It must be though mentioned that the set of these structures in pistils of the plants belonging to different systematical groups is different. Thus, not all of the groups possess an integumental tapetum or antipodal tissues etc. It is interesting to note that E.-N. GERASSIMOVA-NAVASHINA (unpubl. data) has found in some Compositae a compact group of cells with dense cytoplasm under the ovary base and above the conductive bundle. They occupy the same position as S-cells in **Zea mays,** are developing approximately at the same time and probably accomplish the same functions.

As to the « lumps » observed by me in S-cells, the constancy of place and time of their formation, type of the development and their aspect do not seem to give grounds to regard them simply as artefacts. However, their real nature may be clarified only in the course of further investigations.

Within the strict limits of the present article, I shan't be able to describe in all the detail the development of S-cells in the stamens of functionally female and in the pistils of functionally male flowers, as well as in pistils and stamens of the lower sterile female spikelet of **Zea mays** (all these organs die off at an early stage of development). I shall mention now only the fact that they show an absence of correspondence between the development of an organ and its conductive system. Thus, one can observe typical elements of xylem and S-cells with lobed nuclei, vacuolized cytoplasm and « lumps » with granules in a sterile stamen which correspond to the fertile stamen in the phase of the beginning of differentiation of the procambial bundle. It may be supposed that it is in connection with the early development of the connective bundle and S-cells that the surrounding cells grow old very soon and rapidly degenerate.

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