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THE SUSPENSOR AND ITS ROLE IN EMBRYO DEVELOPMENT IN PHASEOLUS (PAPILIONACEAE): A REVIEW

Riassunto — Il sospensore ed il suo ruolo nello sviluppo embrionale in Phaseolus (Papilionaceae). Vengono passati in rassegna i risultati di studi condotti in *Phaseolus* coccineus e P. vulgaris nell'intento di elucidare, utilizzando differenti approcci metodologici, il ruolo svolto dal sospensore embrionale nella embriogenesi.

Le indicazioni raggiunte, di carattere sia strutturale che funzionale, possono essere così riassunte:

1) le cellule del sospensore, ed in particolare quelle altamente politeniche situate nella sua porzione basale, presentano complesse digitazioni delle pareti ed altre caratteristiche strutturali che le indicano come tipiche 'cellule di trasferimento', capaci di trasportare materiali attraverso i plasmodesmi verso l'embrione vero e proprio;

 esperimenti con saccarosio marcato dimostrano che, durante gli stadi embriogenetici iniziali, il sospensore rappresenta il principale sito di assunzione attiva dei nutrienti e che i nutrienti stessi sono effettivamente ed attivamente trasportati dal sospensore all'embrione;

3) in aggiunta alla sintesi di DNA dovuta al processo della endoreduplicazione cromosomica, nelle cellule del sospensore ha luogo sintesi preferenziale di determinate sequenze che è modulata in relazione allo sviluppo dell'embrione. Nelle fasi iniziali della embriogenesi, il tasso di sintesi di RNA per quantità diploide di DNA è più che doppio nel sospensore che nell'embrione;

4) l'attività gibberellino-simile è trenta volte più alta nel sospensore che nell'embrione vero e proprio nello stadio embriogenetico a cuore. Nelle fasi iniziali dello sviluppo, ad una abbondanza nel sospensore di citochinine biologicamente molto attive corrisponde una abbondanza di citochinine con scarsa attività biologica nell'embrione vero e proprio; questa situazione si inverte in stadi di sviluppo più avanzati. Sempre negli stadi embriogenetici iniziali, nel sospensore è presente più che nell'embrione attività auxino-simile e di inibizione;

5) la rimozione del sospensore riduce la crescita di giovani embrioni coltivati *in vitro* e l'effetto è tanto maggiore quanto più precoce è lo stadio di sviluppo. L'aggiunta nel substrato di fattori di crescita si dimostra capace di rimpiazzare il sospensore in embrioni nello stadio a cuore.

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Questi dati contraddicono l'opinione, a lungo espressa da molti autori, che attribuisce al sospensore embrionale una funzione meramente meccanica o di passivo assorbimento. Alla loro luce, il sospensore di *Phaseolus* deve piuttosto essere visto come un organo che rappresenta il sito di attiva assunzione e trasporto di nutrienti verso l'embrione e che soprattutto svolge un fondamentale ruolo di regolazione, costituendo una fonte di sostanze di crescita indispensabili all'embrione nelle fasi iniziali del suo sviluppo. Al di fuori di indebite generalizzazioni, viene suggerito che, in molte specie di Angiosperme, il ruolo che il sospensore esercita durante le fasi iniziali della embriogenesi possa essere più attivo e specifico di quanto sino ad oggi supposto.

Abstract — The present paper reviews the results of those studies in *Phaseolus* coccineus and *P. vulgaris* which, using different methodical approaches, were planned to throw light on the role of the embryo suspensor in embryogenesis.

These results have shed light on many structural and functional aspects of the suspensor, namely:

1) the suspensor cells, and particularly the giant cells with polytene chromosomes in its basal portion, present wall ingrowths and other structural features indicating they are typical 'transfer cells' which can transport material through plasmodesmata in the direction to the embryo proper;

2) experiments using 14 C-sucrose indicate that, during early embryogenesis, the suspensor is the major site of uptake of nutrients and that the process is an active one. These experiments also demonstrate that nutrients are actually transferred from the suspensor to the embryo;

3) in addition to the DNA synthesis due to the process of chromosome endoreduplication, extra DNA synthesis occurs in the suspensor cells; this phenomenon is modulated in relation to embryo development. Early in embryogenesis, the rate of RNA synthesis per diploid copy of DNA is more than twice in the suspensor than in the embryo proper;

4) gibberellin-like activity is thirty times greater in the suspensor than in the embryo proper at the heart stage of development and only at later stages does it rise in the embryo. An abundance of biologically very active citokinins in the suspensor of embryos at earlier developmental stages corresponds to an abundance of cytokinins with low biological activity in the embryo proper and *vice versa* at later embryonic stages. Growth-promoting and -inhibiting activity of metanolic extracts is higher in those from suspensors than in those from embryos proper at the heart stage of development;

5) in *in vitro* culture of isolated embryos, the removal of the suspensor reduces embryo development and the younger the embryo the greater the negative effect. Growth regulators added to the culture medium can replace the suspensor in heart-shaped embryos.

These data contradict the usual view which attributes a merely mechanical function or one of passive absorption to the embryo suspensor. In the light of these findings, the *Phaseolus* suspensor must be seen rather as an organ which functions as the site of the active uptake and transport of nutrients to the embryo and plays a basic regulatory role, acting as a source of growth substances needed for early embryo development. While avoiding inappropriate generalization, it is suggested that, in quite a number of Angiosperm species, the suspensor might play a more specific and active role during early embryogenesis than has previously been assumed.

Key words - Embryo suspensor, plant embryo development, Phaseolus.

THE EMBRYO SUSPENSOR

In *Phaseolus*, as in many Angiosperms, the first division of the zygote is an asymmetric one, thus establishing two cells with different developmental capacities. The apical (chalazal) cell divides to form the embryo proper; the basal (micropylar) cell undergoes only a few divisions to form the suspensor. This short-lived organ has been studied by various authors in *P. coccineus* and *P. vulgaris*, whose suspensors are very similar.

When fully grown, the suspensor attains a typical club-like shape and in *P. coccineus* comprises about two hundred cells. As in other species, the suspensor cells grow by chromosome endoreduplication (cf. NAGL, 1974); its level increases progressively towards the micropylar portion of the organ, in which some twenty giant cells with polytene chromosomes occur, eventually reaching a nuclear DNA content that is as high as 8192C (twelwe endoreduplications; BRADY, 1973).

The polytene chromosomes of *P. coccineus*, which are present in the diploid number (2n=22), since the homologues are not somatically paired (cf. CIONINI *et al.*, 1982), have been the object of a number of studies, which have shed light on various aspects of their structure and functional behaviour (cf. NAGL, 1974; DURANTE *et al.*, 1987). Although they are of interest, the results of these studies will not, however, be reported in this paper, its aim being to consider those data which throw light on the role that the suspensor plays in the development of the embryo.

Even though an embryo suspensor has been known to exist in a number of species for a long time (the embryo suspensor and its massive development in the *Leguminosae* were described by GUIGNARD in 1882), little attention has been paid to this part of the embryo by developmental biologists. It has usually been considered to have only one role, that of anchoring the embryo proper (wherefore the term, suspensor) and of positioning it inside the endosperm, so that the embryo is in a nutritionally favourable environment. As a matter of fact, many years ago, TISON (1919) and SCHNARF (1929) had already drawn attention to the fact that, as a rule, a limited development of the endosperm occurs in species with a highly developed suspensor. This observation may suggest the suspensor plays a more important role in embryogenesis. This view has found sound support in the results of investigations carried out in recent years on the *Phaseolus* embryo suspensor. These results will be summarized below.

Cell structural features

The mature suspensor penetrates the surrounding endosperm and the ovular integument and the walls of the suspensor cells possess prominent partly cork-screw-like, partly tubular ingrowths on those sides which are in contact with the surrounding tissues (AVANZI et al., 1970; SCHNEPF and NAGL, 1970; YEUNG and CLUTTER, 1979). By contrast, the walls between the suspensor cells are thin, with many plasmodesmata (cf. NAGL, 1974). The cytoplasm is very dense with an extended endoplasmic reticulum as the dominant element (Schnepf and Nagl, 1970; Nagl, 1973; Yeung and Clutter, 1979). The basal giant cells, in particular, which contain numerous mitochondria and leucoplasts and which are therefore rich in cytoplasmic DNA (SCHNEPF and NAGL, 1970; YEUNG and CLUTTER, 1979), prove to possess clear polarity in relation to the activity of dictyosomes, which are abundant at the cell pole towards the embryo proper, while the opposite pole is rich in tubular endoplasmic reticulum (cf. NAGL, 1974).

All these structural characteristics indicate that the suspensor cells are typical 'transfer cells' (GUNNING and PATE, 1969), which can transport material through the plasmodesmata towards the embryo proper (NAGL, 1974).

UPTAKE AND TRANSPORT OF NUTRIENTS

That the suspensor is the major site of uptake and transport of nutrients to the young embryo is shown by the results of experiments carried out on both *P. coccineus* and *P. vulgaris* by YEUNG (1980) using ¹⁴C-sucrose.

At the heart stage of embryo development, radioactivity appears

first in the suspensor when labeled sucrose is administered via the base of the excised pod and with time moves to the embryo proper through its suspensor end. The labeling pattern remains unchanged even when the labeled solution is introduced into the endosperm cavity, although the cotyledonary half of the embryo and not the suspensor is nearer to the source of radioactivity. Dinitrophenol, which inhibits the formation of ATP, also inhibits the uptake of the sucrose in the suspensor, thus indicating the process is an active one. Experiments with excised embryos in which ¹⁴C-sucrose was made available only for the suspensor demonstrate that the nutrient is actually transported from the suspensor to the embryo proper. The sucrose uptake pattern is changed at later stages of embryo development, when the cotyledons progressively become the major uptake site for the maturing embryo.

Thus, the role of the suspensor as a 'temporary embryonic root' already suggested by LLOYD (1902) is demonstrated, even though its location in the micropylar portion of the ovule, far from the termination of the vascular strands (chalaza), may appear rather 'anomalous' in this connection.

DNA AND RNA SYNTHESIS

Other studies have demonstrated that the functional role of the suspensor in embryogenesis is even more important and specific than its acting as an uptake and transport site for nutrients. Certain aspects of the metabolism of the nucleic acids in the suspensor cells are among the indications of this.

a) DNA

In addition to DNA synthesis due to the process of chromosome endoreduplication, preferential synthesis of certain DNA sequences leading to their selective amplification in the genome (extra DNA synthesis) has been shown, by means of cytological, autoradiographic and biochemical analyses, to take place during early embryogenesis in the suspensor cells of *P. coccineus* (AVANZI *et al.*, 1970; LIMA-DE-FARIA *et al.*, 1975; CREMONINI and CIONINI, 1977). This phenomenon has been found to exist in other animal and plant materials, in cells engaged in particular, and particularly stringent, physiological activities; such a situation can hardly be believed for an ephemeral organ such as the suspensor without postulating it is the target for requirements coming outside the suspensor itself.

Extra DNA synthesis is shown to occur in the suspensor polytene chromosomes through the formation of 'DNA puffs' (cf. AVANZI *et al.*, 1970): densely Feulgen-stained knobs which enlarge the diameter of the chromosome at those sites where the phenomenon takes place. It has been observed that extra DNA synthesis is modulated in relation to embryo development, since both the frequency of DNA puffs and their chromosomal localization vary in suspensor belonging to embryos at different developmental stages (FORINO *et al.*, 1976, 1979; FREDIANI, 1979; TAGLIASACCHI *et al.*, 1983, 1984). This has been interpreted as being due to the response of the suspensor cells to changes in developmental demands coming from the embryo.

b) RNA

RNA synthesis was measured in the suspensor cells and in those of the embryo proper, at different stages of embryogenesis. The RNA synthetic activity of the suspensor is highest early in development, as is also found in the case of its ATP pool size and specific activity. The rate of RNA synthesis per polytene cell is hundreds of times greater than that in the cells of the embryo proper; even considering the rate per diploid copy of DNA, it is more than twice in the suspensor than in the organogenetic part of the embryo. In the former, after the embryo has reached the heart-shaped stage, RNA synthetic activity declines, whereas it increases throughout development in the embryo proper (WALBOT *et al.*, 1972; CLUTTER *et al.*, 1974).

SYNTHESIS AND TRANSFER OF GROWTH SUBSTANCES

A series of investigations carried out in *P. coccineus* starting from 1975 have raised, and partly solved, the problem of the physiological role of the suspensor in embryogenesis on a hormonal basis. The results of these studies indicate the suspensor is the main if not the only source of growth substances for the embryo in its earlier developmental stages.

a) Gibberellins

The *P. coccineus* embryo suspensor is extremely rich in gibberellins (PICCIARELLI and ALPI, 1986). The gibberellin(GA)-like activity was studied separately in suspensors and embryos proper at two stages of development: i) in the heart-shaped embryo and ii) in the cotyledonary embryo whose suspensor was in the initial stage of degeneration (ALPI *et al.*, 1975).

At the heart stage, total GA activity in the suspensor is about thirty times greater than in the embryo proper. At the cotyledonary stage, a dramatic decrease in the level of GA-like substances occurs in the suspensor, when their level in the embryo proper is increased to ten times what it is at the heart stage.

These results and those obtained by CECCARELLI *et al.* (1981) indicate that GAs are actively synthetized in the suspensor of early embryos. By combined gas cromatography-mass spectrophotometry, it has been shown that GA_1 is the biologically active GA which is mainly present in the suspensors of *P. coccineus* heart-shaped embryos (ALPI *et al.*, 1979). Although the transport of GAs from the suspensor to the embryo proper cannot be demonstrated by the results of ALPI *et al.*, (1975), this hypothesis seems to be acceptable in view of the transition shown to occur in the level of GA activity in the suspensor and the embryo proper during development.

b) Cytokinins

When the cytokinin status of the suspensor and the embryo proper is determined at the same developmental stages as above, it is found that: i) in embryos at the heart stage, the suspensor is active mainly at the level of such less polar cytokinins as zeatin and 2-isopentenyladenosine, whereas more polar cytokinin types as zeatin glucoside and zeatin riboside are prevalent in the embryo proper. This situation is reversed at the cotyledonary stage of development, thus suggesting a transition during embryogenesis such that an abundance of biologically very active cytokinins in the suspensor of embryos at earlier developmental stages corresponds to an abundance of cytokinins with low or very scarce biological activity in the embryo proper, and *vice versa* at later embryogenetic stages (LORENZI *et al.*, 1978).

These results again suggest that in early embryogenesis the suspensor acts as a hormone source for the embryo, which, as also in the case of gibberellins, seems to acquire autonomy for cytokinins only later in development.

c) Auxins and inhibitors

The embryo-suspensor relationships outlined above as far as gibberellins and cytokinins are concerned do not appear to differ when auxins and inhibitors are considered.

The growth-promoting and -inhibiting activities of metanolic extracts from suspensors and embryos were studied at the heart stage of embryo development. Extracts from suspensors showed two inhibitors, one much more active than the other, and two large peaks of growth-promoting activity. The general activity of the extracts from embryos proper was lower and the growth-promoting effect was spread over a large number of the chromatogram fractions (ALPI *et al.*, 1975).

In vitro culture

That the suspensor plays a vital part in the early embryogenesis of *P. coccineus*, as well as in that of *Eruca sativa* (CORSI, 1972), is further demonstrated by the *in vitro* culture of embryos excised from the ovular tissues. These studies also duly confirm several aspects of the hormonal status of the suspensor and the embryo proper as outlined above, and provide further support for the view that the suspensor acts as a hormone source for the embryo in its earlier developmental stages.

When isolated embryos at different stages of development are grown *in vitro*, either intact or deprived of their suspensor, it is found that removal of the suspensor has no effect on the development of embryos which have reached the cotyledonary stage. With younger embryos, on the contrary, removal of the suspensor reduces embryo development; the younger the embryo the greater the negative effect (CIONINI *et al.*, 1976; YEUNG and SUSSEX, 1979). Growth regulators such as GA₃ or kinetin added to the culture medium in appropriate concentrations can replace the suspensor in heart-shaped embryos, whereas they reduce the development of suspensor-deprived embryos at later stages as compared with intact embryos at the same stages grown in hormone-free medium (CIONINI *et al.*, 1976; YEUNG and SUSSEX, 1979).

In these experiments with *P. coccineus*, as with other species (HOMMA, 1955), the pattern of development of the cultured embryos is mainly one of premature germination: the embryo axis and leaflets

develop, whereas there is only slight growth or enlargement of the cotyledons. From the point of view of embryo growth rather than of plantlet formation, it is shown that 90% of intact embryos at the heart stage can grow in the basal medium, versus 60% of suspensor-deprived embryos. Adding abscissic acid plus GA_3 (1 mg/l and 5 mg/l, respectively), 94% of suspensor-deprived embryos grow in culture (YEUNG and SUSSEX, 1979).

CONCLUSIONS

The results obtained using various methodical approaches and reported in the preceding pages, mutually support one another and point to quite a different role of the embryo suspensor from the mechanical one or that of passive absorption which are usually attributed to it. In the light of these findings, the suspensor must be seen as an organ which functions as the site of active uptake and transport of nutrients to the embryo and plays a basic regulatory role, acting as a source of growth substances needed for early embryo development. The endosperm has been well known to carry out this function for some time; its place may be taken, at least in part, by the suspensor.

In this connection, an interesting parallelism has been suggested between the embryo suspensor of Angiosperms and the mammalian trophoblast. Striking similarities exist in the development, structural features and chromosome behaviour of both and both are involved in a similar way in the 'nourishment' of the young embryo (NAGL, 1973).

We are aware any generalization would be out of place, of course. It is hard to believe suspensor plays an important role in embryo development when it is undeveloped, as in the case, for instance, of *Fragaria*. Even in the genus *Phaseolus*, certain species or varieties have small suspensors and no suspensor is formed in *P. tenuiflorus* (NAGL, 1974). However, the fact that an embryo suspensor is present in the vast majority of Angiosperms and that, in various species, its cells possess structural specializations such as those described in *P. coccineus* and *P. vulgaris* (cf. YEUNG, 1980), suggests that in quite a number of Angiosperm species this organ might play a more specific, active role during early embryo development than has previously been assumed.

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