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Review

Histological Approach to the Study of Morphogenesis in Callus Cultures In Vitro: A Review

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Abstract: The use of in vitro callus cultures as experimental model systems allows us to get closer to understanding the patterns and features of morphogenesis in intact plants. In this regard, the problem of realizing the morphogenetic potential of callus cells due to their pluri- and totipotency properties is of great interest. To solve this problem, it is important to use the histological approach, which involves studying the structures of developing tissues, organs and organisms in their interactions and relationships. This review article analyzes data devoted to the study of the histological features of formed primary morphogenic calli (formation of morphogenetic centers and superficial meristematic zones), as well as the in vitro morphogenesis pathways in calli that lead to the formation of regenerants (de novo organogenesis and in vitro somatic embryogenesis). The terminology used is considered. Some questions for discussion are raised. The opinion is expressed that histological (structural) studies should be considered as a methodologic basis for further investigation of various morphogenetic scenarios in in vitro callus cultures, especially in economically valuable plants and for biotechnological purposes.

Keywords: plant morphogenesis; histological analysis; callus in vitro; de novo organogenesis; in vitro somatic embryogenesis; biotechnology

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1. Introduction

Plant morphogenesis is defined as the integrated process of spatial and temporal development of tissues, organs and embryos, controlled by hormones and regulated by a network of genes acting sequentially or in concert (in [1,2]).

Morphogenesis remains the most complex fundamental problem of plant biology. The complexity of this phenomenon in plants is caused by the holistic nature of morphogenetic processes and their dependence on many interacting internal and external factors. In addition, plant morphogenesis occurs during the entire ontogenesis of an individual by the constant functioning of vegetative and floral (reproductive) meristems [3,4].

The model approach of plant cells, tissues and organs in in vitro cultivation allows us to get closer to understanding the patterns and features of morphogenesis in intact plants. This approach makes it possible, with some simplification, to study the details of integrated morphogenetic processes and the mechanisms of their regulation under controlled experimental conditions [5–7]. The basis for the use of such models is the similarity of the main morphogenetic events in plants in planta and in vitro [8,9].

In vitro callus cultures are promising model experimental systems for studying plant morphogenesis. The first publications devoted to obtaining calli in in vitro conditions from the isolated tissue segments of some plants appeared in the late 1930s (in [10]). To date, the ability to form calli in vitro has been revealed in representatives of many plant families. Numerous studies have established that it is possible to use various vegetative, generative and embryonic organs as explants for callus obtaining. A large number of experimental works have been published concerning the study of both in vitro callus formation and

the morphogenesis events in them that lead to the formation of regenerants. Especially great success has been achieved in identifying the molecular aspects of these processes, namely the participation of a number of specific gene systems in them [9,11–15]. Important theoretical generalizations have been made. Thus, the ability to form calli in vitro and produce full-fledged regenerants from them is regarded as one of the manifestations of plant development plasticity, largely due to the attached lifestyle [11,16,17]. Biotechnologies for the mass production of economically valuable regenerants have been developed based on the use of callus cultures in vitro [6,18,19].

At the same time, the problem of implementation of the morphogenetic potential of callus cells in in vitro conditions is far from a final solution. To solve this problem, in our opinion, the histological approach should be used, involving investigation of the structures in developing tissues, organs and organisms in their interactions and relationships.

The importance of using the histological approach is already demonstrated in a definition of the term "callus". In classical studies on in vitro plant tissue cultivation, Skoog and Miller [20] briefly called the "callus" an unorganized growing tissue represented by a mass of dedifferentiated cells. The more complete definition of a callus also reflects its histological characteristics: a callus is an integrated system that is formed as a result of the proliferation of surface or depth cells of various plant tissues; such a system is initially composed of homogeneous cells that are gradually transformed into groups of heterogeneous cells with species-specific morphogenetic potencies, which are realized via various morphogenesis pathways (in [21]).

Attempts have been made to create periodization of callus formation and their development in vitro. In these processes, critical stages [21] and phases of induction and expression [22] are distinguished. In general, this issue is debatable. Apparently, in this single integrated process, one should be able to distinguish (i) the formation of primary morphogenic calli ("callus formation") and the complication of their structure ("callusogenesis"), as a rule, on the in vitro induction medium, and (ii) the development of groups of callus cells according to various morphogenesis pathways ("morphogenesis pathways in calli"), as a rule, on the in vitro regeneration medium.

The aim of this review is to analyze some of the literature and the authors' own data on the histological features of primary morphogenic calli as well as the use of the histological approach to identify the morphogenesis pathways in calli during further in vitro cultivation.

2. Histological Features of Primary Morphogenic Calli

The problem of the competence of explant cells both in in vitro callus formation and callus cells in in vitro morphogenesis was raised in the earliest studies of these processes. Thus, in 1902, Gottlieb Haberlandt (in [23]) proposed the concept of plant cell totipotency as the ability to form a new organism. The modern interpretation of this concept and the used terms are presented, for example, in works [24,25]. Later, the concept of plant cell pluripotency as the ability to form a new organ was elaborated (detailed more in [11,16,17,26,27]). Concepts such as multi-, omni-, oligo- and unipotency of cells have also been proposed and developed (detailed more in [28]). At the same time, we believe that the properties of cell totipotency and pluripotency in the above interpretations should be considered basic during investigation of callus formation, callusogenesis and morphogenesis in calli in in vitro conditions.

It has been experimentally revealed that the success of in vitro callus formation is determined by a complex of interrelated endogenous and exogenous factors. Modern research in this area is largely devoted to the gene regulatory networks and epigenetic regulators involved in callus formation in vitro, including specific mutants of *Arabidopsis thaliana* (e.g., [8]). From a histological standpoint, the presence of targeted morphogenetically competent cells in explant tissues should be considered the main endogenous factor; such cells can be called "initial callus cells". Exogenous factors (mainly hormones in the induction nutrient medium, as well as the effects of stress, e.g., wounds) induce the reprogramming

of such cells in the direction of in vitro callus formation. The principal issue is this: do the initial cells already have the competence to form calli under in planta conditions, or is it the conditions of in vitro cultivation that induce their reprogramming with the acquisition of competence? This and other issues related to callus formation from explant cells should be considered debatable.

Be that as it may, under adequate in vitro conditions, explant cells give rise to primary morphogenic calli. The morphological characteristics of calli that have appeared on the surfaces of various explants and are capable of morphogenesis during further in vitro culturation are quite similar in many plants; they are compact nodular structures [29–32] (Figure 1(1)).

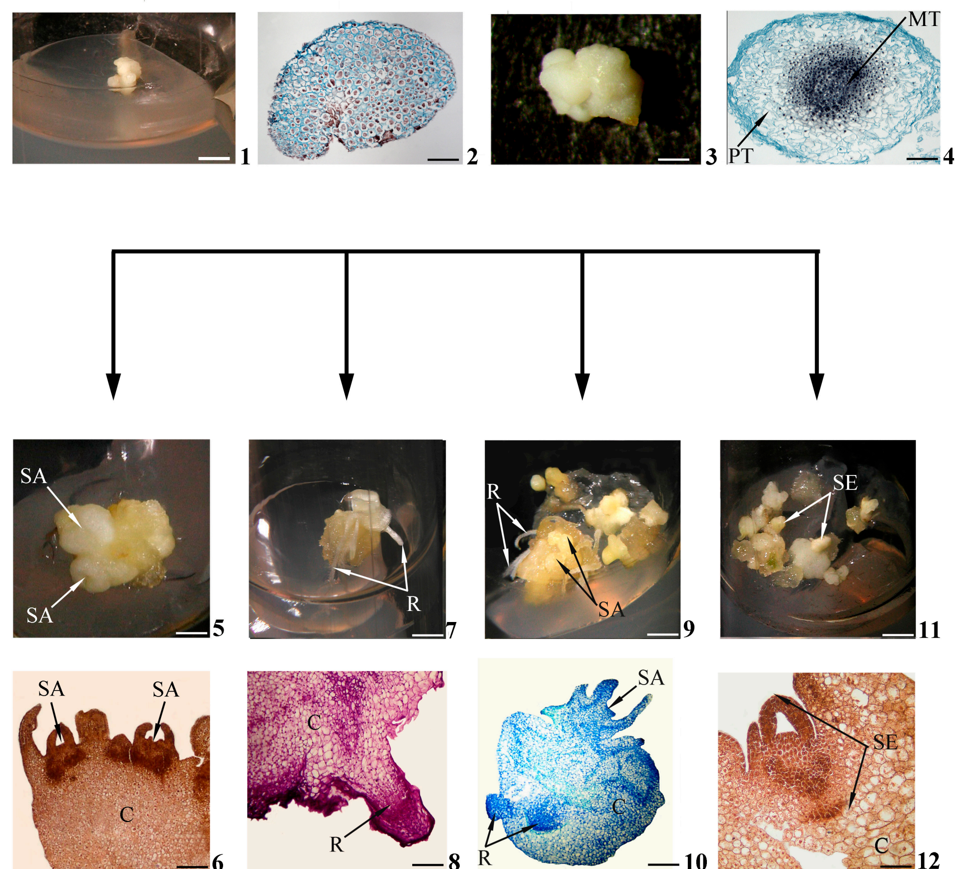

Figure 1. Stages of in vitro morphogenesis in calli. Primary morphogenic callus at initial stage of development according to morphological (**1**) and histological (**2**) data; developed primary morphogenic callus according to morphological (**3**) and histological (**4**) data; shoots (buds) in the morphogenic callus according to morphological (**5**) and histological (**6**) data; roots in the morphogenic callus according to morphological (**7**) and histological (**8**) data; gemmorhizogenic structures in the morphogenic callus according to morphological (**9**) and histological (**10**) data; somatic embryos in the morphogenic callus according to morphological (**11**) and histological (**12**) data. Symbols: C—callus, MT—meristematic tissue, PT—parenchymatic tissue, R—root, SA—shoot apex, SE—somatic embryo. Scale bars: (**1**) = 150 mm; (**2**) = 200 mkm; (**3**) = 3 mm; (**4**) = 100 mkm; (**5**,**7**,**9**,**11**) = 3 mm; (**6**) = 200 mkm; (**8**,**12**) = 100 mkm; (**10**) = 50 mkm.

According to histological data, for example, the primary morphogenic callus obtained from the wheat embryo, in the initial stages of development, is represented by a system of meristematic cells of similar size [33] (Figure 1(2)). However, these histological features do not correspond to all such calli. Thus, the calli that have originated from the lateral root primordia of a number of plants are initially already heterogeneous (in [34]). Apparently,

the histological status of a primary morphogenic callus may differ depending on the explant nature and the in vitro culturation conditions.

Calli intensively increase "critical mass" with repeated mitotic divisions of their constituent cells (Figure 1(3)). Furthermore, there is a gradual occurrence of both cells' heterogeneity in the shapes, sizes, structures and histological zonalities of calli. In the thicknesses of calli (less often on the surface), so-called morphogenetic centers are distinguished. Such centers are represented by two zones of cells. There are the central zone of densely located meristematic cells ("meristematic center" [6,29], "meristemoid" [35], "meristematic node" [36]) and the peripheral zone of loosely located parenchymal cells that have lost meristematic activity [29,37,38] (Figure 1(4)).

It can be assumed that the presence of a morphogenetic center is an obligatory histological feature of primary morphogenic calli, since all future in vitro morphogenesis pathways will somehow be connected with the central meristematic zones of such centers. For example, the formation of meristems (among the authors, promeristems) is regarded as one of the four phases of de novo shoot regeneration in callus [11].

One of the decisive factors in this case is the specialized intercellular interactions of densely located meristematic cells. Such close intercellular contacts are necessary both for the functioning of cells and for the coordination of their activities in the central zone of the morphogenetic center. The opinion was expressed that future morphogenesis pathways would depend on whether a group of cells could establish and maintain coordinated behavior as an integrated unit using symplastic interactions [39]. We agree with this opinion. Indeed, the tight cell–cell symplastic interactions through plasmodesmata in the central meristematic zone of a morphogenetic center differ from those in the surrounding parenchymal peripheral zone, where plasmodesmata are significantly reduced. Symplastic transport provides a reliable exchange of hormones and nutrients between the cells in the central morphogenetic center zone, which makes it possible to consider this zone an integrated structure.

The literature has presented publications devoted to the similarity of the meristem structures in primary in vitro morphogenic calli and in planta root primordia. For example, in *Arabidopsis thaliana*, the structure of the callus tissue obtained on an in vitro induction medium is similar to the structure of the apical meristem of the root of this plant [26]. Interestingly, in *Arabidopsis thaliana*, similarities were also revealed in the molecular mechanisms of in vitro callus formation and de novo root regeneration: in particular, the participation of the *WOX11* gene in both processes [9].

The similarities in the histological features of primary morphogenic calli and root primordia encouraged us to turn to the functions of quiescent centers in root apical meristems in planta. This question was raised, for example, in work [26]. It is known that the quiescent center, consisting of a pool of rarely dividing stem cells (also called pluripotent cells [27]), together with the often-dividing surrounding cells of initials, will form a niche of stem cells; initials give rise to root tissues [40,41]. The key role of auxin in the activation of quiescent centers was revealed in experiments using auxin-responsive reporters or direct endogenous auxin measurements; other hormones are also of great importance, especially cytokinins, which control auxin transport and cell division in quiescent centers (in [42]). We assume that some meristematic cells (possibly stem cells) of morphogenetic centers are activated in primary morphogenic calli under the actions of endogenous auxins and cytokinins. This assumption was confirmed by comparing the data of a histological analysis of wheat calli with the results of an immunohistochemical study of them. It has been established that endogenous auxins and cytokinins are localized in the meristematic cells of actively developing morphogenetic centers in calli [29].

In general, histological prerequisites for the future realization of morphogenesis pathways are created in primary morphogenic calli in the initial stages of in vitro culturation.

3. Histological Approach to the Evaluation of In Vitro Morphogenesis Pathways in Calli

Various morphogenesis pathways were revealed in calli in the subsequent stages of in vitro cultivation (Figure 1(4–11)): organogenesis (gemmogenesis-type or caulogenesis-type, consisting of the formation and development of the shoot; rhizogenesis-type, consisting of the formation and development of the root; or gemmorhizogenesis-type, consisting of the formation and development of the gemmorhizogenic structure that combines both the shoot and the root) and somatic embryogenesis (consisting of the formation and development of somatic embryos) (reviews [15,16,21,33]). Thus, reprogrammed callus cells exhibit the properties of pluripotency and totipotence under adequate in vitro conditions.

Morphogenesis pathways lead to the regeneration of full-fledged plants under further favorable in vitro conditions. The plant regeneration system in calli is called "de novo plant regeneration" [9,16], "in vitro plant regeneration" [15] or "indirect plant regeneration" [43].

The results of studying the greatly important issue of plant regeneration in callus cultures in vitro have been summarized in a number of recent reviews.

Bidabadi and Jain [16], in their extensive review, evaluated the callus as a proliferating mass of dedifferentiated cells. Those authors analyzed in detail the physiological (mainly hormonal), biochemical, (epi)genetic and physical factors and some others that not only affect in vitro plant regeneration but also regulate this process. They paid much attention to the discussion of control molecular mechanisms, the occurrences of somaclonal changes and the role of programmed cell death, as well as many other issues connected to in vitro plant regeneration.

A cycle of works by Ikeuchi et al. [44–49] is devoted to various issues of callusogenesis, including a comparative analysis of events during plant regeneration in calli in planta and in vitro. Those researchers, assessing the callus as an unorganized mass of cells, considered the genetic and epigenetic mechanisms of regenerant formation. Those authors defined regeneration as a manifestation of either the reprogramming of differentiated somatic tissue cells or the activation of relatively undifferentiated somatic tissue cells. They paid special attention to the mechanisms of the molecular control of plant regeneration in calli formed in planta in response to wound exposure.

A number of reviews are devoted to the analysis of organogenesis events in calli. It should be noted that a number of authors use the phrase "in vitro organogenesis" when it comes to the formation and development of shoots with subsequent induction of root formation under the action of specific exogenous hormones. The other authors apply the phrase "de novo organogenesis" when they analyze the regeneration events of the shoots and roots in wound calli or in an isolated shoot or root. As evidenced by the analysis of the literature, the reviews of recent years have mainly been devoted to molecular events during organogenesis in calli. Thus, Zai and Xu [26], using the example of *Arabidopsis thaliana*, assessed the participation of the *WOX5* gene in stimulating the acquisition of pluripotency properties by callus cells. Wang et al. [9] devoted their review to summarizing the achievements in the study of the molecular mechanisms of de novo organ regeneration in calli, especially the role of the *WOX11* gene.

Researchers have paid great attention to in vitro somatic embryogenesis as a manner of plant regeneration in calli. In a theoretical study, Feher [24] posed the important problem of the correct interpretation of the terms "callus" and "somatic embryogenesis", as well as the related terms "dedifferentiation" and "totipotence". Sivanesan et al. [50], considering somatic embryogenesis to be a mode of stimulated plant cell totipotency, presented a review of the works devoted to the influences of major factors (nature of explant, abiotic stresses, concentration and variation of plant growth regulators) on the induction and regulation of somatic embryogenesis, including indirect somatic embryogenesis in callus cultures in vitro. Tretyakova and Mineev [51] analyzed data of indirect in vitro somatic embryogenesis in comparison with another system of asexual reproduction, which is apomixis. Those authors showed that the transitions of somatic cells to the totipotent and embryonic states occur at the physiological–biochemical and molecular genetics levels. A number of reviews have

reflected the great interest of researchers in studying the influences of genetic (microRNA, transcription factors) and epigenetic (DNA methylation, chromatin remodeling) factors on the regulation of in vitro somatic embryogenesis events [52–54]. This direction of research is also demonstrated in a review by Rocha et al. [55]. Those authors analyzed the molecular mechanisms underlying the control of both morphogenetic pathways, de novo organogenesis and in vitro somatic embryogenesis, supported by findings involving proteome-, metabolome- and transcriptome-based profiles.

At the same time, there are relatively few studies in the literature specifically devoted to detailed histological analysis of in vitro morphogenesis pathways in calli. Nevertheless, certain histological patterns of these events have been identified.

Let us consider these histological events during in vitro gemmorhizogenesis, which is the most difficult and thus the most interesting morphogenesis pathway in calli. Schematically, this pathway is shown in Figure 1(1–4,9,10); more detailed histological data are given in Figure 2.

As stated above, a primary morphogenic callus at the initial stage of development (Figure 1(1)) consists of cells that are rather uniform in their sizes and structures (Figure 1(2)). Later (Figure 1(3)), a morphogenetic center is distinguished in the thickness of the callus. Such a center is represented by two cell zones, including the meristematic center as a central zone of densely located cells (Figure 1(4)).

In the process of development, the meristematic center, initially consisting of similar cells, will gradually acquire a distinct zonality. Some cells will remain meristematic, while others will become parenchymatic. Thus, the meristematic center consists of three cellular layers: a central layer presented by weakly vacuolated cells, an intermediate layer of meristematic cells and a peripheral layer of highly vacuolated parenchymatic cells (Figure 2(1)). In the course of subsequent development, the intermediate meristematic layer will increase in size due to the periclinal and anticlinal divisions of cells. This layer will be transformed into an expanded meristematic zone composed of several cellular layers and situated in parallel to the callus surface (Figure 2(2)). Simultaneously with the formation of the meristematic zone, the destruction of central and peripheral layers can be detected. In the upper callus area, where the complete destruction of the peripheral layer occurs, the shoot meristem (Figure 2(3)), the forming shoot apex (Figure 2(4)) and leaf primordia (Figure 2(4,5)) can be observed on the callus' surface. Developing shoots have typical structures for plants in in planta conditions.

With a sufficient degree of shoot development, initiation of root meristems occurs in the part of the meristematic zone remaining inside the callus (as a rule, in the lower part of the callus below the developing shoot) (Figure 2(6)). The root apex and root primordia will gradually be formed inside the callus (Figure 2(7)). The developing roots are characterized by a structure that is typical for the roots of plants in in planta conditions.

As the shoots and roots develop, a connection will gradually be established between them by elements of the vascular system forming in the thickness of the callus. The united gemmorhizogenic structure will be formed (Figure 2(8)).

These analyzed histological events confirm the fact that the initial stages of indirect regeneration in calli are largely associated with the de novo formation of new meristems or the restructuring of previously existing meristems [2]. It has been shown, for example, that the initial realization of de novo organogenesis is closely related to the activity of cells in the superficial (epidermal, subepidermal) meristematic zones of *Amorphophallus rivieri* [35] and wheat [29] calli. Similar events were noted in somatic in vitro embryogenesis in calli (in [24]).

Important, in our opinion, are the data on the participation of the differentiated surface cells of some organs in direct plant regeneration in vitro, without callus formation [56]. It should be noted that in natural conditions in planta, many initial morphogenetic processes, for example, the marking and laying of leaf primordia, will also occur in the meristem, namely in the peripheral zone of the apical meristem, functionally separated from the central zone and the meristem of expectation [57]. Above, we examined the similarities of

histological events in primary morphogenic calli in vitro and root primordia in planta. All these examples may indicate the general mechanisms of regenerant formation in vitro and plant formation in planta.

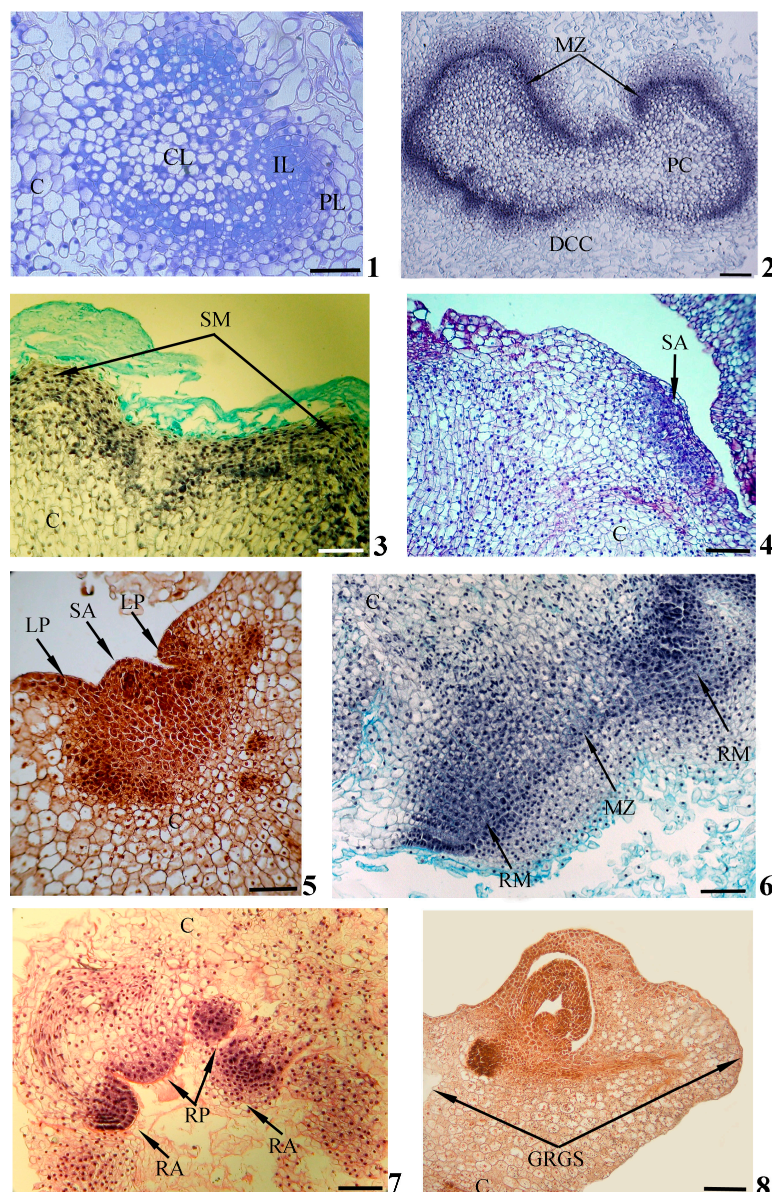

Figure 2. Histological events during in vitro gemmorhizogenesis in calli. Formation of zonality (**1**) and meristematic zone (**2**) within callus; formation of shoot meristem (**3**), shoot apex (**4**,**5**) and leaf primordia (**5**) on callus surface; formation of root meristems (**6**), root apex and root primordia (**7**) inside callus; formation of gemmorhizogenic structure (**8**). Symbols: C—callus, CL—central layer, DCC—destructive callus cell, GRGS—gemmorhizogenic structure, IL—intermediate layer, LP—leaf primordium, MZ—meristematic zone, PC—peripheral cell, PL—peripheral layer, RA—root apex, RM—root meristem, RP—root primordium, SA—shoot apex, SM—shoot meristem. Scale bars: (**1**,**3**–**8**) = 100 mkm, (**2**) = 200 mkm. Modified according to [29], with additions.

In general, histological analysis has proven to be indispensable for the detailed study of events in calli during de novo organogenesis (namely gemmorhizogenesis) and in vitro somatic embryogenesis. Actually, the morphological features of the formed shoot and root are clearly distinguishable (Figure 1(5,7)), but it was very difficult to distinguish the gemmorhizogenic structure (Figure 1(9)) from the somatic embryo (Figure 1(11)) visually,

especially in the late stages of its development. Only the histological callus investigation of the dynamics of development revealed that the gemmorhizogenic structure develops by alternately forming first the shoot on the callus surface and then the root in the callus thickness, followed by the gradual formation of the vascular system between these organs (Figure 2). This pattern of development distinguishes the gemmorhizogenic structure from the somatic embryo, in which the shoot and root are laid almost simultaneously [30]; compare also Figure 1(10,12).

We also note that histological analysis alone did not confirm the formation of somatic embryos during in vitro direct regeneration in cultured petioles of *Pelargonium* × *hortorum* and *Pelargonium* × *domesticum*. It was revealed that leaf-like and shoot-like structures were formed in the conditions of the experiments performed [58].

It is important to emphasize that the data of detailed histological studies contribute to solving one of the fundamental problems of plant development biology, namely the similarities and differences between in vitro somatic embryogenesis and in planta zygotic embryogenesis (detailed more in [51,59,60]).

It is necessary to pay attention to the following aspect: Using the examples of many plants, it is well-established that the inductions of de novo organogenesis and in vitro somatic embryogenesis in calli are largely determined by an optimal balance of endogenous and exogenous phytohormones, and auxin and cytokinin play priority roles in determining callus cell fates [30,61–65]. To identify the mechanisms of endogenous phytohormone participation in these processes, an immunohistochemical method based on the histological approach was used. This method allowed obtaining of data of the contents and distribution of the hormones in plant cells (e.g., [66]). Thus, a comparison of the data of the immunohistochemical detections of endogenous auxin and cytokinin in the callus cells with the results of the histological analysis of the callus showed that, during de novo organogenesis, these hormones are localized mainly in the cells of actively developing organs—shoots and roots [29].

De novo organogenesis and in vitro somatic embryogenesis as systems of indirect regeneration are, as a rule, separately induced in calli. The leading exogenous factor of organ or embryo induction is the introduction of various hormones into the nutrient medium. At the same time, the literature has presented data from a few studies in which the processes of de novo organogenesis and in vitro somatic embryogenesis were revealed in calli using the identical hormonal composition of the nutrient medium. Thus, the formation of either shoots or somatic embryos on a medium of the same composition is morphologically described for the calli of *Valeriana edulis* ssp. *procera* [67], *Metabriggsia ovalifolia* W. T. Wang [68], *Camellia nitidissima* Chi. [69] and the *Clematis* sp. [70]. A number of works have provided data on the simultaneous formation of shoots and somatic embryos in the same callus on a medium of the same composition: for example, in *Lavandula angustifolia* Mill. [19], *Stipagrostis pennata* (Trin.) De Winter [32], *Panax ginseng* [71], *Pogonatherum paniceum* [72] and *Scaevola sericea* [73]. Researchers, as a rule, have not accompanied the presented morphological information with data that has histologically confirmed the formation of shoots and somatic embryos, especially in the dynamics of their development. In our opinion, this once again indicates the need to use the histological approach, which allows the solving of many controversial issues that arise in studying the morphogenesis pathways in callus cultures in vitro. This is especially true for the pathways that lead to mass formation of the regenerants of economically important plants.

One of the possible ways to solve the problem of induction of both de novo organogenesis and in vitro somatic embryogenesis in the same callus is histological analysis of the positional location of the organ or embryo initial cells. The concept of positional information was proposed in order to understand the spatio-temporal organization of morphogenesis in the system of an integral organism [74]. This concept has been regarded ambiguously by researchers. Some authors have actively applied this concept in the analyses of various aspects of the developments of both plants [38,75,76] and animals [77]. Other authors have evaluated the concept as a formal, reductive mechanistic approach [78]. This issue should

also be considered debatable. However, in our opinion, the positive role of this concept in understanding the spatio-temporal organization of morphogenesis in calli is undeniable. In particular, the application of this concept can contribute to solving the questions of with which cells/groups of cells, in which place and in what specific form (organ or embryo) a new structure is formed in a callus as an integrated system.

Numerous experiments have been devoted to the investigation of various aspects of direct in vitro plant regeneration, without the stage of callus formation, as a rule, in response to certain stress treatments and/or exogenous hormone application. Recent reviews have been devoted to generalizing such experimental data. As evidenced by the analysis of the data presented in these reviews, in this case, plants also develop through de novo organogenesis or in vitro somatic embryogenesis. Studies over the last few years have expanded the understanding of the molecular mechanisms of cell reprogramming, and the results of genetic analysis have indicated the key role of epigenetic parameters in the regulation of direct in vitro plant regeneration [2,8,16,59,79–81]. In the context of our review, data of the participation of differentiated surface cells of some organs in direct in vitro plant regeneration are important (see [57]), as well as data on changes in a number of histological parameters (for example, the area of the central cylinder and the cells of the primary root cortex) during direct salt-stress-induced in vitro rhizogenesis [82].

It is important to emphasize that histological events during direct in vitro regeneration largely coincide with similar events, not only during indirect regeneration in in vitro callus cultures but also in intact plants: for example, in case of wound exposure. Such data once again demonstrate the universality of plant morphogenesis events in vitro and in planta.

4. Concluding Remarks

In vitro callus formation, callusogenesis and the morphogenesis pathways in calli have been studied in examples of various plants for quite a long time. In this area of research, in addition to the accumulation of extensive empirical material, important theoretical generalizations have been made.

In vitro morphogenesis in calli is no less complicated than in intact plants in planta. Nevertheless, calli cultivated under strictly controlled conditions are considered promising model experimental systems for evaluating various interacting morphogenetic processes and the mechanisms of their regulation in intact plants. The basis for the use of callus models is both the properties of their cells (pluri- and totipotence) and the main morphogenetic events that occur in calli in vitro (differentiation/dedifferentiation of cells, reprogramming of their development).

However, the most important problem consists of realizing the morphogenetic potential of callus cells in vitro is far from a final solution. To solve this problem, it is important to employ the histological approach, which involves studying the structures of developing tissues, organs and organisms in their interactions and interrelationships. Histological (structural) studies should be considered as a methodologic basis for the further investigation of various morphogenetic scenarios in in vitro callus cultures. In this regard, it is especially important to study the in vitro morphogenesis pathways in calli that lead to the formation of full-fledged regenerants. At the same time, one cannot disagree with the opinion of Rocha et al. [55] on the integration of structural and molecular data as an important strategy for studying the cellular competence in specific pathways of in vitro plant regeneration. The obtained data can contribute to the optimization of existing biotechnological techniques for mass production and the replication of regenerants of economically valuable plants. Moreover, such data is needed in the elaboration of new biotechnologies for breeding purposes: for example, during interspecific hybridization. Such an integrated approach is important to apply when studying regeneration in in vitro callus cultures: not only of traditional objects—representatives of the families Brassicaceae, Solanaceae and Poaceae—but also of plant species of economic importance and that have been previously unexplored in this regard.

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