Determinism and Variability of the Morphogenesis Pathways

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Determinism and variability

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Abstract

Along with a strict determinism of early embryogenesis in most living organisms, the variability of cell fates and developmental pathways exhibits in some of them. We propose that both determinism and variability are established through cell interactions, with the important role played by cell potency, cell sensitivity and cell signaling. The sensitivity of embryonic stem cells is considered to be strong, while the sensitivity of fully differentiated cells is small. This means that high potency correlates with high sensitivity, and vice versa. Experimental data were obtained and analyzed for the early developmental stages of plant species with regular and irregular types of embryogenesis, which explicit correspondingly determinism or variability of developmental pathways. For the irregular type the species with underdeveloped embryos in mature seeds were examined. As the result, we propose three conjectures for explanation of the phenomenon of variability, leading to the invariant final embryo shape, and support each of these cases with the example(s) of actual developmental pathways.

INTRODUCTION

The early stages of development (embryogenesis) are strictly determined in most of living organisms, displaying very high level of regularity of morphogenesis in all taxa of plants and animals (Souèges 1937; Johansen 1950; Meinke 1991 etc). The orientation of cell division planes, the rates of cell division, growth, differentiation occurs in a strictly

determined order and thus define the main course of the embryo's development, in particularly the derivatives of which cell will participate in the construction of embryo body.

Some authors have shown that although the first deterministic cell divisions have a great significance, however, early embryogenesis is determined by the total developmental strategy of the organism, which is established through cell interactions during development and depends on the position of histogens in the embryo (Jürgens 1995; Malinowski, Filipecki, 2002; Long Chen et al. 2018).

Likewise, along with the fact that in most cases the sequence (scheme) of cell events of early embryogenesis is strictly determined, some organisms exhibit irregular types of embryogenesis in which cell events are weakly deterministic, showing a high level of variability of cell fates and developmental pathways (Hutchinson 1964; Kapil, Bhandari 1964). At the same time the final shape of the mature embryo remains the same for all these individual organisms, thus appeared to be determined.

Thus, the question arises – what is the reason of such variability in cell fates paths at early stages at those particular organisms?

In our previous papers (Morozova, Shubin 2013, Morozova, Penner 2015; Minarsky et al. 2018) we have created a theory of morphogenesis, based on several concepts of cell fate determination and realization, and its mathematical formalization.

Here we will show the application of these concepts for the discussion of this question about determinism and variability in pattern formation, first in theory, and next - in the based on this theory analysis of experimental data on two types of embryogenesis of Angiosperms plants - with regular (deterministic) and irregular (variable) types of early embryogenesis.

RESUITS AND DISCUSSION

Formalization of developmental process.

In our previous paper (Bessonov et al. 2019) we have introduced the notions of *cell state* and *cell event,* and proposed a formalization of a development as a graph (tree) with vertexes, corresponding to cell states connected by edges corresponding to cell events (Fig. 1).

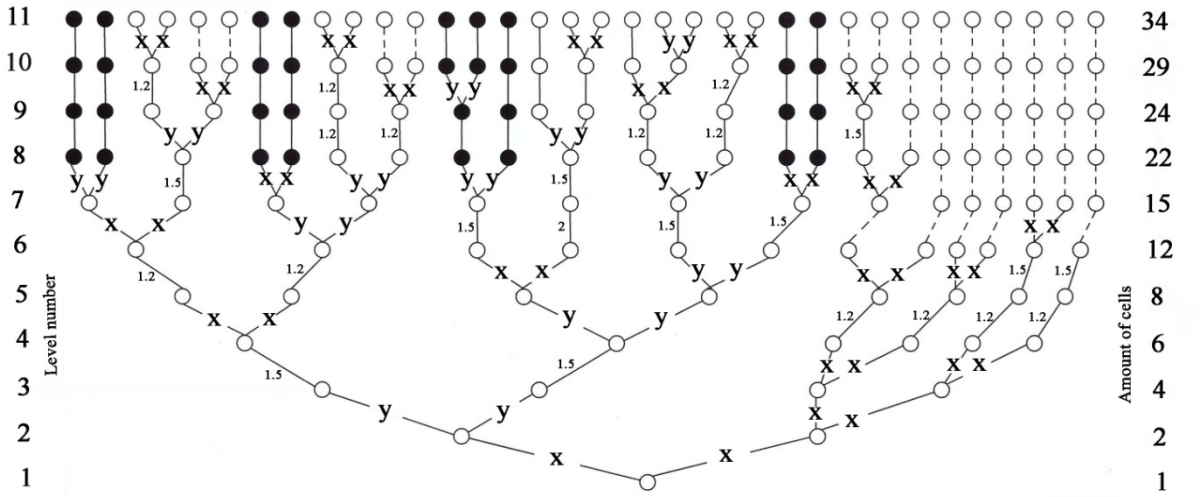


Figure 1. A graph (tree) of cell events, formalizing the process of embryogenesis of *Arabidopsis thaliana.* Cell growth is manifested as an edge with a number coefficient showing cell enlargement in size; "x" corresponds to transverse plane of cell division, "y" corresponds to the longitude plane of cell division.

We considered 5 types of cell events corresponding to the processes of cell division, cell growth, death, cell movement and internal cell event which includes, in particular, cell differentiation. We showed that such a developmental tree with exact parameters of cell events has one-to-one correspondence with embryo morphology at each time slice.

We will use this formalized language of developmental graphs (trees) for discussion the main ideas and concepts of determinism and variability in embryo development.

Our studies on several Angiosperms species (Polygala, Triglochin, Myriophyllum) have shown a high level of determinism in embryogenesis, which was demonstrated by the fact that individual organisms belonging to the particular species have provided the developmental graphs of the same pattern.

Alternatively, the other organisms (e.g. *Fumaria officinalis*) exhibit a high level of variability of embryonic cell fates and developmental pathways, resulting in numerous different developmental trees obtained for the same specie (Fig.2).

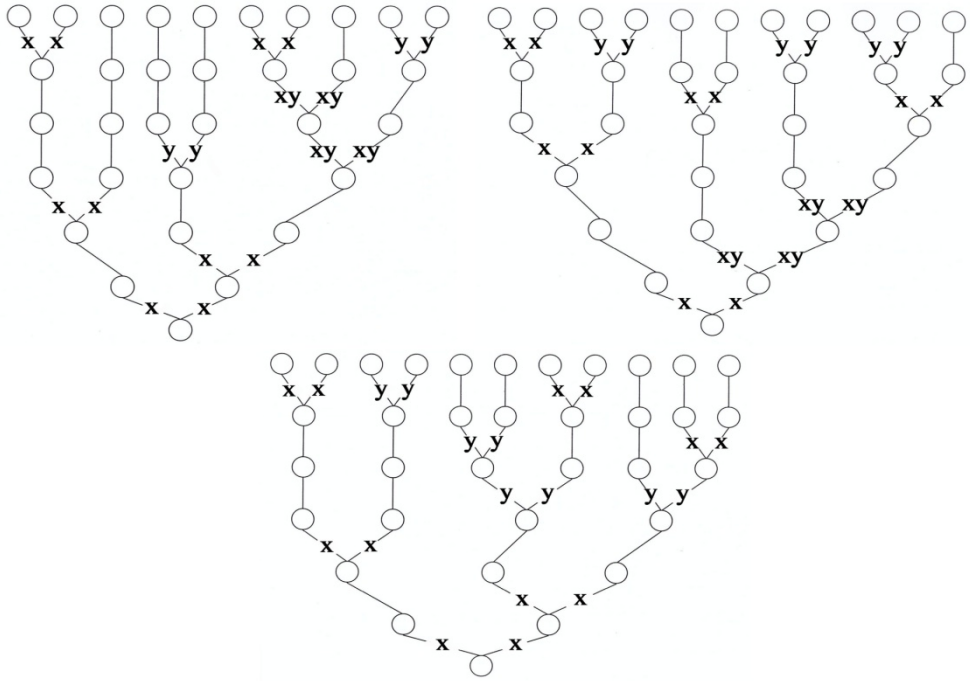


Figure 2. Several developmental trees of *Fumaria officinalis*, a specie with irregular type and underdeveloped embryo in mature seed (created according to figures in Souèges, 1941). Cell growth is manifested as an edge with a number coefficient showing cell enlargement in size; “x” corresponds to transverse plane of cell division, “y” corresponds to the longitude plane of cell division, “xy” corresponds to inclined plane of cell division.

We will notate this phenomenon a **fundamental variability,** meaning a variability of developmental pathways, i.e., a generating of different developmental trees starting from a cell, versus to a **local variability,** which appears in well differentiated tissues and manifests itself in variations of orientations of cell division planes in already formed tissue.

Theory of variability

There are 3 possible conjectures for explanation of ***fundamental variability*** of possible cell fate pathways, leading to the same invariant final shape of an embryo (organism).

1. Existence of **corridors of probabilities** of possible developmental pathways. Those developmental trees, which lead to the invariant final shape, will have a probability close to 1, and thus belong to the basic corridor, while others having small probabilities, exist out of this basic corridor, and may lead to impaired structures or to a death.

2. Some **fragments of a developmental tree can be equivalent** from the point of building a final shape. Then two developmental trees, different in details but built from the fragments equivalent to each other, will be generally equivalent.

3. Variability of developmental pathways can occur **in the structures which having not important morphological significance**, and/or which will be vanished at some stages of embryo development.

We will discuss these theoretical variants of variability using a set of our conjectures together with a set of experimental data obtained on underdeveloped embryos.

Cell potency, sensitivity and signaling

In our previous paper (Minarsky et al. 2018) we have proposed a theory of morphogenesis based on the following fundamental hypotheses:

– For each cell in an organism there exists a cell-surface distribution of molecular substances called its (epigenetic) spectrum governing morphogenesis.

– We call a *signaling* a transmission by each cell its own epigenetic spectrum to a collection of its neighbors.

– Each cell in an organism performs one of several possible cell events, namely, change of spectrum, change of position, change of shape including growth, mitotic division, and apoptosis (that is, programmed cell death).

– There is a collection of universal rules obeyed throughout Nature for a specific cell event for each cell at each instant depending upon its own epigenetic spectrum and the cellular signals it receives.

– For each zygote for each organism, there is an optimal sequence of cell events following the universal rules which describes the normal evolution of the embryo, which can be formalized as developmental graphs (trees). Each cell event in normal (optimal) tree of embryo development can occur only upon its confirmation by the signaling (normal signaling) from the neighbor cells.

– If the optimal cell event is impossible due to amputation, transplantation or malfunction, then the cell response is to de-differentiate and return its spectrum to that of its ancestor cell.

– Cell potency, which is an ability of a cell to produce many different cell types and to change its fate in different circumstances, depends upon an epigenetic spectrum of a cell. The strength of the signal transmitted by a cell is inversely proportional to its potency.

Thus, we have conjectured:

1. The determination of cell events (the determined developmental tree growing from the zygote) by the existence of epigenetic code.
2. Confirmation of each cell event by the signaling from the surrounding.
3. The diversity of the strength of signals emitted by a cell depending on its status of differentiation. The statement that strength of signal emitted by a cell is inversely proportional to its potency means that the emitted signal of a stem cell has weak intensity in comparison with differentiated cells, which produce a strong signal to the neighbors.

Here, in addition to the previous conjectures, we proposed the generalized notion of a ***sensitivity of a cell*** to the signals received from neighbor cells, and hypothesize that different range of sensitivity also depends upon a status of cell differentiation. A ***sensitivity*** means an ability to read incoming signals (spectrums of neighbor cells), e.g., to transform them in a specific way and next to make its summation in a **total accepted signal**.

We assume that the ***sensitivity of embryonic stem cells*** is strong, while the ***sensitivity of a fully differentiated cell*** is small. In other words, we propose a **statement that cell potency directly correlates with cell sensitivity.**

This means that high potency correlates with high sensitivity, and vice versa.

We hypothesize that depending on the interplay of these 3 parameters**:** potency, sensitivity and signaling, a cell will exhibit different types of behavior (deterministic or variable).

Embryonic cells at early stages of embryogenesis undergo precise regular development, their cell events are strictly determined. In plants, cell groups remain in the shoot and root apexes, which consist of undifferentiated (stem) cells, and which present a special type of cells emerged from embryonic stem cells. The regularity of cell events in these shoot and root meristems is much higher than in other cells, thus confirming the statement about deterministic behavior of stem (stem-like) cells.

This means that stem cells have strongly determined program of cell events, independent (or very slightly dependent) upon external signaling, and thus can explain that stem cells emit low signals to each other.

At the same time it is known from tremendous number of experiments that embryonic cells possess a high potency, i.e., an ability to change their fates in different circumstances,

where they get strong external signals. Thus a high potency, which is a characteristic of embryonic stem cells, is a source of possible variability of developmental paths of cells.

More the embryo develops, more (local) variability is manifesting in formation of its tissues. We can notice that differentiated cell does not have a choice of “Internal cell event”, which is the changing of its epigenetic spectrum without any other changes in a cell, thus allowing a cell to change its cell fate (Minarsky et al. 2018; Bessonov et al. 2019). Internal cell event has to be confirmed by signal(s), which means that cells must have ***sensitivity to the signals.*** Apparently, the differentiated cells loose this ***sensitivity*** and at the same time they acquire an indifference to a choice of cell division planes, manifesting in local variability. This can be connected with emitting a strong signal to neighboring cells.

We may suggest that the choice of 1 concrete path for each of embryonic stem cells which is cases of early stages in normal development, occurs under the ***strong received conformational signal***. This ***strong received signal*** is the result of high ***sensitivity to the receiving signals*** by cells of developing embryo, though the signaling of the neighbor cells (also stem-like ones) is rather weak.

In the cases, when embryonic stem cells do not have a high level of ***sensitivity,*** there occurs the case of ***mosaic development***, characteristic for some types of animals (summarized in Gilbert 2013). In this case, each cell continues to implement their developmental program in any environmental conditions independently of signals from surrounding.

From all above we can conclude that:

There is deterministic programming of all cell events, starting from the zygote and resulting in an organism with well determined shape, obeyed by nature (e.g., programmed as an epigenetic spectrum of cells, determining their cell events);

Stem and stem-like cells, due to their high potency, are capable for high fundamental variability; however, under confirmation of normal developmental path (under receiving normal signaling from their environment) stem cells produce the prescribed (optimal) cell event, determined by the epigenetic code. The incoming confirmation signal should be well readable by a cell, which strongly depends on the *sensitivity* of a cell to incoming signals, which is especially important in the case of embryonic stem cells, emitting (according to our theory) low signals. This means that normally, the *sensitivity* of stem and stem-like cells should be very high, that is why being transplanted to another tissue they can change their

cell fates according to the signals from surrounding cells (thus showing capability for fundamental variability).

Application of the theory for the phenomenon of variability of underdeveloped embryos

The investigators of plant embryogenesis have distinguished that the irregular types of development, in which no stable patterns can be identified, are observed in parasitic, epiphytic species and in the species with underdeveloped embryo (UD embryos). In such cases there is no precise scheme of cell events (Fig.3).

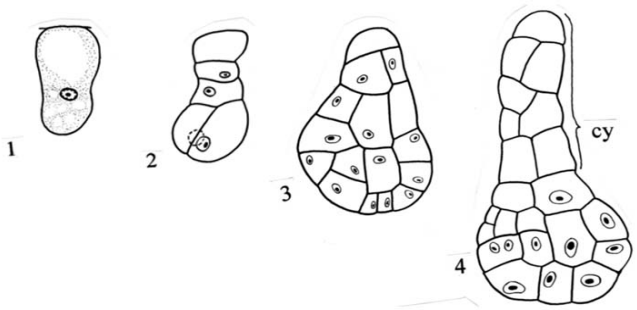


Figure 3. Several embryogenesis stages of *Pulsatilla vulgaris* – a species with irregular type of embryogenesis and underdeveloped embryo in mature seed.

Also, it was revealed that the development of underdeveloped embryos at early stages is very slow, which lead to the fact that seed formation is far ahead of embryo development, leading to falling of the seeds with underdeveloped embryos and their maturation up to normally developed embryo occurs after the seed dissemination.

We have detected that during the time when the cells of normal embryos pass through the whole tree (graph) of cell events leading to a mature embryo, the cells of the underdeveloped embryos pass considerably small number of cell events, and that the developmental trees for all particular embryos are very different, thus exhibiting a high level of variability of cell pathways (Fig. 2).

These observations arise several questions:

1. Why the early stages of UD embryos are developing so slowly?

2. How irregularity in cell fates is connected with the underdevelopment?

3. How irregularity in cell fates is connected with the slowness?

Based on our theoretical conjectures we can give the following response to these questions.

From all discussed above we can notice two correlations:

- between ***sensitivity*** and differentiation (inversed)
- between differentiation ***and variability*** (existence of corridors of possible pathways),

from which we can conclude an existence of inversed correlation between ***sensitivity and (fundamental) variability*** (diversity of developmental paths).

Thus we may assume that the cells of UD embryos has decreased sensitivity to the ingoing signals, contrary to usual high level of sensitivity of embryonic stem cells, and because of it they experience difficulties with processing each next cell event, which should be confirmed by the signal from neighbor cells. This can explain both a time delay with each next step of cell events and a dispersion of the cell events (variability of cell pathways), due to the high potency of cells being of a stem cell nature, and random realization of one of several possible pathways in response to one of the neighbor signals randomly elevated.

More precisely, by further developing our theory we can assume that:

- High potency of a cell may correlate with the wideness of a signal, produced by a cell, in other words, it is possible that undifferentiated cells (stem cells) emit signals (i.e., have such an epigenetic spectrum) which can be read (interpreted) in a wide range of action by neighbor cells. Differentiated cells produce signals readable in very narrower range of action by their neighbor cells, both differentiated and undifferentiated.
- Sensitivity of a cell may create a threshold(s) of ***signal acceptance*** by a cell, and only signals, overcoming this threshold, will be read by a cell.

For example, if a stem cell is surrounded by several differentiated ones, giving the same signal to it, the threshold for this signal will be overcome due to the summation of received signals of the same type.

In embryonic stem-like cells, due to their high level of stemness, each cell receives from its neighbors several different, not precise, wide-range signals, all being of a low strength. In this case, the priority for the signal accepted will be the one that is stronger than the others, well enough to pass the threshold, or the one which be a sum of several equal signals received simultaneously

And in the case of UD embryos, due to the low sensitivity of its cells, most of the signals fail to overcome the threshold of acceptance. Therefore, the priority is taken for a

signal which at some moment appears to be slightly stronger than the others, which may occurs randomly, and that is why the choice of a path displays random pattern.

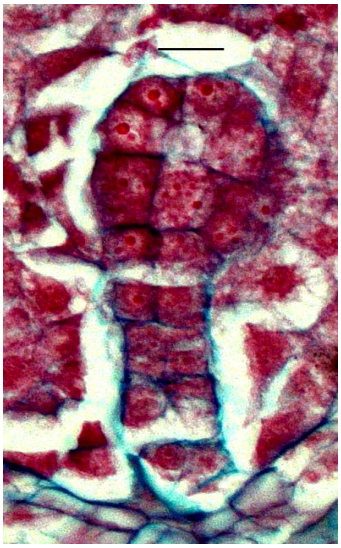
And since this assessment takes time, cellular events occur with considerable delay and the process of embryogenesis goes much slower than in normal embryos; thus the embryo does not reach the fully developed stage at the time of the seed falling.

Next, after the seed dissemination, the embryo accumulates potential for further development from favorable external conditions (temperature and other factors) during a prolonged dormancy, which strengthens the sensitivity of cells to signals. There are good experimental proofs for this assumption (Grushvitsky 1961; Baskin C. C., Baskin, J. M. 2001; Butuzova et al. 2019).

It can be assumed that evolution went towards increasing the potential of the cells (zygotic, embryonic stem and further), therefore in the most advanced taxa the development of the embryo on the mother plant and seed germination after dissemination occurs rapidly, due to the strong signals.

The possible confirmation of this assumption can be found in considering cell walls of these underdeveloped embryos. It was noted that they have thickened walls, unlike those ones with completed development embryo at dissemination (fig. 4). These thickened walls obtain a lot of polysaccharides in intercellular space. According to our theory of the epigenetic code of cell surface, cell wall polysaccharides, especially in the early stages, play a significant role in determining the cellular events in morphogenesis. And the thickening of the cell membranes, in which a large number of substances (excess) of a polysaccharide nature accumulate, can interfere with the reading of signals between adjacent cells.

Such condition may cause the decrease of sensitivity of cells of underdeveloped embryos which remain for a long time, perhaps up to the moment of dissemination.



A B

Figure 4. Proembryos of *Polygala major* (A) and *Pulsatilla vulgaris* (B) at the proembryo stage of development. In *Pulsatilla vulgaris* the thickened cell walls are seen, filling with substances of polysaccharides nature, stained with alcian blue.

In embryos with well differentiated embryos at dissemination such thickness of cell walls can also observed. They distinguish the segments of cells in an embryo deriving from one cell and obtaining the same developmental pathway (fig. 4, B). For example the thickened walls differentiate the sectors that give rise to the right and left cotyledons, as well as the underlying sector in which the hypophysis and embryonic root initials are located.

The so-called complexes of tabular cells can be the evidence of the effect of cell wall thickness on cell events and weakening of contacts between such complexes. These complexes form in the primary cortex of the embryo and in the cotyledons in the late stages of the development and during germination, and are presented by rows of cells, derivatives of one cell, dividing only transversely, and surrounded by a common thickened polysaccharide wall (fig. 5). These complexes play an important role in germination (Lodkina 1966), allowing the embryo to grow in length, but not in width because of the impossibility of longitudinal divisions.

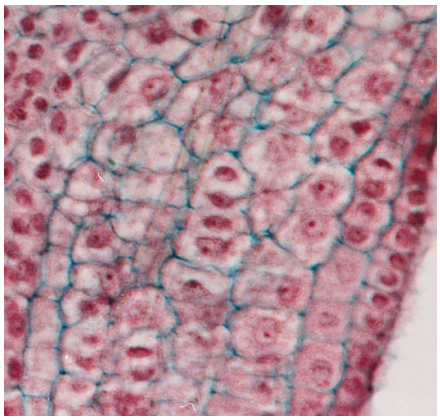


Figure 5. Fragment of embryo hypocotyle in *Aconitum soongaricum* at the stage of postdevelopment completion. The primary core is constituted from the complexes of table cells.

Other cases of variability

The question of the ***variability*** of developmental trees (pathways) can be considered at different stages of embryogenesis and in various structures.

First, we can observe, that the variability of paths of the developmental trees can happen in some concrete places within generally well determined graph of development. For example, in *Triglochin* the embryos variations takes place at the stage of 6-cellular proembryo – the next division in the general series occurs in the apical part, while in some embryos - in the basal part (fig. 6). But the form of the embryo still remains the same for all cases.

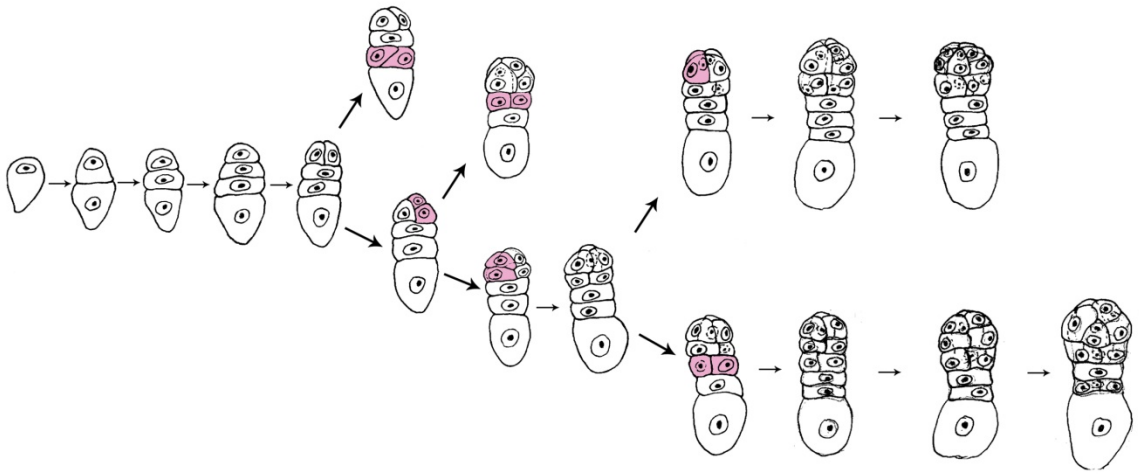


Figure 6. Variability of morphogenesis pathways at early stages of embryogenesis of *Triglochin palustre*. The cells produced by variations in cell events are marked in pink color.

The emergence of variability can also be associated with a contravention in the establishment of regular bilateral symmetry. One example is the early embryos of *Polygala major*, where together with the regular bilateral embryos (Fig. 7, A), the so called “spiral-rowed” asymmetrical embryos were observed (Fig. 7, B).

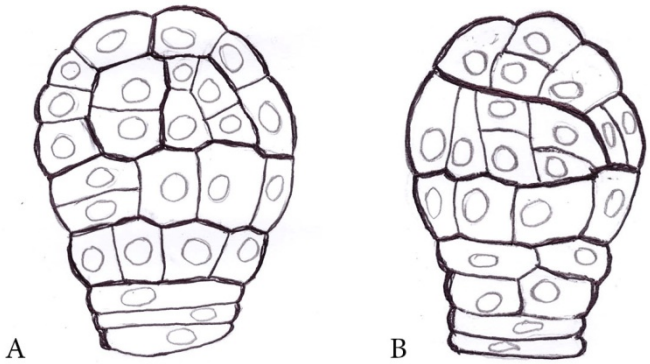


Figure 7. Two embryos of *Polygala major* at approximately the same developmental stage. The normal development with “radial” symmetry (A) and the sample of “spiral-rowed” embryo development (B).

Another interesting observation is that during organogenesis of temporary organs of the embryo – cotyledons, the cellular events have a very high degree of variability (Fig. 8), although the locations of the initiation and the final form of these organs are always strictly determined and specific to the species.

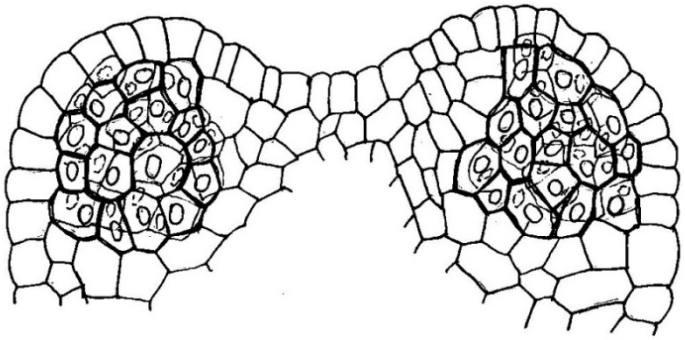


Figure 8. Cotyledons initials in *Polygala major*. The differences in cell event between right and left parts of cotyledons groups are visible.

CONCLUSION

Variability, like determinism, is also causal in morphogenesis and has its own laws. Variability replaces determinism under the influence of various factors - programmed in the epigenetic code, development time, the total mass of cells and cellular events committed by individual cells. Variability manifests itself in different spectra, different corridors of determinism and can be a result of a change in the receiving signals or in the sensitivity to their perception.

As a conclusion, we can provide the examples of 3 cases of ***variability*** of cell pathways, posed in the beginning of the paper. Namely:

1. Existence of **corridors of probabilities** of possible developmental pathways. Those developmental trees, which lead to the invariant final shape, will have a probability close to 1, and thus belong to the basic corridor, while others having small probabilities, exist out of this basic corridor, and may lead to impaired structures or to a death. This can be a case of **embryonic stem cells** which have a high probabilities within the basic “corridor of development”, formatting precise embryo structure, but also have smaller but not zero probabilities for changing their fates in the case of “crises” signals (amputation, transplantation, isolation and growth in cell culture, etc.) and thus to create a developmental paths outside this basic corridor.

2. Some **fragments of a developmental tree can be equivalent** from the point of building a final shape. Then two developmental trees, different in details but built from the fragments equivalent to each other, will be generally equivalent. This is the case of **irregular type of embryogenesis**, particularly, embryogenesis of underdeveloped embryos (underdeveloped embryos).

3. Variability of developmental pathways can occur **in the structures which having not important morphological significance**, and/or which will be vanished at some stages of embryo development (formation of cotyledons and suspensor in plant embryos).

Thus, it is possible to conclude that the manifestation of variability is also deterministic.

Materials and Methods

We used embryos at the progressive early embryogenesis stages of species with regular embryogenesis type (Polygala major, Triglochin palustre) and with irregular type (Pulsatilla vulgaris, Aconitum soongaricum), making sections at every stage according to standart--cytoembryological methods and staining preparations with safranin and alcian blue (for P.vulgaris and A.soongaricum).

The graphs of cell events for the species Arabidopsis thaliana and Fumaria officinalis, were created as described in Bessonov et al., 2019, according to the figures published in the corresponding work (Souèges, 1941).

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