

External and internal control in plant development

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Abstract

Bodies of plants are modularly organized. Development proceeds by adding new modules to open endings with a potential for branching. Each module is autonomous to some extent. Development relies on the self-organized patterns that emerge from the interactions of individual modules. Interactions include both competition and cooperation, and several types of positive and negative feedback loops are involved. Development can be open to external influences, thus enabling the plant to adjust its form to the environment, for example, to the spatial distribution of ecological resources. This paper provides a review on adaptive plasticity in plants.

Keywords

Developmental plasticity, self-organized pattern, phenotypic variation, plant morphogenesis, physiological integration, modular structure

Introduction

Development of most organisms is not strictly prescribed by the genome. As the body is developing, self-organizing processes arise from the interactions of cells locally, and of tissues on a larger scale. Probabilistic effects can largely influence the position and differentiation of individual cells and contacts between cells¹. A problem that should be solved by most organisms is how to channel stochastic, self-organizing processes into one, coherent process that would produce a well-functioning individual. For example, how to exclude selfish elements (c.f. Maynard Smith and Szathmary 1995)? How to reduce developmental noise (c.f. Waddington 1957; Novoplansky 2002)? Coherence and reliability of the developmental process is under strong natural selection.

In addition to internal uncertainties, external effects may also influence development. Protection of the embryo from the environment is an important task, and is solved in various ways by different species (see Gilbert and Raunio 1997). On the other hand, the environment is not only a source of disturbance to development, but can guide development as well. The end-product of development has to match to the habitat in which the organism lives. More precisely, fitness of a genotype is a function of the phenotype and the environment. Therefore, pieces of information that arrive from the environment can be utilized for increasing fitness (Novoplansky *et al.* 1990a; Oborny 1994; DeWitt *et al.* 1998; Alpert and Simms 2002; Givnish 2002).

An important keyword at the core of this problem is phenotypic plasticity. Phenotypic plasticity occurs when the same genotype can be expressed in various phenotypes depending on the environment (Bradshaw 1965; Via *et al.* 1995; Schlichting and Piglucci 1998). Plasticity of development has been demonstrated in a number of species for a large variety of traits (Diggle 2002; Grime and Mackey 2002; Sachs 2002; Piersma and Drent 2003). Nevertheless, the selective consequences of plasticity are not straightforward to assess. Beside the trivial advantage of adjusting the state of organism to the state of environment, there are potential costs and limitations to plasticity that diminish its adaptive advantage, or may even select for non-plastic (rigid) development (DeWitt *et al.* 1998; Diggle 2002; Givnish 2002; Novoplansky 2002; Schlichting and Smith 2002). It is not trivial to ask, to what extent is a particular developmental process controlled internally, by the genetic system, and externally, by the environment.

I review some characteristic features of development in plants, and discuss the means of control with special emphasis on feedback processes. The paper introduces the topic from the basics, with the aim to make it understandable to non-biologist readers. I have chosen plants for the discussion of this general topic, developmental plasticity, because morphogenesis in green plants (outside of the seed) is a readily observable process, and experimental manipulation is also relatively easy. Consequently, there is a large body of empirical literature on the external and internal control mechanisms.

Modular development

We start by a short introduction to some principles of development in plants (Gymnosperms and Angiosperms). The plant body is essentially modularly organized. The smallest, elementary unit of construction in the shoot system is called a ‘metamer’ (Figure 1). Metamers make branches, and branches

¹ This topic has a rich literature since the classical works of Thompson (1917), Turing (1952), Bonner (1963), Meinhardt (1984), Sachs (1991) and Kaufmann (1995). A counter-example was offered by *Caenorhabditis elegans*, in which the fate and position of each cell is pre-determined (Sulston *et al.* 1983), thus, self-organisation does not play a significant role in morphogenesis.

construct branching systems in a hierarchical manner. Each shoot apex is a potential point for further development. Development is an iterative process: the same, finite bit of program is repeated to add new metamers (Harper 1985; Hallé 1986). This add-on nature of development implies that the developmental program is essentially open-ended. Empirical studies have suggested that the number of iterations can be infinite in some species (Watkinson 1988; Gardner and Mangel 1997). In others (for example, in annual plants) iterations certainly terminate, but the number of iterations is not strictly defined; it can depend on the environment (Schlichting and Smith 2002). A trivial consequence of iterative development is that the number of organs is not fixed. For example, the number of leaves of a tree can vary with age and habitat conditions. The first reason for this capability is that organogenesis (formation of organs) is continuous, not restricted to an embryonic stage. Secondly, organs or even larger parts of the body (metamers or branches) are disposable: they can die without the death of the whole organism. The body plan is not pre-determined, but can flexibly change according to the actual interactions of the organism with its environment. These features are in sharp contrast with the development of non-modular (unitary) organisms, such as vertebrates or arthropods (see Oborny *mscr.* for review).

Iterative development and flexible design make plants particularly suitable for studying phenotypic plasticity. Experiments can use multiple units of the same genotype, and can examine whether these units would express different phenotypes according to external stimuli from the environment. Modules can be separated and treated individually. Moreover, spontaneous cloning is a frequent phenomenon among plants (Klimes *et al.* 1997). In such clonal species, researchers can gain genetically identical, physiologically autonomous individuals (ramets) for the experiments. Thus it can be directly studied how different environments would induce different phenotypes, and how each of these phenotypes is selected locally by its own environment or, being transplanted, by another type of environment.

Distributed control

Plants lack any central controller for morphogenesis or behavior. There is no central nervous system or any other morphological structure which would be responsible for coordinating one part of the body with another (c.f. Novoplansky 2002). Indeed, adaptation to the environment seems to hinge on the opposite of centralized control: interactions between individual, semiautonomous modules. Semiautonomy means that a module on any level of the hierarchy (metamer, branch, etc.) is partly independent from the other modules, but the independence is not complete. (See a section about Integration below.)

Events of development (such as adding a new metamer to a growing tip) can proceed parallelly, at multiple locations at the same time. Therefore, life history of a plant is not a single sequence of events, but might rather be described as a set of parallel histories. For example, a branch can develop flowers when another branch is still in a developmentally juvenile stage. A branch can senesce and die while another one is just beginning to start its growth.

Local mechanisms and integration

The domain in which a particular control mechanism can act is an interesting subject for research. Radioactive labeling and other experimental techniques have shown that the pattern of these domains (Integrated Physiological Units; Watson 1986) can be fairly sophisticated. A primary determinant is the pattern of vascular contacts, but states of the modules also matter. State transitions (for example, from vegetative to reproductive) and environmental influences can widen up or narrow down the range of integration. For example, when a branch gets defoliated (e.g. due to herbivore attack), its previous physiological connections to other branches may get re-activated (Watson and Casper 1984; Marshall and

Price 1997), thus, the IPU becomes wider. On the other hand, there are species in which similar treatments cannot change the borderline between IPUs, i.e., sectoriality is strict (Watson and Casper 1984).

An important conclusion from the experiments is that IPUs do not necessarily coincide with developmental modules. Some modules can be strongly connected physiologically, while others may be independent (c.f. Watson and Casper 1984; Marshall and Price 1997; Figure 1). This holds for any level of the hierarchy from metamers up to systems of branches. The highest degree of module independence is achieved by clonal plants, in which each module can develop a self-supporting shoot and root system, and thus, the genetic individual (genet) can get fragmented into independent physiological individuals (ramets). It is remarkable that ramet formation can happen at any level of the developmental hierarchy from metamers (as in *Trifolium repens*) through branches (as in *Ranunculus repens*) up to systems of branches (e.g. in *Robinia pseudo-acacia*, where a ramet is an entire tree).

Let us take the example of a branch that has just started its growth, and thus, consists of a single, undeveloped metamer. This initial branch is certainly not capable for self-maintenance, and relies on carbon import from at least one other branch. Later when the carbon budget becomes positive, the branch can become autonomous. For example, in *Capsicum annuum*, each adult branch has been found to be self-supporting: maturing fruits received assimilate only from leaves on the same branch, and not through the main stem (Steer and Pearson 1976, cited in Watson and Casper 1984). A considerable degree of autonomy can develop even on the level of single metamers. For example, seeds ripening on *Pisum arvense* stems have been found to receive approximately 66% of their carbon supply from the leaves and pod within their own metamer (Flinn and J.S. 1970, cited in Watson and Casper 1984).

Let us consider the import of essential resources other than carbon. Water and mineral nutrients have to be taken up from the soil. Basically, there are two options. The branch in our hypothetical example would either rely on the existing vascular pathway of resource transport from the root through other branches, or can develop its own root system by forming adventitious roots. The second can lead to full autonomy for all resources, i.e., the above-mentioned case of clonal growth. In the first case, the branch would share a root system with other branches. Experiments suggest that shoot-root connections can also be sectorial (Watson 1986; Vuorisalo and Hutchings 1996). In that case, the branch would not have access to resources from the whole root system, only from a part of it (Figure 1).

The means of control

Development can be controlled by two types of substances: resources and hormones.

Resources (carbon, mineral nutrients and water) act directly by limiting growth. Modules are competing for these resources. Those modules in which consumption is relatively faster create a concentration gradient locally. This gradient is a potential driving force for the transport. But this potential is not necessarily manifested. The pattern of vascular connections constrains interactions between modules, and it is the relative states of the modules that finally determines the direction and magnitude of transport (see IPUs).

Hormones can modify the pattern of resource transport on a longer time scale. For example, auxin production by actively growing shoots determines the direction of vascular differentiation (pages 59-63 in Sachs 1991). Besides affecting the connections between modules, hormones can also influence state transitions in each module. For example, gibberellins have been suggested initiate a transition from vegetative to reproductive shoot type in *Hedera helix* (pages 174-175 in Sachs 1991).

Auxin seems to play a central role in the transfer of information about one part of the plant to another part (Sachs and Novoplansky 1997; Sachs 2002). The most remarkable example is apical dominance. A developing shoot apex releases auxin, which flows basipetally, and inhibits lateral branching (i.e. activation of lateral buds) in the neighboring metamers. The regulatory process is sophisticated:

distance from the roots (due to the action of cytokinins) and age of a bud also matters. Any decline in the quality of the apex, for instance, due to shading, would lead to a decrease in auxin production, and thus, to release of the lateral buds from suppression (Sachs 1991). Thus, further growth in the shaded area can be slowed down or even completely abandoned, and a new, lateral direction of growth can be tried. This behavior can be adaptively advantageous in a wide range of patchy habitat types (Oborny 1994).

An important difference between resources and hormones is that resources arrive from the external environment, and thus, once taken up, can only be depleted. In contrast, hormones are synthesized internally, so, there is practically no theoretical limit on their availability. Hormonal actions are finer-tuned than the effects of resources: their concentrations are smaller by magnitudes, and even a small change in hormone concentration may cause large change in the phenotype. The effects can be targeted, and can be specific to organs, tissues, or even cell types (see examples in Sachs 1991). In addition, hormones can act before a change in the resource supply would occur, thus, the plant can utilize anticipatory signals (Sachs 2002). For example, a leaf primordium produces auxin, which causes vascular elements differentiate into the direction of the primordium, where sufficient resource supply would be needed in the future, when the leaf starts to grow (pages 59-63 in Sachs 1991).

As a further example for the adaptive significance of anticipation, Novoplansky *et al.* (1990a) demonstrated that young *Portulaca oleracea* plants can sense neighboring plants from the change of light quality (R/FR ratio), and can respond to this signal by growing away from the direction of the neighbor. Moreover, the response can occur before any significant shading, i.e., before any decline in the amount of resource. Thus, the change in R/FR is a specific, anticipatory signal, and the hormonal system can transmit this to a morphogenetic process. Another example for a predictive signal is photoperiod, which can be used for initiating anthesis before the season for pollination would arrive. This is advantageous, because developing a flower takes time.

The relative importance of resources and hormones in plant development has been debated in the literature. In one of the seminal papers on plant modularity, Harper (1985) emphasized the importance of resource depletion in controlling development. Similarly, Wilson (1988) suggested that the distribution of resources (source-sink relations between modules) would provide a sufficient explanation for plant development. In contrast, Sachs (2002) lists three basic phenomena which support the importance of hormones. (1) Early development in juvenile individuals can proceed in a well-balanced way (maintaining a proper shoot:root ratio) even in the absence of some relevant resources: light or nutrients. Water is necessary, but it does not have to be applied through the roots. (2) Treatments by hormones have been demonstrated to show significant effects on morphogenesis, e.g., on the differentiation of vascular channels. (3) There are cases when a plant part is a sink for resources but a source for hormones. The most extreme example is a bacterium-induced tumor, which consumes substrates from other parts of the plants, and is known to release hormones. Local, exogenous application of auxin and cytokinin in a proper ratio could produce the same, overdominant growth and teratological development (Sachs 2002).

Another, less extreme example for point (3) is apical dominance that is ubiquitous in plants. An interesting, clearly hormonally controlled process is a release from apical dominance by a R/FR signal. Plants can even be 'cheated' by applying a small quantity of light when it has the proper quality. For example, Deregibus *et al.* (1985) placed light-emitting diodes into closed grassland swards. The diodes emitted a small amount of red light, increasing the R/FR ratio. As a consequence, tussocks in the closed grassland started to branch increasingly, as if the plants were growing in an open area, without any competitor. This response was based on a specific mechanism for signal perception and transduction, that is linked to the hormonal system (Schlichting and Smith 2002), and not on the small amount of additional light. Novoplansky and colleagues have demonstrated that even a decrease in the amount of light can induce a high-light growth form when the decrease occurs specifically in the FR spectral range, increasing the R/FR ratio (Novoplansky *et al.* 1990a,b; Novoplansky 1991).

These results underline the importance of hormones in the control of plant development. Control by resources certainly does not suffice when formation of the optimal branching structure implies resource movement against concentration gradients, i.e. when resource-rich branches should get richer.

Feedback loops

We find both positive and negative feedback loops in the control of plant development. A simple example for a positive feedback loop is the above-mentioned effect of auxin in a branch. If a branch grows faster, then it releases more auxin. Auxin suppresses the development of other branches, thus, this particular branch would gain competitive advantage. Getting more resources would result in faster growth, and thus, the loop gets closed.

Negative feedback can be exemplified by the correlative growth of root and shoot systems. It has been demonstrated by numerous studies that the growing plant tissues require a fairly stable ratio of carbon:nitrogen supply. Therefore, biomass of the assimilating shoot (that is a source of carbon) and of the root (that is a source of nitrogen) has to be well balanced. The plant solves this task by a negative feedback. The shoot releases auxin, and presumably other signal molecules, which enhance root initiation. At the same time, the root produces cytokinins, which stimulate the development of shoots. Thus we have two negative feedback loops linked: each system (shoot and root) inhibits its own development by giving advantage to its competitor.

Naturally, negative feedback tends to equalize initial differences between organs to make the system converge to a stable state (e.g. optimal shoot:root ratio), while positive feedback leads to runaway growth. A typical example for the second is offered by split-shoot experiments (Sachs and Novoplansky 1997). Seminal shoot is removed from a young (4 days old) *Pisum sativum* seedling to stimulate growth of the two buds that are in the axils of the cotyledon. The two buds are nearly equal, but there may be a small difference in size by chance. This initial difference is enhanced during development, and growth gets concentrated in one of the branches. The difference between branches increases with time, and in most plants, the subordinate branch stops growing within ten days. It is very interesting to experiment with this system to explore how external stimuli (shading, physical damage, etc.) might change the dominance relations between branches (see Sachs and Novoplansky 1997). A natural role of this positive feedback is to allocate limiting resources into the growth of the stronger branch. More vigorous growth (and thus, more release of auxin) usually indicates better conditions in the local environment. Thus, the plant can preferentially grow toward better sites (Sachs and Novoplansky 1997). The degree of dominance of the stronger branch is a trait that is open to evolutionary optimization: too strong dominance can be disadvantageous in those environments in which the good (high-light) patches are small or ephemeral, because being in a good site is not a guarantee for staying in a good site, and a too strong positive feedback may make reversals costly or impossible (c.f. Oborny *et al.* 2001). This topic, the optimal degree of dominance in various environments, would certainly need more attention from modelers.

Time lags

Most feedback processes are not immediate. Manifestation of a phenotypic change may require time. Physiological changes are usually faster than morphological ones (Bradshaw 1965).

Time delay can be especially important when its scale is similar to or coarser than the scale of environmental fluctuations. In this case, state of the environment at the time of induction may considerably differ from the state of the environment at the time of selection. Thus, the mutual information between the inducing and selecting environment may be too low for promoting the evolution of plasticity at all (Oborny 1994). Jablonka *et al.* (1995) have shown in a Markovian model that the optimal degree of inducibility

increases as the time lag decreases. The degree of inducibility was measured by the probability that an environmental change would cause a corresponding phenotypic change. This result was confirmed by Padilla and Adolph (1996) with the important addition that spatial movement in a patchy environment can have the same effect as temporal fluctuation. (See also Oborny 1994 about spatial and temporal predictability of the environment.)

An extreme example for a long time lag is organ preformation in buds. In some species, for example in *Podophyllum peltatum*, a shoot can be induced to develop reproductive *versus* vegetative buds in year t . So, the presence or absence of inflorescence is determined in year t . But it is only year $t+1$ when the bud is used by the plant to grow. Year $t+1$ can differ from year t in the availability of pollinators, abundance of resources, and many other factors that influence the optimal number of reproductive modules. Nevertheless, the decision cannot be reversed (Geber *et al.* 1997).

An additional problem is called ‘ontogenetic contingency’ (Watson *et al.* 1995). The same environmental signal that arrives at a shoot of *Podophyllum peltatum* can have a different effect depending on the state of that particular shoot. State of a shoot at time t is a result of past, historical events (at $t-1$, etc.). Therefore, developmental history is an important determinant in any actual developmental move (see also Diggle 2002). Of course, if there is no direct transfer of information from the past (e.g. $t-2$ influencing t directly), then this can still be approached by a first-order Markovian model, regarding the state of the plant at time t as a cumulative result of its past history. I think that the most important emphasis in these papers is not on the effects of history, but on the need to consider the state-dependence of changes.

External *versus* internal - Does it make a difference?

Some researchers have suggested to group together all the influences that may affect the development of a particular organ, tissue, or cell as ‘environmental’ influence (Givnish 2002; Sachs 2002; Schlichting and Smith 2002). They suggest to differentiate between an ‘external environment’ (i.e. everything outside of the plant individual) and an ‘internal environment’ (i.e. everything within the plant individual but outside of the organ, tissue or cell that is in the actual focus). Givnish lists the following examples for ‘internal environment’: “positional information based on hormone levels or cellular contact, or the indirect effects of other cells or tissues on abiotic factors such as oxygen tension or red/far red (R:FR) ratio” (page 214 in Givnish 2002). As Sachs wrote, “the growth of the plant itself changes the environment of its individual organs, an obvious example being the shading of lower leaves and branches” (page 244 in Sachs 2002).

Figure 1 provides a summary about external and internal control in this sense. The figure shows a simple, hypothetical plant that consists of some metamers. Let us focus on a single metamer. This metamer can export and import resources and hormones from and to other parts of the plant (arrow [a]). This represents the internal control of its development. At the same time, the metamer can be shaded by other branches of the same plant [b] or of other plant individuals [c]. Shading also controls its development, but [b] and [c] are certainly external. They work by other mechanisms than [a]. In the case of [a], the carrier of information is a resource or a hormone. At [b] and [c], the carrier of information is light.

It is interesting to ask to what extent a plant might differentiate between [b] and [c]. Different species have different composition of photosynthetic pigments. So the species of the shading branch would be likely to matter. But individual distinctions within the same species do not have any empirical support. In case of root systems, there have been interesting indications for self / non-self recognition in some experiments (Schenk *et al.* 1999), but the mechanism is unknown, and certainly more evidence is needed.

For control [a], plants can have heritable genetic variation, so, [a] can be subject to evolution. Controls [b] and [c] cannot be influenced by evolutionary processes directly. [c] is completely inaccessible to the genome. [b] is accessible, but only in an indirect way: the genome codes information about the

architecture of the plant, and architecture influences the probability that a branch would shade another branch (c.f. Bell 1984). So, it is not the mechanism of control but the result of control that can be under selection.

The notion of 'internal environment' is very important, because underlines the dynamic and responsive nature of plant development, including the plant's responses to its own state. However, I think that the idea needs some more clarification. It is obvious that all the somatic cells of the plant individual share the same genome (disregarding somatic mutations). Therefore, the reaction norm that determines a response is coded in all cells, tissues, organs, etc. , although it is not necessarily manifested in all parts of the plant. Fitness of a genotype (a type of reaction norm) depends on the performance of the whole plant individual in its environment. Therefore, the evolutionary unit is the genetic individual (genet). Survival and reproduction of a single branch is relevant only to the extent at which it increases or decreases fitness of the whole plant individual.

Therefore, in an evolutionary sense, it is only the 'external environment' that can be considered as environment. In the sense of proximal, physiological mechanisms I agree that it can be helpful to use the concept of 'internal environment'.

Summary

Development is not simply unfolding a prescribed program. There is a lot of communication between parts of the organism, and the environment can also influence the developmental process. We speak about developmental plasticity when the organism has a genetically inherited rule (a norm of reaction) which determines how an environmental influence would be translated into a phenotypic change.

A plant individual consists of hierarchically nested modules (from metamers through branches up to systems of branches). We may envisage a plant as a collection of modules that are naturally in competition for resources, but are potentially capable for cooperation. The actual form of a plant is a result of these competition / cooperation processes. An example for strong competitive ability of a branch was mentioned when I described the positive feedback in branch development mediated by auxin. An example for cooperation is the case of mutual exchange of resources between roots and shoots, and a negative feedback in the regulation of their relative growth. Both competition and cooperation can increase fitness of the individual, depending on the form that is optimal in a particular environment. Those control mechanisms that bring the form closer to the optimum would be selectively favored during evolution.

In non-modular (unitary) organisms, functional integrity of the organism is an important criterion during development, because a part of an organism (e.g. one leg of a spider) cannot live alone. In modular organisms, such as plants, functional integrity is not obligatory. For example, in clonal plants, the individual can get fragmented into autonomous, self-supporting functional units (ramets). The degree and spatial pattern of integration varies between species, according to some morphological constraints (vascular organization), and more importantly, according to the environment(s) to which the species has adapted. IPU's represent the domains in which local control mechanisms can work.

Development of a plant largely relies on local (distributed) control mechanisms. Global control is not supported by this modular structure, although the borderlines of IPU's can dilate to some extent in response to herbivory or other damage. The purpose of control is to coordinate these parallelly proceeding events, continuously adjusting the plant form to the environment.

The environment has a twofold role in any case of adaptive plasticity: on one hand, it induces a phenotype; on the other hand it selects for or against that phenotype. Fitness relies on the correlation between the inducing and selecting environment, i.e., on the reliability of environmental cues. A time (or space) lag between induction and selection can seriously limit the adaptive value of plasticity, or may even favor rigid development.

Uncertainty about the environment can be reduced by investing more energy into information acquisition (see DeWitt *et al.* 1998) within the habitat or, if possible, by changing the habitat. If uncertainty cannot be reduced, then the developmental process has to cope with it. In this case, optimizing the ratio of external to internal control on development is a great challenge to any organism. Too much external control can disrupt development and/or can cause a mismatch between phenotype and environment.

Acknowledgements

I am grateful to Tsvi Sachs and Ariel Novoplansky for their valuable comments on the manuscript. The research was subsidized by the Hungarian National Research Fund (OTKA T35009, and NWO–OTKA N34028), the Hungarian Ministry of Education (FKFP 0187/1990, István Széchenyi Scholarship), and the International Program of the Santa Fe Institute, NM, USA.

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Figure

Figure 1. Types of control mechanisms in a hypothetical plant: [a] internal control, [b] external control by the same individual, [c] external control by another individual (denoted by gray). The dotted region represents an Integrated Physiological Unit.

