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Morphological Description of Plants: New Perspectives in Development and Evolution

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ABSTRACT

The morphological description of plants has been fundamental in the history of botany and provided the keys for taxonomy. Nevertheless, in biology, a discipline governed by the interest in function and based on reductionist approaches, the analysis of forms has been relegated to second place. Plants contain organs and structures that resemble geometrical forms. Plant ontogeny may be seen as a sequence of growth processes including periods of continuous growth with modification that stop at crucial points often represented by structures of remarkable similarity to geometrical figures. Instead of the tradition in developmental studies giving more importance to animal models, we propose that the modular type of plant development may serve to remark conceptual aspects in that may be useful in studies with animals and contribute to original views of evolution.

Keywords: concepts, description, geometry, structure

INTRODUCTION: PLANTS OFFER NEW APPROACHES TO DEVELOPMENT

The study of development is today a major biological discipline. Although it was traditionally more focused in animal systems, increased emphasis in plant development may open original perspectives. In particular, plant development presents features that may help to understand basic conceptual aspects. In parallel to an increased attention in plant systems, new approaches need to correct a past drawback that has limited perspectives inhibiting original points of view and compromised future results: Development concerns primarily changes in shape, but paradoxically its protocols and strategies are predominantly based on the analysis of the nature and dynamic relationships of molecules. A functional view has been predominant in the analysis and description of all morphological processes. Under this working schema the current views are incomplete and may thus, be unsatisfactory. The main answers offered in response to the developmental questions consist in the description of a series of biochemical elements and their interactions. Primary questions are avoided and substituted by others either because they fall out of current ways of thinking, either because they are too elemental. Some of these primary questions concern the description of the shapes of plants and their changes, for example: why do the flowers of crucifers have the shape of a cross? Others may concern the relationships between different plant structures in evolution: Does the degree of conservation in flower shape in a given family correspond with a parallel degree of conservation in seed shape? In the absence of precise descriptions of plant morphology, development is often seen from a perspective where the main question (morphology) is replaced by a secondary one (the description of the biochemical elements involved).

Tables of contents of journals devoted to development show to what extent research in the field is dominated by the description of genes and proteins: their structure and function, their interactions and regulation are today the basic aspects in the description of development. This reflects a more general situation in Biology, a discipline that has matured from the experimental protocols and views of biochemistry, where the predominant role of experimentation has contributed to a decline in basic aspects that need to be more descriptive, such as those related with morphology. It is true that molecular data provide good information in relation with morphology, but it is also true that the role played by genes and proteins in the maintenance or stability of shapes will be better understood once a sufficient description of plant forms has been done. This needs a strong theoretical basis as well as mathematic support but does not always need sophisticated experimentation.

The limitations of the traditional functional approach to the analysis of plant development need to be considered. The current functional perspective has reached a limit and now needs original inputs from descriptive morphology. In the following paragraphs the historical antecedents to our claim will be commented as well as some recent descriptive issues. In addition, theoretical and conceptual aspects that may be useful for understanding development will be emphasized. The reader will see that plant development may be interpreted as the integration of different independent processes and thus, it may serve as a conceptual framework model for more general approaches. The identification and appreciation of each particular developmental process as an independent entity may contribute to new and productive views of genome organization, development and evolution. In this sense, work in plants may open ways to understand the general principles of development in living beings. The accurate morphological description of plant structures based on a mathematical approach may be a fundamental aspect in the identification of such processes and their role for the integration of plant development.

HISTORICAL VIEW: THE DESCRIPTION OF PLANT SHAPES IS A FUNDAMENTAL ASPECT IN BOTANY

The description of plant shapes is an aspect of traditional importance in the history of botany. From early times, em-

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phasis was made in the geometrical appearance of plant organs and subsequently, many genera and species of plants were named according to their morphological characteristics (*parviflora*, *magnipetala*, *rotundifolia*, etc.). Similarly, many plant families receive their names from characteristics in the shape of their flowers (Papilionaceae, Magnoliaceae, Asteraceae, Campanulaceae, Crucipherae, etc.). Searches in the IPNI database (International Plant Names Index; http://www.ipni.org/index.html) with adjectives indicating morphological characters may yield many examples of this historical trend (Cervantes and Tocino 2009).

Plant ontogeny may be interpreted as periods of continuous growth that stop at reference points or are interrupted by switches to alternative growth patterns. In general, structures representing reference points in development (flowers, seeds, leaves, pollen grains, cones, etc.) approach geometrical forms toward which the growth of a set of cells is accurately regulated. Plant development may thus be seen as an integrated and continuous process that goes through characteristic stages or reference points often characterized by the approximation to a geometric figure.

Fig. 1 illustrates this view for *Arabidopsis*. We may consider the ontogenic development of this species as the continuous transitions between reference points represented by stable geometrical forms (seed, rosette, flower pollen grain). The possibility of a precise morphological description for each of these structures indicates such a reference point. The concept of ontogenetic trajectory (Rice 1997) may be applied either to the transition between two consecutive reference points or to the coordinated developmental program that leads to the establishment of one of such points. Overall, the process of plant ontogeny resembles the current views of evolution with periods of gradual change interrupted (punctuated) by long periods of calm (stasis). Thus, well defined forms may, at least sometimes, indicate the presence of an independent evolutionary process. The resulting geometric forms may be shared by different structures not directly related.

The traditional importance given by botanists to the detailed description of plant shapes often made in Latin, has declined in recent times. The maturity of biology, an experimental science based in the protocols and methods of biochemistry, has relegated the descriptive aspects of nature to a second term giving more emphasis to functional and experimental aspects. Through the XX century a limited number of academic texts were dedicated to the morphological description of organisms. One of them is a classical treatise covering in its own the main aspects of this important field. Under the title “On growth and form”, D’Arcy Wentworth Thompson covered fundamental aspects of the mathematical descriptions of shapes in living organisms illustrating the presence of mathematical constants in nature, explaining the importance of the relation surface/volume and giving means for the representation of morphological relations, such as those based in coordinate axes and the change (scaling) of their relative values. The book, first published in 1917, has been re-edited several times and quoted very often; nevertheless, given the importance of the topic treated, its contents are today insufficient. The description of biological shapes constitutes an important field of study that is being recently recognized in books and articles. New magnitudes are utilized in the description of forms, such as curvature (Zelditch *et al*. 2004; Cervantes and Tocino 2005; Tocino and Cervantes 2008) and methods for data analysis are optimised in morphometrics (Zelditch *et al*. 2004). The emerging panorama reflects the visible side of a question that paradoxically has remained in the shadow, because most studies in development have covered molecular approaches. The precise description of plant structures is still lacking in many cases. In addition to statistics and geometry, such a description provides the basis for discussion on conceptual aspects.

CONCEPTUAL ASPECTS IN DEVELOPMENT: DIFFERENT PROCESSES VERSUS CHANGES IN THE SAME PROCESS

In a recent article entitled “Caterpillars evolved from onychophorans by hybridogenesis”, Donald Williamson (2009) argued in favour of the hypothesis that proposes that insects with a metamorphosis may have evolved modularly. The article is of interest to plant biologists because the hypothesis there proposed may be successfully applied to plant systems. According to this point of view, insect caterpillars would be the result of the integration of onicophoran genomes with pre-metamorphic insect genomes. Independently of the feasibility of the proposed “hybridization” mechanisms, there may be several examples candidates for modular development. For example, different animals sharing a common type of larvae may result from the integration of diverse genomes (an earlier genome for the larva and another for the adult precursor). In theory, this hypothesis may be tested by the genomic analysis but this still remains as an open possibility whose strategy is not yet clear and was not provided by the article. On the other hand, and even if the main hypothesis is not verified by a genomic analysis, the article contributes to an aspect of conceptual importance in the analysis of development that concerns the identification of particular and independent developmental processes. A clear conclusion of this work that particularly affects plant biology (Williamson 2009) is that at least two different processes of development are at play for each of the examples given. For animals with larvae, larval development is different from adult development. For insects with metamorphosis, caterpillar development is different from adult development. The identification of particular developmental processes as independent entities may contribute to give new light to an ancient problem and see plant ontogenesis under new perspectives. No matter whether or not it is proven that the actual genomes are the result of the integration of different ancestors, the analysis of development requires the identification and accurate definition of what is a particular “developmental process”, what are different processes and when a process derives from another as a consequence of modification. Due to the peculiarities of modular growth in plants (Hallé 1986), the identification of independent developmental processes may be addressed better in plants than in animals.

The identification of independent developmental processes may be one example of these questions that being so easy and trivial at the end never get enough attention. Discussing the concept of heterochrony, Rice (1997) made emphasis on the importance of making a clear distinction between different ontogenetic trajectories or processes. Heterochrony was thus defined as a change in the relative timing or rate of development of an ontogenetic trajectory or process. Alberch *et al.* (1979) defined the ontogenetic trajectory as the continuous change in size and shape allowing for diverse classes of heterochrony affecting a particular ontogenetic (developmental) process. This view presents each trajectory (developmental, ontogenetic) as a reflection of the Darwinian evolutionary viewpoint according to which evolution proceeds gradually. But each trajectory (continuous change) affects a single process, and ontogenesis is not always result of a single continuous process but the sum of diverse continuous processes. Development, as evolution, consists in periods of gradual change interrupted by other periods of calm (stasis). Thus trajectory in the sense used by Alberch refers to changes inside a process better than to the transit between two processes. In any case, ontogenesis may be seen as the integrated series of independent ontogenetic processes. In addition to the examples given in animals (Williamson 2009) it may be interesting to explore the possibility that plant development consists in the integration of different ontogenetic processes separated by transitions. In many cases, ontogenetic processes will be characterized by well defined geometric forms. Examples of ontogenetic processes from the plant kingdom may in-

Fig. 1 Development of *Arabidopsis* is presented here as the integration of reference points (ontogenetic processes), each characterized by the approximation to a geometric figure (seed, rosette, flower, pollen grain). The precise morphological description of these structures marks and identifies each ontogenetic process. A series of continuous transitions (seed to rosette, rosette to flower,…) establish links between ontogenetic processes.

clude the formation of flower, seed, rosette leaf or overall aereal plant architecture (**Fig. 1**). Each of them may be interpreted as a continuous- independent process. Transitions between them represent discontinuities. Together, the ordered set of ontogenetic processes and transitions constitute plant ontogeny.

VISIBLE (FORM) AND INVISIBLE (MATTER) AS THE TWO SOURCES OF INSPIRATION IN SCIENCE

Gaston Bachelard (1884-1962) was a scientist (physics) and philosopher. His writings are concerned with epistemology and often deal with the relationship between science and philosophy. The first chapter of his book “De l’eau et les rêves” (1942), is entitled “imagination et matière”. In the introductory paragraphs he indicates two ways to the poetical inspiration that represent as well two creative forces in nature:

> “Les forces imaginantes de nôtre esprit se dévélopment sur deux axes très différents.
> Les unes trouvent leur essor devant la noveauté; elles s’amusent du pittoresque, de la varieté, de l’evenement inatendu. L’imagination qu’elles animent a toujours un printemps à décrire. Dans la nature, loin de nous, déjà vivantes, elles produisent des fleurs.
> Les autres forces imaginantes creusent le fond de l`être; elles veulent trouver dans l’être, a la fois le primitif et l’eternel. Elles dominent la saison et l’histoire. Dans la nature, en nous et hors de nous, elles produisent des germes; des germes ou la forme est enfoncée dans une substance, où la *forme est interne*.
> En s’exprimant tout de suite philosophiquement, on pourrait distinguer deux imaginations: une imagination qui donne vie a la cause formelle et une imagination qui donne vie a la cause matérielle ou plus brièvement, l’imagination formelle et l’imagination matérielle.”
> *The forces of imagination in our spirit develop on two very different routes.*
> *Some find their growth before the novelties; they play with the picturesque, the variety and the unexpected event. The imagination that animates them has always a spring to describe. In nature, away from us and already living, they produce flowers.*
> *The other imagining forces dig the bottom of being, they want to find in being both the original and eternal. They dominate the season and history. In nature, in us and without us, they produce seeds, sprouts where form is embedded in a substance, where form is internal.*
> *Speaking philosophically, one could distinguish between two imaginations: an imagination that gives life to the formal cause and one imagination that gives life to the material cause or more briefly, the formal imagination and material imagination.*

Although the author begins his discourse by talking about the creative forces of human imagination, soon it becomes clear that these forces are not restricted to human imagination, but instead are, general creative forces in nature, and that they belong to each of two classes: formal and material. Following Bachelard’s views, formal forces give the visible shapes of flowers, whereas material forces are responsible for the complexities of seeds.

Although the language used by Bachelard is a poetical one and thus not amenable to strict "biological" validation, several interpretations of his text may not only be possible but also useful contributing to observe the objects of nature in a way that is complementary and thus enriches the points of view of biology.

TWO INTERPRETATIONS AND A PRELIMINARY CONCLUSION

In a first, direct interpretation we may take Bachelard text literally. Then in nature, different forces are at play producing flowers and seeds. Whatever the nature of these different forces at play, the idea suggests independent origins for flowers and seeds. The possibility recalls the article by Williamson suggesting that modular evolution proposed there for holometabolous insects or in diverse animals with larvary stages, for which the genome could be the result of the aggregation of different types of animals (hybridization) could be at play during plant evolution. Their characteristic modular type of development (Hallé 1986) makes of plants better systems to investigate this possibility than animals.

A second interpretation, slightly more complex, may deserve an explanation. It consists in observing natural objects as having two sides: One visible (forms) and other invisible (metabolism and regulation). Observed in this way, the forms in nature may be considered either as "reserves of information" (simple geometric forms) or, in a complimentary way, entropy, display or waste of information (complex geometric forms). The development of particular complex structures in fruits and seeds is associated with assuring a "secure" type of dispersal. On the contrary, simpler structures may involve complex regulation (Cervantes 2008). Organisms with a K strategy belong to the first group, whereas those with an r-strategy to the second. Arabidopsis is clearly an r-strategy organism (Cervantes 2008). Its seeds are simple structures whose images approach the geometrical figure of a cardioid elongated by a factor of ϕ (Cervantes *et al*. 2010). These simple structures may have complex regulatory mechanisms operating during germination and higher variation in germination rates. The seeds of *Erodium cicutarium*, complex structures equipped with hygroscopically active awns that allow self-planting (Stamp 1984) are examples of the opposite strategy. If there is a general correlation between form and regulation, such that structures with complex morphologies have simpler regulation, then simpler morphologies may be better equipped for adaptation to environmental change and be critical for evolution.

Being either simple or complex, it is very important to search for accurate morphological descriptions of plants. They may provide the basis for understanding development as the integration of modular processes of independent origins.

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