



Developmental plasticity in plants: implications of non-cognitive behavior

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Abstract. There has been a surge of interest in phenotypic plasticity in the last two decades. Most studies, however, are being carried out within relatively narrow disciplinary frameworks. Consequently, researchers differ not only in their scientific agenda; they often use different terminologies and conceptual frameworks even when studying the very same phenomena. The diversity of approaches has often generated parallel bodies of theory on subjects that can be best understood in broader interdisciplinary terms. This special issue points out the differences between the concepts and questions that are characteristic of various approaches. Bridging all gulfs may be impossible and not necessarily desirable, yet, awareness of the varied approaches should be instrumental in promoting interdisciplinary advances. It is the contribution to such awareness that is the major purpose of this special issue, and for this reason it deals with molecular, physiological, ecological and evolutionary approaches to the study of developmental plasticity. So as to focus the discussion, six topics have been selected, ranging from the fundamental essence of developmental plasticity to its implications to ecology and evolution. These topics were considered by scholars who were chosen for the diversity of their research, not only their expertise. Rather than a comprehensive body of theory, the current issue thus seeks the *diversity of opinions* on the discussed topics. It is hoped that the confrontation, in its original Latin sense, which includes bringing together and discussion, of scholars who are studying these phenomena at very different levels and from different points of view will generate new insights and promote future interdisciplinary research.

‘The men of experiment are like the ant, they only collect and use; the reasoners resemble spiders, who make cobwebs out of their own substance. But the bee takes the middle course: it gathers its material from the flowers of the garden and field, but transforms and digests it by a power of its own. Not unlike this is the true business of philosophy (science); for it neither relies solely or chiefly on the powers of the mind, nor does it take the matter which it gathers from natural history and mechanical experiments and lay up in the memory whole, as it finds it, but lays it up in the understanding altered and digested. Therefore, from a closer and purer league between these two faculties, the experimental and the rational (such as has never been made), much may be hoped.’

Francis Bacon (1620), *Novum Organum*

Key words: adaptive plasticity, developmental plasticity, differences between plants and animals, hierarchies of plasticity, mechanisms of plasticity, non-cognitive behavior, phenotypic plasticity, plant ontogeny, plasticity and evolution

Introduction

Phenotypic plasticity is often described as the responses of organisms to environmental conditions or stimuli (e.g. Bradshaw, 1965; Schlichting and Pigliucci, 1998). Although depicting the essence of the phenomenon, this definition is extremely broad and overly inclusive. For example, the 'environment', as perceived by ecologists, usually consists of the external surroundings and factors, whereas many other biologists consider the 'environment' in terms of the effects of neighboring cells (e.g. Sachs and Novoplansky, 1993), or morphogenic hormones (e.g. Savidge, 1994; Schlichting and Smith, 2002). However, the diversity of definitions is a mere reflection of deeper gulfs among disciplines in which different aspects of the genetic basis, evolution, adaptive rationale, community-level implications, and physiological and developmental mechanisms of phenotypic plasticity are studied.

One type of phenotypic plasticity that is the subject of most ecological and evolutionary studies of plasticity is *developmental plasticity*. Developmental plasticity can be defined as the developmental changes that follow the perception and integration of environmental information. Although developmental plasticity plays a major role in the adaptation of both animals and plants to heterogeneous conditions (e.g. Agrawal *et al.*, 1999) it is thought to be of particular importance in plants. Reasons for this could be the limitations of motility and 'real behavior' (Bradshaw, 1965) and the continuation of development, including organogenesis, throughout the life in plants.

The purpose of this special issue is to illustrate the diversity of opinions concerning some fundamental questions related to phenotypic plasticity in plants. These opinions are presented by scholars who are interested in different conceptual problems, use different methodologies, and study plasticity at different levels of organization. It is hoped that the special issue will promote an integrative thinking in the study of plasticity by highlighting both the diversity of research and possible unifying conceptual principles. This could be an important role, since there have been only few attempts to bridge physiological, ecological, and evolutionary approaches to plasticity (e.g. Schmitt *et al.*, 1995; Pigliucci, 1996; Sultan, 2000; Pigliucci, 2001).

The structure of the special issue

Due to the interdisciplinary nature of the topic, the structure of this special issue is somewhat unusual. Six topics have been selected, ranging from basic definitions and mechanisms, all the way to implications of developmental plasticity in ecology and evolution. These topics were considered by scholars who were chosen for both their expertise and diversity of backgrounds. An

attempt was made to represent the main scientific disciplines dealing with developmental plasticity: ecology, evolution, development, evolutionary ecology, physiology and eco-physiology. Rather than a comprehensive body of theory, the current issue seeks to cover different ways of thinking about the same phenomena. Each individual contribution comprises answers to the same questions, but, as expected, the authors have understood these in different ways and did not necessarily answer all of them. In most cases an effort has been made to explain how and why answers deviated from the general questions.

The questions

The adaptive domain of developmental plasticity and contiguous phenomena

Environmental heterogeneity is one of the most important selective forces in nature (Hutchings and de Kroon, 1994; Sibly, 1997). As such, it is often recognized as the cause of a wide spectrum of physiological, morphological, and life-history attributes (e.g. Caldwell and Pearcy, 1994; Stuefer, 1998). Although many phenomena fall within the definition of ‘responses to environmental conditions or stimuli’ not all are considered as phenotypic or developmental plasticity. Metamorphosis, differentiation (at the level of an individual) and genotypic diversity (population level; e.g. Woehrmann and Tomiuk, 1988) may serve as alternative or synergistic solutions to spatial and temporal environmental heterogeneity (Lewontin, 1957; Gillespie and Turelli, 1989). In this section a broad conceptual framework was sought, attempting to clarify the differences and relations of these varied phenomena.

Q: What are the modes of operation, the adaptive domain, and the functional limits (Fig. 1) of these related phenomena? Under what circumstances are some of these adaptively superior to others?

Types of developmental plasticity

Different types of developmental plasticity seem to serve different and even contradictory roles. Accordingly, developmental plasticity may allow plants flexibility in at least two ways:

- (a) *Maximizing performance*: allowing the plant to be more opportunistic; increasing its overall performance when resource levels are high, in either time (e.g. Grime *et al.*, 1986; Bilbrough and Caldwell, 1997) or space (e.g. Novoplansky *et al.*, 1989; Caldwell *et al.*, 1991; Wijesinghe and Hutchings, 1997).
- (b) *Sustaining performance*: allowing the plant to remain functional even under limiting and stressful conditions (e.g. Sultan and Bazzaz, 1994).

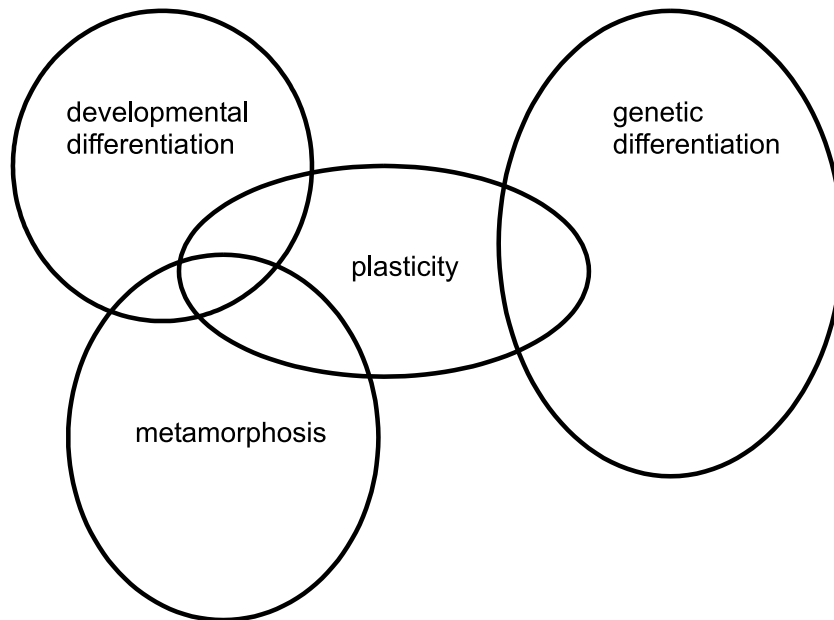


Figure 1. Schematic depiction of the adaptive domain of developmental plasticity and contiguous phenomena.

Superimposed on these expressions of flexibility, developmental plasticity may allow plants to stabilize their performance under varied conditions (e.g. Weiner *et al.*, 1997).

Q: Developmental plasticity may permit greater flexibility or provide greater stability in performance under changing conditions. These may represent very different functions. How can these potentially contradictory capabilities be reconciled?

Phenotypic plasticity is often described as a plant analog to animal behavior (Bradshaw, 1965).

Q: How does developmental plasticity differ between plants and animals?

Mechanisms of developmental plasticity

Unlike animals, in which complex functions and behavior are coordinated by a highly specialized control system, plants are usually considered to be 'simpler' (Harper, 1985) and less strictly coordinated. They often comprise modular units that possess high levels of functional independence (e.g. Watson and Casper, 1984; Marshal and Price, 1997). However, while some plastic responses are relatively local (e.g. Traw and Ackerly, 1995; Bruni *et al.*, 1996), others seem to involve a surprisingly high level of coordination among different parts of the same plant (e.g. Snow, 1931; Norby *et al.*, 1999).

Q: In organisms lacking a nervous system, what are the mechanisms, functional implications and costs of integrating the multiple environmental and internal stimuli? How are these coordinated to enable adaptive plastic responses?

Plant ontogeny involves dramatic changes in the way developing organs interact with their internal and external environments (Watson *et al.*, 1995). It is therefore expected that the mechanisms of developmental plasticity vary with ontogeny.

Q: How do mechanisms of developmental plasticity vary with ontogeny?

Consequences of developmental plasticity for higher organizational levels

While many studies of plasticity consider taxa from different environments, very little is known about the consequences of plasticity for population- and community-level interactions (but see Grime *et al.*, 1997; Bret-Harte *et al.*, 2001; Novoplansky and Goldberg, 2001a, b; Grime and Mackey, 2002). Plasticity may play very different roles at the individual and higher organizational levels. Even when plasticity is significant for the performance of individual plants, it is expected to be meaningful at the population and the community organizational levels only if different members of the population (e.g. plants of different ages) or community (taxa) utilize different levels or types of plasticity (Novoplansky and Goldberg, 2001a, b).

Scaling-up from single organs or individuals to higher organizational levels can be rather complicated (e.g. Grime *et al.*, 1994; Koerner, 1995; Valentini *et al.*, 1995). For example, at the community-level plasticity can produce conflicting (and even opposing) effects – on the one hand it may allow expansion of niche breadth (which should decrease species diversity), while on the other hand it may allow its bearers greater ability to tolerate competition and therefore potentially sustain high species diversity.

Q: What effects could developmental plasticity have on niche breadth under varied environmental conditions?

Q: In what ways could developmental plasticity influence competition and coexistence within and among taxa?

Developmental plasticity and evolution

Developmental plasticity is often considered to require special genetic information (Bradshaw, 1965; Schlichting, 1986; Scheiner and Lyman, 1991; Schlichting and Pigliucci, 1998). Where this is true the relationship between plasticity and evolution can be quite complex: the levels and types of plasticity may be selected directly, and at the same time plasticity itself may buffer or promote various evolutionary processes (e.g. Schlichting and

Pigliucci, 1998). This reciprocity could lead to interesting positive or negative feedback loops along which plasticity is enhanced or truncated by its own action.

Q: What evolutionary scenario(s) could have allowed the emergence of developmental plasticity and under what evolutionary circumstances would you expect it to be enhanced?

Q: How and under what circumstances could developmental plasticity influence macro- and micro-evolutionary processes?

Strategies in studying developmental plasticity

The development of molecular biology may suggest that going ‘from phenotypes to molecules and *vice versa*’ (Pigliucci, 1996) is possible and in the foreseeable future. Accordingly, many of the latest advances in the study of plasticity have been made using ‘plasticity mutants’ (e.g. Callahan *et al.*, 1999; Pigliucci and Schmitt, 1999; Schlichting and Smith, 2002), transgenic plants (Schmitt *et al.*, 1995), and QTL analysis of plastic traits (e.g. Lukens and Doebley, 1999). Although some researchers are pursuing this interdisciplinary endeavor others have expressed concern about its theoretical limitations (Schlichting and Pigliucci, 1998).

Q: Is there an inherent need for a molecular model to understand developmental plasticity?

Q: How should we integrate knowledge at different organizational and scientific levels when studying plasticity? Can we define ‘unbridgeable disciplinary barriers’ and what should be done about them?

Glossary

The following are a few short conceptual explanations of terms that appear in the current issue. Rather than precise textbook definitions, most of these are meant to clarify discrepancies in the usage of key terms and direct the readers to contradictions and controversies.

Adaptive plasticity: plasticity that serves an adaptive role, regardless of whether it is the result of direct selection (Schlichting and Pigliucci, 1998; Alpert and Simms, 2002), or a by-product of selection in a variable environment (Via, 1993). Naturally, the adaptive value of any given plastic response is dependent on the environment in which it is elicited (Schmitt *et al.*, 1995). Thus, a given plastic change may appear adaptive at one spatial or temporal scale and maladaptive in another (DeWitt *et al.*, 1998).

Allometric growth: differential growth of two or more measures of the same organism. Allometric modifications that are resulted by genetically based

ontogenetic changes may phenotypically resemble plastic allocation changes (Coleman *et al.*, 1994; Alpert and Simms, 2002).

Developmental differentiation: the process by which a set of initially similar developmental entities (e.g. cells, organs) become different from each other. Whether or not the process is reversible and allowing developmental totipotentiality (Sachs, 1991), the result of gene expression or a combination of gene expression and the internal environment (Schlichting and Smith, 2002), the products of developmental differentiation may phenotypically resemble those of environmentally induced plastic changes.

Developmental instability: also described as ‘innate variability of unperturbed development’ (Sachs, 2002). It is the random variance or ‘developmental noise’ (Waddington, 1957) around an expected mean of a given trait in a given environment. Thus, developmental instability is the phenotypic variance that cannot be explained by the genotype or the environment (Bradshaw, 1965; Alpert and Simms, 2002). According to an alternative interpretation it could result from small inconsistent environmental effects or perturbations of the internal epigenetic system (Schlichting and Pigliucci, 1998).

Developmental integration and correlation: these supposedly simple terms pertain to a few potentially distinct phenomena (Sachs, 2002; Schlichting and Smith, 2002). Common to these is the notion that a harmonious function of a whole organism must rely on the coordination of its parts (Schlichting and Pigliucci, 1998). Accordingly, integration is recognized at two distinct, although not necessarily mutually exclusive, hierarchies: (a) *phenotypic integration*: the way different traits of the same organism (e.g. petal width and color; Clausen and Hiesey, 1958) correlate to each other during and following ontogeny, and (b) *physiological and information integration*: the dynamic physiological coordination among different organs that develop and function in the same organism (e.g. correlative inhibition among shoots of the same plant; Snow, 1931; Sachs and Novoplansky, 1997). The two types of integration are relatively distinct from each other in animals where most of the development takes place during relatively discrete embryonic stages but typically inseparable in plants and other modular organisms where integration of environmental information and the development of new organs continue throughout the entire lifetime (e.g. Sachs, 2002).

Developmental plasticity: developmental plasticity is likely to be irreversible and is usually complementary to physiological or ‘short-term plasticity’ (Givnish, 2002), that is related to reversible changes at cellular or sub-cellular levels (Bradshaw, 1965; Grime and Mackey, 2002). Developmental plus physiological plasticity are commonly defined as ‘phenotypic plasticity’. Although developmental plasticity is often depicted in terms of reaction norm, it should not be confused with ‘developmental reaction norms’ that are a ‘set of ontogenetic trajectories produced by genotype (or sibship) in response to

naturally occurring (or experimentally imposed) variation' (Schlichting and Pigliucci, 1998).

Environmental information: the information which organisms perceive, process, and integrate and which leads to expressions of plastic development. Depending on the nature of the responding entity (cell, organ, whole organism), the information may be related to the internal or the external environment, reflecting the presence and status of neighboring cells, organs or organisms, or the current and expected availability of resources.

Epiphenotype problem: the limit to the benefit of plasticity due to the fact that phenotypes that are constructed by add-on structures and functions may not be as well-built as those that develop as integrated wholes (DeWitt *et al.*, 1998).

Fixity: absence of phenotypic variability that results from direct natural selection (such as in the case of canalization; Waddington, 1953; Schlichting and Smith, 2002) or from lack of selection for plasticity (Alpert and Simms, 2002). Fixity and plasticity must be judged in their hierarchical context – most commonly, plasticity at one organizational level is selected to maximize fixity at a higher organizational level. Accordingly, biochemical plasticity may allow physiological fixity, and physiological plasticity may allow morphological fixity. For example, when faced by resource patchiness, slow-growing plants of unproductive habitats are expected to demonstrate high physiological plasticity and relative morphological fixity (Grime and Mackey, 2002). Consequently, the magnitude of plasticity and fixity can be only judged for individual characters rather than for entire organisms.

Genetic assimilation: the process by which a character that is initially elicited by environmental triggering (i.e. a plastic response) becomes genetically fixed by natural selection (Schmalhausen's 'stabilizing selection', 1949; Waddington, 1956).

Growth/developmental rules: discrepancies in the use of this term reflect an important conceptual controversy over what information is coded for by genes responsible for plant form. It is used to describe morphological and 'architectural models' that are characterized by relatively inflexible traits (Hallé *et al.*, 1978; Schmid and Bazzaz, 1990; Alpert and Simms, 2002). The term is also used to describe the processes by which the form of a plant is generated, stressing the plastic and often noisy relations among its developing organs (Sachs and Novoplansky, 1995; Sachs, 2002).

Heterochrony: evolutionary changes in the relative timing of developmental processes (*sensu* de Beer, 1930; Gould, 1992). Heterochrony can be the source of large structural and adaptive changes without requiring the evolution of any novel processes.

Metamorphosis: genetically programmed phase changes in the phenotype. Metamorphosis and plasticity are thought to represent two separate processes

that yield similar phenotypic variation (Diggle, 2002) or a threshold differentiation event (Schlichting and Smith, 2002).

Plant foraging: plasticity that maximizes resource capture by developing plant organs (*sensu* de Kroon and Hutchings, 1995). Regardless of the scale at which plants utilize various modes of foraging (Grime and Mackey, 2002), the mechanisms of foraging are still under debate. While some argue that foraging is based on a high degree of organ independence (de Kroon and Schieving, 1990; Diggle, 2002), others point to the importance of physiological integration and correlation among *redundant organs* (Novoplansky, 1996; Sachs, 2002).

Ontogenetic contingency: the dependency of the fate of primordia upon their positional and temporal relationships with their past development and the presence of other organs on the same plant (Diggle, 1994, 2002). Ontogenetic contingency is an example of *developmental correlations* that pertain to any kind of temporal and positional coordination (e.g. apical dominance, resource translocation) among different organs on the same plant (Sachs, 1991, 2002).

Polyphenism: plastic formation of discrete morphs due to coarse grained temporal changes in the environment (Moran, 1992; Schlichting and Smith, 2002).

Redundant organs: organs of the same organism that have the same physiological role (Sachs, 2002).

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