

## Promising directions in plant phenotypic plasticity

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### Abstract

A research agenda for the next phase of plasticity studies calls for contributions from a diverse group of biologists, working both independently and collaboratively, to pursue four promising directions: examining dynamic, anatomical/architectural, and cross-generational plasticity along with simpler growth traits; carefully assessing the adaptive significance of those plasticity patterns; investigating the intricate transduction pathways that lead from environmental signal to phenotypic response; and considering the rich environmental context of natural systems. Progress in these areas will allow us to address broad and timely questions regarding the ecological and evolutionary significance of plasticity and the nature of phenotypic determination.

**Key words:** adaptation, architectural plasticity, cross-generational plasticity, dynamic plasticity, phenotypic determination, transduction pathways

### Introduction

Over the past decade, the study of phenotypic plasticity has both expanded and matured (see Schlichting 2002). At this point there is a wealth of data demonstrating that phenotypic expression varies for many aspects of development, physiology and life-history, depending on all kinds of environmental factors that vary in nature, from atmospheric chemistry to competitive conditions (reviewed by Sultan 2000; Pigliucci 2001). Contrary to earlier neo-Darwinian views of plasticity as anomalous or trivial ‘noise’, plasticity is now recognised to be a major source of phenotypic variation in the real world. Our task now is to more fully understand this variation, in terms of both the individual organism’s capacity for flexible response, and the larger-scale ecological and evolutionary consequences of that capacity. Here I briefly lay out some ideas for a research agenda on plant phenotypic plasticity intended to help address this challenging prospect.

In my view, there are three fundamental questions that serve to motivate and guide future plasticity studies in plants as well as other organisms.

**1. The relation of plasticity to ecological breadth.** In addition to its significance for understanding current distributions of organisms, plasticity may hold both positive and negative implications for future biodiversity conservation, depending on the ecological circumstances and the taxa in question. Species with greater adaptive plasticity may be more likely to survive novel environmental conditions created by human activity, since such changes typically occur too rapidly to allow for an evolutionary (or in some cases a migratory) response. On the other hand, because adaptive plasticity may allow certain species to colonize environmentally diverse sites without the lag time required for local adaptation, it enhances their invasiveness and rapid geographic spread, contributing to the displacement of other taxa (Spencer et al. 1994). Understand-

ing this issue demands targeted studies of plastic response to naturally and human-mediated environmental variation in both widespread invasive or introduced species and narrowly distributed, threatened species (e.g. Williams et al. 1995; Paschke et al. 2003). Selection studies that examine evolutionary potential for ecologically relevant plastic traits such as clonal growth form or reproductive allocation will be of particular predictive value (e.g. van Kleunen et al. 2002; Fischer et al. 2004; see Scheiner 2002 for discussion of selection experiments on plasticity).

**2. The relation of plasticity to evolutionary diversification.** To the extent that plasticity confers adaptive flexibility on individual genotypes, it will influence natural selection and consequently patterns of diversification among populations and ultimately species (see theoretical models by Scheiner 1998; Sultan & Spencer 2002; and references therein). Although this has been clear in principle since Sewall Wright considered the point (Wright 1931), we know very little about the actual evolutionary impact of plasticity. Do plastic responses provide only phenotypic fine-tuning to micro-environmental variation within populations, or can they create the kind of adaptive diversity required to succeed in entirely different habitats? In the latter case, plasticity can preclude population divergence due to local selection (e.g. Novak et al. 1991). Conversely, plasticity may promote evolutionary diversification if phenotypes produced through plasticity provide adaptive diversity that, under continued selection, becomes evolutionarily fixed (Simpson 1953; West-Eberhard 1989, 2003; Pigliucci & Murren 2003; Schlichting, in press). To understand the complex evolutionary role of plasticity, it is necessary to consider how the organism and its environment shape each other (Lewontin 2001): the organism's initial plasticity influences its environmental distribution, and the environmental range encountered conditions subsequent selective evolution. Studies that illuminate these evolutionary questions must characterize patterns of variation among conspecific populations or related taxa for functionally adaptive aspects of plasticity, in conjunction with information on genetic or phylogenetic diversity. They also require careful documentation of environmental variability, gene flow, and realized fitness in nature, all of which will influence evolutionary outcomes, as well as possible genetic constraints to or fitness costs of plasticity (Van Tienderen 1991; Scheiner 1993; DeWitt et al. 1998; Sultan & Spencer 2002; and references therein).

**3. 'Eco-Devo' and the nature of phenotypic determination.** Plasticity studies reveal how specific environmental variables enter into the complex process of phenotypic regulation to give rise to diverse forms,

life-histories, and physiologies. Documenting this variation and its underlying transduction mechanisms has become a major focus of developmental biology, termed 'ecological development' (Gilbert 2001; Gilbert & Bolker 2003; Sultan 2003a). This 'eco-devo' approach links plasticity studies to our general understanding of phenotypic determination in a critical way. Based on a growing body of sophisticated information about regulatory systems, developmental biologists are moving beyond an initial focus on DNA sequences as deterministic blueprints, to understand organisms as developmental systems that continually integrate internal and external signals to modulate gene expression (Carroll et al. 2001; Nijhout 2003). Plasticity research that investigates the molecular and biochemical bases of environmental response will contribute to this newly emerging, unified paradigm for understanding the origin of the phenotype and its diversity (Schlichting & Smith 2002; Sultan & Stearns, in press).

This new understanding of developmental systems holds two important implications for plasticity studies. First, the mechanisms of plastic expression evidently depend upon the same types of genetic elements and transduction networks that underlie other aspects of phenotypic expression, and hence may not entail a unique machinery 'cost' (Schlichting & Smith 2002; Sultan & Stearns, in press). The 'costs' of plasticity may more likely pertain to either construction of particular phenotypes, or limits to their accuracy or adaptive effectiveness in certain environments (DeWitt et al. 1998; Sultan & Spencer 2002). Second, due to environmentally mediated interactions among regulatory components at various points in the developmental process, correlations among phenotypic traits are environmentally contingent (Schlichting 2002). To understand these patterns of phenotypic covariance or 'integration' will require greater knowledge of these regulatory pathways as well as improved analytical tools (Pigliucci & Kolodnynska 2002).

To address these fundamental ecological, evolutionary and developmental issues requires that we add substantially to our existing fund of information on the following aspects of plasticity: (1) its precise expression (i.e. genotypic norms of reaction) for various phenotypic characters within individuals and across generations; (2) its adaptive significance in relation to patterns of environmental variation within and among habitats; (3) its diversity or uniformity of expression among related taxa, populations and individual genotypes; and (4) its underlying transduction pathways and genetic architecture. Below, I note in brief four specific avenues for plasticity research that will provide these kinds of data and hence advance our understanding of the broad and compelling issues outlined above.

## Studying complex aspects of plant plasticity

Much of the foundational work on plant plasticity has documented patterns of environmental response in straightforward growth traits such as biomass, root:shoot ratios, node number, and so on. Having established a basic understanding of growth plasticity, we can focus increasingly on more complex and subtle aspects of plasticity that are likely to be of substantial ecological importance.

The first of these important but little studied types of trait is *cross-generational plasticity*: ways that plants alter traits of their offspring in response to environmental conditions (recently reviewed by Donohue & Schmitt 1998). These cross-generational effects may be negative, in cases where parental resource stress limits the quality or size of offspring, or positive, in cases where they confer specific adaptations to the local environment experienced by the parent plant (Sultan 1996, and references therein). In one stunning example, Agrawal et al. (1999) demonstrated that maternal *Raphanus* plants attacked by lepidopteran herbivores produced seedlings which had higher concentrations of defensive chemicals as well as greater density of feeding-deterrent trichomes. Clearly both adaptive and maladaptive cross-generational effects are important to individual fitness, and consequently may play a role in shaping the ecological distribution of plant taxa and their tolerance of environmental change (e.g. Huxman et al. 1998).

Studies of cross-generational plasticity will be most valuable when the design incorporates the following elements: (1) genetic and environmental effects in the parental generation must be clearly distinguished, through appropriate replication of cloned or inbred parental lines in contrasting treatments (Wulff 1995; Shaw & Byers 1998). (2) To understand these effects it is important to examine specific, functionally important aspects of seedling development such as root and shoot extension rates, rather than to simply measure seed mass as in many earlier studies (Sultan 2000, and references therein). (3) To determine whether cross-generational effects are adaptive, the offspring must be grown in contrasting environmental states rather than in a single 'control' environment. (4) Data on the distribution of environmental states within and across generations, along with propagule dispersal data, will complete an understanding of the fitness consequences and evolution of cross-generational plastic responses (Donohue & Schmitt 1998).

A second intriguing and ecologically important aspect of plastic response to environment is its expression over time or *dynamic plasticity*, including variation in ontogenetic trajectories, rates of phenotypic response, and patterns of developmental iteration. For

example, one key dynamic trait of seedlings that is critical to survival in dense stands is the rate of shoot elongation, part of the well-studied 'shade avoidance syndrome' expressed in response to reduced red:far-red light ratio. Dynamic plasticity in adult plants may also be critical to maintaining fitness, especially when the environment changes over time. For instance, the ability of plants to spatially redistribute their root systems to track change in the location of soil resources such as nutrient ions, moisture and oxygen may be critical to success in variable soil habitats (Fransen et al. 1998). We have found for instance that *Polygonum* species with different field distributions differ significantly in how quickly they are able to produce adventitious and superficial roots at the soil/air interface in response to flooding (Bell & Sultan 1999).

Aspects of developmental trajectories such as meristem fate and reproductive timing constitute an important aspect of dynamic plasticity termed 'ontogenetic contingency' (Diggle 1994; see discussion by Schlichting & Pigliucci 1998). In animals, it is well known that there are 'sensitive periods' in development, typically early or even pre-natally; one related question is how the expression of plant plasticity varies and feeds back during the life-cycle (Weinig & Delph 2001). Undoubtedly these dynamic aspects of plasticity are demanding to study, since traits must be measured repeatedly over time in numerous individuals raised in alternative environments. However, to fully understand the ecological meaning of plasticity this effort is essential, since the adaptive or maladaptive effect of a plastic response may depend strongly on the timing of its expression.

Third, I will briefly mention plasticity for ecologically important *anatomical and architectural traits*, about which surprisingly few published studies exist. For example, functional leaf traits such as stomatal size and distribution, vascularization, fiber size, and thickness of the palisade, hypodermis and cuticle may all vary depending on moisture environment and other factors (Dubé & Morisset 1996; Cordell et al. 1998). In woody plants, anatomical traits important to drought and frost tolerance, such as tracheary element wall thickness and lumen diameter, are known to vary among species (Davis et al. 1999). It would be very interesting to know if these key anatomical traits can show adaptive plasticity, and if so in which species. For instance, do woody taxa with broad geographic ranges express adaptive plasticity for cavitation-resistance traits that are important to survival under frost conditions but disadvantageous in warmer climates, and if so is this plasticity limited to certain taxa? – Architectural traits such as patterns of branching or clonal spread and production of terminal versus axial inflorescences may also vary plastically in certain taxa

(e.g. Wu & Stettler 1998). These traits too are demanding to study, but are likely to provide very important insight into the structural and ultrastructural levels at which phenotypic adjustments take place in the plant body.

## The challenge of interpreting plasticity

One major task relates not to characterizing plasticity but to precisely interpreting it: to what extent are an individual's plastic responses to environmental variation functionally adaptive to the environments in which they are expressed, such that they enhance fitness in each environment? The ecological and evolutionary meaning of a given plasticity pattern depends on the answer to this question. However, demonstrating that a certain phenotypic response does in fact enhance fitness relative to other possible phenotypes in its environment can be quite difficult (discussed in Sultan 2000). One obstacle to empirical tests is that the rapid and continuous phenotypic adjustment to environment that characterizes plants as organisms (Walbot 1996) makes it difficult or impossible to directly compare the relative fitnesses of alternative phenotypic states to a given environment. Schmitt and co-workers have explored some ingenious experimental solutions to this problem, involving plasticity-disabled mutant genotypes and manipulation of environmental cues (Schmitt et al. 1999, and references therein). These elegant experiments have shown that phenotypes produced by plasticity can be quantifiably adaptive (e.g. Dudley & Schmitt 1996); hopefully these manipulative approaches will prove useful in other cases as more becomes known about both the environmental cues and the molecular variants implicated in plastic response.

Statistical methods to quantify a phenotype's contribution to fitness also require refinements for studying plasticity. 'Phenotypic selection analysis' (Lande & Arnold 1983) is particularly problematic in the case of plasticity, where the expressed phenotype is by definition environmentally biased (for discussion of the bias problem see Mitchell-Olds & Shaw 1987; Wade & Kalisz 1990; Stinchcombe et al. 2002; Winn, in press). One solution in the presence of genotype by environment interaction is to use genotypic means as data points (Rauscher 1992) to estimate trait associations to fitness within environmental treatments. However, such analyses require very large sample sizes, because genotypes must be replicated at both treatment and micro-environmental (e.g. block) levels. Furthermore, this approach requires that genotypes differ on average in both trait expression and fitness: when genotypes share an adaptive plasticity pattern, for instance, this

technique cannot confirm its contribution to fitness unless they also differ significantly. A second analytical approach that may prove more flexible is path analysis to assess causal relationships among growth and life history traits that jointly affect fitness (discussed by Scheiner & Callahan 1999). Recently, Scheiner and colleagues have proposed that use of path analysis models which include environmental effects on growth condition can reduce environmental bias in measuring phenotypic selection (Scheiner et al. 2002). Hopefully we will see further progress in these and other analytical tools for assessing adaptive plasticity.

A third way to investigate the adaptive value of plasticity is through comparative studies at the population or species level, to examine the match of qualitatively adaptive patterns of plasticity to the range of environments that taxa inhabit in the field. Such studies use realized field distribution to confirm adaptive interpretations of plastic responses, using a combination of field studies and controlled norm of reaction data for phylogenetically appropriate sets of taxa (e.g. Sultan 2003b, and references therein). Explicitly comparative studies of plasticity will be valuable both as an approach to studying the realized adaptive consequences of specific plasticity patterns, and to provide insight into the evolution of plasticity and its constraints (Callahan et al. 1997). Combining field and controlled studies of particular taxa will also be critical to determine the extent or 'grain' of environmental variation that a given plastic response can adaptively accommodate, and hence illuminate the roles of plasticity and genetically based differentiation as alternative modes of adaptation. For instance, greenhouse studies of plastic response to a particular environmental stress such as shade or drought can be followed by explant experiments testing the effectiveness of that response for tolerance of diverse microsites, sites or habitats.

## Mechanisms of plastic response

Despite a wealth of studies characterizing the diverse phenotypes organisms produce in response to various environments, the underlying mechanisms of plastic systems of phenotypic expression remain largely unknown in both plants and animals. In plants, the well-studied case of developmental response to reduced red:far-red light is the only system to date in which the entire transduction pathway is reasonably well understood, from the perception of the environmental cue to several of the genes that regulate phenotypic expression (see overview and references in Callahan et al. 1997; Schlichting & Smith 2002). Despite substantial increases in knowledge over the past decade, signal

transduction pathways within the plant body involving physical forces, metabolites and ions, and even major growth substances remain little understood, though it is clear that the context-dependent integration of both external and internal environmental signals in regulating gene expression is extraordinarily complex (Voesenek & Blom 1996; Gilroy & Trewavas 2001). Clearly, to fully understand plasticity patterns and their evolution, we need to know much more about these transduction pathways and their biochemical and genetic components, as well as how those components vary at the individual, population and species levels.

We must also increase our focus on the closely related issue of environmental cues and their perception by the organism. Perceiving a relevant environmental signal is the essential first step in any plastic response; identifying these cues and their patterns of variation in diverse natural sites is particularly critical for understanding adaptive plasticity. Indirect cues may be elusive to identify; for instance when factors such as substrate temperature and light intensity interact in natural habitats. Once relevant cues for environmental stresses have been identified, determining their reliability requires intensively repeated environmental sampling. Both the organism's sensory apparatus and the variability of the cues themselves will shape the evolution of plasticity patterns and determine their adaptive effectiveness (Moran 1992; DeWitt et al. 1998; Sultan & Spencer 2002). Taxa with specific phylogenetic or immediate genetic constraints may be unable to effectively sample the environment to perceive certain cues, resulting in reduced capacities for adaptive plasticity to particular conditions. When cues themselves are unreliable predictors of coming conditions or of key selective pressures, maladaptive phenotypic mismatches can occur (Lively 1986; Tufto 2000). Learning more about both cue perception and cue variability in natural habitats may lead to general insights regarding constraints on the evolution of adaptive plasticity for current as well as future environments.

## Understanding the environmental context

To accurately determine patterns of plasticity and to investigate their ecological and evolutionary implications, we also need to better understand the environmental context in which phenotypes are expressed. First, we need to increase our knowledge regarding patterns of spatial and temporal variability both within and among sites, for environmental factors that constitute selective pressures. These selective factors may be either directly or indirectly related to environmental factors that serve as cues for plastic expression

(Dudley & Schmitt 1996). Patterns of environmental correlation from one season or generation to the next will provide key insights into both the selective experience of perennial plants and the fitness consequences of cross-generational plasticity. We also need more precise information about the realized environmental tolerance of taxa in the field in relation to their patterns of plasticity. Such field distribution studies provide an essential complement to single-factor greenhouse experiments, by testing the adaptive consequences of plasticity under the various concurrent stresses that occur in natural habitats.

In general, ecologists are increasingly aware that organisms in nature confront multiple environmental factors that interact in their effects on development and fitness. For instance, we have found that genotypes of annual *Polygonum* species express characteristic, distinct norms of reaction for particular combinations of light, moisture, and nutrients (Sultan 2003b). This kind of response complexity may be an important dimension of adaptive diversity in natural communities (Sultan 2000). Although single-factor studies have been fundamental in plasticity research thus far, at this point we can hope to incorporate more realistic environmental complexity into our experimental designs. We also have a great deal to learn from studies of plastic response to biotic factors, including the presence, density, and identity of herbivores, pathogens, and symbionts, as well as their interactions with abiotic variables.

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