Phenotypic plasticity for plant development, function and life history

Sonia E. Sultan

A single genotype can produce different phenotypes in different environments. This fundamental property of organisms is known as phenotypic plasticity. Recently, intensive study has shown that plants are plastic for a remarkable array of ecologically important traits, ranging from diverse aspects of morphology and physiology to anatomy, developmental and reproductive timing, breeding system, and offspring developmental patterns. Comparative, quantitative genetics and molecular approaches are leading to new insights into the adaptive nature of plasticity, its underlying mechanisms and its role in the ecological distribution and evolutionary diversification of plants.

Individual organisms can alter their development, physiology and life history depending on environmental conditions. These environmental responses are both trait and resource specific, and represent evolved characteristics that vary among genotypes, populations and species. The past 15 years have seen an explosion of interest in this capacity of a given genotype to express different phenotypes in different environments, a phenomenon known as phenotypic plasticity.

Although biologists have long been aware of plasticity (indeed, this is the reason that experiments are performed under controlled environmental conditions), for much of the past century phenotypic response to environment was regarded as ‘environmental noise’ that obscured the ‘true’ genetic characteristics of the organism. Only recently has plasticity been widely recognized as a significant mode of phenotypic diversity and hence as an important aspect of how organisms develop, function and evolve in their environments. This new awareness has led to a redefinition of the genotype as a repertoire of environmentally contingent phenotypic possibilities or ‘norm of reaction’, rather than a blueprint for a single fixed outcome (Fig. 1). In general, biologists are increasingly coming to view the phenotype as the outcome of complex synergistic developmental systems, influenced by multiple interacting genes and gene products as well as by the organism’s internal and external environments.

By the early 1990s, developmental and physiological plasticity had been reported in land plants, algae, marine invertebrates, insects, fish, amphibians, reptiles and small mammals. More recently, plasticity for structure, biochemistry and metabolic activity was documented in a lichen. Plasticity has been studied most intensively in plants, which typically show dramatic effects of environment on growth and development. They can also be more readily cloned (or highly inbred) and raised in alternative environments than many other organisms. Thus, much of our current knowledge of phenotypic plasticity comes from plant studies documenting the range of phenotypes that can be produced by individual genotypes in response to contrasting conditions.

Initial studies of plant plasticity often focused on simple descriptors of growth and morphology such as plant size, branch number and internode length, although some early studies included directly functional aspects of plasticity such as proportional allocation to different plant tissues or assimilation rates. More recent studies have focused on those aspects of plasticity that relate directly to the functional and reproductive success of plants in their environments and hence are both ecologically and evolutionarily important. In addition, researchers are increasingly testing plasticity in experimental environments that are ecologically relevant to the study organism, rather than in arbitrary sets of contrasting conditions.

This emphasis on ecologically, and therefore evolutionarily, meaningful traits and environments has opened several important new avenues of inquiry. Recent research has revealed diverse,
Plants can respond to their environments through developmental plasticity in many aspects of their phenotypes. In addition to allocational and morphological traits, anatomical traits such as leaf vasculature, areas of sclerenchyma and root nodule structure in symbiotic legumes might vary with the environment. Studies of anatomical plasticity shed further light on the subtle ways that plants can adjust their phenotypes to maintain function in contrasting conditions. For example, plasticity for thickness of the water-storing leaf hypodermis layer evidently contributes to the dominance of the indigenous Hawaiian tree *Metrosideros polymorpha* across a broad range of habitats that differ in moisture availability. Such plasticity for anatomical traits might have important implications for plant taxonomy. Plant architecture can also vary in response to the environment, as has been shown for the number and length of sylleptic branches in *Populus* trees. In herbaceous plants, shading can alter the plant's architecture as a result of effects on meristem initiation and fate as well as organ size and structure. Studies of architectural plasticity provide useful insight into the specific developmental components of plastic responses.

The timing of plant development, including plastic responses to the environment, can itself be plastic. Developmental plasticity might be limited to early stages of the life cycle or might vary in timing among different genotypes, populations or species. The effectiveness of functionally appropriate plastic responses to environmental change can be strongly influenced by their timing. For
example, in response to soil flooding, *Polygonum persicaria* rapidly redeployed root systems to aerated surface soil layers and maintained high growth rates, whereas *Polygonum cespitosum* plants showed a similar but significantly slower plastic response that was associated with significantly lower plant biomass.

**Life-history plasticity**

As plasticity studies have extended beyond simple effects on plant growth, researchers have found that key life-history traits such as sex expression and breeding system, reproductive allocation and phenology can vary in response to the environment. For example, the proportions of staminate and hermaphroditic flowers in an andromonoecious *Solanum* were shown to depend on plant resource status, confirming a long-standing ecological hypothesis.

A more surprising finding was that normally self-incompatible plants can switch to self-fertilization in response to floral age and lack of prior fruit development. This plasticity for self-compatibility results in a ‘delayed selfing’ strategy that insures reproduction if outcrossing fails. This case makes it clear that a plastic switch can occur in response to a plant’s internal environment as well as to resource availability or other external cues.

Plastic reproductive timing and allocation have been documented in several herbaceous species. These changes are likely directly to affect plant fitness and therefore population persistence and response to natural selection. For example, *Mimulus* plants flower early in unfavorable conditions, whereas plants in favorable conditions delay flowering to allocate more biomass to vegetative growth. A selection experiment confirmed that these contrasting reproductive patterns reflect different fitness priorities in the two types of environment: in poor sites, plants have shorter...
life spans and maximizing early flower production is advantageous; in favorable sites, where plants live longer, greater allocation to vegetative growth followed by later flowering maximizes fitness22.

Cross-generational plasticity

Plants can respond to environmental conditions not only by adjusting their own phenotypes but also by altering those of their offspring, through changes in the quantity and quality of seed provisioning, and in the structure or biochemistry of the seed coat and fruit tissues. Studies of these cross-generational effects rigorously distinguish environmental from genetic causes of offspring variation and focus on ecologically relevant propagule and seedling traits rather than on propagule mass alone25,26.

Although the mechanisms are not well understood27, offspring structure, development and morphology can be influenced in remarkably specific ways by parent environment. Certain species respond to contrasting growth conditions by changing the structure or thickness of the seed coats or pericarps while maintaining the quantity and quality of the embryo and endosperm tissues that determine initial seedling size26,27. The progeny of the quantity and quality of the embryo and endosperm tissue or thickness of the seed coats or pericarps while maintaining growth rate when seedlings were given even in species that express an immediate ‘CO2 fertilization’ or concentration, there is evidence for negative parental environment effects540. It is these adaptive plastic responses that allow individual organisms to maintain function and hence fitness across a range of diverse environments, and that therefore influence both ecological and evolutionary significance of contrasting plasticity patterns10,11,19,23,36. However, the selective evolution of plasticity in any given population will depend in part on whether the plastic response has high energetic, functional or genetic costs28,29.

Unfortunately, it can be difficult to assess the adaptive value of plastic responses. Because the effect on fitness of the environment and of the organism’s phenotypic response to it are confounded, statistical techniques such as phenotypic selection analysis are not generally suitable for testing adaptive plasticity. A second approach is the classic reciprocal experiment, which tests the adaptive advantage of phenotypes in their own environments by comparing the relative fitnesses of alternative phenotypes within each environment. Generally, reciprocal adaptive comparisons cannot be made of alternative phenotypes produced via plasticity because plasticity itself prevents the plant from producing the ‘wrong’ phenotype in a given test environment (and the phenotypes of plants that have developed in one environment will rapidly begin to change if the plants are then transferred to a test environment).

By separately manipulating the R:FR ratio and the plant density, an elegant reciprocal experiment was performed to test the relative fitness of elongated versus bushy Impatiens phenotypes in both high- and low-density treatments31. Related studies have used constitutively elongated Arabidopsis mutants and transgenic and mutant tobacco plants with suppressed phytochrome-mediated plasticity to compare the phenotypes produced at low and high densities by plastic, wild-type plants with the ‘wrong’ phenotypes expressed in those environments by the genetically modified plants31. The results of both phenotypic manipulation approaches were consistent: the elongated phenotype was advantageous in response. Results, whereas the bushy phenotype had higher fitness in the absence of shading by neighbors. These experiments provide convincing evidence that this common pattern of plastic response to competitive shading is indeed adaptive.

Although the scope of these approaches will necessarily be limited22, further studies of model systems that offer appropriate plasticity-disabled mutants and of systems in which either the environmental cue or the physiological pathway of plastic response can be manipulated will allow direct phenotypic comparisons that provide important information about adaptive plasticity. Comparative studies of ecologically distinct, closely related taxa can also offer insight into adaptive plasticity. Comparative plasticity studies use the realized environmental distribution of taxa rather than correlations with fitness as evidence for the adaptive significance of contrasting plasticity patterns10,11,19,23,36.

Plasticity patterns for ecologically important traits often vary genetically within natural populations, which indicates that the genetic potential for the evolution of adaptive plasticity can exist in many taxa27. However, the selective evolution of plasticity in any given population will depend in part on whether the plastic response has high energetic, functional or genetic costs28,29.

Genetic and hormonal mechanisms of plasticity

The genetic mechanisms that underlie plastic response are as yet poorly known33,39, although it has become clear that several different mechanisms might be involved in different aspects of...
plasticity\textsuperscript{39,40}. These mechanisms are believed to include environmentally dependent regulatory loci as well as non-epistatic loci at which allelic expression varies with the environment\textsuperscript{39}.

The effects of specific photoreception and signal transduction loci on growth plasticity were shown using five single-gene Arabidopsis mutants\textsuperscript{39}. Because plastic responses involve both environmental perception and the production of the appropriate phenotype (which might entail a suite of anatomical, morphological, physiological and other traits), these responses are likely to be influenced by multiple loci. For this reason, and because candidate genes are unknown for the vast majority of cases, quantitative trait loci (QTL) mapping (a DNA-based technique for identifying multiple and/or unknown loci that affect trait expression) might be particularly valuable for investigating the genetics of plasticity\textsuperscript{40,42} (Dorn and Mitchell-Olds, unpublished).

The role of plant hormones in the perception of environmental cues and their transduction into specific plastic responses remains largely to be elucidated. The effects of plant hormones on development are particularly complex, because a given substance and concentration can affect various traits in ways that depend not only on the cell or tissue involved but also on environmental conditions and plant age\textsuperscript{39,44}. Perhaps because of this complexity, surprisingly little is known about even major mechanisms of developmental plasticity such as biomass allocation\textsuperscript{44}. Population differences in both endogenous production and sensitivity to growth hormones might contribute to different patterns of plastic response. For instance, differences in ethylene production and sensitivity influence the ability of alpine Stellaria longipes plants to produce a compact habit in harsh conditions\textsuperscript{45}. Further studies of ecologically distinct populations might provide valuable information about the proximate mechanisms of plastic responses.

**Large-scale ecological and evolutionary implications**

Comparative studies at the population and species levels are revealing several important connections between individual plasticity and higher-level ecological and evolutionary patterns. Species that consist of highly plastic genotypes might show little adaptive diversification at the population level. Conversely, species in which individuals express limited plasticity would be predicted to show greater selective divergence into genetically based local ecotypes (unless these individuals express some sort of non-plastic generalist phenotypes). Differences among taxa in individual adaptive plasticity might thus contribute to differences in large-scale patterns of population and ultimately species divergence.

**Conclusions and prospects for future work**

Continuing research on plasticity for diverse functional, developmental and life-history traits will further illuminate ways that this fundamental property influences plant growth and fitness. One area that merits greater emphasis is the plastic response to biotic environmental factors, including inducible production of plant defense chemicals in response to herbivores and pathogens, and the effects of endophytic fungi and other symbionts on host plant development and life history\textsuperscript{46,50}.

Because plasticity studies should be carefully linked to the organism’s ecological context and differences between microsites and habitats in nature are typically complex\textsuperscript{46}, future studies may increasingly test plastic responses to multifactorial stresses rather than single environmental factors\textsuperscript{46,47}. Research on cross-generational response to environment is just starting to address the ecological consequences of this aspect of plasticity\textsuperscript{48}. Because these consequences depend on the correlation between parental and offspring environments (and therefore on habitat type, dispersal and dormancy properties), such studies are particularly challenging but might provide important insights into individual fitness as well as population persistence.

Further investigation of the genetic architecture and hormonal pathways of environmental perception and phenotypic response will not only improve our mechanistic understanding of these response systems but also illuminate possible constraints on the evolution of adaptive plasticity. These constraints might include the lack of appropriate genetic variation as well as possible costs arising from inherently more complex genetic or physiological systems\textsuperscript{48}. Finally, continued comparative studies will add to our knowledge of the wider ecological implications of plasticity for the distribution, spread and persistence of plant populations, as well as its possible influence on patterns of evolutionary diversification.

**Acknowledgements**

I thank Lisa Dorn for discussion of QTL mapping and Jeffrey Gilarde for image processing assistance. I also thank three anonymous referees for their constructive and thoughtful comments. Research from my laboratory was supported by the US National Science Foundation Population Biology Program, the G.H. and L.Y. Mathers Charitable Foundation, and Wesleyan University.
References

14 Cordell, S. et al. (1998) Physiological and morphological variation in Metrosideros polymorpha, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. Oecologia 113, 188–196
27 Lacey, E.P. et al. (1997) Parental effects on seed mass: seed coat but not embryo/endosperm effects. Am. J. Bot. 84, 1617–1620

Sonia Sultan is at the Dept of Biology, Wesleyan University, Middletown, CT 06459-0170, USA (e-mail sesultan@wesleyan.edu).