# Phenotypic plasticity for plant development, function and life history

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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<sup>1-3</sup>.

By the early 1990s, developmental and physiological plasticity had been reported in land plants, algae, marine invertebrates, insects, fish, amphibians, reptiles and small mammals<sup>4</sup>. More recently, plasticity for structure, biochemistry and metabolic activity was documented in a lichen<sup>5</sup>. 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<sup>6–8</sup>. 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,



Fig. 1. A genotype will vary in its expression depending on the organism's external and internal environments. The phenotypic response pattern of a given genotype is its 'norm of reaction', a term coined by German geneticists at the start of the 20th century. Later researchers typically studied genotypes in a single, standardized laboratory environment, essentially measuring one phenotypic point along each genotype's norm. Norms of reaction can be determined by cloning the genotype and measuring phenotypic traits of interest on the genetically identical replicates in each of several controlled environments. (When cloning is not possible, inbreeding can provide reasonably uniform genetic replicates.) The range of experimental environments might include extreme or unrealistic treatments to investigate the limits of potential phenotypic expression, or might be based on environmental conditions encountered by the organism in nature to provide ecologically and evolutionarily relevant information. A genotype's norm of reaction for any specified trait can be depicted as a twodimensional plot of its phenotypic values for that trait in each experimental environment. Such a plot makes explicit association of a given phenotype with the particular environment in which it is expressed (e.g. phenotype 1 and environment 1 above). Norms of reaction for a group of genotypes can be plotted together to show graphically the pattern of genotypic variance within and across environments.

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**Fig. 2.** (a) Inbred replicates of the same *Polygonum lapathifolium* genotype grown for eight weeks at low light [20% available photosynthetically active radiation (PAR); left] and high light (100% available PAR; right). Low-light plant bears large, thin leaves and few branches. The larger high-light plant bears narrow leaves on many branches and is also more mature, as shown by the senescence of the earliest leaves and the production of mature achenes. (b) Mean norms of reaction for 25 genotypes of *P. lapathifolium* grown at low (20%) and high (100%) light (mean within each treatment plus or minus the standard deviation). Low-light plants have less total biomass (filled circle) but produce far more photosynthetic leaf area per unit mass (unfilled circle) through changes in leaf biomass allocation, morphology and structure.

often subtle and complex modes of plastic response in plants, and has begun to address several fundamental questions about the adaptive significance, genetic and proximate mechanisms and large-scale ecological and evolutionary implications of plant plasticity.

## **Diverse modes of plasticity**

#### Plasticity for functional traits

Traits involved in resource acquisition often show functionally appropriate patterns of plasticity, such as increased biomass allocation to roots in low-nutrient soils or greater leaf area relative to plant biomass under low photon flux density<sup>6-9</sup>. These specific adjustments can partly compensate functionally for the inevitable reductions in total plant growth and biomass that occur under resource limitation (Fig. 2). Such developmental plasticity can allow a given genetic individual to grow and reproduce successfully in contrasting microsites, whereas short-term physiological

plasticity in such traits as leaf angle, stomatal aperture and photosynthetic rate can allow plants to adjust to highly temporally variable aspects of the environment such as light intensity and transpirational demand. Both long- and short-term plastic responses can contribute to the ability of species to occupy diverse and variable habitats in nature<sup>10</sup>.

Although functional shifts in response to different resource levels were initially studied primarily with respect to biomass allocation (e.g. root:shoot ratio), recent plasticity studies also include detailed aspects of shoot and root systems that are more directly related to resource acquisition. These include leaf size and specific area and whole-plant leaf-area: biomass ratio (LAR) (which directly influence photosynthetic light capture) and root specific length, spatial deployment and whole-plant length:biomass ratio (RLR) (which are accurate indicators of root uptake capacity). Including these aspects of morphological plasticity affords greater insight into the diverse ways that plants adjust functionally to environmental stresses (Fig. 3). For instance, a recent study of nutrient-deprived plants grown at different light levels showed that, in spite of strongly reduced biomass allocation to roots, shaded plants maintained root uptake capacity and consequently leaf nitrogen concentration by substantially increasing the length:volume ratio of fine roots<sup>11</sup>.

#### Aspects of developmental plasticity

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<sup>12,13</sup>. 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 waterstoring 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<sup>14</sup>. Such plasticity for anatomical traits might have important implications for plant taxonomy<sup>12</sup>. Plant architecture can also vary in response to the environment, as has been shown for the number and length of sylleptic versus proleptic branches in *Populus* trees<sup>15</sup>. 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<sup>16</sup>. Studies of architectural plasticity provide useful insight into the specific developmental components of plastic responses<sup>17</sup>.

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<sup>9</sup> or might vary in timing among different genotypes, populations or species<sup>18,19</sup>. The effectiveness of functionally appropriate plastic responses to environmental change can be strongly influenced by their timing. For



**Fig. 3.** The many phenotypic differences between genetically uniform *Polygonum lapathifolium* plants grown in dry (a) and flooded (b) soil include dramatic changes to the root system. In addition to increased root biomass, flooded plants produce dense networks of extremely fine roots at the soil surface, where oxygen is readily available. The formation of such dense superficial root systems is a well-known flood tolerance mechanism.

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<sup>19</sup>.

## 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<sup>17</sup>. A more surprising finding was that normally self-incompatible



**Fig. 4.** *Polygonum persicaria* is a cosmopolitan annual found in a broad range of naturally disturbed habitats including open, nutrient-rich sites (a), nutrient-poor sand beaches of freshwater ponds (b) and moderately shaded, mesic habitats (c). Compared with less broadly distributed annual *Polygonum* species, this species has extremely high phenotypic plasticity for functional and fitness traits in response to contrasting light, moisture and nutrient environments.

plants can switch to self-fertilization in response to floral age and lack of prior fruit development<sup>20</sup>. 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<sup>21–24</sup>. 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<sup>22</sup>. 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 fitness<sup>22</sup>.

#### 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 alone<sup>25–28</sup>.

Although the mechanisms are not well understood<sup>27</sup>, 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 size<sup>26,27</sup>. The progeny of nutrient-deprived plants can increase root biomass allocation compared with seedling offspring of plants given ample nutrients<sup>29</sup>. Similarly, the offspring of light-deprived plants can reduce root extension relative to shoot growth compared with offspring of genetically identical plants grown at high light<sup>26</sup>. Such specific plastic changes to seedling growth patterns might allow offspring to maintain critical aspects of function such as root uptake capacity even if the initial seedling biomass is reduced by parental resource deprivation. Seedling offspring of nutrient-deprived Polygonum plants produced thinner roots that extended downward more rapidly into the soil, resulting in root systems that were as long as in seedlings from nutrient-rich parents in spite of their lower mass (S. Elmendorf and S. Sultan, unpublished).

Both positive and negative cross-generational effects can alter offspring quality in ways that affect a population's ability to regenerate. In the case of increased atmospheric  $CO_2$  concentration, there is evidence for negative parental environment effects even in species that express an immediate ' $CO_2$  fertilization' or positive growth response. Significant effects of parental  $CO_2$  environment on seedling development were found in inbred lines of *Arabidopsis thaliana* raised at ambient and elevated  $CO_2$  levels: the offspring of plants grown at high  $CO_2$  produced shorter and less branched roots, possibly owing to reduced seed size and nitrogen content<sup>30</sup>. Similar negative effects of elevated  $CO_2$  on offspring mass, carbon:nitrogen ratio and relative growth rates were found in a study of the annual grass *Bromus rubens*<sup>31</sup>.

The parental environment can also alter the phenotypic plasticity of progeny, including such critical traits as the ability of plants to respond positively to increased atmospheric  $CO_2$ . In the *Bromus* study, only the progeny of plants grown at ambient  $CO_2$  showed the predicted increase in growth rate when seedlings were given high  $CO_2$ , whereas seedling offspring of plants that had been raised at high  $CO_2$  levels failed to show this positive response<sup>31</sup>.

#### Is plasticity adaptive?

Plastic responses include both inevitable effects of environmental limits on growth and physiology, and adaptive adjustments that enhance the organism's success in the environment that elicits them<sup>4</sup>. 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 breadth and response to natural selection. Determining whether plastic responses are functionally adaptive is thus of particular interest to both ecologists and evolutionists.

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).

However, Schmitt and co-workers have developed two innovative experimental strategies that permit reciprocal tests of adaptation for certain plastic responses<sup>32</sup>. They have focused on a particularly well-studied plastic response: the elongated phenotype produced by plants shaded by dense neighbors, which presumably affords greater access to light under intense competition compared with the shorter, bushier phenotype produced at lower densities. The proximate cue for this plastic response is the ratio of red to far-red light (R:FR ratio), which is transduced primarily via phytochrome light receptors. In this case, the environmental cue that induces the phenotypic response (R:FR ratio) and the environmental stress that the response functionally accommodates (above-ground competition) are distinct.

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 treatments<sup>33</sup>. 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 plants<sup>34,35</sup>. The results of both phenotypic manipulation approaches were consistent: the elongated phenotype was advantageous in dense stands, 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 limited<sup>32</sup>, 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 patterns<sup>10,11,19,23,36</sup>.

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 taxa<sup>37</sup>. 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 costs<sup>38</sup>.

#### Genetic and hormonal mechanisms of plasticity

The genetic mechanisms that underlie plastic response are as yet poorly known<sup>3,35,39</sup>, although it has become clear that several different mechanisms might be involved in different aspects of

plasticity<sup>40,41</sup>. These mechanisms are believed to include environmentally dependent regulatory loci as well as non-epistatic loci at which allelic expression varies with the environment<sup>39</sup>.

The effects of specific photoreception and signal transduction loci on growth plasticity were shown using five single-gene *Arabidopsis* mutants<sup>35</sup>. 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<sup>41,42</sup> (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<sup>43,44</sup>. Perhaps because of this complexity, surprisingly little is known about even major mechanisms of developmental plasticity such as biomass allocation<sup>44</sup>. 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<sup>45</sup>. 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 be ecological generalists<sup>4</sup> (Fig. 4), whereas species whose constituent individuals express limited adaptive plasticity might be restricted to narrower, 'specialist' ecological ranges.

In addition to ecological breadth, plasticity might also contribute to a species' invasiveness. Widespread colonizing species are often characterized by high phenotypic plasticity, which should in theory allow them to inhabit diverse new sites without undergoing local genetic adaptation through natural selection. Work on several colonizing species has confirmed that populations across broad geographic and environmental ranges can show remarkably little genetic or morphological differentiation but instead consist of genetically similar populations of highly plastic genotypes<sup>46,47</sup>. Thus plasticity might facilitate the rapid spread of introduced as well as native taxa into new ranges without the evolutionary lag time required to adapt to these unfamiliar habitats through natural selection<sup>46</sup>.

Plasticity might also contribute to the ability of species to withstand sudden environmental changes, such as those caused by human disturbance. Because such changes generally occur at too rapid a pace for evolutionary response and can create conditions not previously experienced during the organism's selective history, species that lack sufficient plasticity to maintain growth and reproduction in altered, degraded and possibly novel environments might be at particular risk of extinction. For this reason, the study of plasticity is particularly timely. One important question is whether plasticity will help plants survive global atmospheric change. Differences among taxa in their adaptive physiological plasticity in response to elevated  $CO_2$  might be an important factor in determining competitive and ultimately extinction outcomes as global atmospheric change continues<sup>48</sup>. However, to predict the ability of plants to maintain populations in spite of environmental stresses, it is essential to consider cross-generational as well as immediate aspects of plasticity. In the case of elevated atmospheric  $CO_2$ , even species that show immediate adaptive plasticity might express negative cross-generational effects that prevent persistence.

Finally, plasticity can influence patterns of evolutionary diversification. If individual genotypes are sufficiently plastic to produce phenotypes appropriate to different local environments, natural selection will not occur for genetically distinct, locally specialized ecotypes<sup>4,7</sup>. Consequently, taxa consisting 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<sup>49,50</sup>.

Because plasticity studies should be carefully linked to the organism's ecological context and differences between microsites and habitats in nature are typically complex<sup>48</sup>, future studies may increasingly test plastic responses to multifactorial stresses rather than single environmental factors<sup>10,11</sup>. Research on cross-generational response to environment is just starting to address the ecological consequences of this aspect of plasticity<sup>51</sup>. Because these consequences depend on the correlation between parental and off-spring 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<sup>38</sup>. 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.

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