



## The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust?

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**Abstract.** Plant populations and species differ greatly in phenotypic plasticity. This could be because plasticity is advantageous under some conditions and disadvantageous or not advantageous under others. We distinguish adaptive from injurious and neutral plasticity and discuss when selection should favor adaptive plasticity over genetic differentiation or lack of phenotypic variation. It seems reasonable to hypothesize that selection is likely to favor plasticity when an environmental factor varies on the same spatial scale as the plant response unit, when the plant can respond to an environmental factor faster than the level of the factor changes, and when environmental variation is highly but not completely predictable. Phenotypic plasticity might also tend to be more advantageous when mean resource availability is high rather than low, when a response can occur late in development rather than early, and when a response is reversible rather than irreversible. There is substantial evidence for the hypothesis that predictability favors plasticity. However, available evidence does not support the hypothesis that high mean resource availability necessarily favors plasticity. Testing hypotheses about when it is good for a plant to adjust is central to understanding the diversity of plasticity in plants.

**Key words:** plant phenotypic plasticity, resource availability, spatial and temporal heterogeneity, unpredictability

### Developmental plasticity and evolution

Plant populations and species differ greatly in plasticity (Linhart and Grant, 1996). This could be because they differ in their capacity to evolve plasticity, but it could also be because plasticity is advantageous under some conditions and disadvantageous or not advantageous under others.

For example, the stolons of some herbs vary their frequency of branching, internode length and direction of growth in response to light or nutrient levels (de Kroon and Hutchings, 1995; Dong, 1995). In contrast, stolons of the herb *Fragaria chiloensis* from a population on coastal dunes grow in a nearly straight line without branching and neither shorten nor lengthen internodes in

shade or nutrient patches (Alpert, 1991, 1996). Stolons do not lack the potential to branch or produce internodes of different lengths; they can respond to damage by branching and typically produce relatively short internodes between the first several offspring on a stolon. Instead, selection may have favored a fixed architecture in *F. chiloensis*. Light and nutrient availability in its sand dune habitat are probably highly dynamic and unpredictable in both time and space (Strong *et al.*, 1995; Alpert and Mooney, 1996). Resource patterns may change as fast as stolon architecture can respond to them, and stolons that randomly and quickly explore the habitat may place more new ramets in favorable patches than stolons with a plastic architecture (Oborny, 1994; Colasanti and Hunt, 1997). A similar lack of plasticity in stolon growth has been documented in a rhizomatous grass from an Asian desert where water availability is unpredictable (Dong and Alaten, 1999).

Under which conditions is it likely to be advantageous for a plant to be plastic? This will depend on both environmental and organismal factors. We will consider four environmental characteristics: spatial heterogeneity, temporal heterogeneity, predictability, and mean resource availability; and six organismal characteristics: size of the responding unit, size of the genetic individual, dispersal range, time required to respond, how late in development a response can take place, and whether a response is reversible.

### **Defining plasticity**

To clarify the discussion, we would first like to define our concept of plasticity. A widely used definition of phenotypic plasticity is environmentally induced variation in the growth or development of an organism (e.g., Bradshaw, 1965; West-Eberhard, 1989; Scheiner, 1993). Plasticity is thus distinguished from variation that is neither environmentally induced nor the result of genotype  $\times$  environment interactions, but rather explained by genotype alone (Table 1). This type of non-plastic phenotypic variation can be subdivided into: (1) genetic differentiation, also termed specialization, genetically based differences between individuals that do not vary with environment; and (2) fixed ontogenetic variation, developmental patterns that are constant across environments. Genetic differentiation in particular is often seen as a major evolutionary alternative to adaptive plasticity. It is further likely, though it may not be possible to show, that some phenotypic variation is explained neither by environment nor by genotype and is instead due to 'developmental instability', i.e., a degree of randomness in developmental outcomes (Table 1).

There are many complexities that can make it difficult to identify whether an individual instance of phenotypic variation qualifies as plasticity. For example, fixity can be mistaken for plasticity as the result of studying 'phantom' traits.

Table 1. Types and subtypes of phenotypic variation

Type of variation	Cause	Type subdivided by cause
1. Explained by environment or environment $\times$ genotype interaction	Selection for phenotypic variation	1.1. Adaptive plasticity
	Inability to prevent variation despite fitness reduction	1.2. Injurious plasticity
	Lack of selection against phenotypic variation	1.3. Neutral plasticity
2. Explained by genotype	Genetic variation between individuals	2.1. Genetic differentiation
	Genetically determined patterns of development	2.2. Fixed ontogeny
3. Explained neither by environment nor genotype	Lack of genetic control	3.1. Developmental instability
4. No variation	Selection against phenotypic variation	4.1. 'Adaptive fixity'
	Lack of potential to vary phenotype	4.2. Genetic constraint
	Lack of selection for phenotypic variation	4.3. 'Neutral fixity'

Fixed but non-linear allometries between root and shoot biomass in plants can be misinterpreted as plasticity for allocation between root and shoot (Coleman *et al.*, 1994; Gedroc *et al.*, 1996; Muller *et al.*, 2000). One remedy may be to identify and aim studies of plasticity at 'growth rules' (Schmid and Bazzaz, 1990; Colasanti and Hunt, 1997). As a second example, even fixed patterns of development may affect plasticity, since a trait may exhibit different degrees or patterns of plasticity at different stages of development (e.g., Newton and Hay, 1996), an interaction nicely termed 'contingent plasticity' (Watson *et al.*, 1995, 1997).

Phenotypic variation that does qualify as plasticity can be subdivided into three subtypes based on the cause of the variation (Table 1). Plasticity in a trait could result from direct selection (adaptive plasticity), from inability to maintain a constant phenotype despite fitness reduction due to variation ('injurious plasticity'), or from lack of selection either for or against variation ('neutral plasticity') accumulated through processes such as mutation or selection on other traits that are functionally related. Of these subtypes, adaptive plasticity is of the most evolutionary and ecological interest.

The important distinctions between adaptive, injurious, and neutral plasticity can be illustrated with a simple conceptual model (Fig. 1), in which plasticity in fitness (measured as plasticity in a trait that is thought to be closely related to fitness) is a function of plasticity in an underlying trait (a trait that

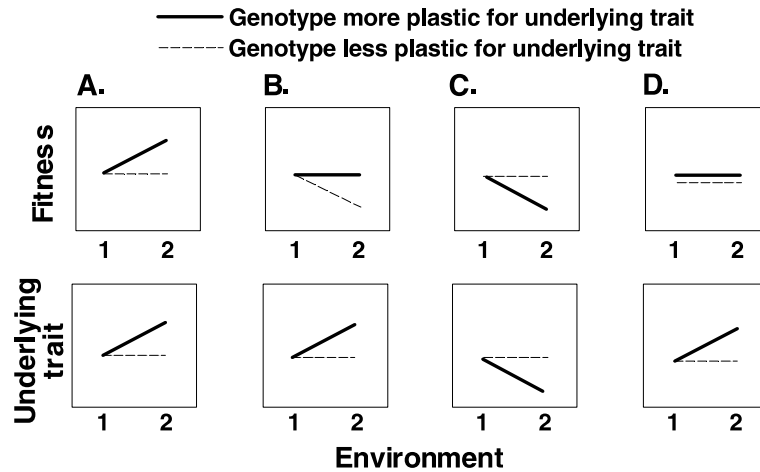


Figure 1. Some types of phenotypic plasticity: (A) adaptive plasticity with increased plasticity in fitness; (B) adaptive plasticity with decreased plasticity in fitness; (C) injurious plasticity; (D) neutral plasticity.

contributes to fitness but is less directly related to fitness than the other trait). To be adaptive, plasticity should increase mean fitness across environments. This might be achieved in at least two different ways, one of which increases and one of which decreases plasticity in fitness. First, increasing plasticity in an underlying trait could increase fitness in one of a set of environments in which fitness was formerly similar, thereby increasing plasticity in fitness (Fig. 1A). This type of adaptive plasticity might be involved in invasions of grassland by non-native grasses in North America. Comparisons between sets of native and non-native, invasive grasses from the same habitats suggest that the non-natives may often have relatively similar growth rates to those of the natives at low levels of water or nitrogen availability but have much higher growth rates than those of natives at high levels of resource availability (Nernberg and Dale, 1997; Claassen and Marler, 1998). It has been hypothesized that capacity for plasticity in general is an important factor in the invasiveness of non-native species (e.g., Williams *et al.*, 1995; Schweitzer and Larson, 1999; Willis *et al.*, 2000).

Second, increasing plasticity in an underlying trait could increase fitness in an environment in which fitness was formerly lower than in other environments, increasing mean fitness across environments while decreasing plasticity in fitness (Fig. 1B). This appears to be the case in two of the best-documented examples of adaptive plasticity in plants, shade-induced stem elongation and induced defense. Some plants respond to shading from other plants by growing longer stem internodes (Schmitt and Wulff, 1993; Schmitt *et al.*, 1995; Dudley and Schmitt, 1996). Increasing internode length (plasticity in an underlying

trait) helps these plants avoid limitation of photosynthesis due to shading by neighbors and thereby increase their seed production under crowded conditions (an environment where their fitness is relatively low). Many plants respond to damage by herbivores by accumulating chemicals or undergoing changes in form that deter subsequent herbivory (Karban and Baldwin, 1997; Tollrian and Harvell, 1999). Plasticity in these underlying traits can help plants to accumulate more biomass and produce more seeds in the presence of herbivores (e.g., Agrawal, 1998).

Plasticity in an underlying trait that decreases mean fitness across environments is 'injurious plasticity' (Fig. 1C). Inability to compensate for environmental stress, such as inability to maintain high water potential and hence growth in an arid environment, is likely to be an example of this type of plasticity. Other examples could include changes in form imposed by physical forces or obstacles, such as 'flagging' of trees near timberline by ice abrasion or the formation of less extensive rhizome systems by plants grown in more compact soil (Schmid and Bazzaz, 1990). Finally, plasticity in an underlying trait might have no effect on fitness and thus be 'neutral plasticity' (Fig. 1D).

In order to discuss the relative advantages of plasticity in different environments, it is also important to distinguish analogous subtypes of the 'null' category of phenotypic variation, which is the absence of variation (Table 1). Like plasticity, absence of phenotypic variation could be due to direct selection ('adaptive fixity'), to lack of variation for selection to act upon (genetic constraint), or to the absence of selection ('neutral fixity'). Adaptive fixity in particular may be a second important evolutionary alternative to adaptive plasticity.

Five key points emerge from this definition. Implicit throughout the definition is the point that plasticity is trait-specific, that genotypes are not plastic but rather can have plastic phenotypic traits. Second, plasticity can be adaptive, injurious, or probably neutral with respect to fitness. Adaptive plasticity is the type of most evolutionary and ecological interest. Third, plasticity is not the opposite of homeostasis. In two of the best-known cases of adaptive plasticity in plants, plasticity in an underlying trait contributes to homeostasis in traits more closely related to fitness. Fourth, to test for adaptive plasticity, one should measure plasticity in traits that contribute to fitness but are not the traits used to measure fitness. Greater plasticity in fitness could be the result of greater adaptive plasticity (Fig. 1A) or greater injurious plasticity (Fig. 1C), and greater adaptive plasticity could cause lower plasticity in fitness (Fig. 1B). Fifth, adaptive plasticity, genetic differentiation, and 'adaptive fixity' are likely to be the three major alternative evolutionary paths along which plants may evolve in response to direct selection on particular traits that is imposed by environmental heterogeneity. When we ask, 'When is it good for a plant to adjust?' we are asking in which environments is it likely that selection will favor adaptive plasticity over genetic differentiation or adaptive fixity.

### Heterogeneity

Whether spatial heterogeneity in the environment will cause selection for plasticity should depend on the scale of heterogeneity relative to the size of the responding unit, the size of the genetic individual, and the dispersal range of offspring. When an environmental factor varies on a scale much smaller than that of a response unit (e.g., a leaf in the case of sun vs. shade leaves, a whole plant or ramet in the case of allocation to roots vs. shoots), each unit may experience the full range of environmental variation. The plant may then perceive the environment as uniform (Ackerly, 1997; Wijesinghe and Hutchings, 1997), and there will be no advantage to plasticity (Fig. 2A). When the environment varies on a scale much larger than that of the plant, the environment will likewise appear uniform to the individual. However, if its offspring disperse into contrasting environmental patches, there could be intergenerational selection for plasticity. Plasticity may thus be advantageous when the environment varies on an intermediate scale, between scales somewhat larger than the size of the response unit and somewhat smaller than the dispersal range of offspring. Within this range, plasticity might be most advantageous when the environment varies on a scale most similar to the size of the response unit (e.g., Wijesinghe and Hutchings, 1997).

A second dimension of spatial heterogeneity is its amplitude, the degree to which an environmental factor varies over a given distance. Plasticity is likely to be advantageous over an intermediate range of amplitude in heterogeneity (Fig. 2A). When amplitude is so small that environmental variation has no effect on performance, plasticity will have no advantage. Above this lower limit, the advantage of plasticity may gradually increase with increasing amplitude (Wijesinghe and Hutchings, 1999). When the amplitude of environmental heterogeneity is so great that plasticity cannot enable a genotype to survive in more than one environment, plasticity should have no advantage (Fig. 2A). Even below this upper limit, locally adapted, phenotypically fixed genotypes might be selected over plastic ones if the range of phenotypes achievable through plasticity is less than that achievable through genetic differentiation (DeWitt *et al.*, 1998).

Whether temporal heterogeneity in the environment will select for plasticity in a trait should depend upon the match between the duration of environmental states and the response time of the trait (Fig. 2B). If the duration of environmental states is brief compared to the time required for a plant to detect and respond, then the environment will appear to be constant, and selection will favor genotypes that produce a fixed phenotype with the greatest average fitness across environments. If the duration of a condition is similar to the time required for response, then the plant may tend to be 'one change behind' and express the 'wrong' phenotype more often than if it maintained a fixed phe-

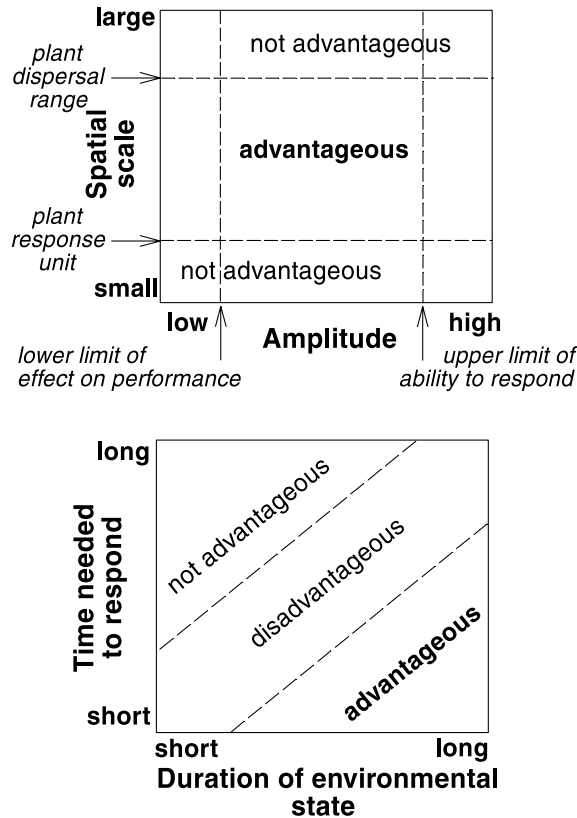


Figure 2. (A) Plasticity is expected to be advantageous only when the scale and amplitude of spatial heterogeneity are within certain bounds. The spatial scale of environmental heterogeneity must be less than the scale of offspring dispersal and more than the scale of the unit of the plant that undergoes the plastic response. The amplitude of environmental heterogeneity must be great enough to affect plant performance but not so great as to exceed the ability of the plant to tolerate the environment after making its maximum response. (B) Plasticity may be advantageous when the duration of temporal states tends to be long compared to the response time of a trait and disadvantageous when duration and response time are similar.

notype, making plasticity disadvantageous (Schmid, 1992). Plasticity is expected to be advantageous only in a trait that responds quickly relative to the duration of environmental states (Levins, 1968; Watson, 1990; Oborny, 1994; Padilla and Adolph, 1996; Cipollini, 1998; DeWitt *et al.*, 1998). However, there is as yet little experimental evidence for effects of temporal heterogeneity on selection for plasticity (Sultan and Bazzaz, 1993; Miller and Fowler, 1994; Schmid *et al.*, 1996).

The spatial and temporal scales of environmental variation might also influence the genetic mechanisms by which plasticity arises (Via *et al.*, 1995; Pigliucci, 1996; Schlichting and Pigliucci, 1998), because they influence whether

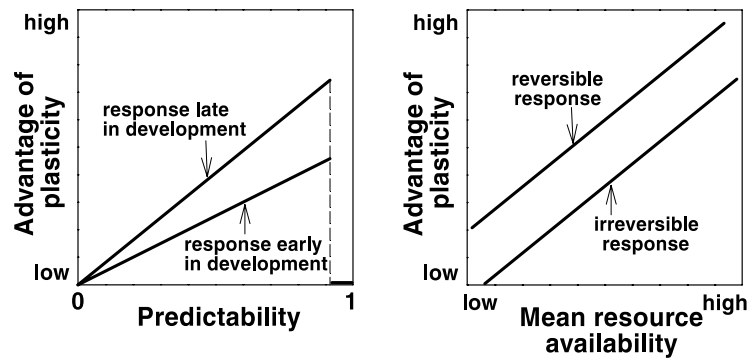
or not there is direct selection on reaction norms at the individual level. For example, spatial variation on the scale of responding modules within plants can impose selection directly on reaction norms at the individual level, since different modules of the same individual can simultaneously express different phenotypes. In contrast, Via *et al.* (1995) propose that spatial variation on the scale of the individual may impose selection only on trait states. However, there could still be direct selection on reaction norms at the lineage level, because different progeny from the same lineage may experience different environments.

Temporal heterogeneity on scales greater than the lifetime of a plant and spatial heterogeneity on scales larger than those of individual plants may select for plasticity when successive generations or different progeny commonly experience contrasting environmental conditions. In this case, lineage-level selection may favor traits that allow tolerance of change, including phenotypic plasticity for somatic characters or, some now argue, for mutation rates (Rosenburg *et al.*, 1998; Macphee, 1999). If the environment changes only slightly or in a constant direction between generations, populations may simply track the environment through evolutionary change without evolving greater plasticity.

### **Predictability and productivity**

Both spatial and temporal heterogeneity should be more likely to favor plasticity when they are more predictable, as when a detectable condition in one place and time reliably indicates a condition in another place or in the future (Levins, 1968; Via *et al.*, 1995, Schlichting and Pigliucci, 1998) (Fig. 3A). For instance, theoretical models suggest that seasonal environmental variation is likely to select for temporal plasticity in storage of carbohydrates in underground organs, whereas unpredictable environmental variation is more likely to select for continuous storage (Iwasa and Kubo, 1997). The hypothesis that predictability favors plasticity has experimental support. For example, a low ratio of red to far red light near the ground in grasslands reliably indicates higher light availability in the vertical but not in the horizontal directions. Accordingly, length tends to be more plastic in vertical than in horizontal organs of grassland herbs (Huber, 1997; Huber and Hutchings, 1997). In forests, low red:far red light ratio does not indicate higher light availability in the vertical direction for herbs, and length of vertical organs tends to be less plastic in woodland than in grassland herbs (e.g., Dong, 1995). Similarly, agricultural populations of the weed *Abutilon theophrasti* show reduced plasticity in stem elongation compared to populations from weedy fields, where *Abutilon* is more likely to be able to overtop neighbors (Weinig, 2000).





*Figure 3.* Advantage of plasticity as a function of environmental predictability and mean resource availability. (A) Plasticity may be more advantageous when the environment is more predictable, except that plasticity should have no advantage when the environment is completely predictable. The two solid lines indicate that, at most levels of predictability, a response that can be made late in development may be more advantageous than a response that must be made early in development. (B) Plasticity may be more advantageous when mean resource levels are higher. The two solid lines indicate that, at a given mean resource availability, a reversible response may be more advantageous than an irreversible one.

At very high levels of predictability, there may be a sudden breakpoint in the relationship between environmental predictability and the advantage of plasticity (Fig. 3A). Selection in extremely predictable habitats may favor fixed phenotypes (Levins, 1968; Schlichting and Pigliucci, 1998), either through fixed patterns of ontogeny or as subpopulations specialized for different conditions, such as for specific seasons or other periodic events.

At a given level of environmental predictability, plasticity that depends upon responses that can be made late in development may be more advantageous than plasticity that requires a response early in development (e.g., Schmid, 1992) (Fig. 3A). Response later in development does not require the plant to predict the environment as far in advance. Late responses may also be less disruptive to development.

Indirect cues may sometimes give more reliable predictions of longer-term environmental change than direct cues and help avoid disadvantageous responses to small or transient events (Levins, 1968). For example, photoperiod is a more reliable indicator of seasonal temperature change than temperature itself. In temperate habitats, cuing traits such as dormancy and flowering to photoperiod instead of temperature may help avoid breaking dormancy or flowering during an early thaw before a late frost (Harper, 1977). An indirect relationship between the environmental factor that selects on a trait and the factor that cues plasticity in the trait could lead to difficulty in determining whether plasticity in that trait is advantageous.

Plasticity could be more advantageous in habitats where resource availability is higher overall (Fig. 3B). Plants are likely to grow faster and to add

and turn over modules more rapidly when resources are more abundant (Chapin, 1980). This should reduce the time required for many responses and allow plants to effectively reverse responses that are irreversible at the level of the module by producing new modules. Moreover, a maladaptive plastic response, due for example to an unreliable cue, may be less likely to cause death when there is less stress due to low resource availability. Finally, at a given level of mean resource availability (Fig. 3B), reversible responses should be more advantageous than irreversible ones, because a reversible response does not permanently commit the plant to a maladaptive decision.

There is little empirical support for a relationship between resource levels and plasticity. Species from more extreme habitats may be less plastic (e.g., Emery *et al.*, 1994). However, species from habitats with different mean levels of nutrients do not appear to differ consistently in plasticity (Hutchings and de Kroon, 1994; de Kroon *et al.*, 1996; Dong *et al.*, 1996; Reynolds and D'Antonio, 1996; Fransen *et al.*, 1998). Competition between species (Grime, 1994) or selection for conflicting functions may complicate the effects of resource availability on selection for plasticity.

### **Conclusion**

In sum, it is reasonable to hypothesize that plants should have adjustable phenotypes when an environmental factor varies on the same spatial scale as a response unit, when the response of the plant is faster than the change in the environment, and when environmental variation is highly but not completely predictable. Phenotypic plasticity might also tend to be more advantageous when mean resource availability is higher, when a response can occur late in development, and when a response is reversible. There is substantial evidence for the hypothesis that predictability favors plasticity and against the hypothesis that high mean resource availability necessarily favors plasticity. Testing hypotheses about when it is good to adjust is central to understanding the diversity of plasticity in plants.

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