

## SETTING THE STAGE: PHENOTYPIC PLASTICITY AS HABITAT SELECTION

Kathleen Donohue<sup>1</sup>

Department of Organismic and Evolutionary Biology, Harvard University Herbaria, 22 Divinity Avenue,  
Cambridge, Massachusetts 02138, U.S.A.

The ability of plants to sense their environment gives them the capacity to respond to it plastically. Plastic responses, in turn, frequently alter the environment that plants experience. Plants can modify the environment they experience through many mechanisms—some approximate but others quite precise. The ability of plants to modify the environment they experience can strongly influence the evolution of characters expressed subsequently. A review of some theoretical models of habitat selection and of the coevolution of characters and their environments highlights the importance of habitat selection in plants. Novel evolutionary trajectories and outcomes result when organisms are capable of modifying the environment they experience. Specifically, characters can evolve even if they have no genetic variation, and plasticity in environment-determining characters may promote specialization in others. Divergence and reproductive isolation may even be augmented by habitat-selecting behavior in plants. An understanding of basic character evolution and the evolution of plasticity in plants requires an appreciation of the ability of plants to modify the environment they experience.

**Keywords:** correlated selection, evolving environments, germination, indirect genetic effects, review, seed dispersal, shade avoidance, specialization.

### Introduction

Niche construction occurs when organisms alter the environment they experience (Odling-Smee et al. 1996). It can occur through habitat selection, direct habitat modification, or simply resource garnering or depletion. In sessile organisms such as plants, one of the most effective ways to alter their environment is through phenotypic plasticity. Phenotypic plasticity is the ability of a genotype to alter its phenotype in response to the environment. To do so requires the ability to perceive environmental cues. With this ability comes the potential for distinguishing environmental qualities most suitable for growth and reproduction. I give some examples of how phenotypic plasticity can be considered a form of niche construction or habitat selection by plants. By responding to environmental cues, plants can control to some degree the ecological environment that they experience. This has important consequences for character evolution, since the environment can influence both the phenotypic expression of subsequent characters and the agents of natural selection to which these characters are exposed.

Some evolutionary consequences of niche construction and habitat selection have been explored thoroughly in the literature on animal behavior and in theoretical treatments. Such literature emphasizes the importance of habitat selection for specialization and divergence. More recently, the evolutionary quantitative genetics of “indirect genetic effects” on phenotypic evolution have been explored, framed again within the context of the evolution of animal behavior. Indirect genetic

effects refer to the genetic component of a social environment that influences the evolution of other phenotypes. The concept is innovative in giving the environment—in this case, the social context—the ability to evolve. I argue that if phenotypic plasticity has a genetic basis and can evolve, then plasticity can result in the evolution of the ecological environment experienced by plants. Similar to indirect genetic effects, this coevolution of phenotypes and environments can have novel evolutionary trajectories and outcomes.

First I provide some examples in which plasticity can alter the environment that plants are exposed to. Then I discuss some of the evolutionary consequences of this ability to alter the environment. I do so by discussing literature, primarily from animal behavior, that explores the consequences of niche construction in general, habitat selection in particular, and the coevolution of environments and phenotypes through indirect genetic effects.

### Plasticity as Niche Construction and Habitat Selection: Some Empirical Examples

Niche construction, or environmental modification, in plants can occur through various mechanisms. Resource depletion, litter accumulation, allelopathy, canopy formation, and even flammability are all examples of niche construction whereby plants alter their environment. When plants actually sense the environment and respond to it in ways that influence their experience of it, habitat selection results. Habitat selection for plants may be less familiar a concept than it is for animals, since plants are less mobile. However, by altering growth form and phenology in response to environmental stimuli, plants can nevertheless alter the environment that they experience and sometimes even the life stage that is exposed

<sup>1</sup> E-mail kdonohue@oeb.harvard.edu.

to different environments. The lack of mobility of plants, on the one hand, increases the importance of plasticity of sessile life stages in mediating the experienced environment and, on the other hand, increases the importance of responses to environments experienced during nonsessile stages.

Bazzaz (1991) has reviewed several mechanisms whereby plants alter their resource environments through modifications of their modular structure. Plants can express morphological changes that enable a plant to grow beyond areas with scarce resources and changes that enable plants to remain in and take advantage of areas with abundant resources. Foraging behavior by clonal plants has been investigated intensively as a mechanism whereby plants sample over wide spatial areas and harvest resources in areas of their abundance (review Bazzaz 1991; de Kroon and Hutchins 1995; Huber et al. 1999). Such sampling most frequently takes the form of plastic meristem development, whereby photosynthesizing structures develop in areas of higher light availability or roots develop in areas of higher nutrient or water availability (de Kroon and Hutchings 1995). Nonclonal plants have also displayed plasticity to resource availability in ways that can increase resource uptake through selective root development or leaf placement (review de Kroon and Hutchins 1995; Sultan 2000).

Not all responses to variable resource environments result in an improvement of the quality of the environment that a plant inhabits. Some responses, such as decreased biomass and developmental rates, may merely reflect the limitation of resources or the presence of stress (Sultan 1987, 1995; Schlichting and Pigliucci 1995). In fact, plasticity in a single character may simultaneously include passive responses to resource limitation and active plastic responses that ameliorate the adverse effect of resource limitation (Sultan and Bazzaz 1993a, 1993b, 1993c; Sultan 1995). One goal is to distinguish changes in morphology, physiology, and phenology that reflect resource limitation and stress from adaptive plastic responses that alleviate such adverse environmental challenges. The distinction between “passive” responses due to resource limitation and “active” responses that alter resource acquisition (Schlichting and Pigliucci 1995) is not always appropriate; however, “passive” responses to resources may actually increase total resource acquisition, and resources themselves may stimulate “active” adaptive responses (Forde 2002). Nevertheless, this distinction is appropriate when plants respond to environmental cues and, by doing so, increase the availability of resources. In such cases, responses to cues can be considered habitat selection. Distinguishing responses to cues versus resources is frequently difficult, but the distinction is necessary to identify traits most closely associated with habitat selection. The examples below illustrate how such distinctions can be made by using a well-characterized system of plastic responses to light.

#### *Plastic Shade Avoidance Responses: Plasticity to Cues and Resources*

Photomorphogenic shade avoidance responses illustrate how plasticity to cues of environmental quality can alter the resource quality experienced by subsequent characters and thereby alter their expression. This example serves to (a) demonstrate how to distinguish between responses to cues com-

pared with responses to resources, and thereby to identify potential habitat-selecting characters, and (b) show that habitat selection through plasticity to cues can influence the phenotypic expression of other characters, including important life-history characters.

The shade avoidance response is a classic example of phenotypic plasticity in plants (Smith 1982; Casal and Smith 1989; Ballaré et al. 1990; Smith et al. 1990; Schmitt and Wulff 1993; Schmitt et al. 1995, 1999; Schmitt 1997). It refers to morphological and phenological responses to altered light quality caused by vegetation shade. In this well-studied system, much is known about both the molecular basis of the environmental sensing involved in the response and the ecological context of those environmental cues. This example, therefore, serves to illustrate the relationship between sensing environmental cues and altering the quality of the environment experienced by responding to those cues.

*Distinguishing responses to cues compared with resources.* Plants can sense the presence of neighbors through sensing variations in light wavelengths. Green leaves absorb red light and transmit or reflect far-red light. Beneath or beside a vegetation canopy, therefore, not only is the availability of photosynthetically active radiation (PAR) lower, but the red to far-red ratio (R : FR) of light is also lower. A family of photoreceptors, the phytochromes, senses the R : FR, and plants can respond to this cue even before they experience direct competition for the light resource (Smith 1982, 1995; Casal and Smith 1989; Smith and Whitelam 1990). Hence, the response to R : FR is termed the “shade avoidance response.” Plants grown at high density frequently exhibit pronounced stem elongation, reduced branching, and early flowering (Weiner 1985, 1990; Schmitt et al. 1986; Geber 1990; Weiner and Thomas 1992).

In *Impatiens capensis*, Donohue and Schmitt (1999) compared responses to vegetation shade caused by high density and responses just to the R : FR cue that predicts density. They used selective light filters to manipulate the R : FR cue independently from density and found that stem elongation and flowering rate responded directly to the R : FR cue, with low R : FR causing longer internodes and faster flowering. Branch production did not respond to R : FR, but it nevertheless responded to high density, with plants at high density suppressing branch production. Therefore, some traits responded to the environmental cue of R : FR, while other traits responded to other aspects of the density environment, such as light availability.

Shade avoidance responses have also been studied extensively in *Arabidopsis thaliana* (Levy and Dean 1998; Pigliucci and Schmitt 1999; Botto and Smith 2002), which accelerates flowering in response to low R : FR characteristic of vegetation shade. By manipulating light quality independently of density using selective light filters, Dorn et al. (2000) dissected responses to density into responses to the R : FR and responses to light availability. They observed delayed reproduction at low density when the light resource alone (PAR) was reduced, and this plasticity to low PAR was maladaptive. However, plants responded to low R : FR by accelerating flowering and by flowering at a smaller size, and this plasticity to low R : FR was adaptive. This adaptive plasticity counteracted the adverse effects of slower growth rates under low PAR and

vegetation shade. The combined responses led to very little plasticity to density itself. In this example, a single character responded to both cues and resources, with the plastic response to cues being the adaptive response.

As the physiological mechanisms of plastic responses become characterized in other systems, such independent manipulations of cues and resources will be possible. These manipulations can identify characters that respond to resource cues as opposed to resources themselves. These characters may be more likely to exhibit adaptive plasticity than characters that respond to resource availability itself (Sultan 1987, 1995; Sultan and Bazzaz 1993a; Schlichting and Pigliucci 1995), since characters that respond to cues can respond before resource limitation actually occurs. Therefore, characters that respond to cues might be particularly good candidates for “habitat-selecting” traits that can influence the environment experienced at later life stages.

*Shade avoidance influences environmental quality.* By elongating internodes in response to low R : FR, plants can overtop their neighbors, avoid direct shading, and increase the light available to them. The effectiveness of this response is visually striking in the field, since one views small, suppressed individuals pining beneath a heavy canopy of taller, flourishing neighbors. The improved quality of the environment accompanying stem elongation has been demonstrated in several studies of natural selection on shade avoidance responses. For example, Weinig (2000a, 2000b) found evidence in *Abutilon theophrasti* that stem elongation was advantageous only when it resulted in increased light availability. Elongation throughout life increases light availability when the plants are grown in weedy fields, and elongation was found to be adaptive in these sites. In soy fields, however, light is limiting only later in life after the soy becomes established, and elongation only late in life was shown to be adaptive. In cornfields, where plants cannot overtop corn, elongation later in life does not increase light availability, and it was found to be maladaptive because of carbon costs of elongation. Shade avoidance responses have also been found to be more pronounced in populations that evolved under open-canopy conditions than under closed-canopy conditions where elongation is not effective at overtopping tree canopies (Morgan and Smith 1979; Dudley and Schmitt 1995; Donohue et al. 2000b), suggesting adaptive variation in shade avoidance. In these examples, the adaptive nature of plasticity depends directly on the ability of plasticity to alter the resource environment.

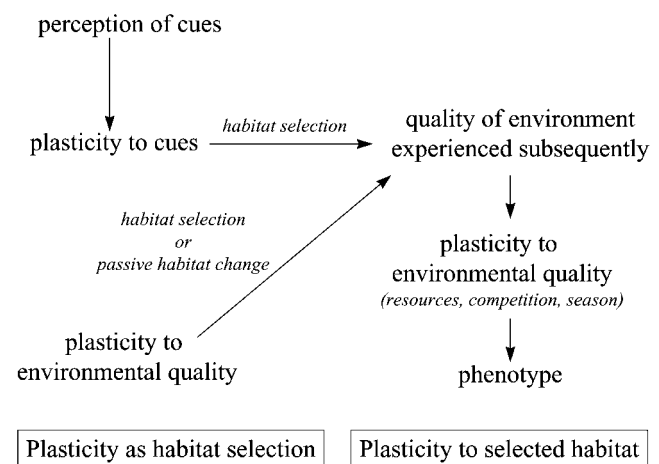
Flowering time also responded directly to the R : FR cue. This phenological response can alter the resource availability experienced by critical life stages, such as developing fruits. By flowering early, plants may mature fruits before canopy closure when light resources are still available. Flowering time can determine the environmental quality during seed maturation in a more general manner when environmental quality deteriorates or the probability of mortality increases predictably over time (Schemske 1984; Lacey 1986; Fox 1990; Bennington and McGraw 1995; Bierre 1995). In the *Impatiens* system (Donohue et al. 2000b), plants died earlier at high density, and plants that flowered earlier set more fruits before they died. In this example, the cue of low R : FR was not only a cue of high density but also a cue of conditions that led to early mortality. By flowering earlier, plants were able to mature

fruits before they experienced conditions of stress and imminent senescence. In this manner, plasticity in this phenological trait determined the environmental quality experienced during fruit maturation.

These two examples of shade avoidance responses through elongation and accelerated flowering demonstrate how effective plasticity to cues can be in determining the quality of the environment that plants experience. Both morphological and phenological responses have the potential to alter the environmental quality experienced by plants.

*Plasticity in shade avoidance characters influences phenotypic expression of other characters.* Habitat selection can influence the expression of other characters whose phenotype depends on environmental quality. In particular, the plasticity of characters that respond to cues, such as stem elongation, can in turn alter the expression of characters that respond to resources, such as branch production. In the *Impatiens* system (Donohue et al. 2000a), this dynamic is evident from the relationship between elongation and meristem allocation at high density. Poorly elongated plants—those lower in the canopy of the high-density stands—allocated most meristems directly to flowers and thereby flowered earlier. Plants that elongated the most at high density, in contrast, tended to keep meristems inactive or allocated them to branches. Therefore, the elongation response at high density apparently altered the environment experienced by the plants and thereby altered their pattern of meristem allocation. Thus, plasticity as habitat selection can influence the phenotypic expression of characters associated with general life history such as size and timing of reproduction.

*Double plasticity.* In summary, the above are examples of plasticity to environmental cues and environmental quality. Plasticity in characters that respond to cues can determine the environmental quality experienced by the plant and can thereby influence further phenotypic expression and fitness (fig.



**Fig. 1** Double plasticity. Plasticity to cues can be considered habitat selection, which changes the quality of the environment experienced subsequently. Passive or active responses to environmental quality itself can also alter the environmental quality experienced subsequently. Other characters, in turn, respond plastically to the altered environment.

1). This plasticity can result in habitat selection in space, as in the example of stem elongation, or habitat selection in time, as in the examples of flowering time. A second episode of plasticity is the plasticity of subsequent characters in response to the environment created by the first. Such plasticity can be distinguished experimentally from plasticity to cues of resource availability.

Future physiological studies can identify particular ecological cues that elicit plastic responses and can determine which resources or environmental stresses the cues predict. With this knowledge, experimental manipulations that independently alter cues and resources can identify key plastic characters that respond to cues directly. We can then determine how plasticity in such characters alters the environmental quality experienced by subsequent characters through genetic studies such as those described. Studies that investigate how suites of plastic characters respond to environmental variation should take into account the fact that the relationship among plastic characters may depend not only on the shared genetic basis of these characters but also on the manner in which some characters modify the environment that determines the expression of other characters.

To explore further how variation in some characters can influence the expression of other characters, I focus now on examples in which the temporal priority of character expression is explicit. I will give two examples of how plasticity in characters of early life stages influences the environment experienced at later life stages.

#### *Seed Dispersal: Voting with Their Seed*

A seed is the most mobile stage in a plant's life history, and for some plants it is the only mobile stage. Seed dispersal, therefore, offers plants the rare opportunity to change location if the maternal site is unsuitable. Dispersal directly to high-quality sites can occur when animals disperse seeds to friable anthills, nutrient-rich animal droppings, or light gaps, for example (review Howe and Smallwood 1982; Bazzaz 1991). Passive dispersal can enhance site quality by decreasing sibling competition. Variation in the timing of dispersal can also influence environmental conditions experienced by offspring by determining the availability of dispersing agents (Willson and Traveset 2000) and the seasonal environment experienced by seeds (Lacey and Pace 1983; Baskin and Baskin 1984). Frequently, however, the choice offered by dispersal is simply whether to stay in the maternal home site.

It is nevertheless precisely this choice that structures all models of the evolution of dispersal (review Ronce et al. 2001). The premise behind these theoretical treatments is that this choice of whether or not to disperse influences the quality of the environment experienced by progeny. Plasticity in the dispersal of one's progeny therefore has the potential to determine both the environmental quality and the variation in the environment experienced across generations. It has been shown theoretically (McPeck and Holt 1992) that plasticity of dispersal can significantly alter its evolution, favoring habitat-specific dispersal even in temporally stable environments.

Any habitat selection through dispersal would occur through plasticity of the maternal parent, since seed dispersal is determined by the maternal parent, not by the seeds themselves

(Roach and Wulff 1987; Theide and Augspurger 1996; Donohue 1999). Plasticity in seed dispersal is probably common but has seldom been documented. Plasticity in maternal phenology can cause variation in the timing of dispersal (Lacey and Pace 1983; Lacey 1986), and plasticity in maternal architecture and inflorescence structure can cause plasticity in the seed shadows themselves (review Donohue and Schmitt 1998). In particular, many characters of plant size and productivity that strongly influence postdispersal seed shadows are also highly plastic to environmental quality. Dispersal itself, therefore, is likely to exhibit plasticity in response to environmental quality.

Such plasticity raises the possibility that maternal parents alter the dispersal of their progeny when conditions at the home site are poor. A few studies have demonstrated that maternal plants growing in poorer conditions tend to disperse their seeds more effectively (Donohue 1999; Imbert and Ronce 2001), but many other species decrease the proportion of readily dispersing seeds under stressful conditions (Venable and Levin 1985; Imbert and Ronce 2001 and references therein).

Although efficient dispersal can influence the quality of the environment experienced by seeds, it is not at all clear that plasticity in dispersal is, in the strict sense, habitat selection, even in examples in which plasticity did result in dispersal away from poor conditions. In *Cakile edentula*, for example (Donohue 1998), plasticity in dispersal resulted primarily from variation in the number of branches and in the overall size of plants; plants growing in favorable sites were larger and had more branches that trapped the more numerous fruits, thereby impeding dispersal. That is, the observed plasticity in dispersal appears to be the result of responses of the maternal plant directly to resources rather than to cues of resource availability. In this sense, the plasticity is a "passive" response (Sultan 1987; Schlichting and Pigliucci 1995) rather than active habitat selection. It is possible that other plastic responses less closely related to the condition of the maternal parent may influence progeny dispersal. For example, qualities of fruit morphology, pericarp structure, and abscission properties may influence dispersal more independently of plant condition and may therefore be characters that evolve more through their consequences for dispersal rather than through their association with maternal fitness. Imbert and Ronce (2001) argued that pure developmental constraints of inflorescence morphology in *Crepis sancta* would result in fewer dispersing seeds under stressful conditions, on the basis of observations in other Asteraceae, yet they observed an increase in dispersing seeds under stressful conditions. Their result indicates that the plasticity in dispersal they observed was not simply due to developmental constraints associated with maternal vigor. Very few empirical studies have sought to distinguish these possibilities, but such distinctions are likely to enhance our currently meager understanding of the evolutionary potential of dispersal.

It remains, however, that resources during fruit maturation and dispersal very likely do predict resources available for progeny at that site. In this manner, responding to a resource is the same as responding to a cue, since the resource in one generation is a cue for resource availability in the next generation. The distinction between cues and resources, therefore, may be less informative for maternally determined characters,

such as seed dispersal, than for nonmaternal characters, such as shade avoidance.

Whether plasticity in dispersal is an example of habitat selection or, more probably, merely a correlated response of plasticity (adaptive or not) of maternal characters to habitat quality is to some degree irrelevant. Either way, plasticity in dispersal will very likely influence the environment experienced by progeny. It is, therefore, an example of niche construction even if not of habitat selection. Whether such plasticity results in predictably higher- or lower-quality environments for progeny or results in increased or decreased variation in environmental quality across generations depends on the nature of the plastic responses of maternal characters and how specific maternal characters determine dispersal.

The postdispersal environment is clearly crucial for determining phenotypic expression by dispersed progeny (Murren et al. 2001). Site quality, intensity of competition, and seasonal conditions all can vary with dispersal and all strongly influence morphological, phenological, physiological, and life-history expression. Habitat selection through dispersal, or simply plasticity in dispersal that results in niche construction, will influence the expression of many crucial postdispersal characters.

#### *Germination: The Importance of Timing*

When to germinate is a very important decision for a seed, since, by germinating, the seed essentially commits the seedling to grow in whatever conditions elicited germination. This initial decision can influence the plant for the rest of its life, since it determines the environment that postgermination stages must contend with. This environment can influence not only phenotypic expression of postgermination life stages but also the environment of natural selection experienced by these stages. Therefore, plastic germination responses can influence life-history evolution in a very general manner by influencing life-history expression and natural selection on life-history characters.

*Germination cueing as habitat selection.* Examples of germination cueing are abundant in the literature (Baskin and Baskin 1998). Temperature is a cue of seasonal conditions to which many seeds respond precisely in their germination behavior. Seeds usually require very particular temperature regimes in order to germinate; certain temperatures are often required to break dormancy, and other temperatures are required to allow germination after dormancy is broken. Such temperature requirements for germination accurately determine the season of germination. Other germination requirements also predict seasonal conditions (Guterman 1994). Desert plants often have very thick seed coats that require scarification in order to germinate. Scarification most frequently occurs during dispersal by seasonal flood waters; the requirement for scarification thereby insures adequate water for growth. Other desert plants require prolonged periods of water to germinate if the temperature is high. In some species, this requirement is mediated by the concentration of salt that accumulates in soils, such that low soil salinity indicates that adequate rains have arrived. Other odd germination requirements include extreme heat, which increases the probability of establishment in high nutrient, noncompetitive conditions after fire, and acid treatment, which can prevent germination

before a seed has been dispersed by an animal (Baskin and Baskin 1998).

In addition to responding to cues experienced by seeds after dispersal, germination can respond to environmental cues experienced during seed maturation on the maternal plant (review Baskin and Baskin 1998; Guterman 2000). Like dispersal, germination is controlled in part by the maternal parent, since the pericarp and seed coat are maternal tissue and can act as mechanical constraints or environmental filters for the embryo (Roach and Wulff 1987). Cues experienced in the maternal generation can interact with postdispersal cues to determine the conditions for germination. For example, in *A. thaliana*, a short photoperiod during seed maturation was shown to increase the ability of postdispersal cold to break dormancy, thereby providing a mechanism whereby seeds that were matured under short days can germinate in the spring as opposed to waiting until autumn (Munir et al. 2001). Also in *A. thaliana*, a low R : FR environment experienced by the maternal plant during seed maturation, indicative of a vegetation canopy, induced a light requirement for germination in its seeds (McCullough and Shropshire 1970; Hayes and Klein 1974), thereby decreasing the probability that seeds will germinate into competitive conditions beneath a vegetation canopy. These numerous examples demonstrate that germination requirements, or plastic germination behavior, can act as extremely precise mechanisms of habitat selection.

*Germination timing influences life-history expression.* This initial act of habitat selection can have profound influences on the rest of the life of the plant. Much fundamental life-history variation depends on variation in the timing of germination. Examples abound in which variation among taxa in germination responses and life history indicate that these traits have evolved into adaptive syndromes (review Baskin and Baskin 1998). For example, serotiny—the requirement for fire in order for seeds to be released from cones and to germinate—and traits related to performance in postfire environments are associated in pines (Schwilk and Ackerly 2001). Within species, variation in germination has also been shown to influence life-history expression. In *Campanula americana*, seeds germinate either in the autumn or in the spring (Baskin and Baskin 1984; Kalisz and Wardle 1994). Those that germinate in the autumn exhibit an annual life history, whereas those that germinate in the spring are biennials because of a requirement for cold vernalization for reproduction. Therefore, environmental conditions that influence the season of germination also influence life-history expression (Galloway 2001a, 2001b). Similarly, germination timing in *A. thaliana* determines whether a plant will be a summer annual or a winter annual and may even determine whether two generations can be completed within a single year (Thompson 1994; Munir et al. 2001). Therefore, plastic germination responses can influence fundamental life-history expression.

*Germination influences natural selection on postgermination characters.* By determining the environment to which later life stages are exposed, plastic germination behavior can influence not only the expression of life-history characters but also natural selection on those characters. In *A. thaliana*, the timing of germination in the autumn was shown to influence not only the size and timing of reproduction in the spring but also the strength and mode of natural selection on these life-

history characters (Donohue 2002). In this example, the change in natural selection was not because the plants experienced different environments when they germinated at different times. Rather, the plants were exposed to similar agents of natural selection but at different life stages, and the quality of natural selection depended on the life stage that experienced a particular selective environment. One could easily imagine, however, that germination timing could determine exposure to completely different selective agents, such as winter temperatures, which would contribute to differences in natural selection on life histories. Weinig (2000a) found evidence that selection on stem elongation depended on germination timing, since germination timing influenced the competitive environment experienced by newly emerged seedlings. Germination responses are therefore likely to strongly influence natural selection on life histories and morphology by influencing which selective environments plants are exposed to and which developmental stage is exposed to selection.

These examples illustrate how plastic germination responses can be precise mechanisms of habitat selection and how they can influence the environment experienced by later life stages. Plastic germination responses to environmental cues can determine not only the phenotypic expression of later life stages but also the environment of natural selection experienced by the plant at all stages.

### Evolutionary Consequences of Plasticity as Habitat Selection

#### *Character Coevolution: A Different Sort of Genotype-Environment Interaction*

The above examples illustrate how plasticity in one character can influence the environment experienced by other characters. In the examples of foraging and shade avoidance, the light environment of the plant was determined by its plastic responses. In the case of dispersal, the density or general quality of the environment varied with variation in dispersal, and in the case of germination, the seasonal environment experienced by later life stages depended on the initial germination response of the seed. Plastic responses of such characters, therefore, can influence the evolution of other characters through two sources: first, they can influence the opportunity for selection by influencing phenotypic expression, and second, they can influence what the agent of natural selection on those characters may be.

The opportunity for selection depends on the phenotypic variation in the character under selection and how far from the optimum the mean of the character distribution is. In the above example of germination in *Arabidopsis thaliana*, plants that had germinated later in autumn were smaller, farther from the optimum, and therefore exposed to stronger selection (Donohue 2002). Likewise, they flowered later, shifting the distribution closer to the fatal end-of-season drought period, and thereby experienced stabilizing selection rather than simply directional selection for delayed flowering at a larger size, as was observed in earlier germinating plants. Thus, variation in phenotypic expression alone can alter the strength and mode of natural selection. When the agent of selection changes as well, character evolution can be fundamentally altered.

The combined ability of habitat-selecting plasticity to influence the opportunity for selection and the agent of selection on other characters implies that many characters coevolve with plastic characters. Evans and Cabin (1995) proposed that character coevolution could be strongly influenced by the ability of germination responses to determine the ecological environment experienced by postgermination stages. On the basis of their system of *Lesquerella fendleri*, a desert mustard, they maintained that moisture requirements for germination are expected to coevolve with postgermination physiological properties, such as water use efficiency. By determining the degree of water stress to which seedlings are exposed, germination responses essentially mediate the intensity of selection to which postgermination stress-response characters are exposed. If the postgermination characters have responded to such mediated selection, they argue, then one expects genetic associations between germination responses and postgermination physiology.

Such an argument has great generality beyond the system of germination and physiology. Any character that alters the environment experienced by subsequent characters is subject to the same dynamic. For instance, plants that have great resistance to herbivory may have altered selection on tolerance to herbivory (Tiffin and Rausher 1999) and may evolve to be less tolerant to herbivory (Fineblum and Rausher 1995). Water-conservation strategies may evolve less when the plant is able to alter the moisture environment by foraging. Adaptations to shade environments may be less developed in plants that are able to elongate above a canopy or place ramets in high-light locations. Cold tolerance or desiccation resistance of seedlings may not evolve in plants that require warm conditions or abundant water for germination. In fact, many physiological capacities may evolve in concert with phenotypic responses that ameliorate environmental challenges. The evolution of physiological limits and phenological patterns of life histories may strongly depend on the degree of plasticity in other characters and the efficacy of plasticity to alter selective environments.

Environments that organisms experience can evolve through the evolution of plastic habitat-selecting characters. The evolutionary significance of this is that character coevolution depends not only on the genetic basis of the phenotypic expression of characters but also on how some characters alter the environment experienced by other characters. In typical formulations of phenotypic plasticity, a genotype-environment interaction refers to how a particular genotype responds to the environment. In this formulation, how the environment that an organism experiences depends on a particular genotype is equally crucial.

The ability of plants to modify the environment they experience has important consequences for the evolution of other traits. I explore these consequences by reviewing briefly the literature on habitat selection and that on the coevolution of environments and characters.

#### *Evolutionary Consequences of Niche Construction and Habitat Selection*

When organisms alter the environment they experience through any mechanism of niche construction, the altered environment can impose different modes of natural selection than

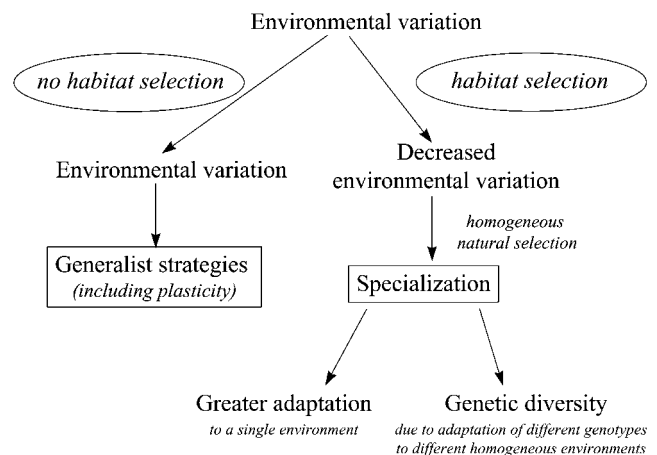
would otherwise be experienced. The different mode of selection can cause different phenotypes to be favored. Theoretical models have shown that niche construction can cause the fixation of alleles that would otherwise be deleterious, eliminate alleles that would otherwise be favored, and alter states of stable polymorphism (Laland et al. 1996, 1999; Odling-Smee et al. 1996). For example, when niche-constructing behavior improves the environment, the allele that performs best in the improved environment would be favored instead of the allele that would have been favored had the environment remained poor.

Habitat selection is a form of niche construction whereby organisms inhabit a particular environment more frequently than would be expected on the basis of its frequency in the landscape. It frequently includes some sort of perception of environmental conditions and a choice or response to those conditions. The most robust theoretical consequence of habitat selection is that specialization to the chosen habitat becomes more likely. As a consequence, adaptive polymorphisms become more stable (fig. 2).

The role of habitat selection in promoting specialization was recognized very early (Levins 1968). As organisms experience more variable environments, generalist strategies evolve more easily. Habitat preference reduces the exposure of organisms to one environment and thereby enables the divergence of the population into genotypes that are adapted to the habitat of choice (Levins 1968; Holt 1987; Rosenzweig 1987; Brown 1990). As adaptation to one environment is maximized, extreme morphology and physiology can be manifest (Rosenzweig 1987; Brown and Pavlovic 1992), which in turn can contribute to reproductive isolation (Maynard-Smith 1966; Rausher 1984; Rice 1987; de Meeus et al. 1993). Such divergent specialization can facilitate the maintenance of diversity, though sometimes subtly (Hoekstra et al. 1985; Jaenike and Holt 1991). Habitat selection is especially effective at maintaining diversity under soft selection (that is, when fitness is locally rather than globally regulated such that groups with different genetic composition contribute equally to the next generation; Maynard-Smith 1966; de Meeus et al. 1993) and when habitat preference is correlated to performance in the preferred habitat (Templeton and Rothman 1981; Rausher 1984; Garcia-Dorado 1986).

Even without the conflicting requirements of adaptation to different environments, habitat selection can increase rates of evolutionary response to selection (Whitlock 1996). This effect is primarily due to the more homogeneous selective environment experienced by individuals with narrow niches; this homogeneity is more effective at fixing favorable and purging deleterious alleles. Holt (1987) also proposed that habitat selection can reduce gene flow, increase population growth rates and population size, and consequently increase adaptation through indirect mechanisms such as reduced drift and gene flow. Therefore, habitat preference can increase the mean fitness of populations and result in more specialized adaptation, even without trade-offs in performance across environments.

These consequences of habitat selection depend on the mechanism of habitat preference. Hypothesized mechanisms include preference for natal sites (Maynard-Smith 1966; Hoekstra et al. 1985), preference for a site type independent of performance in that site, and preference for a site in which perform-



**Fig. 2** Evolutionary consequences of habitat selection. Habitat selection reduces the degree of environmental variation experienced subsequently, promoting specialization and divergence.

ance is maximized (Jaenike and Holt 1991; de Meeus et al. 1993). The last sort of habitat preference is most effective at promoting specialization and maintaining diversity (Jaenike and Holt 1991; de Meeus et al. 1993). How common these different mechanisms are in natural plant systems is not known.

In order for habitat selection to promote divergence and maintain polymorphism, it must be variable within populations (Rausher 1984; Jaenike and Holt 1991; de Meeus et al. 1993). One mechanism that can maintain variation in habitat preference is frequency-dependent selection on habitat preference such that preference for alternative habitats is favored when the optimal habitat becomes too crowded (Templeton and Rothman 1981; Rausher 1984; Rausher and Englander 1987; Jaenike and Holt 1991). Another mechanism, more recently identified, is the temporal stochasticity in the reception of cues of environmental quality (Storch and Frynta 1999). If habitat choice is predicated on discriminating “better” from “worse” environments, the preference necessarily depends on the environments experienced previously by a population. If environments are experienced in a random temporal sequence, then different habitat preferences can evolve. A third mechanism to maintain variation in habitat preference depends on polymorphism in loci that influence adaptation to different habitats. If such variation exists, then a new variant of habitat choice can be favored in individuals that are adapted to the alternative habitat (Jaenike and Holt 1991). This mechanism, however, requires a correlation between preference for a habitat and performance in a habitat.

Many models that include habitat preference postulate such a correlation; namely, that organisms prefer the habitat in which they perform best. Such correlations between preference for a habitat and performance in a habitat can evolve when both habitat preference and habitat-specific performance are genetically variable (Taylor 1976; Garcia-Dorado 1986; Jaenike and Holt 1991). The correlations can occur through either pleiotropy or physical linkage or when habitat choice itself is based on performance (Jaenike and Holt 1991). Correlations caused by selective linkage disequilibrium alone are more dif-

difficult to acquire (Garcia-Dorado 1986), and when frequency-dependent habitat selection is present, such correlations may not occur at all (Rauscher 1984). Empirical evidence, in fact, does not always find such correlations. Surprisingly, melanic moths, for example, express genetic variation for both body color and for the color of resting sites. However, pale moths did not prefer pale resting sites (Grant and Howlett 1988). This example emphasizes the need for empirical investigations of the genetic relationship between habitat preference and loci under selection in different habitats. This is especially important since this relationship determines the effectiveness of habitat selection in altering the evolutionary dynamics discussed above.

Recall that such correlations between habitat selection and performance have also been predicted in plant systems. Specifically, Evans and Cabin (1995) argued that germination cueing is an effective method of habitat determination and that postgermination physiological characters should show genetic correlations with germination behavior. Very few studies in plants have tested the hypothesis of genetically based associations between habitat-selecting characters and other characters under selection, nor the hypothesis of correlational selection among such characters (see Schwilk and Ackerly 2001 for an example with a niche-constructing character). The presence of such correlations is a fundamental component of models with habitat selection and has consequences for degrees of adaptation, adaptive divergence, and even reproductive isolation. The dearth of empirical studies in plants to test whether such correlations exist most likely derives simply from the lack of recognition of the various methods by which plants determine the environment they experience.

Several pressing empirical questions in plant evolutionary ecology become obvious in light of the theory on habitat selection. In particular, (a) Does variation in habitat preference exist in plant populations? (b) If so, what causes it? Frequency-dependent selection is hypothesized to be a major contributor to variation in habitat selection in animals, but its comparable role in plants is completely unknown. Further studies on mechanisms of cue acquisition and the accuracy of cues in predicting selective environments could contribute to our knowledge of how variation in habitat selection might be maintained in plants. (c) How strong are correlations between habitat selection and performance within a habitat? Estimates of such correlations would provide valuable information on whether habitat-selecting behaviors in plants are likely to contribute to specialization and divergence. (d) What is the genetic basis of correlations between habitat preference and performance, if they exist? In particular, distinguishing between pleiotropy, linkage, and linkage disequilibrium would reveal how likely such correlations are that contribute to increased adaptation and/or divergence. (e) Given the much stronger effect of habitat selection under soft selection than hard selection, what is the relative importance of soft selection in plant populations? (f) Finally, does habitat selection (especially temporal habitat selection, it seems) contribute to population divergence and reproductive isolation in plants? The contribution of habitat selection to specialization and divergence in plants has rarely been evaluated. The extent to which habitat selection can increase the degree of specialization of genotypes, increase the mean fitness of populations, and contribute to divergence and

even reproductive isolation necessitates explicit studies of habitat selection in plants.

### *Coevolving Environments and Phenotypes: Indirect Genetic Effects*

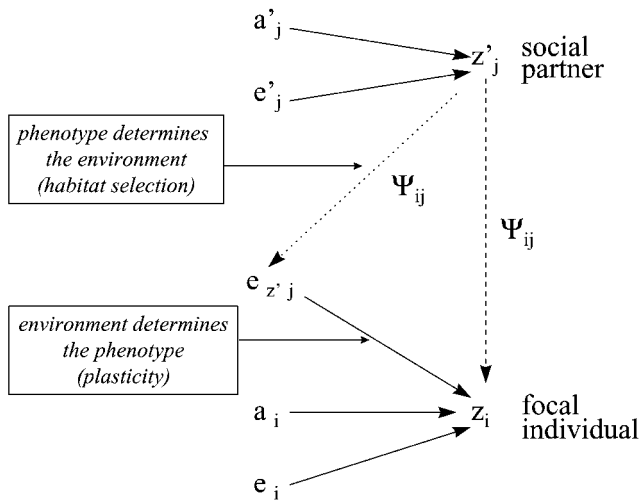
The above discussion of habitat selection reviewed population genetic models of the coevolution of phenotypes and the probability of experiencing a particular environment. The following discussion reviews quantitative genetic models of the coevolution of phenotypes and environments when those phenotypes exhibit plasticity to the environment. Recent theoretical investigations of “indirect genetic effects” concern the coevolution of traits and their environments. These models were originally developed to explain the evolutionary dynamics of social interactions, including parental care. With a slightly modified orientation, they can also be applied to the coevolution of habitat-selecting traits and other traits whose expression depends on the selected habitat.

These quantitative genetic models are uniquely appropriate for investigating these dynamics because they postulate that the environment that an individual inhabits—the social environment—is in part genetically determined and therefore can evolve. It is the evolution of the environment itself that contributes the special evolutionary dynamics. The environment is termed the “social environment” because it is determined by other individuals that possess evolving genotypes. These individuals can be unrelated to a focal individual expressing a trait of interest, they can be related as kin, or they can be parents. Who determines the environment of the focal individual is flexible in these models. In the empirical examples of habitat determination in plants above, it was usually either the individual itself or its maternal parent that determined the environment.

Griffing (1981a, 1981b, 1981c, 1981d, 1989) introduced the concept of “indirect genetic effects” to model how the “social environment” of plants, or the genetic composition of competitors, influences evolutionary outcomes. Moore et al. (1997, 1998) further developed the quantitative genetic evolutionary dynamics of this phenomenon as an investigation of traits that exhibit plasticity in response to the environment created by individuals with whom an individual interacts (fig. 3). The first important component of phenotypic expression in their model is therefore (a) plasticity, in this case, to the social environment. This is measured by the interaction coefficient and is given the notation  $\Psi_{ij}$ . The second important component is (b) the genetic basis of traits in the interacting conspecifics that influence the expression of interacting phenotypes, that is, the genetic basis of that social environment, or  $a'_j$ . This genetic component is termed the “indirect genetic effect.”

In a slightly later formulation (Wolf et al. 1998; fig. 3), separate paths are explicitly indicated in their figures for the effect of one phenotype,  $z'_j$ , on the environment experienced by another phenotype,  $e_{z'_i}$  (this path coefficient also being designated  $\Psi_{ij}$ ), and for the effect of that environment,  $e_{z'_i}$ , on the expression of another phenotype,  $z_i$ . The first path corresponds to the effectiveness of habitat selection in the empirical examples above (how a character influences the environment), and the second corresponds to the plasticity of other characters





**Fig. 3** Indirect genetic effects. Modified from Moore et al. (1997) and Wolf et al. (1999);  $a'_j$  is the additive genetic contribution to the environment-determining phenotype,  $z'_j$ ;  $e'_j$  is the environmental contribution to that phenotype;  $a_i$  and  $e_i$  are the additive genetic and environmental contributions to the phenotype,  $z_i$ , that responds to the environment created by  $z'_j$ ;  $e_{z'_j}$  is the environmental contribution to phenotype  $z_i$  caused by phenotype  $z'_j$ . Two paths with  $\Psi_{ij}$  are shown since  $\Psi_{ij}$  was presented differently in the figures of these two publications. The “social partner” of Moore et al. (1997) can be, in the examples here, the individual itself or a parent that determined the subsequent environment.

to the selected habitat. Therefore, both the determination of the environment by genotypes and the response of phenotypes to the environment are included.

Selection on traits that respond to their social environment comprises “natural selection” associated with expressing a phenotype and “social selection” on that phenotype operating through the environment created by the interaction between individuals (Wolf et al. 1999). The covariance between the focal character,  $z_i$ , and the social environment,  $z'_j$ , creates correlated selection on the focal character by selection acting on the environment-determining character.

The covariance term between the focal character and the social environment includes covariance due to plasticity to the social environment (i.e.,  $\Psi_{ij}$ ) as well as genetic covariance (Wolf et al. 1999). The genetic covariance includes both the shared genetic basis of character expression of the two traits due to pleiotropy or linkage disequilibrium and the covariance due to relatedness between the focal individual and the individuals that create the social environment. This last component of the covariance will always be larger when the individual itself determines or when parents determine the environment, as in many examples of habitat selection in plants mentioned above, than when other individuals determine the environment. Hence, the dynamics described in the model below will be even more pronounced for the examples in plants discussed above.

Because of the correlated response to selection, evolutionary change in one character,  $\Delta \bar{z}_i$ , depends not only on the genetic variation in that character and natural selection acting directly on that character but also on the genetic and phenotypic relationship between that character and its “social” environment

and on selection acting on that environment-determining character. This is described by the following equation:

$$\Delta \bar{z}_i = (G_{ii} + \Psi_{ij}G_{ji})\beta_i + (G_{ij} + \Psi_{ij}G_{jj})\beta_j, \quad (1)$$

where  $G_{ii}$  is the genetic variance of the focal character,  $z_i$ ;  $G_{jj}$  is the genetic variance of the character,  $z_j$ , that influences the expression of  $z_i$ ;  $\Psi_{ij}$  is the interaction coefficient (which measures the effect of  $z_j$  on  $z_i$ );  $G_{ji}$  is the genetic covariance between  $z_i$  and  $z_j$ ;  $\beta_i$  is the magnitude of selection acting directly on  $z_i$ ; and  $\beta_j$  is the magnitude of selection acting directly on  $z'_j$ .

Lande (1979) originally described the coevolution of correlated characters as (eqq. [1a], [1b] of Lande [1979], with notation adapted to be comparable to that of Moore et al. [1997])

$$\Delta \bar{z}_i = G_{ii}\beta_i + G_{ij}\beta_j. \quad (2)$$

The only difference between Moore et al.’s formulation and that of Lande is the interaction coefficient,  $\Psi_{ij}$ , that describes the response of one phenotype to the environment created by the other. The interaction has two modes of influence. First, it modifies the response to selection acting directly on a character,  $\beta_i$ , by adding a contribution acting through the genetic covariance between the two characters  $G_{ji}$ . Second, it introduces an additional component to the response to selection; selection on the environment-determining character  $\beta_j$  is mediated by the additive genetic variance for that character,  $G_{jj}$ , in addition to the genetic covariance,  $G_{ij}$ . This means that even if the two characters are not genetically correlated, i.e.,  $G_{ij} = 0$ , selection on the environment-determining character can still contribute to evolutionary change in the character that is influenced by the environment.

The main novelties of the dynamics arise because of this interaction, namely, because the focal character changes its phenotypic value as a result of an evolutionary change in the social environment. This simple outcome leads to two important conclusions: (1) the rate of the evolution of the focal character can be slower or faster than it would be without the influence of the social environment, depending on the direction of the evolution of the social environment and the nature of the plastic response to the social environment, and (2) the focal character can evolve even when it, itself, has no genetic variance; if the social environment evolves, phenotypic expression of the focal character will change according to its plastic response to that evolving environment. This can be seen from equation (1) by setting  $G_{ii}$  and  $G_{ij}$  to zero. The character can still evolve as long as  $G_{jj}$  and  $\Psi_{ij}$  are greater than zero.

Most empirical evidence supporting the outcomes of these models comes from investigations of parental care in insect or mammalian systems. Estimates of the evolutionary potential of offspring characters such as body size have been shown to be considerably larger when indirect genetic effects due to parental care were considered in addition to the additive genetic variance of body size alone. This was found for red squirrels (McAdam et al. 2002) and for dung beetles (Hunt and Simmons 2002). Elegant studies on burying beetles, who supply their offspring regurgitated carrion for provisions, have demonstrated significant indirect genetic effects on body size and

growth rates (Rauter and Moore 2002a). Studies on this system have also included experimental manipulations of parental care, and thereby the indirect component of genetic variation, to experimentally test the importance of indirect genetic effects on the evolution of size (Rauter and Moore 2002b). Similar creative quantitative genetic studies of indirect genetic effects could be expanded beyond animals with nasty habits to include the more civilized behavior of plants. Such studies would complement the well-developed literature on maternal effects in plants. These studies can proceed by investigating the genetic basis of habitat-selecting characters, such as those discussed above, and the plasticity of subsequently expressed characters that respond to the environment created by habitat selection.

#### *Further Theoretical Work Is Needed*

The above quantitative genetic models are not fully adequate to describe the evolution of plastic characters as we know them. Although plasticity is incorporated in the models in the form of a response of one phenotype to the environment created by another, this plastic response is a fixed parameter and does not evolve. The models describe character evolution, given plasticity. To fully understand how plastic characters coevolve, we need to allow for the evolution of their plasticity.

Standard models of the evolution of plasticity allow for the empirical fact that the genetic and phenotypic variance-covariance relationships among characters vary with the environment (Falconer 1952; Via and Lande 1985; Schlichting 1986; de Jong 1990a, 1990b). Many standard models of the evolution of plasticity solve this difficulty by defining a plastic character as two or more characters: one character expressed in each of multiple environments (Via and Lande 1985; Van Tienderen 1991) or even in an infinite number of environments (Gomulkiewicz and Kirkpatrick 1992). Other models of the evolution of plasticity include the phenotype as a continuous function of the environment (Scheiner and Lyman 1989; de Jong 1990a, 1990b; Gavrillets and Scheiner 1993). The differences in genetic variance expressed in the different environments is incorporated in the genetic variance of the parameters that describe the plasticity function. These latter models may be more easily adapted to describe the coevolution of traits and environments, since the environment is already included as a variable in the function (albeit a nonevolving variable).

Another staple of models of the evolution of plasticity is environment-dependent selection in which the adaptive value of a character depends on the environment. Standard models of plasticity, by defining separate traits in each environment, can also define selection separately in each environment. A model in which the environment itself is a character needs to include correlational selection (Lande and Arnold 1983) between the environment-determining character and the character that responds to the environment. Such correlational selection would describe how selection on a character depends on the environment created by another character.

Finally, the frequency of the selective environments experienced by a genotype is key in models of the evolution of plasticity and determines whether plasticity or specialization will evolve. Evolutionary change in the variance of the environment through habitat selection or niche construction (Lewontin 1983) would alter the adaptive value of plasticity of pheno-

types in response to the environment created by other phenotypes, or  $\Psi_{ij}$ . This is the parameter that is responsible for the unique evolutionary dynamics of the coevolution of phenotypes with their environment. By altering the adaptive value of the interactions, these interactions themselves could evolve. Additional theoretical work is necessary to determine the dynamics when the interaction,  $\Psi_{ij}$ , can evolve in response to the changing environment.

### **Habitat Selection and Character Evolution in Plants**

#### *Interpreting the Theory*

The results from the models of indirect genetic effects have important implications for character and life-history evolution in plants. Plants have mechanisms that alter the environment they experience, as the empirical examples above illustrate. If these mechanisms have a genetic basis—and they do in many systems—then the environment that plants experience can evolve, just as the “social environment” in the above model evolves. Likewise, the empirical examples above illustrate several cases in which the physiological or life-history characters expressed by plants depend on the environment that they experience. In the model of indirect genetic effects, phenotypes depend on the environment created by other phenotypes. The similarity between these examples and the theoretical model implies that similar conclusions pertain. Specifically, (a) the evolutionary rates and trajectories of physiological and life-history characters can strongly depend on the evolution of habitat-selecting characters and on the plastic responses of life-history characters to the selected environment and (b) physiological and life-history characters can evolve even if they have no genetic variation, as long as the environment that influences their expression continues to evolve.

For example, branching in *Impatiens*, which responds to light availability, can evolve as long as the shade avoidance response evolves, even without genetic variation in branch production itself under a constant environment. This is because an evolutionary response in shade avoidance will cause an evolutionary change in the light environment experienced by developing meristems, which in turn determines branching. Similarly, evolutionary changes in plant morphology, physiology, and life history can occur through the evolution of dispersal, even without genetic variation for these characters. Dispersal can determine competitive environments, resource availability, and density-dependent selective agents. If morphology, physiology, or life history responds to these environmental factors, evolutionary changes in these characters will accompany evolutionary changes in dispersal. Perhaps the most spectacular possibility is the evolutionary potential for life-history evolution through the evolution of germination cueing. An evolutionary conversion from a summer annual to a winter annual life history or a change from an annual to a biennial life history can result from an evolutionary change in the season of germination, even without genetic variation for the expression of these alternate strategies. The possibility that fundamental life-history strategies can evolve without genetic variation for life histories is indeed a startling thought, but it is a highly probable occurrence in natural plant populations.

In the empirical examples cited above, the environment is

determined either by the maternal parent or by the individual itself. In the latter case, the statement that evolution of life histories can proceed without genetic variation might be more accurately stated as follows: a genetic basis to environmental determination can create pleiotropic genetic variation for life-history traits that otherwise would not exist. That is, as long as different environment-determining genotypes are permitted to inhabit their different environments, these genotypes will also differ in life history; genetic variation for life history would be expressed even if none were expressed if all were constrained to inhabit the same environment. Thus, environmental determination can actually create genetic variation in life-history characters that can contribute to evolutionary responses.

The theoretical treatments of habitat selection emphasize a different consequence of the coevolution of characters and their environment. With habitat selection, or reduced variation in environmental conditions experienced by organisms, organisms more easily evolve specialized adaptations to the selected environment. Adaptive evolution proceeds more quickly, and organisms more closely approach the selective optimum for the chosen environment. With habitat selection, organisms therefore have higher fitness both because they inhabit a more suitable environment and because they are more highly adapted to that environment.

A corollary to the evolution of increased adaptation to a particular environment is the possibility of corresponding decreased generalist adaptation to a heterogeneous environment. In particular, the evolution of phenotypic plasticity is less likely when organisms experience a less variable environment, as would be the case with habitat selection. Therefore, plasticity in habitat-selecting characters is likely to influence the evolution of plasticity and the degree of specialization in other characters.

#### *Can Plasticity Promote Specialization?*

A major theoretical limitation to the evolution of plasticity in a variable environment is the trade-off between the ability to be plastic and the ability to perform optimally in a given environment. Plastic individuals are predicted not to be able to express the optimal phenotype in any given environment because of genetic correlations between the trait expressed in the different environments (Via and Lande 1985; Van Tien-deren 1991; Gomulkiewicz and Kirkpatrick 1992). Nonzero genetic correlations across environments have been observed often in plants (Platenkamp and Shaw 1992; Schmitt 1993; Thomas and Bazzaz 1993; Donohue et al. 2000a). With these constraints on plasticity, specialists are predicted to have higher fitness in their native environment than do plastic generalists, and this too has been observed (Donohue et al. 2000b). Thus, plasticity can compromise plant performance in any given habitat.

With habitat selection, the degree of environmental variation experienced by a genotype is reduced. With reduced environmental variation, specialization can more easily evolve. Therefore, with plasticity in a habitat-selecting character, subsequent characters may experience less environmental variation and can evolve a higher degree of specialization. Such increased specialization can enable a higher level of adaptation to one

version of a variable environment. Ironically, plasticity may increase the overall adaptation of organisms to variable environments by enabling plants to better specialize.

The ability of plasticity to alter the environment experienced by plants needs to be recognized and quantified in order to make accurate predictions about which characters should exhibit plasticity and which should exhibit specialization in a variable environment. Plasticity in some characters may actually promote specialization in others and a corresponding ability to express a more optimal phenotype. Thus, investigations of genetic constraints on the expression of optimal phenotypes should consider the role of plasticity in ameliorating environmental variation that might constrain the evolution of specialization. One previously unrecognized evolutionary advantage of plasticity may be its role in enabling ecological specialization.

#### *Conclusions*

Plants clearly have sophisticated methods of determining the environment they experience. This ability has important consequences for the evolution of morphology, physiology, and life history. First, the evolution of environment-selecting characters can cause correlated selection in all other characters whose expression is influenced by the chosen environment. This alleviates the most fundamental requirement for character evolution: genetic variation for the evolving character. Morphology, physiology, or life-history traits can evolve even if they harbor no genetic variation in a given environment. As long as the environment-determining character evolves, these characters can evolve due to their plasticity to the selected environment. In the less extreme case, the evolution of the environment-determining character will alter evolutionary rates of the characters whose expression depends on the environment.

Second, habitat selection by plants can alter the degree of environmental variation experienced by later life stages. As such, it can influence the evolution of plasticity of later characters, since the adaptive value of plasticity depends on the degree of environmental variation experienced by a genotype. With decreased environmental variation because of habitat selection, greater specialization can evolve in other characters, leading to a higher overall level of adaptation in morphological, physiological, or life-history characters.

To understand fully the evolution of plastic characters and their contribution to adaptation requires recognizing the numerous ways plants modify the environment they experience. Ecological and physiological work can identify which environmental cues elicit plasticity in certain characters and how responses by specific characters to such cues alter the environment experienced subsequently. The plasticity of later characters to the environment determined by earlier ones needs to be characterized in order to determine the evolutionary potential of these characters through indirect mechanisms. The genetic basis of both the subsequent characters and the environment-determining characters needs to be determined in order to predict the evolution of any character that displays plasticity to the modified environment. Finally, both theoretical and empirical work needs to address the evolution of plasticity within the context of evolving environments.

### Acknowledgments

I am grateful to David Ackerly, Lisa Dorn, Lauren Griffen, Jason Wolf, and an anonymous reviewer for many helpful

comments on earlier drafts of the manuscript. This was written with support from National Science Foundation grant DEB0079489, USDA grant CREES-2001-35311-09845, and a Bullard Fellowship from the Harvard Forest.

### Literature Cited

- Ballaré CL, AL Scopel, RA Sanchez 1990 Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* 247:329–332.
- Baskin CC, JM Baskin 1998 Seeds: ecology, biogeography and evolution of dormancy and germination. Academic Press, San Diego, Calif.
- Baskin JM, CC Baskin 1984 The ecological life cycle of *Campanula americana* in north central Kentucky. *Bull Torr Bot Club* 111: 329–337.
- Bazzaz FA 1991 Habitat selection in plants. *Am Nat* 137(suppl): S116–S130.
- Bennington CC, JB McGraw 1995 Natural selection and ecotypic differentiation in *Impatiens pallida*. *Ecol Monogr* 65:303–323.
- Biere A 1995 Genotypic and plastic variation in plant size: effects on fecundity and allocation patterns in *Lychnis flos-cuculi* along a gradient of natural soil fertility. *Ecology* 83:629–642.
- Botto JF, H Smith 2002 Differential genetic variation in adaptive strategies to a common environmental signal in *Arabidopsis* accessions: phytochrome-mediated shade avoidance. *Plant Cell Environ* 25:53–63.
- Brown JS 1990 Habitat selection as an evolutionary game. *Evolution* 44:732–746.
- Brown JS, NB Pavlovic 1992 Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evol Ecol* 6: 360–382.
- Casal JJ, H Smith 1989 The function, action and adaptive significance of phytochrome in light-grown plants. *Plant Cell Environ* 12: 855–862.
- de Jong G 1990a Genotype-by-environment interaction and the genetic covariance between environments: multilocus genetics. *Genetica* 81:171–177.
- 1990b Quantitative genetics of reaction norms. *J Evol Biol* 3: 447–468.
- de Kroon H, M Hutchings 1995 Morphological plasticity in clonal plants: the foraging concept reconsidered. *J Ecol* 83:143–152.
- de Mees T, Y Michalakakis, F Renaud, I Olivieri 1993 Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. *Evol Ecol* 7: 175–198.
- Donohue K 1998 Maternal determinants of seed dispersal in *Cakile edentula*: fruit, plant, and site traits. *Ecology* 79:2771–2778.
- 1999 Seed dispersal as a maternally influenced character: mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *Am Nat* 154:674–689.
- 2002 Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. *Ecology* 83:1006–1016.
- Donohue K, E Hammond-Pyle, SM Heschel, A Messiqua, J Schmitt 2000a Density-dependence and population differentiation of genetic architecture in *Impatiens capensis* in natural environments. *Evolution* 54:1969–1981.
- Donohue K, D Messiqua, E Hammond-Pyle, SM Heschel, J Schmitt 2000b Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade avoidance responses in *Impatiens capensis*. *Evolution* 54:1956–1968.
- Donohue K, J Schmitt 1998 Maternal environmental effects: adaptive plasticity? Pages 137–158 in TA Mousseau, CW Fox, eds. *Maternal effects as adaptations*. Oxford University Press, Oxford.
- 1999 Genetic architecture of plastic responses to density in *Impatiens capensis*. *Evolution* 53:1377–1386.
- Dorn L, E Hammond-Pyle, J Schmitt 2000 Plasticity to light cues and resources in *Arabidopsis thaliana*: testing for adaptive value and costs. *Evolution* 54:1982–1994.
- Dudley SA, J Schmitt 1995 Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens capensis* from open and woodland sites. *Funct Ecol* 9: 655–666.
- Evans AS, RJ Cabin 1995 Can dormancy affect the evolution of post-germination traits? the case of *Lesquerella fendleri*. *Ecology* 76: 344–356.
- Falconer DS 1952 The problem of environment and selection. *Am Nat* 86:293–298.
- Fineblum WL, MD Rausher 1995 Trade-off between resistance and tolerance to herbivore damage in a morning glory. *Nature* 377: 517–520.
- Forde BG 2002 The role of long-distance signalling in plant responses to nitrate and other nutrients. *J Exp Bot* 53:39–43.
- Fox GA 1990 Drought and the evolution of flowering time in desert annuals. *Am J Bot* 77:1508–1518.
- Galloway LF 2001a The effect of maternal and paternal environments on seed characters in the herbaceous plant *Campanula americana* (Campanulaceae). *Am J Bot* 88:832–840.
- 2001b Parental environmental effects on life history in the herbaceous plant *Campanula americana*. *Ecology* 2001:2781–2789.
- García-Dorado A 1986 The effect of niche preference on polymorphism protection in a heterogeneous environment. *Evolution* 40: 936–945.
- Gavrilets S, SM Scheiner 1993 The genetics of phenotypic plasticity. V. Evolution of reaction norm shape. *J Evol Biol* 6:31–48.
- Geber MA 1990 The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* 44:799–819.
- Gomulkiewicz R, M Kirkpatrick 1992 Quantitative genetics and the evolution of reaction norms. *Evolution* 46:390–411.
- Grant B, RJ Howlett 1988 Background selection by the peppered moth (*Biston betularia* Linn.): individual differences. *Biol J Linn Soc* 33:217–232.
- Griffing B 1981a A theory of natural selection incorporating interaction among individuals. I. The modeling process. *J Theor Biol* 89: 635–658.
- 1981b A theory of natural selection incorporating interaction among individuals. II. Use of related groups. *J Theor Biol* 89: 659–677.
- 1981c A theory of natural selection incorporating interaction among individuals. III. Use of random groups of inbred individuals. *J Theor Biol* 89:679–690.
- 1981d A theory of natural selection incorporating interaction among individuals. IV. Use of related groups of inbred individuals. *J Theor Biol* 89:691–710.
- 1989 Genetic analysis of plant mixtures. *Genetics* 122: 943–956.
- Gutterman Y 1994 Strategies of seed dispersal and germination in plants inhabiting deserts. *Bot Rev* 60:373–425.
- 2000 Maternal effects on seeds during development. Pages 59–84 in M Fenner, ed. *Seeds: the ecology of regeneration in plant communities*. 2d ed. CABI, New York.

- Hayes RG, WH Klein 1974 Spectral quality influence of light during development of *Arabidopsis thaliana* plants in regulating seed germination. *Plant Cell Physiol* 15:643–653.
- Hoekstra RE, R Bijlsma, AJ Dolman 1985 Polymorphism from environmental heterogeneity: models are only robust if the heterozygote is close in fitness to the favoured homozygote in each environment. *Genet Res* 45:299–314.
- Holt RD 1987 Population dynamics and evolutionary processes: the manifold roles of habitat selection. *Evol Ecol* 1:331–347.
- Howe HF, J Smallwood 1982 Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228.
- Huber H, S Lukacs, M Watson 1999 Spatial structure of stoloniferous herbs: an interplay between structural blue-print, ontogeny and phenotypic plasticity. *Plant Ecol* 141:107–115.
- Hunt J, LW Simmons 2002 The genetics of maternal care: direct and indirect genetic effects on phenotype in the dung beetle *Onthophagus taurus*. *Proc Natl Acad Sci USA* 99:6828–6832.
- Imbert E, O Ronce 2001 Phenotypic plasticity for dispersal ability in the seed heteromorphic *Crepis sancta* (Asteraceae). *Oikos* 93: 126–134.
- Jaenike J, RD Holt 1991 Genetic variation for habitat preference: evidence and explanations. *Am Nat* 137(suppl):S67–S90.
- Kalisz S, GM Wardle 1994 Life history variation in *Campanula americana* (Campanulaceae): population differentiation. *Am J Bot* 81: 521–527.
- Lacey EP 1986 The genetic and environmental control of reproductive timing in a short-lived monocarpic species *Daucus carota* (Umbelliferae). *J Ecol* 74:73–86.
- Lacey EP, R Pace 1983 Effect of parental flowering and dispersal times on offspring fate in *Daucus carota* (Apiaceae). *Oecologia* 60: 274–278.
- Laland KN, FJ Odling-Smee, MW Feldman 1996 The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. *J Evol Biol* 9:293–316.
- 1999 Evolutionary consequences of niche construction and their implications for ecology. *Proc Natl Acad Sci USA* 96: 10242–10247.
- Lande R 1979 Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. *Evolution* 33:402–416.
- Lande R, SJ Arnold 1983 The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Levins R 1968 Evolution in changing environments. Princeton University Press, Princeton, N.J.
- Levy YY, C Dean 1998 The transition to flowering. *Plant Cell* 10: 1973–1989.
- Lewontin RC 1983 Gene, organism, and environment. Pages 273–285 in DS Bendall, ed. *Evolution from molecules to men*. Cambridge University Press, Cambridge.
- Maynard Smith J 1966 Sympatric speciation. *Am Nat* 100:637–650.
- McAdam AG, S Boutin, D Reale, D Berteaux 2002 Maternal effects and the potential for evolution in a natural population of animals. *Evolution* 56:846–851.
- McCullough JM, W Shropshire Jr 1970 Physiological predetermination of germination responses in *Arabidopsis thaliana* (L.) HEYNH. *Plant Cell Physiol* 11:139–148.
- McPeck MA, RD Holt 1992 The evolution of dispersal in spatially and temporally varying environments. *Am Nat* 140:1010–1027.
- Moore AJ, ED Brodie III, JB Wolf 1997 Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. *Evolution* 51:1352–1362.
- Moore AJ, JB Wolf, ED Brodie III 1998 The influence of direct and indirect genetic effects on the evolution of behavior: social and sexual selection meet maternal effects. Pages 22–41 in TA Mousseau, CW Fox, eds. *Maternal effects as adaptations*. Oxford University Press, Oxford.
- Morgan DC, H Smith 1979 A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145:253–258.
- Munir J, L Dorn, K Donohue, J Schmitt 2001 The influence of maternal photoperiod on germination requirements in *Arabidopsis thaliana*. *Am J Bot* 88:1240–1249.
- Murren CJ, R Juliard, CD Schlichting, J Clobert 2001 Dispersal, individual phenotype, and phenotypic plasticity. Pages 261–272 in J Clobert, JD Nichols, E Danchin, A Dhondt, eds. *Dispersal*. Oxford University Press, Oxford.
- Odling-Smee FJ, KN Laland, MW Feldman 1996 Niche construction. *Am Nat* 147:641–648.
- Pigliucci M, J Schmitt 1999 Genes affecting phenotypic plasticity in *Arabidopsis thaliana*: pleiotropic effects and reproductive fitness of photomorphogenic mutants. *J Evol Biol* 12:551–562.
- Platenkamp GAJ, RG Shaw 1992 Environmental and genetic constraints on adaptive population differentiation in *Anthoxanthum odoratum*. *Evolution* 46:341–352.
- Rausher MD 1984 The evolution of habitat preference in a subdivided population. *Evolution* 38:596–608.
- Rausher MD, R Englander 1987 The evolution of habitat preference. II. Evolutionary genetic stability under soft selection. *Theor Popul Biol* 31:116–139.
- Rauter CM, AJ Moore 2002a Evolutionary importance of parental care performance, food resources, and direct and indirect genetic effects in a burying beetle. *J Evol Biol* 15:407–417.
- 2002b Quantitative genetics of growth and development time in the burying beetle *Nicrophorus pustulatus* in the presence and absence of post-hatching parental care. *Evolution* 56:96–110.
- Rice WR 1987 Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evol Ecol* 1: 301–314.
- Roach DA, RD Wulff 1987 Maternal effects in plants. *Annu Rev Ecol Syst* 18:209–235.
- Ronce O, I Olivieri, J Clobert, E Danchin 2001 Perspectives on the study of dispersal evolution. Pages 341–357 in J Clobert, JD Nichols, E Danchin, A Dhondt, eds. *Dispersal*. Oxford University Press, Oxford.
- Rosenzweig ML 1987 Habitat selection as a source of biological diversity. *Evol Ecol* 1:315–330.
- Scheiner SM, RF Lyman 1989 The genetics of phenotypic plasticity. I. Heritability. *J Evol Biol* 2:95–107.
- Schemske DW 1984 Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. *Evolution* 38: 817–832.
- Schlichting CD 1986 The evolution of phenotypic plasticity in plants. *Annu Rev Ecol Syst* 17:667–693.
- Schlichting CD, M Pigliucci 1995 Gene regulation, quantitative genetics and the evolution of reaction norms. *Evol Ecol* 9:154–168.
- Schmitt J 1993 Reaction norms of morphological and life-history traits to light availability in *Impatiens capensis*. *Evolution* 47: 1654–1668.
- 1997 Is photomorphogenic shade avoidance adaptive? perspectives from population biology. *Plant Cell Environ* 20:826–830.
- Schmitt J, SA Dudley, M Pigliucci 1999 Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade avoidance responses in plants. *Am Nat* 154(suppl):S43–S54.
- Schmitt J, DW Ehrhardt, M Cheo 1986 Light-dependent dominance and suppression in experimental radish populations. *Ecology* 67: 1502–1507.
- Schmitt J, AC McCormac, H Smith 1995 A test of the adaptive plasticity hypothesis using transgenic and mutant plants disabled in phytochrome-mediated elongation responses to neighbors. *Am Nat* 146:937–953.
- Schmitt J, RD Wulff 1993 Light spectral quality, phytochrome and plant competition. *Trends Ecol Evol* 8:47–51.

- Schwilk DW, DD Ackerly 2001 Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94:326–336.
- Smith H 1982 Light quality, photoreception, and plant strategy. *Annu Rev Plant Physiol* 33:481–518.
- 1995 Physiological and ecological function within the phytochrome family. *Annu Rev Plant Physiol Plant Mol Biol* 46:289–315.
- Smith H, JJ Casal, GM Jackson 1990 Reflection signals and the perception by phytochrome of the proximity of neighbouring vegetation. *Plant Cell Environ* 13:73–78.
- Smith H, GC Whitelam 1990 Phytochrome, a family of photoreceptors with multiple physiological roles. *Plant Cell Environ* 13:695–707.
- Storch D, D Frynta 1999 Evolution of habitat selection: stochastic acquisition of cognitive clues? *Evol Ecol* 13:591–600.
- Sultan SE 1987 Evolutionary implications of phenotypic plasticity in plants. *Evol Biol* 21:127–178.
- 1995 Phenotypic plasticity and plant adaptation. *Acta Bot Neerl* 44:363–383.
- 2000 Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci* 5:537–542.
- Sultan SE, FA Bazzaz 1993a Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. *Evolution* 47:1009–1031.
- 1993b Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture and the maintenance of genetic diversity. *Evolution* 47:1032–1049.
- 1993c Phenotypic plasticity in *Polygonum persicaria*. III. The evolution of ecological breadth for nutrient environment. *Evolution* 47:1050–1071.
- Taylor CE 1976 Genetic variation in heterogeneous environments. *Genet Res* 83:887–894.
- Templeton AR, ED Rothman 1981 Evolution in fine-grained environments. 2. Habitat selection as a homeostatic mechanism. *Theor Popul Biol* 19:326–340.
- Theide DA, CK Augspurger 1996 Intraspecific variation in seed dispersal of *Lepidium campestre* (Brassicaceae). *Am J Bot* 83:856–866.
- Thomas SC, FA Bazzaz 1993 The genetic component in plant size hierarchies: norms of reaction to density in a *Polygonum* species. *Ecol Monogr* 63:231–249.
- Thompson L 1994 The spatiotemporal effects of nitrogen and litter on the population dynamics of *Arabidopsis thaliana*. *J Ecol* 82:63–68.
- Tiffin P, MD Rausher 1999 Genetic constraints and selection acting on tolerance to herbivory in the common morning glory. *Am Nat* 154:700–716.
- van Tienderen PH 1991 Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution* 45:1317–1331.
- Venable DL, DA Levin 1985 Ecology of the achene dimorphism in *Heterotheca latifolia*. I. Achene structure, germination, and dispersal. *J Ecol* 73:133–145.
- Via S, R Lande 1985 Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.
- Weiner J 1985 Size hierarchies in experimental populations of annual plants. *Ecology* 66:743–752.
- 1990 Asymmetric competition in plant populations. *Trends Ecol Evol* 5:360–364.
- Weiner J, SC Thomas 1992 Competition and allometry in three species of annual plants. *Ecology* 73:648–656.
- Weinig C 2000a Differing selection in alternative competitive environments: shade-avoidance responses and germination timing. *Evolution* 54:124–136.
- 2000b Plasticity versus canalization: population differences in the timing of shade-avoidance responses. *Evolution* 54:441–451.
- Whitlock MC 1996 The Red Queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *Am Nat* 148:S65–S77.
- Willson MF, A Traveset 2000 The ecology of seed dispersal. Pages 85–110 in M Fenner, ed. *Seeds: the ecology of regeneration in plant communities*. 2d ed. CABI, New York.
- Wolf JB, ED Brodie III, AJ Moore 1999 Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. *Am Nat* 153:254–266.
- Wolf JB, ED Brodie III, JM Cheverud, AJ Moore, MJ Wade 1998 Evolutionary consequences of indirect genetic effects. *Trends Ecol Evol* 13:64–69.