Shade tolerance plasticity in response to neutral vs green shade cues in *Polygonum* species of contrasting ecological breadth

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Summary

- Here we examined species differences in perception and response to two distinct types of shade cue, reduced photosynthetically active radiation (PAR) with and without reduced red : far red ratio (R : FR), in *Polygonum persicaria* and *Polygonum hydropiper*, two closely related annuals of contrasting ecological breadth.
- We compared plasticity data for light-gathering traits from glasshouse experiments at equivalently reduced PAR under neutral shade (R : FR 1.03) and green shade (R : FR 0.702).
- Species shared the ability to distinguish between the two types of shade, as shown by the ability of each to respond differently to neutral vs green shade for one or more traits. However, the species' responses to these cues differed significantly. *Polygonum persicaria* expressed stronger shade-tolerance responses (increased leaf allocation and leaf area ratio) to reduced PAR alone than to green shade. By contrast, *P. hydropiper* expressed slightly less plasticity for these traits in neutral than in green shade.
- The pronounced plastic response of *P. persicaria* to neutral shade may contribute to the range of habitats this widespread species can occupy, which includes neutral-shade environments such as urban settings.

Key words: available PAR, light cues, neutral shade, phenotypic plasticity, *Polygonum hydropiper*, *Polygonum persicaria*, R : FR ratio.

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Introduction

One aspect of adaptive diversity among species that is of growing interest to ecologists is different patterns of individual phenotypic plasticity. Adaptive plasticity requires that an organism perceives some aspect of its environment as a specific cue, and then that it responds to that cue by expressing particular phenotypic adjustments. A difference among taxa in the plasticity individuals express under given conditions can reflect underlying variation at either point in the process. Because functionally adaptive plasticity promotes environmental tolerance, differences among species in plasticity patterns may contribute to differences in ecological breadth, persistence in novel environments, and evolutionary diversification (Novak *et al.*, 1991; Williams *et al.*, 1995; Sultan, 2000, 2004; Paschke *et al.*, 2003). Despite the fundamental importance of species' differences in plasticity, we know very little about their precise nature or their effects on environmental tolerance.

A key requirement for the evolution of adaptive plasticity is the presence of reliable and timely environmental cues (Lively, 1986, 1999). Such cues may be indirectly related to selective conditions, as when shorter daylength signals coming decreases in temperature and resource availability. Cues for phenotypic response may also consist of directly perceived aspects of the environment, such as immediate resource limits. For example, many plants grown in dry or nutrient-poor soil allocate a greater proportion of biomass to root production. Thus, a wide range of both indirect and direct signals can serve as plasticity cues, enabling organisms to adaptively respond to changing conditions (Levins, 1968; Moran, 1992; Gilroy & Trewavas, 2001). Identifying the specific aspect or aspects of the environment that cue plastic response can be difficult

(Sultan, 1995; Denver *et al.*, 1998). Natural environments consist of numerous, partly covarying elements: for plants, correlations exist between insolation, temperature, soil moisture and transpiration demand, between water and mineral availability, and so forth. In any given environment, species may be able to detect one or more of these partially covarying elements as cues. Adaptive patterns of plastic response reflect both perception of relevant cues and the patterns of covariance between particular environmental cues and selective conditions in which the organism evolved.

An organism's ability to perceive a given cue depends on environmental sampling, sensory apparatus, and external signal transduction. Once perceived, environmental information conditions phenotypic response through a complex series of biochemical steps based on cell-, tissue-, organ- and stage-specific sensitivity thresholds and feedbacks that ultimately regulate gene activity (Voesenek & Blom, 1996; Gilroy & Trewavas, 2001). In plants, genes associated with environmental perception, as well as signal transduction, regulation and expression have been identified (Callahan *et al.*, 1999; Schlichting & Smith, 2002). A difference between taxa in plastic response to a given environmental cue can arise from an evolved difference at any point in this complex regulatory cascade (Sultan & Stearns, 2005). However, little is known about variation in these systems among naturally occurring populations or even closely related species.

Differences among species in either cue perception or response pathways may be important in shaping their relative ecological breadth and evolutionary trajectories. Because the correlation between specific cues and selective conditions varies among habitats, the particular cue or cues that a species is able to perceive can influence the range of habitats in which it expresses an appropriate phenotype (Galen *et al.*, 2004; Huber *et al.*, 2004). Moreover, species that use several environmental elements as cues may more accurately detect diverse habitats. Differences in response pathways may also influence ecological breadth. Because the adaptive value of a particular response may depend on a variety of microsite conditions (Huber *et al.*, 2004), species that are better able to modulate phenotypic response by integrating complex environmental signals are more likely to persist in a broad range of habitats. In addition, species' differences in perception or response pathways may shape the further evolution of adaptive plasticity. Plasticity is not predicted to evolve if organisms cannot accurately perceive a salient environmental cue, or cannot express a timely, effective phenotypic response (Moran, 1992; DeWitt *et al.*, 1998; Tufto, 2000; Sultan & Spencer, 2002). Since the perception and response aspects of plasticity may depend on distinct genetic components or transduction pathways, they may be subject to different evolutionary constraints or opportunities. To understand the nature of species differences in plasticity and the ecological and evolutionary implications of those differences, it is important to consider cue perception and response as distinct aspects of plasticity.

Plant plasticity to shaded vs open conditions provides an excellent system in which to examine perception of, and plastic response to, specific environmental cues. In natural habitats, both quantity of photosynthetically active radiation (PAR) and its spectral quality (red : far red ratio, or R : FR) can vary widely. Reduction in either aspect of the light environment can have pronounced phenotypic consequences including adaptive plasticity (Sultan & Bazzaz, 1993; Stuefer & Huber, 1998; Dorn, 2000). Yet, very little is known about how these cues covary, or the way in which they are jointly perceived. Shaded sites or microsites may show strongly correlated reductions in PAR and R : FR ratio, for example under a mature tropical forest canopy (Lee, 1987). However, these elements of shade can also vary somewhat independently: depending on canopy composition and on shade sources such as cliffs, boulders and tree-trunks, reduced light is not always accompanied by a particular degree of spectral change (Smith, 1982). Indeed, at all but extremely low light levels (i.e. < 10% of full sun), the correlation between PAR and R : FR can be quite weak (Lee, 1987). In general, low PAR is a consistent feature of shade habitats, while concomitant reduction in R : FR may or may not occur in such habitats depending on the precise sources of shade. Thus, the ability to perceive and respond to reduced PAR *per se* in addition to R : FR changes may provide adaptive shade cues for a greater range of habitats than low R : FR ratio alone.

The way in which plants perceive and respond to these two aspects of shade conditions is only partly understood. Although perception and transduction of R : FR signals are common to diverse taxa (reviewed by Smith, 2000; Schlichting & Smith, 2002), less is known about the perception of reduced PAR in the absence of spectral alteration (Smith, 1994, and personal communication). Some authors consider that low PAR is perceived by plants simply as reduced photosynthetic rate, and that light quantity is a resource limit rather than a cue that provides the organism with environmental information (see Dorn, 2000 and references therein). However, cases of functionally appropriate responses to reduced PAR indicate that in some taxa low light *per se* can indeed function as a plasticity cue (Ryser & Eek, 2000; Sultan, 2003). Thus, species may differ in their ability to perceive low PAR as a cue in the absence of altered R : FR ratio. Alternatively, species may share perception abilities for these different shade cues but differ in their evolved phenotypic responses to the cues, owing to differences in selective history and/or genetic constraint. Depending on the distribution of shade cues in natural habitats, either type of difference might influence present distributions in various types of shade environment.

Here, we examine species differences in perception and response to two distinct types of shade cue by comparing plasticity in two closely related annual species to reduced PAR with and without reduced R : FR ratio. *Polygonum persicaria* is a generalist, weedy species that occurs in a broad range of conditions including full sun, light to moderate canopy shade, forest margins and city streets, whereas *Polygonum hydropiper* is restricted to open sites (Mitchell & Dean, 1978; Sultan *et al.*, 1998). As a result of this distribution, *P. persicaria* encounters reduced PAR both with concomitant reduction in R : FR ratio (under canopy or neighbor shade) and without such reduction (near tree-trunks or buildings). Because *P. hydropiper* does not grow under canopy shade or in urban settings, it encounters shade primarily caused by herbaceous neighbors (Sultan *et al.*, 1998; T. Griffith, personal observation), which impose a strong correlated reduction in R : FR and PAR.

Separate experiments testing plastic response to neutral and green shade revealed that the *Polygonum* species differed in their responses to reduced PAR with and without reduced R : FR ratio. Since the two shade environments imposed similar reductions in total available PAR, differences in response to these cues were not confounded with different levels of light deprivation and consequent growth constraint. Here, we draw on data from these two experiments to distinguish responses to reduced light quantity alone (neutral shade) from responses to reduced light quantity with altered spectral quality (green shade), in a suite of traits associated with light-gathering capability. We address two questions: (1) Are both *Polygonum* species capable of perceiving the two distinct types of shade environment, low PAR *per se* and low PAR accompanied by low R : FR ratio? (2) If so, do the species express similar or different phenotypic responses to the two types of shade cue? We discuss the results in the context of the contrasting ecological distributions of the two *Polygonum* species.

Materials and Methods

Study system and experimental material

Polygonum persicaria L. and *P. hydropiper* L. (Polygonaceae) are closely related species within a monophyletic section of the genus (Löve & Löve, 1956; Mitchell & Dean, 1978). The species have similar life histories as obligate annuals with mixed breeding systems, found in disturbed habitats (references in Sultan *et al.*, 1998). Both species were introduced to North America where they now have similar geographic ranges and often co-occur in moist, open sites (Mitchell & Dean, 1978; Gleason & Cronquist, 1991).

Achenes were obtained from inbred lines derived from field families of four populations per species (details in Sultan, 2001). Populations were chosen from sites representing each species' range of habitats in north-east North America (Sultan *et al.*, 1998). Because plants in the neutral shade experiment comprised part of a large multifactorial study, sample size was smaller than for the green shade experiment; despite such sample inequalities valid statistical tests can be made through bootstrapping methods (Efron & Tibshirani, 1993, see Data Analysis). The neutral shade experiment included two inbred lines per population (one treatment replicate per line), and the green shade experiment included those lines plus an additional 8–11 lines from the same populations (four treatment replicates per line).

Experimental treatments

Experimental achenes were stratified in distilled water at 4°C for 6 wk and then sown into moist vermiculite (18 March 1996 for neutral shade experiment, 16 June 2002 for green shade experiment). Once seedlings reached the first true leaf stage, they were transplanted singly into 0.8 l clay pots filled with a 1 : 1 : 1 mixture of sterilized sandy loam–coarse sand–Turface fritted clay (Hummert International, Earth City, MO, USA) with 2.5 g of granular 15 : 18 : 12 NPK fertilizer (Agway Inc., Syracuse, NY, USA). Plants received two equal-volume water pulses per day (morning and midday) from an automatic watering system (Chapin Watermatics, Watertown, NY, USA). The amount of water per pulse was varied with plant age and light treatment to maintain all plants at constant field capacity throughout the experiments. Plants were grown in a glasshouse under natural daylengths at 25°–36° day/18° night temperatures and ≥ 40% relative humidity (r.h.).

Each glasshouse experiment consisted of a full-sun treatment (High Light) and a shade treatment, neutral shade in the first experiment, green shade in the second. For both experiments, plants were randomly assigned to positions and treatments in a complete block design on eight glasshouse benches, and arranged in a hexagonal design with sufficient distance among individuals to prevent competition for light. In the neutral shade experiment, plants were placed under vertically adjustable frames covered with black neutral-density shade cloth (Hummert International, Earth City, MO USA) that reduced PAR by *c.* 85% (R : FR = 1.03). To create the green shade treatment, frames were covered with a combination of neutral-density shade cloth and green plastic film (#138 Lee Filters, Burbank, CA USA), perforated with 0.6 cm holes to allow air flow. The R : FR ratio under green shade was 0.702 ± 0.020 and PAR was reduced by approx. 79%. This R : FR ratio is within the range reported for deciduous and coniferous forests in other studies (Smith, 1982) and agrees with measured levels under the kind of canopy shade in which annual *Polygonums* grow (D. Sloan & S. Sultan, unpublished).

Data collection

In both experiments, plants were grown till senescence (10–12 wk) and then harvested. At the time of harvest, a representative subsample of five leaves per plant was selected from intermediate nodes of primary branches, scanned in a leaf area meter (LI-3100; Li-Cor, Lincoln, NE, USA), oven-dried, and weighed to compute mean individual leaf area (MLA) and specific leaf area (SLA, cm^2 leaf g^{-1} leaf biomass). Shoots and roots were dried to a constant mass and leaves separated from the remaining plant tissue, to compute per cent biomass allocated to leaf mass (total leaf biomass: total plant biomass).

Whole-plant leaf area ratio (cm^2 leaf g^{-1} of plant biomass; LAR) was estimated as the product of per cent leaf biomass and specific leaf area (Sultan & Bazzaz, 1993).

Data analysis

We used standard *t*-tests and boot-strapping procedures to allow robust significance tests of the salient comparisons both within and across the two experiments (Efron & Tibshirani, 1993). First, we tested whether plants of each species altered phenotypes in response to light environment (sun vs. shade) by performing separate *t*-tests for each species in each experiment (Zar, 1984). The SLA and LAR were square-root transformed to reduce variance inequality among light levels within each experiment. Similarity of sample sizes and variances permitted variances to be pooled in the computation of *t*-statistics (Snedecor & Cochran, 1989).

To assess whether each species' phenotypic response to neutral shade differed from its response to green shade, we examined each trait for each species using hypothesis testing procedures for bootstrapped data (Dixon, 1993; Efron & Tibshirani, 1993). All comparisons were performed following Efron & Tibshirani (1993, Chapter 16). For each set of comparisons, *t*-statistics (assuming unequal variances) were calculated for 1000 bootstrapped samples. Samples were drawn with replacement from the original data in each treatment, with the number of observations per treatment in each sample equal to that of the original data set. Treatment means of the original data were adjusted to the grand mean so that differences in the resampled data represented the range of between-treatment differences that could occur due solely to sampling error. The achieved significance level (ASL) was measured as the per cent of bootstrapped *t*-statistics greater than the observed *t*-statistic (Efron & Tibshirani, 1993). To confirm the validity of these comparisons (i.e. that growth conditions in the two experiments were comparable apart from the deliberate difference in shade treatment), we compared phenotypic values expressed by plants of each species in the High Light treatments of each experiment. Final assessment of significant differences was made using a species-wide sequential Bonferroni test (Rice, 1989).

Results

Both *P. persicaria* and *P. hydropiper* exhibited plastic responses to each type of shade, significantly increasing SLA, per cent leaf mass, and LAR under both neutral shade (reduced PAR alone) and green shade (reduced PAR and R : FR ratio) (Fig. 1a–c, Table 1).

Both species were able to distinguish between the two types of shade environment, since each species expressed different phenotypic responses to neutral vs green shade for one or more traits (Table 2; Fig. 1b–d). For example, both species maintained mean leaf area (MLA) in the low-light, green shade treatment: *P. persicaria* plants actually increased MLA slightly but significantly in green shade compared with full sun, while there was no change in *P. hydropiper* (Table 1, MLA in green shade experiment; Fig. 1d). By contrast, both species reduced leaf size significantly when grown in neutral shade compared with full sun (Table 1, MLA in neutral shade; Fig. 1d). This decrease was particularly steep in *P. hydropiper*; leaves produced by *P. persicaria* in neutral shade were nearly

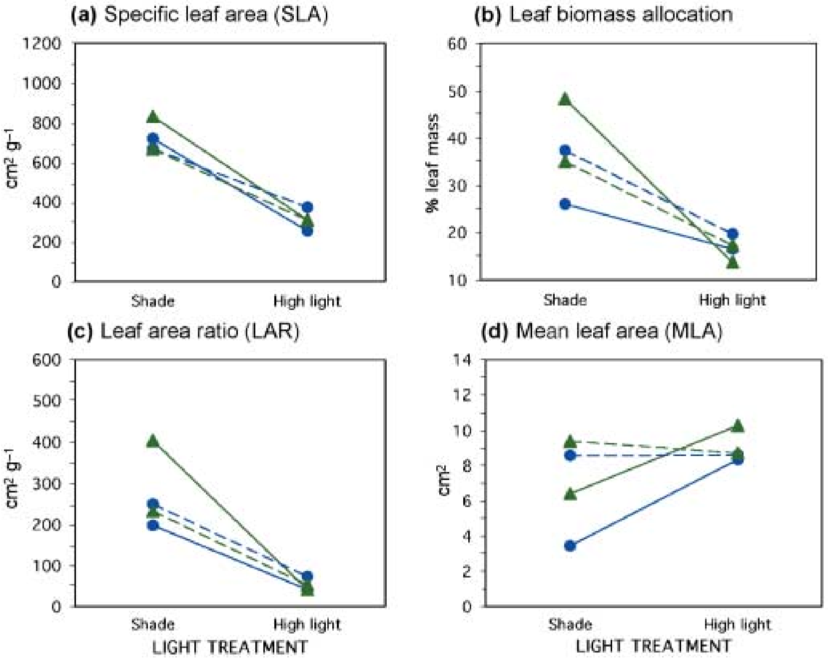

Fig. 1 *Polygonum persicaria* (triangles) and *Polygonum hydropiper* (circles) responses to high and low light in a neutral shade (solid lines) and a green shade (dashed lines) experiment. (a) Specific leaf area; (b) per cent leaf mass; (c) leaf area ratio; (d) mean leaf area.

Table 1 *t*-Test comparisons of trait means in full sun vs low light for each species and shade experiment

	SLA	% Leaf mass	LAR	MLA
Polygonum hydropiper				
Neutral shade experiment	9.29*** *n* = 13	2.56* *n* = 13	5.41*** *n* = 13	−4.93*** *n* = 13
Green shade experiment	42.79*** *n* = 280	46.06*** *n* = 278	56.06*** *n* = 270	−0.21 *n* = 266
Polygonum persicaria				
Neutral shade experiment	8.61*** *n* = 13	11.62*** *n* = 13	11.22*** *n* = 13	−2.57* *n* = 13
Green shade experiment	60.21*** *n* = 359	57.94*** *n* = 345	87.30*** *n* = 346	3.50*** *n* = 354

SLA, specific leaf area; LAR, whole-plant leaf area ratio ; MLA, mean individual leaf area. Shade experiments consisted of a full-sun treatment and either a neutral or a green shade low-light treatment. Top number: *t*-statistic; lower number: *n* for both full sun and low light.
*, **, ***, $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively, after sequential Bonferroni correction.

Table 2 *t*-Test comparisons of trait means in the low-light treatments of the neutral and green shade experiments

Low-light treatments	SLA	% Leaf mass	LAR	MLA
Polygonum hydropiper				
Neutral vs green shade experiment	−0.85 *n* = 5, 140	2.52 *n* = 5, 138	0.95 *n* = 5, 138	9.88** *n* = 5, 135
Polygonum persicaria				
Neutral vs green shade experiment	−2.43* *n* = 6, 178	−5.47* *n* = 6, 170	−3.79* *n* = 6, 172	2.24* *n* = 6, 179

SLA, specific leaf area; LAR, whole-plant leaf area ratio; MLA, mean individual leaf area. Top number: *t*-statistic; lower numbers: *n* for the neutral and green shade experiments, respectively. The *t*-statistics were calculated without assumption of equal variances. The probability of different means (i.e., achieved significance level, ASL), was assessed as the per cent of 1000 bootstrapped samples with *t*-statistics exceeding the observed value (see the Materials and Methods section for full details).
*, **, ASL < 0.05 and ASL < 0.01 after sequential Bonferroni correction.

twice as large as those produced by *P. hydropiper* plants in this treatment (Fig. 1d).

However, the species exhibited different responses to the two types of shade they perceived. In general, *P. persicaria* plants expressed even more pronounced plasticity in response to neutral shade than to green shade, while *P. hydropiper* plants expressed either comparable or nonsignificantly less plasticity in response to neutral shade. For example, both *P. persicaria* and *P. hydropiper* plants increased leaf biomass allocation by 90–100% in green shade compared with allocation at full sun, but in neutral shade, *P. persicaria* plants showed a dramatic increase of 211% (significantly greater than the response to green shade), while *P. hydropiper* plants increased leaf allocation by only 57% (Table 2; Fig. 1b). Both species also increased whole-plant LAR similarly in green shade (from 52–73 $cm^2 g^{-1}$ plant tissue at full sun to 235–249 $cm^2 g^{-1}$ plant tissue), but again *P. persicaria* plants expressed significantly more plasticity in neutral than green shade while *P. hydropiper* plants expressed slightly less (Table 2, Fig. 1c). The two species also increased SLA equally sharply in green shade compared with full sun; in this case too *P. persicaria* plants expressed an even steeper response to neutral shade (Table 2; Fig. 1a). However, in the case of SLA, *P. hydropiper* plants expressed equally high plasticity to neutral and green shade (Table 2; Fig. 1a).

Because response to shade was measured in two separate experiments, it is possible that ambient environmental differences among experiments could have contributed to observed divergence in response patterns. However, the similarity of trait expressions in the full-sun treatments of the two experiments (Fig. 1, High Light treatment, all traits) confirms that ambient environmental conditions were indeed comparable.

Discussion

In this study, we compared the ability of closely related annual species with differing shade distributions in the field to perceive and respond to light quantity and quality cues associated with shade environments. We found that both *P. persicaria* and *P. hydropiper* could perceive and distinguish between neutral shade (reduced PAR) and green shade (altered spectral quality as well as reduced PAR). Both types of shade induced phenotypic change in the two species, but the degree and/or direction of phenotypic response depended on the type of shade cue for certain traits in each species. Thus, these closely related species differed in their patterns of plasticity not because of differences in perception of neutral and green shade cues, but because they initiated different responses to these cues. Comparative studies of other taxa, ecological forms, and phylogenetic levels are needed to assess the generality of these perception abilities among plants; studies of additional types of environmental signals will reveal whether closely related taxa may differ in other aspects of cue perception.

Although the species responded similarly to the green shade environment by plastically increasing light-harvesting traits, they expressed very different plastic responses to neutral shade. Interestingly, *P. persicaria*, which inhabits a broad range of light habitats, expressed significantly stronger shade-tolerance responses to neutral than to green shade, while the more narrowly distributed *P. hydropiper* expressed slightly less plasticity to neutral than green shade. Specifically, *P. persicaria* plants exhibited very high leaf allocation and leaf area ratio in response to reduced PAR alone. Increases in these traits can improve the ability of individuals to capture light by increasing the ratio of leaf surface area relative to the amount of energy invested in the production of leaf or other plant tissue (Chapin *et al.*, 1987; Bazzaz, 1996; Fitter & Hay, 2002). Collectively, these traits are considered part of a shade-tolerance syndrome that can be advantageous in habitats where the source of shade cannot be overtopped, for example near trees or in the presence of rocks, buildings, etc. (Sultan & Bazzaz, 1993; Smith, 1994). Thus, to the extent that neutral shade (or a R : FR ratio closer to neutral, for example near conifers) is more consistently associated with such environments, the pronounced plastic response of *P. persicaria* to neutral shade may contribute to the range of habitats this widespread species can occupy. Possibly, these responses evolved under selection near buildings or tree trunks at forest margins, where maximizing light interception in the absence of reduced R : FR would be advantageous. Regardless of their evolutionary origin, these responses likely contribute to the present distribution of *P. persicaria* in neutral-shade environments such as urban settings.

By contrast, *P. hydropiper* plants did not express a pronounced plastic response to neutral shade for allocational and leaf area ratio. Possibly, past selection in this species has occurred in sites where low PAR correlates more consistently with low R : FR, such as in the presence of neighbor shade. *Polygonum hydropiper* may have been restricted to such sites for other environmental reasons, such as edaphic conditions, which would have precluded selection under a low PAR cue in the absence of altered spectral quality. The inability of *P. hydropiper* to produce a shade-tolerant phenotype in response to low PAR alone may contribute to its relatively narrow distribution with respect to light conditions. However, to fully understand the ecological meaning of these response differences and their likely evolutionary basis, more must be known about the correlation between light quantity and quality cues in diverse natural habitats, as well as the fitness consequences of alternative response patterns.

In this study, we found that closely related species can share the ability to perceive distinct aspects of the light environment and yet express very different patterns of phenotypic plasticity in response to those distinct shade cues. This result suggests that the previous selective experience of the two species and/or possible genetic constraints have altered the developmental pathway linking perceived environmental signals to realized phenotypic expression. Although these results are preliminary in nature, they raise some intriguing questions about species differences in plasticity and their ecological and evolutionary implications. Further comparative studies decoupling environmental perception and phenotypic response may contribute to our understanding of how adaptive plasticity evolves. A growing body of research is investigating the genetic variation that underlies reaction norm variation, particularly for light perception and response in plants (Callahan *et al.*, 1997; Pigliucci & Schmitt, 1999; Schlichting & Smith, 2002). Perception mechanisms (i.e. phytochrome genes) as well as downstream components of developmental regulation have been found to vary within as well as between species (Smith, 2000; Schlichting & Smith, 2002). Currently, little is known about the relative evolutionary importance of variation in these respective pathways. Further work linking the perceptual and developmental mechanisms underlying plasticity to both species' ecological ranges and their phylogenetic history can advance our understanding of species differences in adaptive plasticity.

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