

# Is photomorphogenic shade avoidance adaptive? Perspectives from population biology

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## ABSTRACT

**Photomorphogenic shade avoidance responses provide an ideal model system for integrating genetic, physiological and population biology approaches to the study of adaptive plasticity. The adaptive plasticity hypothesis predicts that shade avoidance phenotypes induced by low ratios of red to far-red light (R:FR) will have high relative fitness in dense stands, but will suffer a fitness disadvantage at low density. Experiments with transgenic and mutant plants in which photomorphogenic genes are disabled, as well as phenotype manipulation by means of altered R:FR, strongly support the shade avoidance hypothesis. The observation of photomorphogenic ecotypes in different selective environments also suggests that the shade avoidance response has undergone adaptive evolution. Quantitative genetic variation in R:FR sensitivity has been detected in wild populations, indicating that the evolutionary potential exists for response to natural selection. However, evolutionary response may be constrained by genetic correlations among developmentally linked traits. Therefore it cannot be assumed that an observed suite of photomorphogenic responses represents an adaptive optimum for every trait.**

*Key-words:* adaptive plasticity; ecotypes; genetic correlations; natural selection; phenotypic plasticity; photomorphogenesis; phytochrome.

## INTRODUCTION

The evolution of phenotypic plasticity, that is, the capacity for response of a genotype to environmental variation, is a subject of intense theoretical interest for population biologists (e.g. Via & Lande 1985; Schlichting 1986; Thompson 1991; Van Tienderen 1991; Gomulkiewicz & Kirkpatrick 1992; Scheiner 1993; Schlichting & Pigliucci 1995; Via *et al.* 1995; Pigliucci 1996). For plasticity to be adaptive, the phenotype induced by each relevant environment must confer high fitness in that environment relative to alternative phenotypes. For adaptive plasticity to evolve, natural selection on a trait must differ among environments, and genotypes within populations must vary in phenotypic

expression of the trait across those environments (i.e. in 'norms of reaction'). Theory predicts that the evolution of plasticity may be constrained by strong genetic correlations between traits across or within environments or by costs of plasticity (Via & Lande 1985; Van Tienderen 1991; Gomulkiewicz & Kirkpatrick 1992). Unfortunately, the hypothesis that plasticity is adaptive has rarely been tested in any organism. Information is also needed on the nature of genetic variation for plasticity within and between populations, as well as on potential genetic constraints on the evolution of plasticity (Via *et al.* 1995).

Photomorphogenic responses of plants to crowding and vegetation shade provide an ideal model system for integrating genetic, physiological and population biology approaches to the study of adaptive plasticity. Many plant species display characteristic 'shade avoidance' responses, such as shoot elongation and reduced branching, to the decreased ratio of red to far-red light (R:FR) characteristic of foliage shade (Smith 1982). These responses are also elicited by crowding (Schmitt & Wulff 1993; Ballaré 1994). Plants can perceive the R:FR reflected from nearby vegetation as an accurate indicator of neighbour proximity and respond morphologically even before they are directly shaded (Ballaré *et al.* 1987; Ballaré, Scopel & Sánchez 1990). Such shade avoidance responses are largely mediated by light-stable phytochromes, including phytochrome B (Smith 1995). It has been hypothesized that phytochrome-mediated sensitivity to R:FR is adaptive because it enables plants to anticipate and avoid competition for light in dense stands (Ballaré *et al.* 1987; Casal & Smith 1989; Ballaré *et al.* 1990; Schmitt & Wulff 1993). Until recently, however, the effect of shade avoidance responses on performance and fitness has not been investigated explicitly. Here I review methods for testing the adaptive plasticity hypothesis. I also discuss approaches to investigating the basis of quantitative genetic variation in shade avoidance responses within and between natural populations, as well as possible constraints on the evolution of adaptive plasticity in this system.

## EXPERIMENTAL TESTS OF ADAPTIVE PLASTICITY

The adaptive plasticity hypothesis predicts that shade avoidance phenotypes induced by low R:FR will have high relative fitness in dense stands, but will suffer a fitness disadvantage at low density (Casal & Smith 1989; Schmitt &

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Wulff 1993). Light is a critical resource for plants, and photomorphogenic responses such as shoot elongation at high density may confer an important advantage in asymmetric competition for light (Schmitt & Wulff 1993; Ballaré 1994). However, in the absence of competition, allocation of resources to height at the expense of leaves, roots or branches may reduce growth and reproduction, and elongated stems may have a greater risk of mechanical damage (Casal & Smith 1989; Schmitt & Wulff 1993). To test these predictions, it is necessary to compare the performance of 'appropriate' and 'inappropriate' morphologies in both crowded and isolated plants. Such alternative phenotypes can be obtained by either genetic modification or phenotype manipulation.

### Transgenic and mutant plants

Transgenic and mutant plants in which photomorphogenic genes are overexpressed or disabled have proved important in elucidating gene function (Whitelam & Harberd 1994; Smith 1995). Such plants also provide a valuable opportunity for investigating the adaptive significance of photomorphogenic responses. By comparing their relative fitness at high and low density with that of wild-type plants expressing normal shade avoidance responses, it is possible to test both predictions of the shade avoidance hypothesis. For example, overexpression of introduced oat *PHYA* under a constitutive promoter in transgenic tobacco results in suppression of normal shade avoidance responses, due to persistence of the FR-high-irradiance response (McCormac *et al.* 1991; McCormac, Whitelam & Smith 1992; Casal & Sánchez 1994). To test the prediction that phytochrome-mediated stem elongation is favoured under competitive conditions, Schmitt *et al.* (1995) used two lines (Y10 and Y12) of transgenic tobacco (*Nicotiana tabacum* cv. *xanthi*) which overexpress the oat *PHYA* gene at moderate levels. At low density, these lines are phenotypically similar to wild-type plants, but in crowded stands they display a dramatic reduction in stem elongation (Schmitt *et al.* 1995; Robson *et al.* 1996). When grown in mixture with normally elongating wild type, the transgenic plants had significantly lower relative fitness (measured as dry biomass) than in pure stands. This result supports the prediction that phytochrome-mediated stem elongation is advantageous for crowded plants.

Complementary experiments with constitutively elongated mutants also support the second prediction of the adaptive plasticity hypothesis: that stem elongation is disadvantageous in the absence of competition. Schmitt *et al.* (1995) compared the fitness of the *Brassica rapa ein* mutant with that of wild-type controls. This mutant, deficient in phytochrome B, displays an elongated phenotype even at high R:FR (Devlin *et al.* 1992). Mutant plants were grown in mixture with wild-type plants displaying normal shade avoidance responses in both high- and low-density stands. The fitness of *ein* relative to wild type at low density (measured both as dry biomass and as number of reproductive structures) was only half its relative fitness at

high density (Schmitt *et al.* 1995). In cucumber, seedlings of the phytochrome-B-deficient long-hypocotyl mutant (*lh*) suffered mechanical damage and increased mortality relative to wild type when grown in isolation in the field (Casal *et al.* 1994). This observation is consistent with the adaptive plasticity hypothesis, although conclusive support would require demonstration that the fitness disadvantage of the mutant is density-dependent.

At present, the use of genetic modification to test evolutionary hypotheses is limited to a few model species in which mutants have been isolated or transgenic lines constructed. However, this approach is potentially valuable for investigating natural selection on photomorphogenesis in wild plant species. Creation of transgenic lines in a variety of species, in which specific genes are overexpressed, or blocked by expression of antisense genes, could provide a valuable tool for ecophysiological and evolutionary studies (Smith 1995). Ideally, such studies should be conducted using null segregants as an appropriate control for the effects of transformation (Linder & Schmitt 1994, 1995; Purrington & Bergelson 1997).

### Phenotype manipulations

Another powerful method for testing the adaptive plasticity hypothesis is to manipulate phenotypes directly within natural populations and measure the impact on performance or fitness (Dudley & Schmitt 1996; Schmitt & Dudley 1996). Phytochrome-mediated photomorphogenesis is a particularly attractive system for this approach, because R:FR is easy to manipulate, resulting in expression of alternative phenotypes. However, only a few studies have examined the effects of the R:FR response on performance or fitness. Ballaré *et al.* (1991) used R:FR manipulation in a glasshouse to test for an opportunity cost of stem elongation, by comparing growth and biomass allocation of elongated and non-elongated *Amaranthus quitensis* plants in dense stands and at low density. At both densities, elongated plants had greater biomass, due to increased allocation to stems, although the magnitude of the difference appeared to be somewhat larger at high density. Thus, if biomass is considered a fitness estimator, this study supported the prediction that elongation is advantageous in dense stands, but found no evidence for a disadvantage of elongation at low density. However, elongated plants did display lower proportional allocation to roots. It would be interesting to determine whether this shift in root/shoot ratio could result in reduced drought tolerance under conditions of water stress.

Dudley & Schmitt (1996) used phenotype manipulation to test for density-dependent selection on stem elongation in a natural population of *Impatiens capensis*, a common North American annual. Elongated and non-elongated seedlings, produced by exposure to low and high R:FR, were transplanted into high-density and low-density stands in the field. Plants harvested after 2 weeks displayed a pattern similar to that observed by Ballaré *et al.* (1991): elongated seedlings had higher above-ground biomass than

non-elongated seedlings, but the magnitude of the difference was much greater at high density. However, measurements of lifetime reproductive fitness supported both predictions of the adaptive plasticity hypothesis: initially elongated plants had higher relative fitness than non-elongated plants at high density, and lower relative fitness at low density. Multivariate phenotypic selection analysis (Lande & Arnold 1983; Mitchell-Olds & Shaw 1987; Wade & Kalisz 1990) revealed that the fitness difference between elongated and non-elongated plants at high density was attributable to direct selection for increased height (Dudley & Schmitt 1996). However, direct selection on height did not explain the lower fitness of elongated plants at low density, suggesting an intrinsic physiological cost of the shade avoidance phenotype independent of selection on above-ground morphology. A testable hypothesis is that elongated plants were more vulnerable to water stress under field conditions (Dudley & Schmitt 1996).

### COMPARATIVE APPROACHES TO THE SHADE AVOIDANCE HYPOTHESIS

Comparative approaches provide a useful complement to experimental studies of selection for testing hypotheses about adaptive evolution. It has been suggested that phytochrome-mediated shade avoidance responses are more advantageous in open habitats, where R:FR is a reliable cue of neighbour proximity, than in woodland habitats, where elongation elicited by low R:FR beneath the forest canopy could be maladaptive (Morgan & Smith 1979). Comparative data indicate that woodland species are often less responsive to R:FR than species of open habitats (Morgan & Smith 1979; Corré 1983; Van Hinsberg 1996; Van Tienderen & Van Hinsberg 1996) as predicted by this hypothesis. So far, no published study has tested the shade avoidance hypothesis using modern phylogenetic methods to control for the effects of ancestry (Felsenstein 1985; Harvey & Pagel 1991), and such analyses are clearly needed. To determine whether a given plastic response represents an adaptation to a particular selective environment, the baseline should be the reaction norm of the ancestral taxa (Doughty 1995).

It is also important to ask whether ecotypic differentiation in photomorphogenesis can occur among natural populations experiencing different selective pressures. Relatively little information is available concerning intraspecific genetic differentiation in shade avoidance responses. Field populations of *Galium aparine* show evidence of greater responsiveness to R:FR than hedgerow populations (Bain & Attridge 1988). Hayfield populations of *Plantago lanceolata* are more plastic than pasture populations in terms of plasticity of growth form to R:FR, although population differences in plasticity are small compared with differentiation in trait means (Van Hinsberg 1996; Van Tienderen & Van Hinsberg 1996). In *Impatiens capensis*, plants derived from an open habitat display greater stem elongation in response to reduced R:FR than plants from woodland populations (Dudley &

Schmitt 1995). This population difference is localized in the first internode, leading to the intriguing suggestion that different internodes may be capable of evolving independently. If canopy closure occurs at a particular developmental stage in the field, then different internodes might experience very different selective pressures. This hypothesis is testable by phenotypic selection experiments in the field.

The identification of photomorphogenic ecotypes in wild species clearly deserves additional effort. In addition to providing insight into how selection acts on photomorphogenesis in different natural environments, such ecotypes may be extremely useful for future studies of adaptive evolution at specific photomorphogenic loci. Analysis of hybrid segregants (Gottlieb 1984; Orr & Coyne 1992), and more recently molecular mapping of quantitative trait loci (Mitchell-Olds 1995) provide increasing evidence that major genes may play an important role in plant evolution, adaptive differentiation and speciation. The specific photomorphogenic loci identified by molecular and developmental genetic studies provide attractive candidate genes for investigations of adaptive genetic differentiation in wild species. It will be of considerable interest to determine which, if any, of these genes contribute to quantitative genetic variation in shade avoidance responses within and between natural plant populations. QTL mapping of shade avoidance ecotypes may also help to identify additional loci with important functional roles in photomorphogenesis.

### GENETIC VARIATION WITHIN NATURAL POPULATIONS

For shade avoidance responses to evolve in response to natural selection, there must be variation within populations in reaction norms to vegetation shade (Via & Lande 1985). Such quantitative genetic variation can be detected by replicating clones, inbred lines, or sibships across experimental treatments and testing for significant genotype  $\times$  environment interaction using mixed-model analysis of variance. Quantitative genetic variation in shade avoidance responses can also be detected directly by examining responses to artificial selection. Several recent studies have detected genetic variation in R:FR responses in wild plant species (Solangaarachchi & Harper 1987; Skávllová & Krahulec 1992; K. Donohue & J. Schmitt, unpublished results). In *Plantago lanceolata*, genetic variation in response of leaf length to light quality was observed both within and among lines subjected to bidirectional selection on leaf length under low and high R:FR (Van Hinsberg 1996). Lines selected in the direction of response to the environment (i.e. selection for increased leaf length under low R:FR and decreased leaf length under high R:FR) were more plastic than lines selected in the direction opposite to environmental response (selection for decreased leaf length under low R:FR and increased leaf length under high R:FR). These studies suggest that within-population quantitative genetic variation in shade

avoidance responses, and thus the potential for evolutionary change, may be relatively common in the wild, although additional data are needed.

### CONSTRAINTS ON THE EVOLUTION OF SHADE AVOIDANCE RESPONSES

In predicting how photomorphogenesis may evolve in response to variation in natural selection in variable light environments, it is important to remember that selection acts on the multivariate phenotype, not independently on individual traits. Direct selection on one character may also result in indirect selection on a correlated trait. The evolutionary response to selection towards the optimal reaction norm for a given trait may be constrained by strong genetic correlations across or within environments (Via & Lande 1985; Gomulkiewicz & Kirkpatrick 1992). For example, in *Plantago lanceolata*, shade avoidance traits such as leaf length are genetically correlated across R:FR environments (Van Hinsberg 1996). Moreover, direct selection on leaf length results in correlated responses of other traits, such as leaf number and leaf angle, indicating that they are genetically linked (Van Hinsberg 1996). Thus, direct selection on a single trait in one light environment may result in evolutionary responses in correlated traits that are not necessarily adaptive.

If a suite of characters is controlled by the same developmental pathway, then the independent evolution of reaction norms may be especially limited (Van Tienderen 1990). In *Plantago lanceolata*, shade avoidance responses to R:FR involve integrated plasticity of a suite of traits such as leaf length, leaf number, leaf angle, rosette number and scape length; the same integrated morphological response is elicited by application of gibberellic acid, indicating developmental linkage (Van Hinsberg 1996; Van Tienderen & Van Hinsberg 1996). Such developmental constraints may be common in plants due to integrated action of growth regulators or meristem allocation patterns (Gottlieb 1986; Chapin, Autumn & Pugnaire 1993). Integrated plasticity of the multivariate phenotype may well be shaped by correlative selection on individual traits in different environments, or by selection on the underlying physiological mechanism itself (Schlichting & Pigliucci 1995). However, the trajectory of response to such selection will depend upon the genetic architecture of shade avoidance traits in natural populations. Although there is considerable evidence that plastic shade avoidance is the product of adaptive evolution, it cannot be assumed that the suite of photomorphogenic responses observed for a given species represents an adaptive optimum for every trait. To test this hypothesis requires direct measurement of selection on multivariate phenotypes and genotypes in natural populations.

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