

RESPONSES OF CARBON ACQUISITION TRAITS TO IRRADIANCE AND LIGHT QUALITY IN *MERCURIALIS ANNUA* (EUPHORBIACEAE): EVIDENCE FOR WEAK INTEGRATION OF PLASTIC RESPONSES¹

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It is often suggested that traits will be integrated, either because of pleiotropy or because natural selection may favor suites of integrated traits. Plant responses to different environments can provide evidence of such integration. We grew *Mercurialis annua* plants in high-density stands in high irradiance, in neutral shade, and in high red to far-red (R:FR) shade, resulting in environments of high irradiance, low R:FR; low irradiance, low R:FR; and low irradiance, high R:FR. We measured gas exchange, leaf morphology, stem elongation, and biomass traits and tested the prediction that traits within each functional group would show higher trait integration, as evidenced by high correlations among traits within environments, higher correlations of trait plasticity, and lower plasticity of trait correlations. Overall, we found evidence of only moderate integration for some groups of traits. Functionally related groups of traits, or pairs of traits, could be strongly integrated by one criterion but weakly integrated by another of the criteria. Stem elongation traits, though often observed to be strongly integrated in other taxa, showed little evidence of integration. Internode traits exhibited a novel pattern of responses to low R:FR, with increased elongation of the hypocotyl, decreased elongation of the first internode, and no change in the second internode. We propose that these responses to light are more likely to be the result of natural selection than the consequence of constraints imposed by pleiotropy.

Key words: androdioecy; gas exchange; phenotypic plasticity; plasticity integration; R:FR; stem elongation.

In evolutionary biology, the phenotype can be studied as a suite of correlated traits (Lande and Arnold, 1983). Researchers may even define new traits, e.g., the amount of insect damage as a trait of the plant (Rausher and Simms, 1989; Simms and Rausher, 1989) or flower size in males and females as genetically correlated traits (Meagher, 1994). However, the use and value of the character concept are areas of intense discussion (e.g., Wagner, 2001, and references therein). For example, critiques of such trait-focused approaches to evolution have been articulated by Gould and Lewontin (1979): “organisms are integrated entities, not collections of discrete objects. Evolutionists have often been led astray by inappropriate atomization... .”

In the plant literature, several authors have suggested that the integrated expression of many traits is explained by variation in primary, more fundamental traits (Kudoh, Ishiguri, and Kawano, 1996). For instance, Chapin, Autumn, and Pugnaire (1993) have suggested that many plant traits are so completely correlated with seed size that it may determine many lifetime characteristics. Other candidate “master traits” in-

clude plant size (Coleman, McConnaughay, and Ackerly, 1994), timing of reproduction and size at reproduction (Kudoh, Ishiguri, Kawano, 1996), and meristem allocation (Geber, 1990; Schmitt, 1993). Candidate master traits are identified either by strong phenotypic correlations (positive or negative) among traits, and from arguments based on the underlying biology of the traits. If master traits exist, then the problem of understanding how the multivariate phenotype evolves is greatly simplified. Instead of the multivariate phenotype being shaped by selection on individual traits and the constraints on these traits, the “master trait” hypotheses suggest that the multivariate phenotype is largely the consequence of pleiotropy.

One way of understanding integration among traits is to evaluate the patterns of phenotypic correlations in response to different environments. Both the magnitude and the sign of phenotypic correlations frequently change in response to differing environments (Schlichting, 1989a, b; Pigliucci, Schlichting, and Whitton, 1995; Pigliucci and Marlow, 2001). This “plasticity of trait correlations” is considered one aspect of plasticity integration (Schlichting, 1989b; Pigliucci, 2001). Low plasticity of trait correlations is suggested to show higher integration among traits (Schlichting, 1989b).

A second aspect of plasticity integration is the “correlation of character plasticities” i.e., do traits respond similarly or independently to a change in environment (Schlichting, 1989a)? Studies have found different degrees of plasticity integration for the correlation of trait plasticities. For example, in a study by Pigliucci, Schlichting, and Whitton (1995), the trait of life span exhibited high plasticity integration with flowering time; both traits had increased values in the low light and low nutrient treatment compared to the optimal and the low water treatment. However, the trait of number of leaves

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showed low plasticity integration with life span; it had a decreased value in the low nutrient treatment where life span had increased and remained comparable to the optimal, low water values in low light where life span had increased. A study of components of yield found high integration (Marshall, Levin, and Fowler, 1986) in response to different stresses. Plants have shown both low (Pigliucci, Cammell, and Schmitt, 1999) and high (van Hinsberg, 1997a, b) integration in the correlation of their responses to density and to light quality, which is a cue of density.

If master traits exist, then groups of traits should show high integration by all three measures: highly positive or negative phenotypic correlations among traits within an environment, low plasticity of trait correlations, and high correlation of trait plasticities. Only a few studies have looked at all aspects of plasticity integration and asked whether suites of traits that are more functionally or developmentally related are more apt to show plasticity integration. Waitt and Levin (1993) found higher plasticity integration in functionally related traits for both aspects of plasticity integration. However, their analysis did not analyze each functional group separately, though measures of size appeared more strongly integrated than the flower and leaf traits. Donohue and Schmitt (1999) found high integration in response to density and light quality in phytochrome-mediated traits, but variation in responses of non-phytochrome-mediated traits. Here we ask how functionally interacting traits related to carbon acquisition and allocation respond to different light cues.

Functionally androdioecious hexaploid populations of *Mercurialis annua* L. sensu lato (s.l.) (Euphorbiaceae) were used as a model system for our investigations. The populations are found distributed around the Mediterranean (Pannell, 1997a, b), primarily in open disturbed ruderal habitats. These populations consist of male individuals with staminate flowers on erect peduncles above the plant and hermaphroditic individuals with axillary clusters of staminate and pistillate flowers. Character differences between male and hermaphroditic individuals potentially provide another axis to examine for integration. In quantitative genetic studies, gender dimorphism is often treated analogously to phenotypic plasticity (Meagher, 1994).

We grew *Mercurialis annua* plants in high-density stands in high irradiance, in neutral shade, and in high red to far-red (R:FR) shade, resulting in environments of high irradiance, low R:FR; low irradiance, low R:FR; and low irradiance, high R:FR, respectively. We measured photosynthetic rates, stomatal conductance, leaf mass, leaf area, height, internode lengths, aboveground vegetative biomass, and male biomass for males and hermaphrodites, and number of fruits for hermaphrodites grown in these three environments. We used this data to ask how the traits are integrated within functional groups, which are defined in MATERIALS AND METHODS. We asked (1) whether functionally related traits were more apt to be strongly correlated within environments; (2) whether the plasticity of trait correlation across environments is less plastic for functionally related traits; (3) whether traits responded similarly to the light environments; and (4) whether the trait plasticities were more likely to be correlated for functionally related groups of traits. Finally, we determined whether these different measures give consistent assessments of integration.

MATERIALS AND METHODS

Environments—The experiment incorporated three shading treatments: (1) high light, (2) neutral shade, and (3) high R:FR shade, placed over high-

density stands. Plant responses to density constitute a well-studied example of phenotypic plasticity. Plant plasticity to density can be adaptive (Schmitt, McCormac, and Smith, 1995; Dudley and Schmitt, 1996). The light cues that plants use to sense density are well known (Smith, 1982, 1995; Smith and Whitelam, 1990) and easily manipulated (Ballaré, Scopel, and Sánchez, 1991a; Dudley and Schmitt, 1995, 1996). The primary and best-studied cue for density is light quality. The photoreceptor phytochrome alters state in response to photons of red and far-red light. Light transmitted or reflected by living plants has a low red to far-red ratio (R:FR) because chlorophyll absorbs more strongly in the red than the far-red part of the spectrum. Consequently, the phytochrome signal transduction chain allows plants to sense and respond to vegetation shade. Plants in high light and neutral shade both received the light quality cue from the presence of neighbors, but received different irradiance. Plants in high R:FR shade were prevented from perceiving the light quality cues from presence of neighbors, but received the same irradiance as neutral shade plants.

Photon fluence, or irradiance, induces phenotypic responses both because it is a resource and because it is an environmental cue (Ballaré, Scopel, and Sánchez, 1991b; Jenkins et al., 1995). Although the light-dependence of photosynthesis implies that many responses to irradiance, particularly in size, are resource related, other responses, particularly changes in morphology, may be the consequence of the cryptochrome-mediated signal transduction response chain, which is cued by blue light (Jenkins et al., 1995). It is common to find that traits respond similarly to low irradiance and low R:FR in both sun and shade plants (Fitter and Ashmore, 1974; Morgan and Smith, 1981; Corrê, 1983; Lee, 1988; Ballaré, Scopel, and Sánchez, 1991b; Turnbull, 1991).

These light quality and irradiance combinations allowed us to understand how the plants responded to the cues of vegetation shade, light quality, and irradiance. However, they also have equivalents in nature; (1) high irradiance, low R:FR corresponds to high intraspecific density, (2) low irradiance, low R:FR corresponds to competition from taller interspecific neighbors or overhead canopy shade, and (3) low irradiance, high R:FR corresponds to shade not arising from living plants.

Because both low irradiance and low R:FR are associated with vegetation shade and with high density, we predicted that many trait responses to both aspects of light will be similar, e.g., internodes are predicted to elongate in response to both low irradiance and low R:FR. Other trait responses are expected to combine resource-related responses and cues, e.g., height should be greater in high irradiance and low R:FR than in low irradiance and low R:FR because of increased growth rates for plants in high irradiance.

Suites of traits—We measured four suites of carbon acquisition and allocation traits: leaf morphology, gas exchange, height, and biomass traits in *Mercurialis annua*, an annual herb. The first three suites affect rates of carbon acquisition. Leaf morphology (leaf mass, leaf area, and specific leaf mass) determines the area photosynthesizing and can affect rates of gas exchange. A second suite comprised the gas exchange traits (photosynthetic rate, stomatal conductance, water use efficiency) that measure the rate of carbon acquisition per unit leaf area and the associated water loss. These traits are affected by light quality (Maliakal et al., 1999; Sleeman and Dudley, 2001) and irradiance (Boardman, 1977). The third suite includes traits related to stem elongation, such as the height of the plant and length of internodes (Smith, 1995). These are the best-studied responses to light quality. Height is a carbon acquisition trait in the broad sense because at high density, taller plants receive more light (Casal and Smith, 1989). The fourth suite includes measures of vegetative and reproductive biomass, which give an indication of carbon allocation. We predicted that these traits would increase with irradiance. The four suites of traits that we considered allow us to examine plasticity integration to irradiance and R:FR along a hierarchy of functional interrelationships. We asked whether all traits exhibit high plasticity integration or whether plasticity integration is stronger within the carbon acquisition traits, for leaf traits vs. stem traits, or within each of the four suites of traits. Of course, at the most trivial level, plasticity integration can be expected of composite traits and their component traits, e.g., water use efficiency is the ratio of photosynthetic rate to stomatal conductance, and height is the sum of the lengths of the internodes.

Experimental design—*Mercurialis annua* L. s.l. seeds were collected from a natural population in the precincts of Pabellón de Cuba in southern Spain during March 1994 (see Pannell, 1997b for details). On 3 September 1997, seeds were planted in ten $8.0 \times 29.5 \times 37.0$ cm plastic trays containing pure, washed river sand. The seeds were set 1.0 cm below the surface of the media in seven rows with 350 seeds per row providing high density stands of $\sim 22,500$ plants/m². The seeds were allowed to germinate in high light at the glasshouse facilities at the Royal Botanical Gardens in Burlington, Ontario, Canada, with top watering performed daily for the duration of the experiment.

After the majority of plants had emerged, the trays were randomly assigned to the different light quality treatments. Growth in the greenhouse was slower than expected. Because of the slow growth rates and the limited availability of greenhouse space, we were forced to harvest the plants at an earlier life stage than planned. At the time of harvest, 60 d after planting, $\sim 26\%$ of plants had developed only a first and second internode, 57% had developed a third internode, and 17% had developed a fourth internode. Many of the plants had begun to flower and were developing fruits upon harvest. Of the male plants, $\sim 96\%$ of plants were producing male flowers at the time of harvest. With respect to the hermaphroditic plants, $\sim 90\%$ were producing both male and female flowers, of which $\sim 75\%$ had developing fruits at the time of harvest. These estimates are based on gender frequencies assessed at a later harvest (data not shown). Seed maturation and dispersal were also noted in $\sim 26\%$ of hermaphrodites.

Light quality treatments—The experiment incorporated three shading treatments: high light, neutral shade (NS), and high R:FR. The combination of the high-density planting and these shading treatments yielded three light environments: high irradiance, low R:FR; low irradiance, low R:FR; and low irradiance, high R:FR. The design included two replicates (hereafter trays) of each of the high R:FR and neutral shade treatments and one replicate of the high-light treatment. All trays were randomized with respect to their position on the bench every other week. From each tray 20 male and 20 hermaphrodites were randomly selected for measurement of gas exchange and biomass allocation. Nonflowering plants were not selected because they could not be assigned a gender. Though the flowering plants consisted of the vast majority of the population, plants with either lower vegetative biomass or low early allocation to flowering were underrepresented compared to the population as a whole.

For the high-light treatment, the trays were unshaded, receiving ambient greenhouse light. The two shade treatments consisted of 43.8×74.3 cm filters placed at an initial height of 25 cm above the top of the trays and provided an irradiance of $45\% \pm 5\%$ of the high light intensity. The light filters were subsequently raised an additional 18 cm each time when plants grew as tall as the level of the treatment. Both filters were raised at the same time to maintain comparable conditions between them.

The high R:FR treatment was imposed using a solution of 45 g/L of CuSO₄ in distilled water to selectively filter out far-red light (FR: 710–730 nm) (Ballaré, Scopel, and Sánchez, 1991a). Enough distilled water was used to fill the $15.2 \times 45.7 \times 76.2$ cm box made of 0.95 cm clear acrylic plastic to a depth of 3 cm. The box had an open top and was filled with distilled water as required. In this treatment, filtering out far red light raises the incident R:FR reaching the stand and suppresses the shade avoidance response to neighbors (e.g., Ballaré, Scopel, and Sánchez, 1991a; Dudley and Schmitt, 1996). The neutral shade treatment consisted of one layer of 50% black plastic shade cloth with a layer of 0.16 mm clear thin vinyl to further reduce light intensity and to help match the microclimate of the high R:FR treatment. In this treatment, the R:FR is not altered from that of the incident light. Here the plants are able to detect the presence of neighbors and to respond to the associated changes in the light quality (Schmitt and Wulff, 1993; Smith, 1995).

The high R:FR and NS treatments were enclosed in frames that were 56 cm wide \times 81 cm long \times 101.5 cm tall with their sides covered in aluminum foil. The foil was used to block diffuse light from the sides and to reflect the imposed light quality back onto the stands.

Gas exchange measurements—Twenty males and 20 hermaphrodites were randomly selected from each of the five trays of plants. Plants near the edges

of trays were excluded by selecting plants at least five positions in from the edge in rows 2 through 6. On 12 November 1997, the most recently fully expanded leaf on each plant was sampled for gas exchange measurements. The net photosynthetic rate (assimilation of CO₂ in micromoles of CO₂ per square meter per second) and rate of stomatal conductance (millimoles of H₂O per square meter per second) of this leaf were measured within 60 s of having cut the plant's stem at its base to remove it from the tray. Gas exchange was measured with a Ciras-1 portable photosynthesis system using a Parkinson Leaf Cuvette attached (PP Systems, Hitchin Herts, UK). To maintain a relatively consistent and uniform measurement environment, measurements were taken after the leaf had equilibrated for 45 s in the cuvette. The Ciras-1 unit was adjusted to the following settings: internal airflow rate ~ 200 mL/s, cuvette air temperature $\sim 25^\circ\text{C}$, and photosynthetic photon flux density $800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Boundary-layer resistance was determined using methods described in the Ciras-1 operator's manual (version 2). Because boundary-layer resistance is correlated with leaf size, a calibration curve estimating resistance as a function of leaf area was used for calculation of photosynthetic rates and stomatal conductance. Photosynthetic rate and stomatal conductance were calculated according to equations described in the Ciras-1 manual. Effects of date and time were removed from the calculated photosynthetic rates and stomatal conductance (Winn and Evans, 1991). For the high R:FR shade treatment, environmental variables did not explain variance in gas exchange. For high irradiance, the effects of time and time \times date were removed, and for neutral shade, date and air temperature from photosynthesis and date, time \times date, and air temperature from stomatal conductance.

Morphological measurements—Immediately after the gas exchange measurements were performed, the measured leaf was sectioned into the portion within the cuvette and the remainder. The area of both portions was measured using an AM-100 leaf area meter (Analytical Development Co., Hoddeson, UK). The leaf was then dried and weighed to obtain leaf mass. Internode lengths and total height were measured for all plants. Plants were stripped of remaining leaves, male and female flowers, and fruits. The leaves, flowers, fruits, and stem portion were dried at 65°C for at least 1 wk and then weighed.

Statistical analysis—All parametric tests were performed with SAS version 6.12 for Windows (SAS Institute, 1996, Cary, North Carolina, USA). Plants with missing traits (1–2 in each shade treatment) were kept in analyses not involving that trait. An analysis of variance (ANOVA) with light treatment as the main effect was used to determine effects of the treatments on the measured traits. We analyzed shade treatment, gender, and shade treatment \times gender effects on internode lengths, height, dry masses for vegetative and male mass biomass, and covariate-corrected values of photosynthetic rate (A), stomatal conductance (g), and water use efficiency (WUE, the ratio of A/g), using the general linear modelling (GLM) procedure. Tray was nested within treatment. Because the among-tray variance was not relevant for the plasticity responses to the light cue, we did not test treatment effects over the tray variance (Newman, Bergelson, and Grafen, 1997). We analyzed shade treatment and tray nested within shade treatment effects on fruit number, for hermaphrodites only.

An analysis of covariance (ANCOVA) was performed with PROC GLM to determine treatment differences in the relationship between height and shoot mass, which measures elongation. Because this relation was curvilinear, both mass and mass \times mass were included in the model. We found no significant interactions between shade treatment or gender and mass or mass \times mass and consequently omitted any interactions between mass and the discrete variables from the final model.

Plasticity integration—The first measure of plasticity integration is the plasticity in the phenotypic correlation matrices. For each environment, we calculated Pearson correlations (PROC CORR) among traits. In this and subsequent analyses all individuals were used to estimate the correlations except for the correlations with fruit number, where only hermaphrodites were used. We tested for differences among the three correlation matrices for the three environments using hierarchical principal components analysis (Flury [1988]; program available from Patrick Phillips, University of Oregon, Eugene,

Oregon, USA at <http://www.uoregon.edu/~pphil/programs/cpc/cpc.htm>). This technique determines whether matrices share similarity at different hierarchical levels by testing a series of hypotheses about matrix similarity against the null hypothesis that the matrices are completely dissimilar. At the lowest level of similarity, the matrices share one principal component (eigenvector). Hypotheses of increasing similarity include sharing more than one principal component (up to $p - 2$ principal components, where the matrix has dimensions of $p \times p$), being proportional such that matrices share all principal components but differ in eigenvalues, or being completely equal with similar principal components and similar eigenvalues (Flury, 1988).

We display the second measure of plasticity integration, the correlations in character responses across environments, in a plot of the standardized character responses in environment space (Wickens, 1995). All characters were first standardized to a mean of 0 and a standard deviation of 1. Then the averages were calculated for each environment. The neutral shade treatment is set to be the 0,0 point. Distance along the x -axis, which measures the response to R:FR, is the difference between the high R:FR shade treatment and neutral shade treatment. Distance along the y -axis, which measures the response to irradiance, is the difference between the high-light treatment and the neutral shade treatment.

We estimated the Pearson correlation (r) between character responses to these environments from the cosine of the angle between character vectors (Wickens, 1995), e.g., vectors at 0° have a correlation of 1, vectors at 180° have a correlation of -1 , and vectors at 90° have a correlation of zero. Correlations tended to be high because of the curvilinear nature of the relation between angle and cosine. To test whether these correlations differed from zero, we bootstrapped (Manly, 1997) the angle estimate by randomly subsampling from the original individuals to obtain 10000 sample populations. For each sample population, the phenotypic values were standardized, shade treatment means and standard deviations estimated, and the angles of the pairs of sample vectors calculated as for the original populations to obtain the probability distribution of each angle. We tested each measured angle against the null hypothesis that the angle was 90° (i.e., that the correlation was zero).

For the third measure of plasticity integration, we tested the hypotheses that the correlations within the a priori defined groups of traits were higher (either more positive or more negative) than correlations among less related traits, using a Monte Carlo simulation (Manly, 1997). This was done within each of the three within-environment correlation matrices and for the across-environment correlation matrix. The average of the absolute values of the correlation within the a priori defined group of traits was compared to the probability distribution derived from 10000 random draws from the absolute value of the correlations from the matrix. Traits were considered significantly integrated if the average was greater than the 95 percentile of the distribution (one-tailed test).

RESULTS

Plant height—The plants in the two low-irradiance treatments were taller than plants in high irradiance (Fig. 1a, Table 1). The hypocotyl, first internode, and second internode were significantly longer in both shaded treatments (Fig. 1b–d, Table 1). The plants in both shaded treatments were significantly taller for a given vegetative biomass than plants in high irradiance (Figs. 1e and 2, Table 2). For the shaded treatments, hypocotyls were significantly longer in plants grown under neutral shade than for plants grown in high R:FR shade, as expected (Fig. 1b, Table 1). However, the plants grown under high R:FR shade had longer first internodes than plants grown under neutral shade (Fig. 1c, Table 1). Plants from the two shaded treatments did not differ significantly in the length of the second internode (Fig. 1d, Table 1). Furthermore, the plants grown under neutral shade were not more elongated than plants grown under high R:FR shade (Fig. 1e, Fig. 2). There was a significant interaction between biomass and gen-

der in their effects on height, indicating that males were more elongated than hermaphrodites (Fig. 1e, Table 2).

Biomass traits—An analysis of variance revealed no significant differences between treatments or genders for vegetative biomass (Table 3). There were no significant differences between genders, or between treatments, for male reproductive biomass. However, the plants grown in high irradiance produced significantly more fruits than those in the two shaded treatments (Table 3).

Leaf traits—Leaf traits also showed significant treatment differences but no gender differences. The area of the most recent fully expanded leaf that was used for gas exchange measurements differed significantly between all treatments. Plants from neutral shade had the largest leaves, and plants from high irradiance had the smallest leaves (Fig. 3a, Table 4). Specific leaf mass, a measure of mass relative to area, also showed significant treatment differences (Table 4). The mean specific leaf mass was highest in high irradiance and lowest under neutral shade (Fig. 3b). Leaf mass, however, was not affected by the treatments (Fig. 3c, Table 4).

Physiological traits—Gas exchange was not affected by gender. Significant treatment differences were found for photosynthetic rate and stomatal conductance (Table 5). Photosynthetic rates were highest in plants grown under high R:FR shade and lowest in high-irradiance plants (Fig. 4a). Stomatal conductance differed significantly between all treatments and was highest in plants under high R:FR shade and lowest in high irradiance (Fig. 4b, Table 5). There was no significant difference in water use efficiency between plants in the different shade treatments (Fig. 4c, Table 5).

Plasticity integration—The within-environment correlations are presented in Tables 6–8. The only significant evidence of trait integration, as measured by higher average absolute correlations within a trait group, was found for stem traits in high irradiance (Table 6). For the correlation matrix as a whole, the correlations among traits differed significantly among environments (Table 9). Within functional groups, there was evidence of some plasticity integration. The within-environment correlation matrices for the gas exchange traits shared one common principal component (Table 9). The within-environment correlation matrices for the biomass traits were found to be similar, with no difference in correlation matrices (Table 9).

Correlation of trait plasticities in responses to the light quality and irradiance were high and frequently significant (Fig. 5, Table 10). Only hypocotyl length, specific leaf mass, and leaf area showed the same direction in their responses to low R:FR and low irradiance. Only female fruit number showed the increase with higher irradiance expected as a response to the higher light resource. Significant evidence for trait integration, as measured by higher average absolute correlations within a trait group, was found for gas exchange traits and for biomass traits (Table 10).

DISCUSSION

In this study we measured functional and plasticity integration in several groups of traits in response to light environments and between genders. If master traits exist, then groups of traits should show high integration by all three measures:

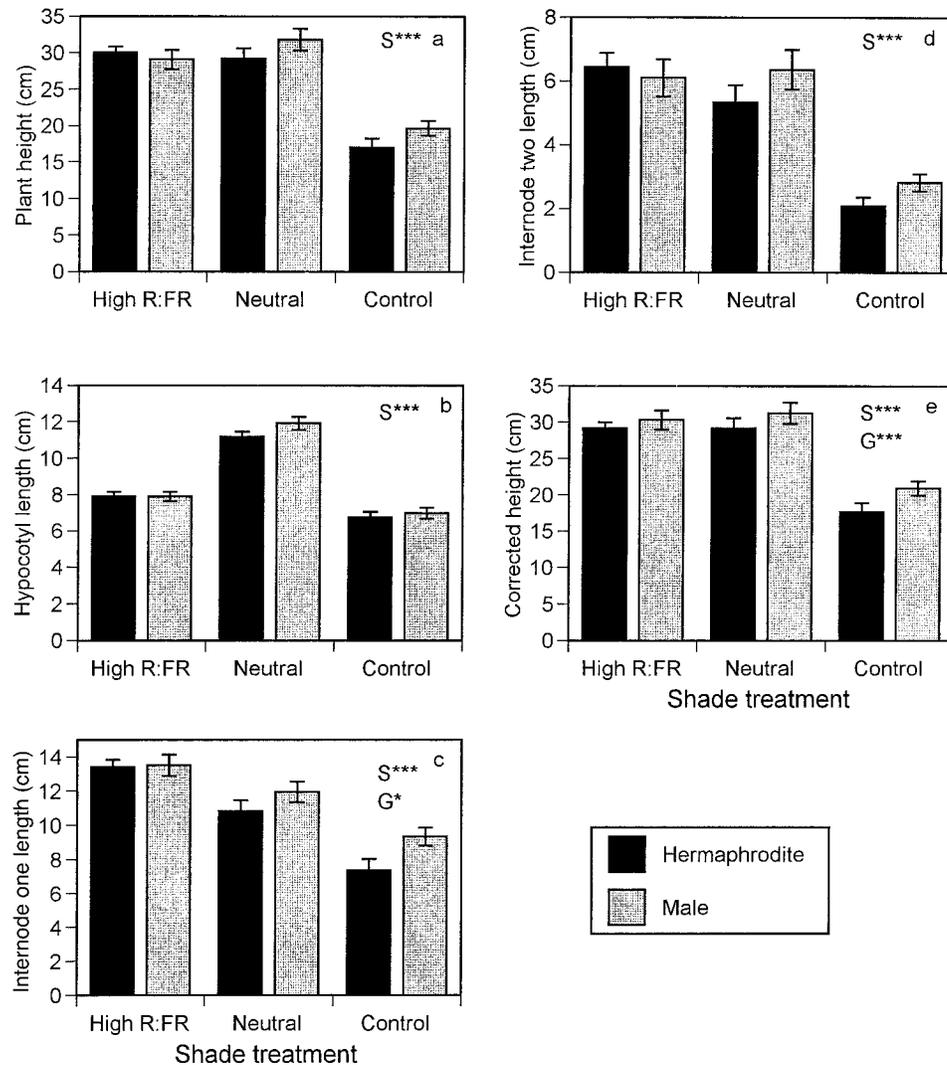


Fig. 1. Effects of shade treatment and gender on (a) height, (b) hypocotyl length, (c) internode one length, (d) internode two length, and (e) height corrected for biomass in glasshouse-grown populations of *Mercurialis annua*. The corrected heights are obtained from the least square means for the analysis of covariance in Table 2. $N = 193$. Bars indicate ± 1 SE. Effects of Shade (S) and Gender (G) are indicated when significant. * $P < 0.05$, *** $P < 0.001$.

highly positive or negative phenotypic correlations among traits within an environment, low plasticity of trait correlations, and high correlation of trait plasticities. Though the lack of differentiation between genders gave little evidence to judge integration, the strong though often unpredicted plasticity responses to the shade environments for nearly all traits gave considerable evidence about how these traits are integrated. For each measure of integration, we found evidence of moderate integration for at least one group of functionally related traits. However, no functional group could be assessed as either consistently integrated or consistently not integrated. Instead, the assessment of integration depended on how it was measured. This complexity in the integration results suggests that there is no simple answer, such as the "master trait" hypothesis, to the problem of understanding the evolution of multiple traits. Consequently, our results suggest that the unexpected plasticity shown by *M. annua* in response to R:FR is unlikely to be the consequence of constraints imposed by trait and plasticity integration.

Gender dimorphism—Gender dimorphism has been observed in physiological traits in several dioecious species (reviewed in Dawson and Geber, 1999). However, in our study, gender dimorphism in vegetative traits was found only in longer first internodes, resulting in greater elongation in males, similar to results found in a previous study of this species (Pannell, 1997a). This is hypothesized to be an adaptive difference; because pollen is wind-dispersed in this species, greater height should lead to more effective dispersal. The finding of dimorphism in only one trait does suggest a lack of integration in gender dimorphism. We did find gender dimorphism in correlations among traits (S. A. Dudley, J. D. Sleeman, J. R. Pannell, and S. C. H. Barrett, unpublished data). Contrary to a previous study of *M. annua* (Pannell, 1997a), there were no significant differences between genders, as well as between treatments, for male reproductive biomass. Reproductive allocation was observed to be relatively low compared to *M. annua* in other studies (Pannell, 1997a, and personal observation). This suggests that the plants may have been rel-

TABLE 1. Analysis of variance for the height variables in response to shade treatment and gender in glasshouse grown populations of *Mercurialis annua*. Effects of tray were nested within shade treatment; however, we did not test over the between-tray variance.

Source	df	Total height		Length of hypocotyl		Length of first internode		Length of second internode	
		F	P	F	P	F	P	F	P
Shade (S)	2	39.69	0.0001	126.14	0.0001	29.96	0.0001	22.58	0.0001
Gender (G)	1	1.38	0.2417	1.35	0.2462	4.47	0.0358	0.66	0.4161
Tray[S]	2	4.41	0.0135	0.47	0.6270	6.05	0.0029	7.48	0.0008
S × G	2	1.48	0.2311	0.97	0.3800	0.93	0.3962	1.49	0.2272
Error	185								

atively early in their reproductive stage, which was further supported by the fact that relatively few plants had dispersed seeds at the termination of the experiment. We attribute this difference to the low light intensities they experienced in this study compared to their native habitat. The growth environment and the early life stage in which we measured the traits should certainly have influenced the results we found.

Responses to light treatments—However, overall we found striking plasticity in response to the light environments. We measured the responses of several carbon acquisition and allocation traits to irradiance and R:FR and examined the pattern of plasticity integration shown by these traits. We found that the male flower biomass, vegetative biomass, leaf mass, and water use efficiency were not very responsive to the environmental cues, while other traits were. For all the traits, correlations among traits were often high, but the correlation matrices differed among environments. We found that the correlations of trait plasticities were often significant. We then asked whether traits within functional groups were more integrated than the group of all traits: were they more likely to be highly correlated within an environment, were correlations within functional groups constant across environments, and were trait plasticities to different environments more highly correlated within functional groups?

A surprising result was that few traits exhibited either of the predicted patterns of responses to irradiance and R:FR. We had first predicted that, because irradiance and R:FR are both associated with vegetation shade, many traits should either respond positively to both cues or negatively to both cues. However, only responses for a few traits (hypocotyl length, specific leaf mass, and leaf area) were consistent with this prediction. The alternative patterns of response we found were (1) traits that responded only to irradiance (female biomass, height, in-

ternode 2) and (2) traits that responded positively to R:FR but negatively to irradiance (internode 1, photosynthetic rate, and stomatal conductance). The second prediction was that greater light availability would result in greater growth in high irradiance. However, only female biomass showed a positive response to irradiance. These results contrast with several studies finding similar responses to these cues or differences explainable by light as a resource as well as a cue (Fitter and Ashmore, 1974; Morgan and Smith, 1981; Corré, 1983; Ballaré, Scopel, and Sánchez, 1991b; Turnbull, 1991). This lack of the expected patterns in *M. annua* appears to result from both a novel strategy in response to density and some evidence of stress in high irradiance.

Stem traits—The results for the stem traits were surprising in both the lack of integration that they demonstrated and the relatively weak and variable response to R:FR. Internode lengths are usually strongly affected by phytochrome-mediated stem elongation in weedy plants of disturbed, high light communities. Other studies have shown high integration (van Hinsberg, 1997a, b; Donohue and Schmitt, 1999) for phytochrome-mediated traits. The predicted similarity in response to irradiance and R:FR was found only for the hypocotyl. Responses to irradiance were strong and consistent among the stem traits, with the typical reduced elongation (Corré, 1983; Ballaré, Scopel, and Sánchez, 1991b; Dudley and Schmitt, 1995) in response to irradiance. However, *M. annua* showed highly unusual and uncorrelated responses to decreased R:FR, with the hypocotyl showing the expected increased elongation at low R:FR (Smith, 1982, 1986, 1995; Schmitt and Wulff, 1993), the first internode showing reduced elongation in low R:FR, and the second internode not responding to R:FR at all. Height was unaffected by R:FR. Though other studies have found differences among internodes in the degree of their responsiveness to R:FR (Dudley and Schmitt, 1995; Weinig,

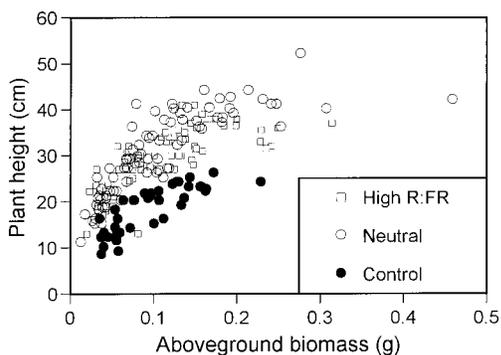


Fig. 2. Scatterplot of height vs. vegetative biomass for plants from the three shade treatments in glasshouse-grown populations of *Mercurialis annua*. *N* = 193.

TABLE 2. Analysis of covariance for height as function of vegetative biomass, shade treatment, and gender in glasshouse-grown populations of *Mercurialis annua*. Significance effects of shade treatment or gender indicate differences in stem elongation. The slope of height with biomass did not differ between the treatments or genders, so these effects were not included in the model.

Source	df	Height	
		F	P
Vegetative biomass (B)	1	235.11	0.0001
B × B	1	73.02	0.0001
Shade (S)	2	123.26	0.0001
Gender (G)	1	13.01	0.0004
S × G	2	0.72	0.4863
Tray[S]	2	2.59	0.0780
Error	183		

TABLE 3. Analysis of variance of shade treatment and gender on vegetative and reproductive allocation in glasshouse-grown populations of *Mercurialis annua*. For the analysis of number of fruits, only hermaphroditic plants were included, and only the effects of shade treatment and tray nested within shade treatment were included within the model.

Source	df	Vegetative biomass		Male reproductive biomass		No. of fruits	
		F	P	F	P	F	P
Shade (S)	2	0.70	0.4962	0.31	0.7340	7.83	0.0007
Gender (G)	1	1.36	0.2442	1.22	0.2698		
Tray[S]	2	0.62	0.5391	2.42	0.0915	0.08	0.9264
S × G	2	0.88	0.4146	1.40	0.2494		
Error (fruits)	187 (94)						

2000), no previous work has observed reduced elongation of internodes in response to low R:FR.

The consequence of the responses to R:FR is a lack of correlation in plastic responses for these traits. The only evidence of integration was found for the within-environment correlations, a measure of trait integration, in the high irradiance environment, where plants were least elongated. However, in the other environments, hypocotyl length tended to be uncorrelat-

ed with other elongation traits. The high plasticity of correlations across environments was consistent with low integration of traits.

Leaf traits—A somewhat surprising result was that the overall leaf group, including both morphological and gas exchange traits, showed no evidence of integration at any level. This was surprising because all of these measures were taken on the same leaf for each plant and because leaf morphology and gas exchange are often highly correlated (Bhagsari and Brown, 1986), and it is argued that leaf morphology will have causal effects on gas exchange (Korner, 1991; Lambers and Poorter, 1992).

Leaf morphology traits—We did not find any statistically significant evidence of integration, even though leaf area and leaf mass were highly correlated within all three environments and specific leaf mass is directly calculated as the ratio of these two traits. However, a notable result was the contrast between the correlation of trait plasticities and the within-environment trait correlations. Despite the high correlations of leaf mass and leaf area within environments, there was a complete lack of correlation of trait plasticity for leaf area and leaf mass. And despite the lack of correlation within environments between specific leaf mass and leaf area or leaf mass, the plasticity response for specific leaf mass was highly negatively correlated to the plasticity response for leaf area.

The decreased leaf area in high irradiance together with the lack of change in leaf mass explains the increase in specific leaf mass in response to irradiance, the ratio of leaf mass to leaf area. These responses are consistent with the common sun shade responses. A higher specific leaf mass, commonly a thicker leaf for a given area, is typical of plants experiencing water stress, as well as the phenotype for leaves in high light (Boardman, 1977). In *M. annua*, these responses were only cued by irradiance, though frequently both light quality and irradiance cue changes in leaf size and morphology (Morgan and Smith, 1981; Kwesiga and Grace, 1986; Lee, 1988).

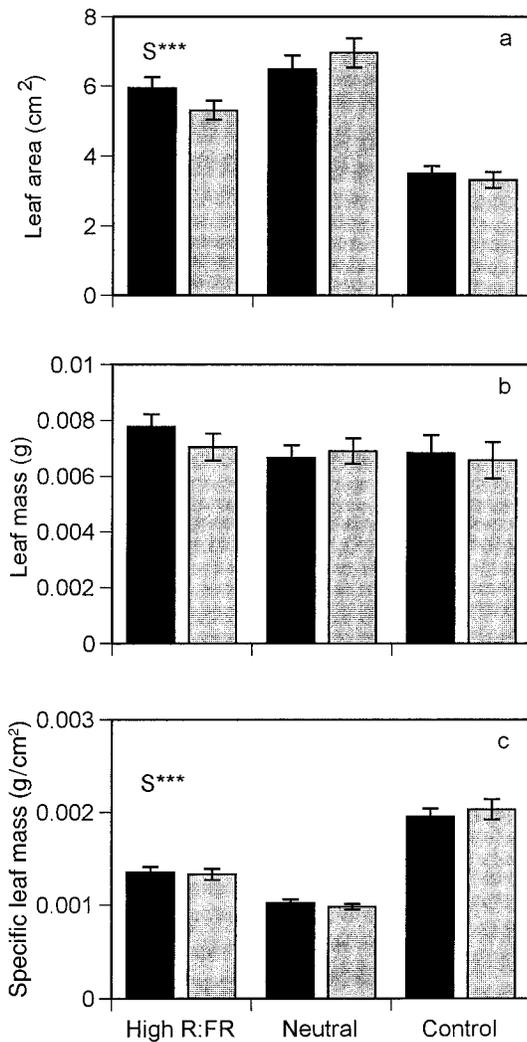


Fig. 3. Effects of shade treatments and gender on (a) leaf area, (b) leaf mass, and (c) specific leaf mass in glasshouse-grown populations of *Mercurialis annua*. Bars indicate ± 1 SE. $N = 193$. Effects of shade (S) that are significant are indicated. *** $P < 0.001$.

TABLE 4. Analysis of variance of shade treatment and gender on leaf morphology in glasshouse-grown populations of *Mercurialis annua*. Specific leaf mass is the ratio of leaf mass to leaf area.

Source	df	Leaf area		Leaf mass		Specific leaf mass	
		F	P	F	P	F	P
Shade (S)	2	33.20	0.0001	1.22	0.2990	113.83	0.0001
Gender (G)	1	0.10	0.7527	0.31	0.5778	0.00	0.9639
Tray[S]	2	2.15	0.1188	1.33	0.2682	0.34	0.7120
S × G	2	1.22	0.2990	0.53	0.5874	0.46	0.6347
Error	187						

TABLE 5. Analysis of variance of shade treatment and gender on gas exchange traits in glasshouse-grown populations of *Mercurialis annua*. The water use efficiency was estimated as the ratio of photosynthetic rate over stomatal conductance.

Source	df	Leaf area		Leaf mass		Specific leaf mass	
		F	P	F	P	F	P
Shade (S)	2	45.67	0.0001	30.50	0.0001	1.49	0.2272
Gender (G)	1	2.10	0.1488	0.41	0.5169	2.99	0.0853
Tray[S]	2	2.71	0.0691	8.16	0.0004	1.00	0.3715
S × G	2	2.43	0.0911	1.36	0.2580	1.28	0.2816
Error	187						

Gas exchange traits—Gas exchange traits showed evidence of integration for two measures: high correlation of plasticities and relatively low plasticity of correlations. For these traits, there was no similarity of responses to irradiance and R:FR. Though the responses for gas exchange traits to these environments were not correlated, they were significantly integrated, with photosynthetic rate, stomatal conductance, and water use efficiency all responding positively to R:FR and negatively to irradiance. The positive response to high R:FR for these gas exchange traits was consistent with the results of Maliakal et al. (1999) and Sleeman and Dudley (2001), who also found more elongated plants to have lower photosynthetic

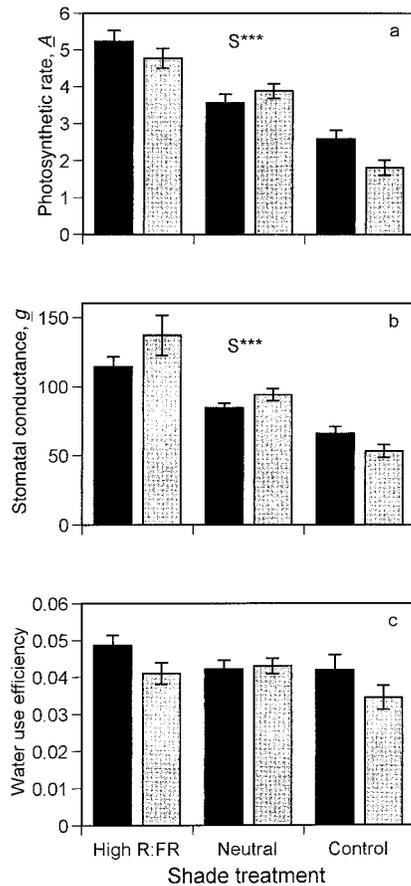


Fig. 4. Effects of shade treatments and gender on (a) photosynthetic rate, (b) stomatal conductance, and (c) water use efficiency in glasshouse-grown populations of *Mercurialis annua*. Bars indicate ± 1 SE. $N = 193$. Effects of shade (S) that are significant are indicated.

TABLE 6. Correlations among traits in the plants grown in low R:FR, high irradiance. Correlations shown in boldface type are significant at a tablewide 0.05 level after sequential Bonferroni correction. Tests that each correlation differs significantly from zero are indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. A Monte Carlo randomization was used to test the hypothesis that suites of traits within the boxes had a higher average correlation than would a random draw from the matrix (stem traits, $P < 0.001$; leaf traits, $P > 0.05$; leaf morphology traits, $P > 0.05$; gas exchange traits, $P > 0.05$; carbon allocation traits, $P > 0.05$); significant results are indicated by a solid line around the box. For correlations with fruit number, $N = 18$, otherwise $N = 38$.

	Height	Hyp.	Int. 1	Int. 2	Leaf area	Leaf mass	SLM	A	g	WUE	Veg. mass	Male mass	Fruit no.
Height													
Hyp.			0.95***	0.86***	0.29	0.51***	0.40*	-0.01	-0.19	0.08	0.81***	-0.12	0.47*
Int. 1			0.59***	0.48**	0.04	0.22	0.31	0.01	0.06	-0.10	0.51**	-0.05	0.32
Int. 2				0.79***	0.37*	0.57***	0.37*	-0.09	-0.28	0.06	0.76***	-0.09	0.48*
Leaf area						0.38*	0.35*	0.05	-0.19	0.17	0.69***	-0.12	0.44
Leaf mass						0.77	-0.21	-0.19	-0.34	0.00	0.48**	-0.10	0.50*
SLM							0.44**	-0.01	-0.22	0.06	0.77***	-0.02	0.41
A							0.28	0.15	0.15	0.11	0.48**	0.06	-0.06
g								0.54***	0.70***	0.70***	0.18	0.18	-0.34
WUE									-0.17	-0.17	-0.13	0.38*	-0.06
Veg. mass											0.25	-0.11	0.32
Male mass												-0.06	0.43
Fruit no.													0.28

Note: A, photosynthetic rate; g, stomatal conductance; Int., intermode; SLM, specific leaf mass; Veg. mass, vegetative mass; WUE, water use efficiency.

TABLE 7. Correlations among traits in the plants grown in low R:FR low irradiance. Correlations shown in boldface type are significant at a tablewide 0.05 level after sequential Bonferroni correction. Tests that each correlation differs significantly from zero are indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. A Monte Carlo randomization was used to test the hypothesis that suites of traits within the boxes had a higher average correlation than would a random draw from the matrix (stem traits $P > 0.05$; leaf morphology traits $P > 0.05$; gas exchange traits $P > 0.05$; carbon allocation traits $P > 0.05$). For correlations with fruit number, $N = 40$, otherwise $N = 79$.

Height	Hyp.	Int. 1	Int. 2	Leaf area	Leaf mass	SLM	A	g	WUE	Veg. mass	Male mass	Fruit no.
Height	0.42***	0.91***	0.92***	0.59***	0.75***	0.62***	0.63***	0.26*	0.51***	0.70***	0.31**	0.53***
Hyp.		0.29**	0.16	0.07	0.13	0.23*	0.17	0.15	0.14	0.18	0.19	0.46**
Int. 1			0.80***	0.53***	0.68***	0.58***	0.59***	0.26*	0.45***	0.65***	0.22	0.47**
Int. 2				0.62***	0.74***	0.52***	0.60***	0.21	0.48***	0.76***	0.25*	0.41*
Leaf area					0.89***	0.12	0.59***	0.26*	0.39***	0.76***	0.33**	0.33*
Leaf mass				Morphology		0.53***	0.71***	0.34**	0.47***	0.92***	0.41**	0.49**
SLM							0.48***	0.27*	0.34**	0.61***	0.29*	0.52***
A								0.49***	0.72***	0.71***	0.43***	0.51***
g									-0.20	0.32**	0.28*	0.31
WUE								Gas exchange		0.50***	0.25*	0.38*
Veg. mass											0.52***	0.51***
Male mass												0.48**
Fruit no.												

Note: A, photosynthetic rate; g, stomatal conductance; Int., intermode; SLM, specific leaf mass; Veg. mass, vegetative mass; WUE, water use efficiency.

TABLE 8. Correlations among traits in the plants grown in low irradiance, high R:FR shade. Correlations shown in boldface type are significant at a tablewide 0.05 level after sequential Bonferroni correction. Tests that each correlation differs significantly from zero are indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. A Monte Carlo randomization was used to test the hypothesis that suites of traits within the boxes had a higher average correlation than would a random draw from the correlation matrix (stem traits, $P > 0.05$; leaf traits, $P > 0.05$; leaf morphology traits, $P > 0.05$; gas exchange traits, $P > 0.05$; carbon allocation traits, $P > 0.05$). For correlations with fruit number, $N = 40$, otherwise $N = 77$.

Height	Hyp.	Int. 1	Int. 2	Leaf area	Leaf mass	SLM	A	g	WUE	Veg. mass	Male mass	Fruit no.
Height	0.29**	0.81***	0.88***	0.38***	0.56***	0.33**	0.68***	0.28*	0.33**	0.73***	0.18	0.41**
Hyp.		0.20	0.00	-0.05	-0.02	0.02	0.08	0.19	-0.14	0.01	-0.09	0.04
Int. 1			0.56***	0.32**	0.44***	0.19	0.51***	0.20	0.24*	0.50***	0.24*	0.29
Int. 2				0.35**	0.55***	0.34**	0.66***	0.24*	0.36**	0.71***	0.09	0.27
Leaf area					0.79***	-0.20	0.17	-0.20	0.42***	0.67***	0.17	0.14
Leaf mass				Morphology		0.43***	0.47***	-0.04	0.52***	0.85***	0.27*	0.25
SLM							0.45***	0.18	0.21	0.36**	0.21	0.21
A								0.40***	0.46***	0.65***	0.21	0.30
g									-0.51***	0.06	0.00	0.02
WUE								Gas exchange		0.51***	0.11	0.36*
Veg. mass											0.30**	0.39*
Male mass												0.41**
Fruit no.												

Note: A, photosynthetic rate; g, stomatal conductance; Int., intermode; SLM, specific leaf mass; Veg. mass, vegetative mass; WUE, water use efficiency.

TABLE 9. Common principal components (PC) analysis for the three within-environment correlation matrices and for groups of functionally related traits using a Flury hierarchy analysis. The table presents a hierarchical series (from no to all common comparisons) of hypothesis tests, each comparing a specific model to the null hypothesis of no common structure for the three matrices. Each series stops at the level at which the null hypothesis can be rejected. The hypothesis to be accepted is specified under outcome.

Functional group of traits	Hypothesis tested	χ^2	df	P
All traits	1 common PC; outcome: no common components	119.288	24	0.000
Elongation	1 common PC; outcome: no common components	22.488	6	0.0010
All leaf	1 common PC; outcome: no common components	37.178	10	0.0001
Leaf morphology	1 common PC; outcome: no common components	16.161	4	0.0028
Gas exchange	1 common PC; common PCs; outcome: one common component	4.687 23.771	4 6	0.3210 0.0006
Biomass	1 common PC; common PCs; proportional components; equality; outcome: equality	1.826 2.035 11.390 12.488	4 6 10 12	0.7677 0.9165 0.3279 0.4073

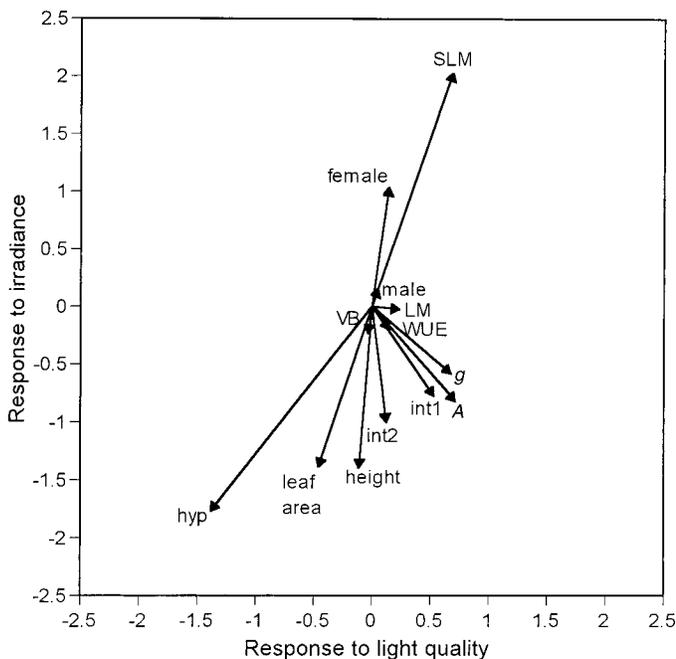


Fig. 5. Responses for standardized traits to irradiance and light quality are indicated by vectors for glasshouse-grown populations of *Mercurialis annua*. The neutral shade treatment is set to be the 0,0 point. Distance along the x-axis, which measures the response to R:FR, is the difference between the high R:FR shade treatment and neutral shade treatment. Distance along the y-axis, which measures the response to irradiance, is the difference between the high light treatment and the neutral shade treatment. Correlations between character plasticities are measured by the cosine of the angle between two vectors; i.e., vectors at 0° have a correlation of 1, vectors at 180° have a correlation of -1, and vectors at 90° have a correlation of zero. Abbreviations used for traits: A, photosynthetic rate; g, stomatal conductance; male, male reproductive biomass; female, number of fruits; SLM, specific leaf mass; WUE, water use efficiency; LM, leaf mass; hyp, hypocotyl length; int1, internode 1 length; int2, internode 2 length; VB, vegetative biomass.

rates. However, the negative response for these gas exchange traits to irradiance was unexpected. Most commonly plants have increased photosynthetic rates when grown in high light (Boardman, 1977). The reduced photosynthetic rates and stomatal conductance may indicate that our study plants experienced some drought stress in the higher irradiance and responded with reduced stomatal opening. The high-light treatment was observed to dry more quickly and to require more frequent watering than the other treatments.

This similarity of responses for photosynthetic rates and stomatal conductance suggests that the plasticity is explicable by changes in stomatal conductance. However, the moderate correlations within environments are considered indicative of a moderate level of stomatal control of photosynthesis (Farquhar and Sharkey, 1982), but with some variance in the metabolic control of photosynthesis. Some plasticity integration as measured by lack of plasticity of correlations across environments was found. The within-environment correlation matrices share a principal component. In contrast, trait integration, as measured by high correlations within an environment, was not found.

Biomass allocation traits—The biomass allocation traits showed evidence of integration, with high correlation of plasticities and relatively low plasticity of correlations. However, these results must be interpreted cautiously because the biomass traits showed little significant plasticity to the environment. Surprisingly, vegetative biomass did not differ between high and low irradiance environments. This lack of change in vegetative biomass is consistent with the low photosynthetic rates these plants expressed in high irradiance. Biomass of male flowers was also unresponsive. Female reproduction did increase in high irradiance, a response that may be resource related or may indicate plasticity in allocation. Despite the insignificant responses in vegetative biomass and male biomass to the environments, the responses to the environments were found to be significantly integrated.

Within environments, we did not find trait integration as measured by high correlations within an environment, but we did find plasticity integration as measured by lack of plasticity

TABLE 10. Correlations in trait responses to R:FR and irradiance among traits in glasshouse grown *Mercurialis annua*, estimated from vectors shown in Fig. 5. Tests from a bootstrap of vector angles that each correlation differs significantly from zero are indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Correlations shown in boldface type are significant at a tablewide 0.05 level after sequential Bonferroni correction. Boxes indicate suites of traits expected to be highly correlated. A Monte Carlo randomization was used to test the hypothesis that suites of traits within the boxes had a higher average correlation than would a random draw from the matrix (stem traits, $P > 0.05$; leaf traits, $P > 0.05$; leaf morphology traits, $P > 0.05$; gas exchange traits, $P < 0.01$; carbon allocation traits, $P < 0.01$); significant results are indicated by a solid line around the box.

	Hyp.	Int. 1	Int. 2	Leaf area	Leaf mass	SLW	A	g	WUE	Veg. mass	Male mass	Fruit no.
Height	0.83***	0.77***	0.98***	0.97***	0.03	-0.97***	0.70***	0.59***	0.74***	1.00***	-0.97***	-1.00***
Hyp.		0.30*	0.71***	0.94***	-0.53	-0.94***	0.19	0.04	0.25	0.87***	-0.95***	-0.87***
Int. 1			0.89***	0.61***	0.65	-0.60***	0.99***	0.97***	1.00***	0.74***	-0.59	-0.74***
Int. 2				0.90***	0.23	-0.90***	0.83***	0.74***	0.86***	0.97***	-0.90***	-0.97***
Leaf area					-0.21	-1.00***	0.51***	0.38**	0.56	0.98***	-1.00***	-0.98***
Leaf mass						0.22	0.74***	0.83***	0.69	-0.03	0.22	0.03
SLW							-0.50***	-0.37***	-0.55	-0.98***	1.00***	0.98***
A								0.99***	1.00***	0.65	-0.50*	-0.65***
g									0.98***	0.54	-0.37	-0.54***
WUE										0.70***	-0.55	-0.70***
Veg. mass												-0.98***
Male mass												-1.00***
Fruit no.												0.98***

Note: A, photosynthetic rate; g, stomatal conductance; Int., internode; SLM, specific leaf mass; Veg. mass, vegetative mass; WUE, water use efficiency.

of correlations across environments. It should be remembered we do not distinguish gender differences in this analysis, though there are some significant differences between genders in correlations involving biomass (S. A. Dudley et al., unpublished data).

Conclusions—These results do not reflect strong integration, either for the overall phenotype or among functionally related traits. In particular, though correlations among phenotypic traits within an environment were often high, they were no more likely, with one exception, to be higher within functional groups of traits than among traits from different functional groups. It was also clear that groups or pairs of traits could be significantly integrated for one measure and unrelated by another, e.g., leaf area and leaf mass or photosynthetic rate and stomatal conductance. The exception was that both groups that showed significant correlation of trait plasticities also had some similarity in trait correlations across the environments. While not conclusive, this trend is worth further exploration.

The moderate levels of integration indicate that the plasticity responses, including the very unusual internode length responses to R:FR, are more unlikely to be the result of strong constraints. It is intriguing that several features of the high irradiance, low R:FR phenotype evoked by intraspecific competition in *M. annua* are consistent with a hypothesized noncompetitive strategy. The typical increased stem elongation in response to high density benefits the tallest individuals within a stand because taller plants should receive more light. But it is hypothesized that for maximal productivity of a stand, plants should not elongate and so waste biomass in stem allocation (Givnish, 1982; Smith, 1992). *Mercurialis annua* plants only showed the expected elongation response to neighbors during the growth of the hypocotyls. However, the high-irradiance, high-density stand had the lowest elongation. In high irradiance and high intraspecific density, plants had small leaves that did not tend to shade competitors. Consistent with this is the lack of a height-photosynthetic rate correlation, so no cost was imposed by not elongating above these intraspecific neighbors. But if plants were in low irradiance, as would occur if they were shaded by interspecific competitors, they showed more classic responses to density. They did elongate, made bigger leaves, and taller plants had higher photosynthetic rates. Consequently, we speculate that the stem elongation responses we observed may have resulted from natural selection for an alternate strategy for intraspecific competition.

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