

Quantification of plasticity of plant traits in response to light intensity: comparing phenotypes at a common weight

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Summary. Plasticity of plant traits is commonly quantified by comparing different phenotypes at the same age. In this paper, we present a method in which the effect of resource conditions on plant weight is used as a basis for quantifying the plasticity of individual plant traits. *Abutilon theophrasti* individuals were grown in, and some transferred between, high and low intensity light conditions, resulting in four phenotypes. Plant traits were found to exhibit different degrees of plasticity, decreasing in this order: height; specific leaf area; allocation to branch roots; allocation to leaf area; number of nodes; allocation to tap roots; allocation to stem; allocation to leaf weight. Under these conditions, individuals of the four phenotypes had very similar heights when compared at the same age, but very different heights when compared at the same plant weight. The latter comparison indicates that light intensity influences height independently of its influence on plant weight. Individuals that were transferred from high to low light had greater allocation to leaf weight than did individuals of the same age that had not been transferred, but individuals of all phenotypes had nearly the same leaf weight allocation when compared at the same plant weight. The latter comparison indicates that light intensity influences leaf weight allocation mostly by influencing plant weight. In the phenotype resulting from the transfer of plants from low to high light, reproduction was stimulated much less than plant weight and axillary leaf growth, and reproductive allocation was delayed relative to the other three phenotypes. We conclude that when plasticity is measured by comparing phenotypes at the same plant weight, the effects of resources on plant size can be excluded from the quantification.

Key words: Plasticity – Light intensity – Allocation – *Abutilon*

Plasticity occurs if exposure of plants to different environmental conditions results in trait differences. These differences are usually measured on sets of plants that are all the same age. However, individuals grown in high resource

conditions are larger than individuals grown in low resource conditions if both are measured at the same age. Moreover, high resource conditions may cause plant characteristics to change over time more rapidly than is the case in low resource conditions (Peterson and Bazzaz 1978; Flint and Palmblad 1978; Hunt and Bazzaz 1980; St. Omer and Horvath 1983; Garbutt and Bazzaz 1984; Benner and Bazzaz 1985; Lacey 1986). In both of these ways, high resources have not only stimulated phenotypic adjustments to environmental conditions but have also stimulated growth, relative to low resource conditions. In this paper, we suggest that effects of size or growth rate should be avoided in the quantification of plasticity. This can be done by making comparisons between high-resource and low-resource phenotypes at the same plant weight rather than at the same age.

Plasticity can be quantified for sets of conspecific plants whether or not they are genetically identical. If they are not, then the environmental component of the trait differences represents the average plasticity of the genotypes present.

In this paper we quantify the plasticity of ten traits in *Abutilon theophrasti*, an annual colonizing plant of the eastern USA, in response to differences in incident light intensity during growth.

Methods and materials

Seeds of *Abutilon theophrasti* Medic. were obtained from central Illinois populations and seedlings were grown in 250 ml plastic cups whose sides and bottoms were punctured to allow aeration and drainage. Each cup was filled with compost of clay soil, sand, peat, vermiculite, and perlite in equal proportions. Several seedlings were established in each cup and were thinned to one per cup during the first two weeks.

The experiment was conducted in growth chambers maintained at 27/22° C (day/night) with a 16-h photoperiod. High light (H) individuals were raised at about 900 $\mu\text{E m}^{-2} \text{s}^{-1}$ photosynthetically active radiation, and low light (L) individuals were raised at about 200 $\mu\text{E m}^{-2} \text{s}^{-1}$ photosynthetically active radiation in separate chambers illuminated by different numbers of light banks. Plants were fertilized on day 12, then all plants were fertilized one day prior to each harvest, with 20 ml of

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20-20-20 NPK inorganic fertilizer diluted to 20 mg ml⁻¹, except for the first five harvests, when the fertilizer concentration was one-third strength because of the greater frequency of the harvests at this time.

Half of the individuals of each treatment were transferred to the other treatment: from high to low (HL) and from low to high (LH) light, resulting in four phenotypes. Because this species has been observed in previous investigations to accumulate weight more slowly in low than in high light, the transfer of plants from low to high light and the harvest of LH and L individuals was delayed relative to the transfer from high to low light and the harvests of HL and H individuals. Transfer of HL individuals occurred on day 14, of LH individuals on day 27. H and HL individuals were first harvested on day 15, L and LH individuals on day 28. Harvests occurred daily on the first five days, then once every five days until days 39, 54, 57, and 52 in treatments H, HL, L, and LH respectively. Eight individuals were harvested on each of these days from each treatment. On the final harvest date in each treatment terminal differentiation of the apex into reproductive activity was beginning. During the harvest period, plants were placed in plastic tubs and supplied with water to insure continually favorable soil moisture status.

Leaf areas were obtained with an area sensor (Lambda Instruments Corp.). Leaves, stems (including petioles and branches), axillary leaves, and fruits were dried separately at about 50° C. Beginning of fruitfill was recognized when the developing capsules exceeded calyx length. Roots were washed and dried, and branch roots were stripped away from the taproot and weighed separately.

For each treatment, regressions were obtained of several plant traits as quadratic functions of dry weight, both axes logarithm-transformed. The seven traits were height, number of nodes, leaf area, leaf weight, stem weight, branch root weight, and tap root weight.

The grand mean plant weight of all individuals in all treatments was calculated. The predicted value of each trait in each treatment, from the above regressions, transformed back to the original units and with confidence limits, was calculated at this grand mean plant weight. The ratio of a trait in one phenotype relative to the same trait in another served as an index of plasticity for each trait (as in Bazzaz and Carlson 1982; Langenheim et al. 1984). The larger value was always used in the numerator. Comparisons were made between treatments H and L, between treatments H and HL, and between treatments L and LH.

In order to quantify plasticity of an eighth trait, specific leaf area (SLA; leaf area divided by leaf weight), leaf area as a quadratic function of leaf weight (both axes logarithm-transformed) was obtained for each treatment. The between-treatment ratios were calculated at the grand mean leaf weight.

Only nonzero values were used in the analysis of reproductive allocation. Because there was no overlap of the plant weights of the reproductive plants of treatment LH with those of the other treatments, there was no plant weight common to all the treatments, and plant weight could not be used as the independent variable. Instead plant weight was analyzed as a quadratic function of fruit weight, both axes logarithm-transformed. From these were obtained, for each treatment, the predicted values of plant weight at the grand mean fruit weight. From these plant and fruit weights, reproductive allocation was calculated.

A predicted value of plant weight was also obtained at the fruit weight of "first fruitfill", which was the average weight of immature fruits. A large plant weight at first fruitfill indicates that the onset of reproduction was delayed relative to plant weight increase.

Only nonzero values were used in the analysis of axillary leaf development. Quadratic regressions were obtained of whole-plant leaf weight as a function of axillary leaf weight and of plant weight as a function of axillary leaf weight. We chose to use plant weight and whole-plant leaf weight as dependent variables in order to allow comparisons to be made between this set of analyses and those of reproductive allocation, in which whole-plant weight was also used as a dependent variable. In the two treatments in which individuals exhibited axillary leaf development, there was little overlap of plant weights, total leaf weights, or of axillary leaf weights. Comparisons could not in this case be made at a common value of the independent variable. Therefore predicted values of the dependent variable were calculated for each treatment at its own mean.

In order to determine whether significant change in a trait had occurred within one day after transfer from one set of light conditions to another, ratios of the trait to plant weight were obtained for each observation on the first harvest date after transfer for treatments HL and LH, and for the harvest dates of treatments H and L on which their plant weights corresponded most closely to those of HL and LH respectively. Normalized scores were substituted for these ratios (using tables from Harter 1961) in the comparison of H with HL and the comparison of L with LH, which was performed by t-test.

All analyses, except the t-test, were performed with routines MU and NP from the STAT package (University of Nebraska Computing Systems 1976).

Results

The grand mean plant weight was 679 mg. Individuals in treatments HL and LH had been experiencing their new light conditions for at least five days by the time they attained this weight. This grand mean weight was similar to each of the separate mean weights of the treatments. The grand mean leaf weight was 351 mg, which was similar to each of the mean leaf weights of the separate treatments. Predicted values of traits at these plant and leaf weights were calculated from cubic regressions (Rice 1987a). The null hypothesis (lack of plasticity) was rejected if the predicted values differed significantly from one another.

The traits with greatest plasticity were height, SLA, branch root weight, and leaf area, while leaf weight showed the least plasticity (Table 1). The ranking of the traits in the three columns of Table 1 are in significant agreement (Kendall's coefficient of concordance = 0.912, $\chi^2_7 = 19.16$) indicating that some traits showed greater plasticity than others over both long and short periods of growth.

Plants raised in, or transferred to, low light were taller (Fig. 1 a-c), had more leaves and greater leaf area, greater allocation to stems, but less allocation to branch roots and taproots than plants raised in or transferred to high light, when compared at a common plant weight (Table 1). Plants raised in or transferred to low light had a greater SLA than plants raised in or transferred to high light, when compared at a common leaf weight (Table 1). Even after one day, plants transferred to low light had significantly greater

Table 1. Trait values at grand mean plant weight, and plasticity ratios (mean, lower and upper 95% confidence limits of prediction)

Trait (ratio relative to plant weight)	Phenotype			LH	Plasticity ratios			
	H	HL	L		H vs. L	H vs. HL	L vs. LH	Average rank
Height (mm g ⁻¹)	87.6 (82.6–92.8)	237 (225–250)	327 (315–340)	168 (150–186)	3.73	2.71	1.95	1.7
SLA* (cm ² g ⁻¹)	348 (339–356)	815 (783–846)	821 (803–838)	402 (385–419)	2.36	2.34	2.04	2.5
Branch root weight	19.0% (17.4%–20.1%)	8.2% (7.4%–9.1%)	4.2% (3.7%–4.6%)	7.0% (6.4%–7.8%)	4.57	2.29	1.69	2.7
Leaf area (cm ² g ⁻¹)	209 (196–222)	504 (468–543)	493 (477–510)	299 (271–328)	2.36	2.41	1.65	3.2
Node number (g ⁻¹)	11.1 (10.8–11.4)	15.8 (15.3–16.5)	18.6 (18.1–19.0)	14.3 (13.5–15.0)	1.67	1.42	1.30	5.0
Tap root weight	3.0% (2.8%–3.3%)	2.3% (2.0%–2.5%)	2.0% (1.8%–2.2%)	1.6% (1.4%–1.7%)	1.56	1.35	1.25	6.0
Stem weight	21.1% (20.0%–21.9%)	27.4% (26.2%–28.7%)	31.8% (31.1%–32.7%)	28.4% (27.4%–29.6%)	1.51	1.30	1.12	7.0
Leaf weight	58.9% (55.4%–62.7%)	59.1% (56.7%–61.7%)	63.2% (61.9%–64.7%)	69.1% (63.5%–75.1%)	1.07	1.00 ns	1.09 ns	8.0

* At grand mean leaf weight

(All ratios significant at $\alpha=0.05$ unless *ns* indicated)

Table 2. Allocation changes after one day. Percentage changes for eight traits for the first harvest dates of HL (day 15) and LH (day 28), and the harvest dates of H (day 15) and of L (day 31) on which their plant weights corresponded most closely to those of HL and LH respectively. The traits, except SLA, are divided by plant weight. * = significant at $\alpha=0.05$

Trait	HL vs H	LH vs L
Height	+22%*	-21%*
Leaf area	+23%*	-29%*
SLA	+33%*	-29%*
Branch roots	+11%	+8%
Nodes	+25%*	-17%*
Stem weight	-4%	+1%
Tap root weight	+45%	0%
Leaf weight	-6%	+1%

height, and number and area of leaves, after correction was made for plant weight, and significantly greater SLA, than plants that remained in high light. And after one day, plants transferred to high light had significantly lesser height, and number and area of leaves, after correction was made for plant weight, and significantly lower SLA, than plants that remained in low light (Table 2). However, growth in or transfer to low light did not alter allocation to leaf weight in comparison to growth in or transfer to high light, when comparison is made at a common plant weight (Fig. 2a–c; Table 1).

Plants raised in high light differed very little from plants raised in low light in either plant weight at onset of fruitfill or in reproductive allocation at the grand mean fruit weight (Table 3). Plants transferred from high to low light had a significantly smaller plant weight at onset of fruitfill than the other phenotypes, but did not differ from phenotypes H and L in reproductive allocation at the grand mean fruit weight (Table 3). As a result, the relationship between plant

weight and fruit weight is almost the same in these three phenotypes (Fig. 3). Plants transferred from low to high light, however, had a much greater plant weight at onset of fruitfill and much lower reproductive allocation at the grand mean fruit weight (Table 3). The relationship between plant weight and fruit weight in the LH phenotype was entirely distinct from that of the other three phenotypes (Fig. 3).

Axillary leaf development was completely suppressed in low light conditions. Moreover, the high-light phenotypes (H and LH) differed in axillary development. Phenotype LH had much greater axillary leaf weight allocation at its mean total leaf weight than did phenotype H at its mean total leaf weight (Table 3). In treatment H, 36 mg of axillary weight was accumulated considerably later than was 36 mg of fruit weight. But in treatment LH, 36 mg of axillary weight was accumulated before 36 mg of axillary leaf weight was accumulated.

Almost all branching in treatment LH was at nodes that had young fully-expanded leaves at the time of transfer (usually nodes 7–10). Nodes at which leaves developed after transfer exhibited little branching.

Discussion

The observed patterns of plasticity of height, leaf area, and root weight allocation in *Abutilon theophrasti* were in general agreement with previous research with this species (Paterson et al. 1978) and with other herbaceous species (Blackman and Wilson 1954; Hughes and Evans 1962; Cooper 1967; Hurd and Thornley 1974; McLaren and Smith 1978; Mahall et al. 1981). Furthermore, lack of plasticity of leaf weight allocation has been observed in herbaceous species by other workers (Blackman and Black 1959; Evans and Hughes 1961; Hughes and Cockshull 1971). Agreement of our results with those of other workers oc-

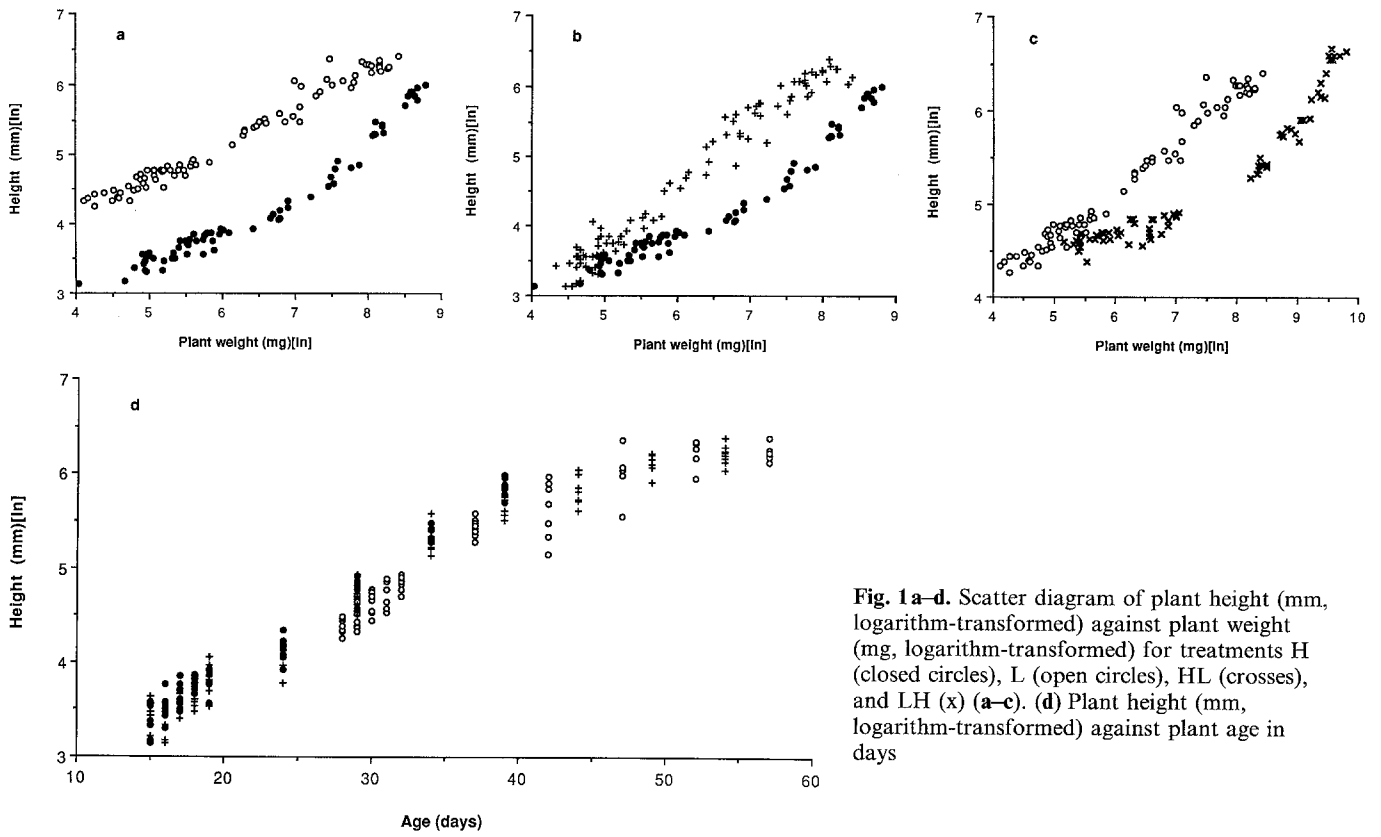


Fig. 1 a–d. Scatter diagram of plant height (mm, logarithm-transformed) against plant weight (mg, logarithm-transformed) for treatments H (closed circles), L (open circles), HL (crosses), and LH (x) (a–c). (d) Plant height (mm, logarithm-transformed) against plant age in days

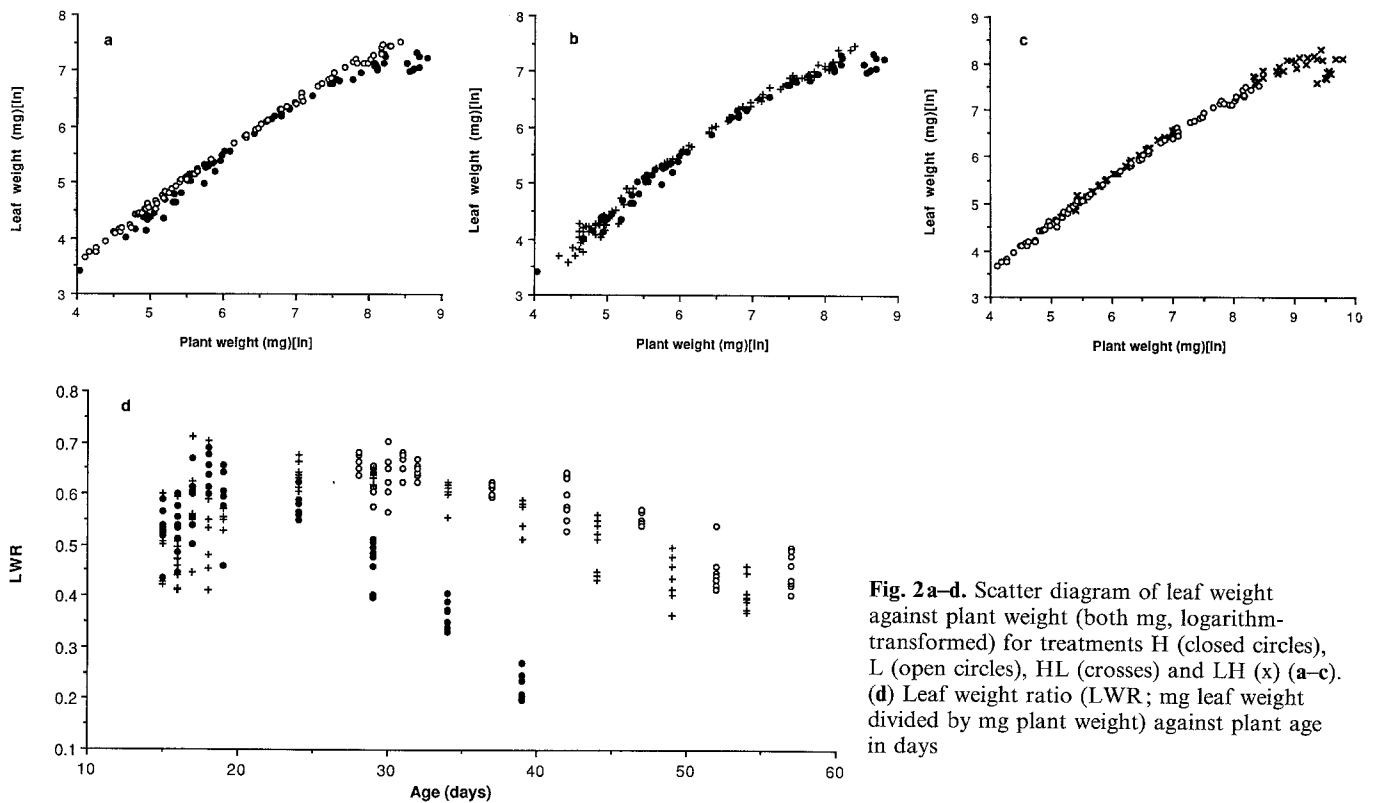


Fig. 2 a–d. Scatter diagram of leaf weight against plant weight (both mg, logarithm-transformed) for treatments H (closed circles), L (open circles), HL (crosses) and LH (x) (a–c). (d) Leaf weight ratio (LWR; mg leaf weight divided by mg plant weight) against plant age in days

currred despite the fact that their studies made comparisons between phenotypes at the same age.

Reekie and Bazzaz (1987) found greater reproductive allocation in high light than in low light phenotypes. This is the result we would have obtained if we had made com-

parisons among phenotypes at the same age. Our results instead indicated that reproductive allocation was not reduced in plants grown in or transferred to low light, and that transfer to high light, but not continuous growth in high light, resulted in reduced reproductive allocation.

Table 3. Reproductive and axillary allocation. (Means and 95% confidence intervals)

Plant weight at fruit weight = 36 mg	2289 mg ± 221 mg	1533 mg ± 428 mg	2282 mg ± 526 mg	6395 mg ± 2020 mg
Reproductive allocation at grand mean fruit weight	16.3% ± 1.44%	19.8% ± 3.00%	15.5% ± 5.91%	6.7% ± 1.61%
Plant weight at axillary leaf weight = 36 mg	4230 mg ± 834 mg	–	–	2048 mg ± 731 mg
Axillary allocation ^a	3.0% ± 0.18%	–	–	8.8% ± 0.05%

^a At treatment mean axillary leaf weight (35 mg for H, 164 mg for LH)

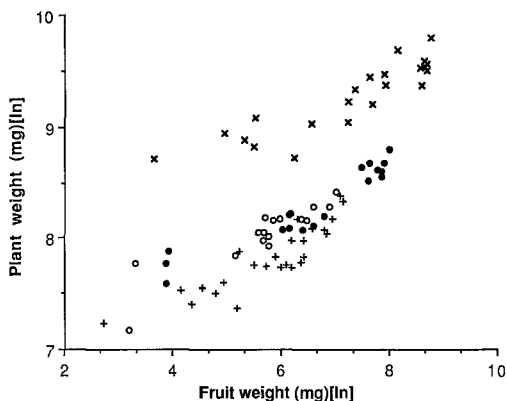


Fig. 3. Scatter diagram of plant weight against fruit weight (both mg, logarithm-transformed) for treatments H (closed circles), L (open circles), HL (crosses), and LH (x)

Individuals in treatments H, L, and HL had nearly identical heights (Fig. 1d) and node numbers when compared at the same age. In *Abutilon theophrasti*, unlike *Fragaria virginiana* (Jurik and Chabot 1982), these two traits could be considered stable rather than plastic. However, we choose to consider them plastic because there was less inhibition of internode elongation and leaf development than of plant weight growth by the low light conditions. Relative to their weight, plants in low light had greater height (Fig. 1a–c) and leaf number, which compensated for the slower weight increase in low light to produce the apparent stability.

After thirty days of age, the leaf weight allocation of individuals remaining in high light diverged greatly from that of individuals in the other treatments (Fig. 2d). This trait could be considered plastic. However, we choose to consider leaf weight allocation a stable trait because leaf weight was reduced to the same extent that plant weight was reduced by this transfer (Fig. 2a–c). Larger plants have lower leaf weight allocation. Individuals of the H phenotype had a lower leaf weight allocation because they were larger than those of the HL phenotype during the latter part of the harvest period.

The reduced reproductive allocation in the low light individuals upon transfer to high light may be an example of a phenotypic response that does not confer benefit. In *Abutilon theophrasti*, solitary flowers develop in the axils, and under high resource conditions branches develop in addition (pers. obs.). Transfer of low light individuals to high light caused an immediate stimulation of growth and photosynthetic rates (Rice and Bazzaz 1989), and may have caused an above-normal abundance of carbohydrates in the vicinity of the axillary buds of the youngest leaves that were fully-expanded at the time of transfer. If branch development is normally limited by the selective partitioning of photosynthates, water, minerals, and growth substances toward the apex (Phillips 1975; McIntyre 1977; Chapin 1980),

this above-normal supply of carbohydrates to the axillary buds may have stimulated development of leaves at the expense of flower and fruit production. Thus the initial delay in onset of, and reduced allocation to, reproduction in treatment LH may not itself be an adaptive response to the change in light conditions. As L individuals transferred to high light undergo phenotypic changes, the reproductive disadvantage may be overcome.

Light intensity, light quality, soil moisture, atmospheric humidity, temperature, and nutrient conditions interact. Therefore several of the phenotypic responses reported in this paper, elicited by light intensity, may confer adaptive benefit primarily in response to other environmental factors, particularly moisture. Differences in light intensity (as well as quality) can induce plasticity of stem elongation and root weight allocation (McLaren and Smith 1978), leaf area (Morgan and Smith 1981), and leaf thickness (Bjorkman 1981). An increase in root weight, however, can increase water uptake, and a reduction in leaf area can reduce water loss under conditions of high light intensity. Greater height can be associated with reduced cross-sectional area of stem xylem (Rice 1987b), thus with reduced transpiration (Rice and Bazzaz 1989), in this species. Light-induced differences in SLA may reflect not only differences in mesophyll thickness (Yun and Taylor 1986) but also differences in leaf vascularization (Charles-Edwards et al. 1974), which will affect leaf water status.

We conclude that for some purposes it is valuable to quantify plasticity of plant traits by comparing phenotypes at the same plant weight rather than at the same age.

Acknowledgements. The authors gratefully acknowledge assistance from L. Rice in preparing the experiment, from K. Garbutt in statistical analysis, and from C.K. Augspurger, G.O. Batzli, R.W. Carlson, J.M. Cheeseman, and D.C. Tremmel in manuscript preparation. This paper was adapted from the Ph.D. thesis by S.A.R.

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Received December 7, 1988