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Growth consequences of plasticity of plant traits in response to light conditions

Stanley A. Rice[1,]* and F.A. Bazzaz[2]

[1] Department of Plant Biology, University of Illinois, 289 Morrill Hall, 505 S. Goodwin Ave., Urbana IL 61801, USA
[2] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

Summary. We present a method for quantifying the growth advantage, if any, that results from the plasticity of plant traits in response to growth in high vs. low resource levels. The method, which uses two phenotypes and two resource levels, quantifies the average advantage that a phenotype has, in its own set of conditions, over the other phenotype. The method is applied to the growth of two phenotypes of *Abutilon theophrasti*, induced by high and low light intensity, in response to two levels of incident light intensity. We calculated the growth advantage first using relative growth rate, and second using whole-plant photosynthetic assimilation rate, as the response variable. Then we used the photosynthetic responses to changes in light intensity to calculate changes in growth rates of each phenotype when exposed to a change in light conditions. These three quantifications of growth advantage broadly agree with one another. Despite the great plasticity of its traits induced by growth in high vs. low light intensity, whole-plant plasticity did not allow *Abutilon theophrasti* to exhibit a significant growth advantage under these conditions. Indeed, the relative growth rate of the low light phenotype greatly exceeded that of the high light phenotype in high incident light conditions. This may have resulted from the higher leaf area ratio of the low light phenotype. Furthermore, the high light phenotype had significantly greater transpiration rate in both light conditions. For these reasons we suggest that light-induced plasticity of traits in *Abutilon theophrasti* may confer advantage in response to the variation in vapor pressure deficit that is associated with variation in light intensity. Light-induced plasticity may also be advantageous because under high incident light conditions the high-light phenotype has greater reproductive allocation than the low-light phenotype.

Key words: Plasticity – Growth rate – Photosynthesis – *Abutilon*

Rice and Bazzaz (1989) quantified plasticities of traits, considered independently of one another, in *Abutilon theophrasti* in response to growth in two levels of light intensity. Some plant traits exhibited greater plasticity than others, since the plasticity of some traits may allow the homeostasis of others (Bradshaw 1965, 1974; Caswell 1983), particularly those essential for vital function. The overall effect of the plasticity of some traits and stability of others should be to allow a genotype to have a growth advantage under heterogeneous conditions.

If the observed set of plastic responses allows the stimulation of growth by high resources to be greater, and the diminution of growth by low resources to be less, than would some other set of phenotypic responses, then plasticity can be said to confer a significant growth advantage under heterogeneous resource conditions. We therefore predicted that the phenotype induced by high light would have more rapid growth in constant high light conditions than would the phenotype induced by low light, and that the phenotype induced by low light would have more rapid growth in constant low light conditions than would the phenotype induced by high light. The expression of both phenotypes (plasticity) should be advantageous to growth in heterogeneous conditions only if both of these comparisons are significant. We therefore averaged two ratios (representing the growth advantage in each light intensity) to obtain *G*, the growth advantage attributable to plasticity.

If a growth advantage is not observed in both phenotypes, then we would expect natural selection to confer an advantage on the expression of one rather than two phenotypes under these conditions.

In this paper we test two hypotheses:

1. Each phenotype possesses a growth, and whole-plant photosynthetic assimilation, advantage over the other phenotype in its own set of conditions.
2. Immediate response of growth rate to a change in resource conditions can be predicted if the growth rate in constant resource conditions, and the photosynthetic response to changes in conditions, are known.

Methods and calculations

Growth conditions and measurement techniques. Growth conditions of these *Abutilon theophrasti* individuals were described in Rice and Bazzaz (1989). Only the youngest individuals were analyzed for this paper. H individuals were those that were grown at 900 $\mu E\ m^{-2}\ s^{-1}$ photosynthetically active radiation (PAR) and L individuals were those that were grown at 200 $\mu E\ m^{-2}\ s^{-1}$ PAR. Linear regressions of the natural logarithm of plant weight as a function of age were obtained for the first five harvest dates for

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* *Current address:* Department of Biology, The King's College, Briarcliff Manor, NY 10510, USA

Offprint requests to: F.A. Bazzaz

H individuals exposed to high light intensity ("H(h)"), for H individuals transferred to low light intensity ("H(l)"), for L individuals exposed to low light intensity ("L(l)"), and for L individuals transferred to high light ("L(h)"). All four sets of plants were harvested over similar plant weight ranges. Slopes of these regressions are the relative growth rates.

Whole-plant photosynthetic rates of six individuals each of the H and L phenotypes were measured by infrared gas analysis in the open system that was used by Bazzaz and Carlson (1982). Each of these individuals was measured in high (900 µE m^{-2} s^{-1} PAR) and low (200 µE m^{-2} s^{-1} PAR) incident light intensity, at 28° C air temperature and 1.5 m s^{-1} windspeed. Ambient relative humidity was maintained between 50% and 70% and ambient carbon dioxide concentration between 315 and 335 µl/l. Water was provided to the plants during the measurements.

Calculation of G *and testing of hypothesis 1.* We predicted that the phenotype that has developed in one set of conditions will have a greater response, "R", in that set of conditions than the phenotype that developed in the other set of conditions. Thus the response of H individuals to high resource conditions, "RH(h)", will exceed that of L individuals immediately upon their transfer to those high resource conditions ("RL(h)"); and the response of L individuals to low resource conditions, "RL(l)", will exceed that of H individuals immediately upon their transfer to those low resource conditions ("RH(l)").

A growth advantage of the H phenotype over the L phenotype in high resource conditions is demonstrated if RH(h) significantly exceeds RL(h), and the magnitude of the advantage is the ratio of RH(h) to RL(h). Similarly, a growth advantage of the L phenotype over the H phenotype in low resource conditions is demonstrated if RL(l) significantly exceeds RH(l), and the magnitude of the advantage is the ratio of RL(l) to RH(l).

In order for plasticity to be considered beneficial in a heterogeneous environment, each of the phenotypes should posses a growth advantage. Therefore, for hypothesis 1 to be accepted, both the comparison between RH(h) and RL(h) and the comparison between RL(l) and RH(l) should be significant. Otherwise the phenotype that developed in one of the resource states would be as successful as or more successful than the other phenotype in both of the resource states. A quantification of the growth advantage (*G*) in a heterogeneous environment can be obtained as the average of the two ratios RH(h)/RL(h) and RL(l)/RH(l). Relative growth rate and whole-plant net photosynthesis were used for R in these quantifications. Reproductive growth rate cannot be used for R in this quantification because reproduction is mostly a response to past rather than to current resource availability. It therefore does not respond to a step change in environmental conditions as well as dry weight growth or photosynthetic assimilation.

Since the response of one phenotype is compared to that of the other within one resource state in each of these ratios, *G* does not quantify the advantage conferred by plasticity over a constancy of gene expression, but rather the average advantage that expression of the H phenotype in high light and the L phenotype in low light confers relative to the expression of the H phenotype in low light and the L phenotype in high light.

Relative growth rate depends strongly on plant weight (Hunt 1978). Therefore the treatments must be harvested over a similar plant weight range. Since plants grow more slowly in low than in high resource conditions, the low-resource plants must be harvested on later dates than the high-resource plants. A range of harvest dates rather than a single harvest is necessary because the plant weights cannot be precisely known before harvest. For these reasons, a large number of plants is required for this method if relative growth rate is used as the response variable.

We also investigated an alternative procedure, in which values of RH(l) and of RL(h) are predicted rather than measured, and which therefore requires the harvest of fewer plants. If the assumption is made that the proportional increase in whole plant photosynthesis caused by the transfer of L individuals to high resource conditions, PL(h)/PL(l), is the same as that of relative growth rate, the predicted value of RL(h) would be RL(l) multiplied by PL(h)/PL(l). If the assumption is made that the proportional decrease in whole-plant photosynthesis caused by transfer of H individuals to low resource conditions, PH(l)/PH(h), is the same as that of relative growth rate, the predicted value of RH(l) would be RH(h) multiplied by PH(l)/PH(h).

Testing of hypothesis 2. The assumption that relative growth rates respond to resource changes in the same proportion that photosynthesis responds to these changes will be tested as an hypothesis both broadly and narrowly. The narrow confirmation of the hypothesis will be recognized when the predicted values of RL(h) and RH(l) fall within the confidence limits of the measured values. The broad confirmation of the hypothesis will be recognized if the predicted values of RL(h) and RH(l) bear qualitatively the same relationships to RH(h) and RL(l), respectively, as do the measured values. If the hypothesis is not accepted narrowly, then the predicted values cannot completely substitute for the measured values of RH(l) and RL(h). However, if the hypothesis proves correct in the broad sense only, then the predicted values allow at least a rough estimate of *G*. If the rough estimate is used along with the quantification of *G* using photosynthetic light responses, and if both quantifications lead to the same results, then the growth advantage attributable to plasticity can be quantified with a sample size much smaller than would otherwise be the case. If the hypothesis is not accepted broadly, then the predicted values should not be used at all.

Results

Tests of hypothesis 1

The relative growth rate of treatment L in low light exceeded that of treatment H when transferred to low light by a factor of 3.65 (Table 1, Fig. 1b, c). However, the relative growth rate of treatment H in high light was only 68.9% as great as that of treatment L when transferred to high light (Table 1, Fig. 1a, d). Thus the low-light phenotype grew faster in both light regimes. *G* was 2.17, but Hypothesis 1 was not accepted when relative growth rate was used as the response variable.

In low incident light conditions, the photosynthetic rates of the two phenotypes did not differ significantly (ratio = 1.03) (Table 2). In high light conditions, the photosynthetic rate of the H individuals far exceeded that of the L individ-

Table 1. Measured and predicted relative growth rates

Measured RGR[a]	Confidence limits		Predicted RGR[b]
	Upper	Lower	
RH(h)[c] = 0.257	0.316	0.198	
RH(l) = 0.074	0.115	0.033	0.072
RL(l) = 0.270	0.319	0.221	
RL(h) = 0.373	0.422	0.324	0.489

[a] Measured relative growth rates are slopes of regressions of natural logarithms of plant weight on the first five harvest dates

[b] Predicted relative growth rates were calculated as explained in text

[c] RH(h) and RH(l) are relative growth rates of the high light phenotype in high incident light and immediately upon transfer to low light, respectively; RL(l) and RL(h) are relative growth rates of the low light phenotype in low light and immediately upon transfer to high light, respectively

Table 2. Photosynthetic gas exchange data

	Photosynthesis[a] 95% confidence limits			Transpiraton[b] 95% confidence limits		
	Mean	Lower	Upper	Mean	Lower	Upper
H Phenotype						
Low incident light	6.7	5.9	7.5	5.3	4.9	5.7
High incident light	23.6	22.3	24.9	7.4	7.0	7.8
Light response[c]	0.28	0.19	0.56	0.75	0.59	1.04
L Phenotype						
Low incident light	6.9	5.8	8.0	2.5	1.9	3.1
High incident light	12.4	11.6	13.2	3.4	2.9	3.9
Light response[d]	1.81	1.32	2.30	1.38	1.05	1.71

[a] µmol carbon dioxide m^{-2} s^{-1}

[b] mmol water vapor m^{-2} s^{-1}

[c] rate in low incident light as a proportion of the rate measured in high light

[d] ratio of rate in high relative to that in low incident light

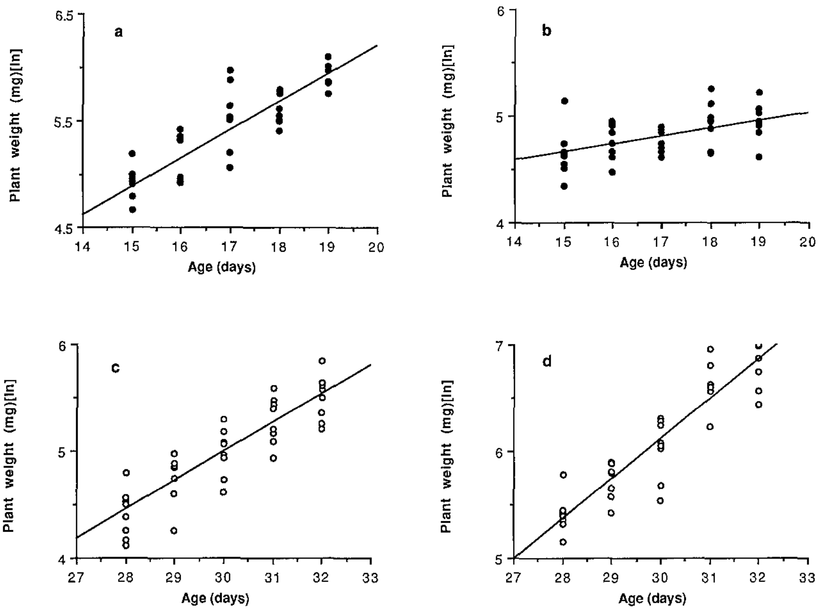

Fig. 1a–d. Scatter diagram and regression of plant weight (mg, logarithm-transformed) against age (days) for the first five harvests of treatment H (**a**), H individuals transferred to low light (**b**), for L individuals (**c**), and L individuals transferred to high light (**d**). Regression coefficients are the relative growth rates presented in Table 1

uals (ratio = 1.90) (Table 2). *G* was 1.47 but Hypothesis 1 was not accepted when photosynthetic rate was used as the response variable.

Tests of hypothesis 2

Transfer of H individuals to low light reduced their photosynthetic rate to 28% of its previous level, and transfer of L individuals to high light stimulated their photosynthetic rates by 81% (Table 2). The predicted value of RH(l) was within the 95% confidence limits of the measured RH(l), in narrow agreement with hypothesis 2. The growth advantage resulting from plasticity in response to low light conditions, calculated from the predicted value of RH(l), is 3.75, very similar to the growth advantage calculated from measured relative growth rates (3.65), even though the predicted and measured values of RH(l) were calculated from independent data sets.

The predicted value of RL(h), however, is outside the 95% confidence limits of the measured value, thus the narrow interpretation of hypothesis 2 could not be accepted. The ratio of the relative growth rates in high light conditions, 0.525, was less than the ratio calculated from measured values (0.689).

However, both the predicted and measured values of RH(l) were less than RL(l), and both the predicted and measured values of RL(h) exceeded RH(h), broadly confirming hypothesis 2. *G* calculated from predicted values (2.14) was similar to *G* predicted from measured values (2.17).

Water use characteristics

Regardless of incident light intensity, the H phenotype had significantly greater transpiration than the L phenotype (Table 2).

Discussion

The H phenotype had a much higher photosynthetic rate in high light than did the L phenotype, but the L phenotype had a much higher relative growth rate in high light than did the H phenotype. Thus the more rapid growth of the L phenotype in high incident light conditions could not be attributed to a greater photosynthetic capacity. Neither could it be attributed to a higher tissue nutrient concentration in the L phenotype, although elevated nutrient levels can stimulate photosynthetic rate in this species (Mooney et al. 1981). The high-light phenotype in a previous experiment (Rice unpublished work), in which all conditions were the same as the experiment reported here except for higher nutrient levels, did not have a significantly higher relative growth rate than did the high-light phenotype in this experiment.

The higher relative growth rate of the L phenotype in high light can probably be attributed to its much greater leaf area ratio (Rice and Bazzaz 1989). Under high resource conditions, greater allocation to photosynthetic surface results in higher growth rate (Elmore 1980; Gifford and Evans 1981; Potter and Jones 1977). The higher relative growth rate of *Abutilon theophrasti* than of other annuals (Patterson and Flint 1983) and of low light phenotypes than of high light phenotypes under high light conditions in *Helianthus annuus* (Blackman and Wilson 1954) and *Impatiens parviflora* (Hughes and Evans 1962), have been attributed to higher leaf area ratio. The greater leaf area ratio of the L phenotype also allowed it to grow as rapidly in low light as the H phenotype grew in high light (Table 1), a result also observed by Evans and Hughes (1961), Myerscough and Whitehead (1966), and Loach (1970).

If the growth of the L phenotype exceeds that of the H phenotype in both high and low light conditions, what advantage could genotypes within *Abutilon theophrasti* obtain by the expression of the H phenotype? We suggest that the H phenotype may be superior to the L phenotype (1) in response to low atmospheric moisture conditions and (2) in reproductive allocation under high light conditions.

In natural situations high light is often associated with high vapor pressure deficit, which even under conditions of adequate soil moisture can reduce stomatal conductance (Turner et al. 1984). High light conditions cause greater heat load on leaves than low light conditions. The increased root weight allocation of the high light phenotype, which was the most plastic of the trait responses (Rice and Bazzaz 1989) may supply water needed by the leaves to dissipate this heat load by transpiration. The reduction of leaf area ratio in high light conditions (Rice and Bazzaz 1989) may allow more water to be available to each unit of leaf surface area and thus confer an advantage under these conditions despite the growth rate reduction that it causes. In this experiment, very favorable moisture and air advection conditions were maintained, allowing no opportunity for the leaves of the L individuals to experience water stress or excessive heat load. Yun and Taylor (1986) have also reported that leaf characteristics promoting a favorable water balance are induced by high light intensity in *Abutilon theophrasti*.

Furthermore, when individuals of the L phenotype experience high intensity light, a significant reduction of reproductive allocation initially occurred (Rice and Bazzaz 1989). High reproductive allocation appears to be advantageous in species (such as *Abutilon theophrasti*) that live in areas of high disturbance or unpredictability (Bazzaz 1983). Therefore the expression of an H phenotype in high light may give genotypes of *Abutilon theophrasti* a higher fitness, despite a slower growth, than would the expression of an L phenotype in those conditions. The L phenotype did not have a lower reproductive allocation, however, under low light conditions (Rice and Bazzaz 1989).

Therefore phenotypic plasticity may be advantageous in this species because efficient light interception, even at the expense of water uptake and conductance, is favored in low light conditions while more efficient reproductive allocation and more efficient water uptake and conductance, even at the expense of growth rate, is favored in high light conditions. The general possibility is raised that the environmental factor that induces a plastic response is frequently not the factor in response to which a growth advantage accrues.

The conclusions and quantifications obtained by this method are specific to the kind of resource being investigated. In order to apply the method, the resource must be altered abruptly, to a known degree, and without significant after-effect, so that RH(l) and RL(h) can be either measured or estimated. It would be difficult to quantify the growth advantage of plasticity in response to different nutrient levels in this manner because the plant, due to its nutrient storage and translocation ability, cannot be forced to experience an abrupt nutrient decrease. Light, temperature, and carbon dioxide are, however, suitable resources for the use of this method.

This method is limited to the consideration of two resource levels at a time. Further, it cannot show the superiority of plasticity over the lack of plasticity. Its contribution to the methodology of research in this subject is that it allows the integrated effects of all traits on the growth of the observed phenotypes to be quantified. In addition, the use of the estimated growth rates adequately serves as a rough estimate of the average growth advantage resulting from the plasticity of traits.

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