

# Above-ground competition does not alter biomass allocated to roots in *Abutilon theophrasti*

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## SUMMARY

We tested whether plants allocate proportionately less biomass to roots in response to above-ground competition as predicted by optimal partitioning theory. Two population densities of *Abutilon theophrasti* were achieved by planting one individual per pot and varying spacing among pots so that plants in the two densities experienced the same soil volume but different degrees of canopy overlap. Density did not affect root:shoot ratio, the partitioning of biomass between fine roots and storage roots, fine root length, or root specific length. Plants growing in high density exhibited typical above-ground responses to neighbours, having higher ratios of stem to leaf biomass and greater leaf specific area than those growing in low density. Total root biomass and shoot biomass were highly correlated. However, storage root biomass was more strongly correlated with shoot biomass than was fine-root biomass. Fine-root length was correlated with above-ground biomass only for the small subcanopy plants in crowded populations. Because leaf surface area increased with biomass, the ratio between absorptive root surface area and transpirational leaf surface area declined with plant size, a relationship that could make larger plants more susceptible to drought. We conclude that *A. theophrasti* does not reallocate biomass from roots to shoots in response to above-ground competition even though much root biomass is apparently involved in storage and not in resource acquisition.

Key words: Above-ground competition, *Abutilon theophrasti* Medic., biomass allocation, leaf surface area, light quality, phenotypic plasticity, root length, root:shoot ratio.

## INTRODUCTION

Plasticity in root:shoot ratios is thought to reflect optimal allocation of plant biomass for resource uptake. Allocation adjustments are presumed to maximize capture of the most limiting resource so that all resources become equally limiting (Bloom, Chapin & Mooney, 1985; Chapin *et al.*, 1987). Models of plant growth are often built on the assumption that the ratio of carbon (C) to nitrogen (N) (or some other nutrient) in plant tissues or the relative uptake of these resources controls partitioning of biomass between above-ground and below-ground structures (see Wilson, 1988; Reynolds & D'Antonio, 1996 for reviews). A large body of empirical data generally supports the idea that, in the absence of plant–plant interactions, resource avail-

ability influences biomass allocation (Wilson, 1988). Root:shoot ratios often increase under limited nutrients and decrease under low irradiance.

It is not clear that plants reallocate biomass in the same way when resources are reduced by competition from other plants. Plants perceive the presence of neighbouring canopies through changes in the ratio of red to far red wavelengths (R:FR), and above-ground growth responses can occur even before direct shading takes place (Aphalo & Ballaré, 1995). Responses to reduced R:FR include rapid stem elongation with disproportionately less above-ground biomass allocated to leaves, reduced branching, greater specific leaf area, and changes in leaf shape and chlorophyll content (Morgan & Smith, 1981; Smith 1982; Weiner & Thomas, 1992; Schmitt & Wulff, 1993; Aphalo & Ballaré, 1995).

Much less is known about possible concomitant changes in below-ground structures. Interspecific

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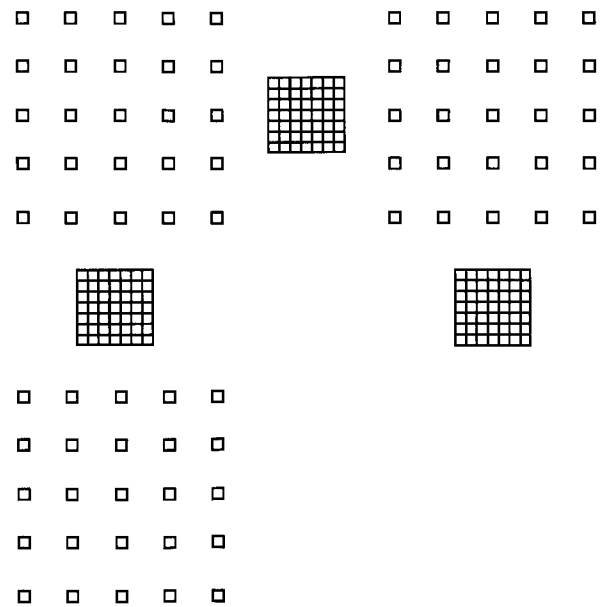
variation and phenotypic plasticity in root:shoot allocation patterns are considered important in maximizing uptake of those resources most reduced by neighbouring plants (Grime, 1979; Tilman, 1985; Grime *et al.*, 1991). Although plasticity is likely to vary among species, changes in root:shoot ratios should reflect the relative importance of above-ground vs. below-ground competition. Size should confer more of an advantage in above-ground competition specifically, since competition for light is asymmetric (Weiner, 1990; Schmitt, McCormac & Smith, 1995), while below-ground competition appears size-symmetric (Casper & Jackson, 1997; Schwinning & Weiner, 1998).

In order to evaluate optimal partitioning theory in the context of plant interactions, we examined root:shoot partitioning in the annual *Abutilon theophrasti* Medic. when plants only experienced competition above ground. We also considered how biomass was apportioned among different parts of shoots and roots. Since optimal partitioning theory concerns allocation to structures involved in resource uptake, we wanted to measure biomass directly involved in uptake functions. We separated shoots into leaves, stems and reproductive structures and whole-root systems into fine roots, which are primarily involved in resource uptake, and taproots, which function more in storage and anchoring. Only recently have studies of root:shoot ratio taken allocation to different root functions into account (e.g. Gebauer, Reynolds & Strain, 1996; Reynolds & D'Antonio, 1996).

## METHODS

### Plant species

Commonly called velvet leaf, *Abutilon theophrasti* Medic. is native to Asia but now a widespread agricultural weed throughout much of the western hemisphere. Plants have strong vertical stems that can reach over a metre in height, and large heart-shaped leaves. Small yellow flowers (1.5–2.5 cm in diameter), borne in leaf axils, are normally auto-gamous but capable of outcrossing (Garbutt & Bazzaz, 1987). The plant produces a distinct taproot, with most lateral roots originating in four vertical columns within 10 cm of the top of the taproot. The species tolerates a wide range of nutrient and light conditions (Parrish & Bazzaz 1982; Garbutt & Bazzaz, 1987) and has been used in many studies of biomass allocation, intraspecific competition and the formation of population size hierarchies (e.g. Hartegrink & Bazzaz, 1984; Pacala & Silander, 1990; McConnaughay & Bazzaz, 1992a; Shumway & Koide, 1995; Casper & Cahill, 1996). Population densities used in this study are typical of those in many natural populations (Cahill, pers. obs.).



**Figure 1.** Layout of the three crowded and three sparse populations within the experimental plot. Squares represent 10 × 10 cm pots.

### Growth of conditions

The experiment was conducted from mid-June to mid-August in a sunny outdoor plot on the University of Pennsylvania campus. Two levels of above-ground competition were achieved by planting seedlings individually in 10 × 10 × 35 cm pots and varying spacing between pots. Three replicate populations of each density were arranged alternately within the experimental garden (Fig. 1). Sparse populations, with a density of approx. 7 m<sup>-2</sup>, consisted of five rows of five pots 35 cm apart. Crowded populations, with a density of 100 m<sup>-2</sup>, consisted of seven rows of seven pots with their sides touching. To minimize edge effects in crowded populations, plants in the 24 perimeter pots were ignored, and the remaining 25 measured.

Plants were grown in pots in order to prevent below-ground competition and to ensure identical soil volume and nutrient availability. Pots were submerged below the soil surface so that soil in the pots was level with that in the garden, in order to minimize temperature variation, which greatly affected plant growth in a preliminary experiment. Seedlings were started in the greenhouse and transplanted into the pots when they were 7–9 d old.

The planting medium consisted of a homogeneous mixture of garden soil, a commercial soilless potting medium, and commercial dehydrated cow manure in a 16:2:0.6 ratio. The garden soil had been amended with organic fertilizers and large quantities of sand in previous years. The soilless medium consisted of vermiculite, ground sphagnum, perlite and washed sand. Although nutrient levels were probably higher than those in some soils in which *A. theophrasti* naturally occurs, they should not have been high

enough to produce maximum plant growth, based on previous experiments with *A. theophrasti* in which different quantities of commercial manure were added to the same garden soil (Casper & Cahill, 1996, 1998). Ambient rainfall was supplemented by watering roughly every other day with a garden sprinkler. Drainage was through a 7 cm-diameter hole in the bottom of each pot, which was regularly weeded of all volunteer seedlings.

#### Harvests and measurements

The experiment was harvested after 8 wk, a time when many plants had begun to flower but before any fruits had ripened. Plants were cut at the soil surface and shoots separated into three components: (1) leaf laminae, (2) stems and petioles, and (3) flowers and fruits. Total leaf area per plant was determined by summing the surface area of all leaves, measured using a Delta-T<sup>®</sup> video image analyser. Leaf area was used in calculating specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ). Shoot parts were then placed in paper bags, air-dried in a glasshouse, then dried to constant biomass in an oven at 70 °C. Mass was measured to the nearest 0.1 mg. Total above-ground biomass was calculated as the sum of the three shoot components.

Roots were separated from the sandy soil and washed, care taken to recover as many of the fine roots as possible. Whole roots were refrigerated until they could be separated into fine roots, which were arbitrarily defined as less than 1 mm in diameter, and storage root (taproot). Fine roots and storage roots were then placed in separate paper bags, oven-dried to constant biomass, and weighed. Mass of the two components was summed for total root biomass. For a subset of the plants in each density, the total length of all fine roots was measured using the video image analyser before they were dried. The analyser employs a line intercept method to measure root length and was calibrated with meter-lengths of string cut into 8–10 pieces. Fine-root length was used in calculating root specific length ( $\text{cm g}^{-1}$ ). These measurements were taken for 12 individuals selected arbitrarily from sparse populations. In crowded populations, 12 individuals were selected from among the canopy plants (greater than the median height), and 15 from subcanopy plants.

#### Treatment of data

The main statistical approach employed ANCOVA to partition variance in one size measure (e.g. total root biomass, root specific length) into that attributable to density (fixed effect) and population nested within density (random effect) when plant size was controlled statistically by using another size measure as a covariate. When a covariate was significant, the slopes of the regression relationships of densities were compared. Significantly different slopes in-

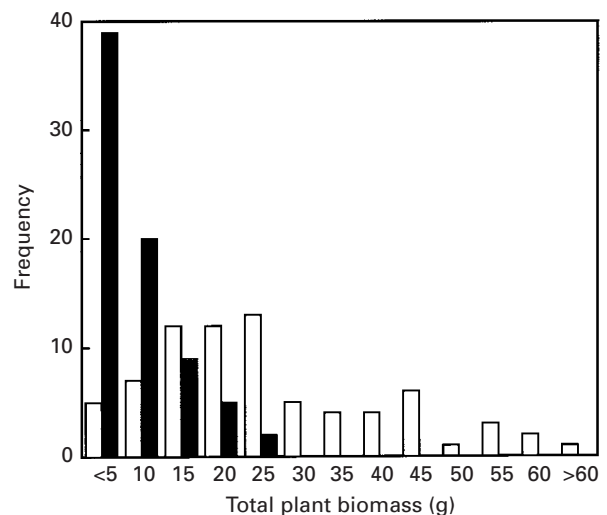
dicate a difference in the ratio of the two size measures and thus a density-dependent response in biomass partitioning. In using ANCOVA to examine density effects on root length or root specific length, plants from sparse populations were compared only with canopy plants from dense populations. Omitting subcanopy plants maintained homogeneity of variance, and ensured that plants of similar size from the two densities were compared. This was appropriate, since the goal was to determine whether above-ground competition affected root characteristics independent of its effect on plant size.

Regression analysis was employed to examine relationships between certain root characteristics and plant size. Multiple regression was used to determine whether fine-root biomass or storage-root biomass was more highly correlated with total shoot biomass. Regression relationships between shoot biomass and fine-root length and root specific length were also examined. Separate analyses were conducted for the 12 canopy and 15 subcanopy plants in crowded populations and for the 12 plants in sparse populations; data were not normally distributed when these categories were combined. Changes in leaf surface area and fine-root length as a function of above-ground biomass were examined graphically.

Statistical analyses were conducted using Statistica for the Macintosh (StatSoft, 1994). All variables were  $\log_e$  transformed.

## RESULTS

Above-ground competition greatly affected plant performance. Mean plant biomass was lower, and the size structure of the population more skewed, in crowded populations (Fig. 2). A greater percentage of plants had begun to flower in the sparse (95%) than in the crowded populations (76%). Among

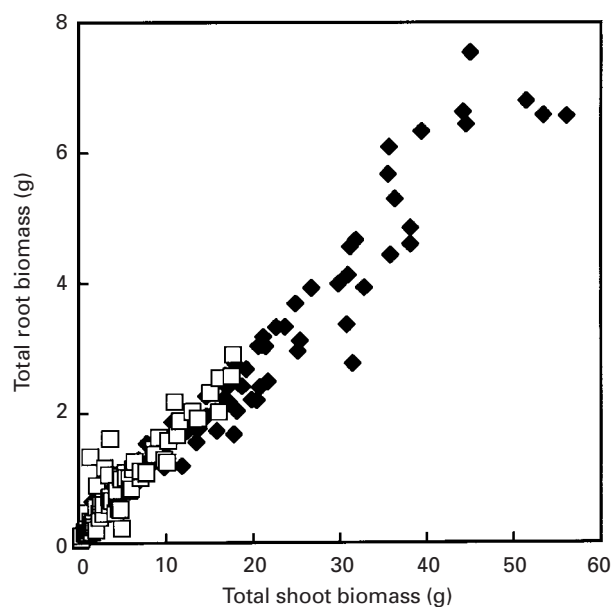


**Figure 2.** Comparison of plant-size distributions for the crowded (■) and sparse (□) densities. Data are combined across populations.

**Table 1.** Results of ANCOVA and ANOVA examining variation in the distribution of plant biomass as a function of population and density

Dependent variable	Independent variable	d.f.	MS <sub>effect</sub>	MS <sub>error</sub>	P
Total root mass	Covariate (shoot mass)	1, 143	77.665	0.089	< 0.001
	Density	1, 4	0.170	0.154	0.756
	Population	4, 143	0.154	0.089	0.145
Total leaf mass	Covariate (stem mass)	1, 143	121.039	0.277	< 0.001
	Density	1, 4	14.412	0.904	0.014
	Population	4, 143	0.904	0.277	0.016
Specific leaf area	Covariate (none)				
	Density	1, 4	4.585	0.303	0.017
	Population	4, 144	0.303	0.059	< 0.001
Fine root mass	Covariate (storage root mass)	1, 143	0.712	0.032	< 0.001
	Density	1, 4	0.004	0.137	0.873
	Population	4, 143	0.137	0.032	0.003
Fine root length	Covariate (shoot mass)	1, 17	0.002	0.290	0.943
	Density	1, 4	0.211	0.104	0.227
	Population	4, 17	0.104	0.290	0.835
Fine root specific length	Covariate (shoot mass)	1, 17	0.133	0.265	0.488
	Density	1, 4	0.072	0.149	0.524
	Population	4, 17	0.149	0.265	0.695

Population was treated as a random variable and nested within density.

**Figure 3.** Allocation of biomass between roots and shoots for plants in crowded ( $\square$ ) and sparse ( $\blacklozenge$ ) populations.

flowering individuals, the mean biomass of reproductive structures was also greater in sparse (1.237 g; SE = 0.215) than in crowded populations (0.345 g; SE = 0.085).

Despite the strong effect of above-ground competition on overall plant performance, root:shoot ratio was unaffected. ANCOVA revealed no differences between densities or among populations in mean root biomass when total above-ground biomass was used as a covariate (Table 1). Above-ground and below-ground biomass were highly correlated (Table 1, Fig. 3), but the slope of the regression relationship

between total below-ground biomass and total above-ground biomass did not differ between densities (Table 2, Fig. 3).

Density did affect the distribution of biomass among above-ground plant parts as expected. Leaf mass decreased with crowding and differed among populations within densities (Table 1). Total stem biomass (including petioles) was significant as a covariate. The slope of the regression relationship between stem biomass and leaf biomass differed between densities (Table 2, Fig. 4), reflecting a higher stem to leaf biomass ratio in crowded than in sparse populations. Specific leaf area increased with crowding and differed among populations (Table 1).

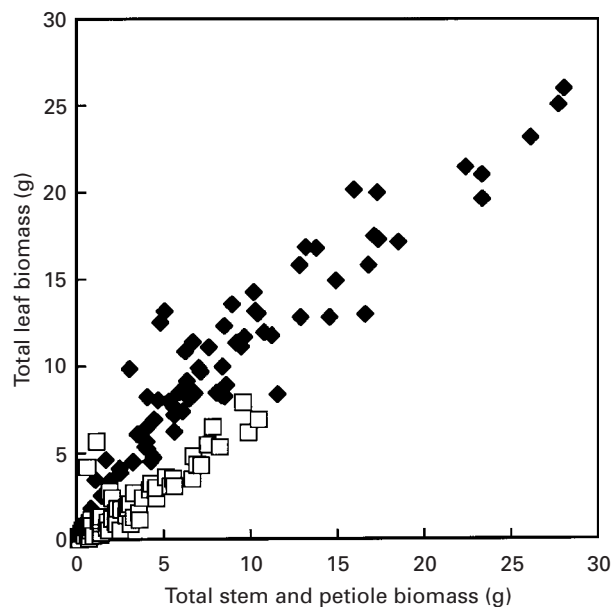
In contrast, the allocation of biomass between fine roots and storage roots was unaffected by density. Biomass allocated to fine roots was positively correlated with biomass allocated to storage roots (Table 1), and the slopes of the regression relationships for the two densities were not statistically different (Table 2). When storage-root biomass was accounted for as a covariate, mean fine-root biomass differed among populations but not between densities (Table 1).

Further analysis revealed interesting relationships between root characters and plant size. Storage-root biomass was more highly correlated with total shoot biomass than was fine-root biomass (Table 3), when both were used as independent variables in multiple regression. Neither fine-root length nor root specific length (shown in Fig. 5) was correlated with shoot biomass either for plants in sparse populations or for canopy plants in dense populations. For subcanopy plants in dense populations, which were the smallest, fine-root length was

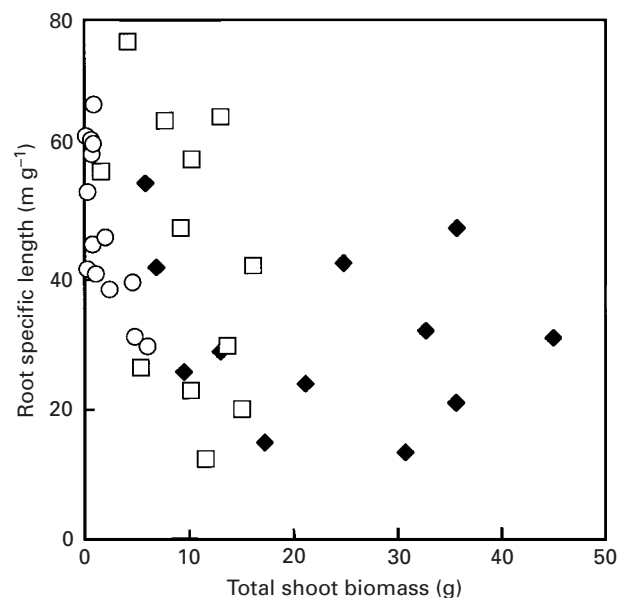
**Table 2.** Results of ANOVA comparing slopes of regression relationships between densities for covariates found to be significant in Table 1

Dependent variable	Covariate	MS <sub>effect</sub>	MS <sub>error</sub>	P
Total root mass	Total shoot mass	0.090	0.090	0.320
Fine root mass	Storage root mass	0.020	0.035	0.450
Total leaf mass	Stem and petiole mass	2.153	0.282	0.006

Significance (d.f. = 1, 146) indicates that the slopes are not parallel.

**Figure 4.** Allocation of above-ground biomass between leaves and stems (including petioles) for individuals in the two densities; crowded ( $\square$ ), sparse ( $\blacklozenge$ ).

positively correlated with shoot biomass (slope = 0.3204), while root specific length was negatively correlated with shoot biomass (Fig. 5; slope = -0.1531);  $r^2$  values were 0.338 and 0.437, respectively. Figure 6 shows leaf surface area and fine root length as a function of shoot biomass for the subset of plants for which root-length data were available. Transpirational surface area increased greatly as shoot size increased, while fine-root length, which should correlate with root-surface area, increased very little.

**Figure 5.** Root specific length as a function of shoot biomass for plants sampled at random from sparse populations ( $\blacklozenge$ ) and for canopy ( $\square$ ) and subcanopy ( $\circ$ ) plants in crowded populations. Canopy plants were taller and subcanopy plants shorter than the median height.

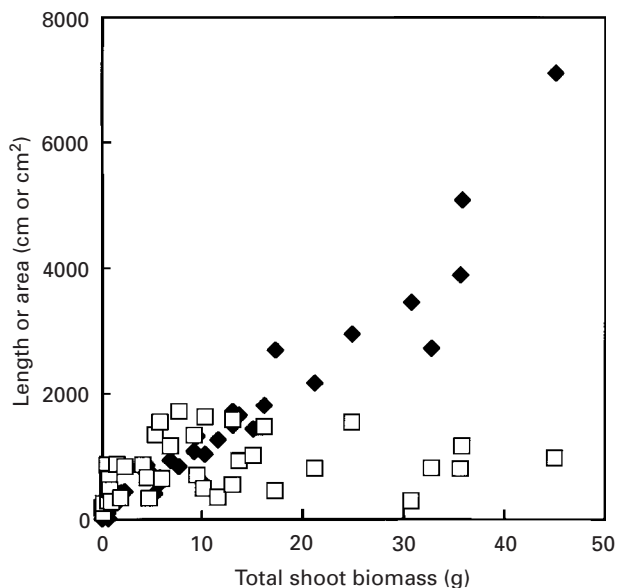
#### DISCUSSION

Optimal partitioning theory is not supported by our results. *Abutilon theophrasti* does not reallocate biomass from below-ground to above-ground plant parts when light availability is reduced through above-ground competition. Root:shoot ratios were remarkably constant over the broad range of plant size achieved in the two densities. Individuals in the crowded populations predictably allocated relatively

**Table 3.** Results of multiple regression analysis examining the relationship between fine root biomass and storage root biomass and the dependent variable total shoot biomass

Independent variable	Partial correlation coefficient	t value	P
Fine root mass	0.172	2.113	0.036
Storage root mass	0.955	38.862	< 0.001

The regression equation ( $n = 150$ ) has an  $r^2$  value of 0.949,  $F = 1374.783$ ,  $P < 0.001$ .



**Figure 6.** Fine-root length (□) and leaf surface area (◆) as a function of total shoot biomass of plants in both crowded and sparse populations for which root-length data were available.

more above-ground biomass to stems and petioles, but increase in stem biomass was apparently at the expense of leaves and not roots. Thus, these plants do not exhibit above- vs. below-ground biomass trade-offs in their ability to compete for light vs. below-ground resources. The results contrast with the lower root:shoot ratios obtained under reduced light intensity in a number of other studies (reviewed by Wilson, 1988).

We expected root:shoot ratios to decrease with above-ground crowding in *A. theophrasti* because of the disproportionate advantage of above-ground size in competing for light (Weiner, 1990), and because this species is plastic in its allocation to roots vs. shoots under variable nutrient conditions (Gedroc, McConnaughay & Coleman, 1996). In general, placing relatively more biomass above ground should improve overall competitive ability because size apparently does not confer a disproportionate advantage in below-ground competition (Weiner, 1990; Weiner, Wright & Castro, 1997). The lack of root:shoot response in *A. theophrasti* is surprising, since most of the root biomass consists of taproot, which must play little part in acquiring resources. One possible explanation is that taproots provide structural support, and strong root anchoring could be increasingly important as plants increase stem to leaf ratio in response to above-ground competition.

Few other studies have examined below-ground responses to above-ground competition. Aerts, Boot & van der Aart (1991) examined root:shoot ratios for two shrub species, *Erica tetralix* and *Calluna vulgaris*, and the perennial grass *Molinia caerulea* in several competition treatments in pots, including one in which plants only interacted above ground. Plants were grown in monoculture and in species mixtures

in both fertilized and unfertilized conditions. Above-ground competition alone affected proportionate allocation to roots in only four of the 18 fertilization treatment  $\times$  species combinations. Root:shoot ratio decreased under above-ground competition in two of these cases but increased in the other two. In different studies, *Impatiens capensis* allocated proportionately less biomass to roots in higher-density monocultures (Maliakal *et al.*, 1996), and root:shoot ratio of *Taraxacum officinale* decreased in response to above-ground competition from grasses, while that of *Rumex longifolius* did not (Houghland, 1993).

Whereas many studies have found reduced root:shoot ratios under lower light levels, most of them have not reduced R:FR as occurs when shading comes from other plants. In one experiment, varying light quality, Ballaré, Scopel, & Sánchez (1991) used filters to reduce R:FR for *Amaranthus quitensis*. They found an increase in stem biomass but no compensatory decrease in allocation to either leaves or roots. Likewise, reduced R:FR produced the expected increase in stem to leaf biomass ratio in *Eucalyptus grandis* but no change in root:shoot ratio (Hoad & Leakey, 1994). Reduced light quantity decreased root:shoot ratio in three species of *Veronica*, but only one exhibited a further reduction in root:shoot ratio when light quality was also altered using a plant canopy of *Ricinus zanzibariensis* (Dale & Causton, 1992).

Based on these few studies, it is difficult to generalize about plastic biomass allocation that might reflect trade-offs in the ability of plants to compete above ground and below ground. The results of Aerts *et al.* (1991) suggest that allocation response might depend on whether competition is intraspecific or interspecific. Considering that reduced light quantity alone often changes root:shoot ratio, it seems possible that growth responses to low resources might depend on whether the resources are reduced by competitors or represent inherently low levels in the environment. However, since most natural light reduction is caused by shading from other plant canopies, experimental protocols that change quantity but not quality of light might have little ecological relevance (Dale & Causton, 1992).

Several plant attributes, leaf mass, fine root mass and leaf specific area, differed among populations, indicating plastic plant responses to environmental variation within the experimental plot. Moreover, the fact that the ratios of fine-root biomass to storage-root biomass differed among populations suggests that biomass partitioning within roots is plastic even if above-ground competition has no effect on this partitioning. This population-level variation in allocation patterns could have resulted from uneven drainage of the rocky substrate underlying the soil and/or from some shading by a building located just northeast of the plot.

Examining biomass partitioning as a function of plant size revealed one pattern that could have importance in plant water relations. Fine-root length was not correlated with shoot biomass except among the small subcanopy plants. Because leaf surface area continues to increase with increases in plant biomass, the ratio of root absorptive surface area to transpirational surface area should decline greatly in larger plants, which could mean that they are less likely to meet transpirational water demands under conditions of water stress. A size-dependent response to drought occurs in at least some species (Watkinson, 1982; Rice, 1990; Casper, 1996).

A concern in pot experiments is that root growth might be artificially restricted. In our experiment, the tall pots forced lateral roots to grow further down than they would *in vivo*, but pot volume was five times that used for the same species by Gedroc *et al.* (1996) who detected variation in root:shoot allocation. Possible shifts in allocation as a function of ontogeny or plant size are other considerations (Wilson, 1988; Gedroc *et al.*, 1996; Coleman, McConnaughay, & Ackerly, 1994), but these should not have been a factor in our experiment, since plants were of the same age, and we accounted for plant size in statistical analyses.

From our study and others (McConnaughay & Bazzaz, 1992*a, b*), a great deal is known about biomass allocation responses of *A. theophrasti* in the presence of real or simulated neighbours. While root:shoot partitioning appears unresponsive to above-ground competition, neighbours seem to affect both the distribution of biomass among parts of the shoot and the physical placement of leaves (McConnaughay & Bazzaz, 1992*b*). Less is known about whether or how plants detect the presence of neighbours below-ground (Aphalo & Ballaré, 1995), but there is evidence that *A. theophrasti* also does not alter root:shoot ratio under different degrees of below-ground competition (Cahill, 1997).

In conclusion, *A. theophrasti* lacks plasticity in either root:shoot partitioning or in allocation to fine roots in response to above-ground competition, but we recognize that more species need to be examined in different competition regimes before optimal partitioning theory can be fully evaluated in the context of plant interactions.

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