

RELATIVE GROWTH RATES AND PLANT ALLOCATION PATTERNS

Shipley and Peters (1990) suggested that the results of their study of seedling growth rates and biomass partitioning could test some recent theoretical predictions (Tilman 1988). Their desire to test theory and the rapidity with which they did so are gratifying. I commend them, also, for publishing a table of their actual data, which allows for further analyses. I offer three comments on their results. First, although their results are interesting, they misinterpreted aspects of my theory and have thus not refuted it. Second, their data contradict numerous published relationships between morphology and relative growth rate (RGR; see review in Poorter 1989), perhaps because of methodological problems (Poorter and Lambers 1991). Third, further analysis of their data, presented below, shows that the maximal growth rates they observed are highly dependent on the habitat affinities of the species.

Shipley and Peters said that their results failed to support what they asserted was an essential assumption of my theory of plant allocation and competition and thus rejected the theory. However, Shipley and Peters (1990, p. 139) were incorrect in asserting that it is a "fundamental assumption of Tilman's model . . . that the maximum relative growth rate of a plant is negatively correlated with the ratio of the mass of its non-photosynthetic tissues to that of its photosynthetic tissues." That relationship was not an assumption at all but a prediction of the model for a case in which all individual plants were assumed to have similar physiologies (Tilman 1988, pp. 55-56).

I supported this by deriving a simple model:

$$\text{RGR}_{\max} = P_m[1 - (S + R)/B] - r, \quad (1)$$

where RGR_{\max} is the maximal relative growth rate, P_m is the maximal rate of photosynthesis per unit leaf biomass, r is the respiration rate per unit biomass, B is the total biomass of the individual plant, R is its root biomass, S is its stem biomass, and leaf biomass (L) is $L = B - S - R$. I assumed that physiologies were similar so as to mathematically explore the effects of plant morphology on RGR_{\max} (Tilman 1988, p. 56). Given this restriction, RGR_{\max} is an increasing function of leaf allocation, that is, $\text{RGR}_{\max} = P_m L/B - r$. Contrary to the statements of Shipley and Peters, the model can include physiological differences, and it only predicts that RGR_{\max} will necessarily increase with leaf allocation for plants with similar physiologies (equal P_m and equal r). If the plant species being compared differ as much or more in physiology as in morphology, a valid test of the model would require measurement of both allocation patterns and physiology.

Shipley and Peters (1990) erred in equating leaf allocation with shoot allocation.

The data they collected provide a poor test of my model because they did not separate leaves from stems but lumped the two together as "shoot." My model states that RGR_{max} should be a decreasing function of allocation to stem and root (eq. [1]) but an increasing function of allocation to leaf. It can make no prediction about the relationship between RGR_{max} and shoot allocation. Such a prediction would depend on the relative proportions of stem and leaf in the shoot, which Shipley and Peters did not measure. They justified their failure to separate leaves from stems by asserting that stems are often photosynthetic. However, Reekie and Bazzaz (1987) found that the green stems of *Agropyron repens* (quack grass) had a maximal photosynthetic rate one-fifth that of leaves. Clearly, leaves are the major photosynthetic organ. The inclusion of stems introduces unknown biases in the data of Shipley and Peters that make them a questionable test of my hypothesis.

The weak positive correlation that Shipley and Peters (1990) found between root-shoot ratio and growth rate for one of their two sampling dates (after they discarded four data points) contradicts many published studies. In reviewing more than 60 different studies of controls of plant growth rates, Poorter (1989) found that RGR increased with increasing allocation to leaf in about 85% of the studies. Poorter and Remkes (1990) also found this in a detailed comparison of 24 plant species. It is interesting that the best correlation found by Poorter and Remkes (1990) was between leaf-area ratio (leaf area divided by total plant mass) and RGR, not simply leaf allocation, because much of the mass of thicker leaves was not photosynthetic tissue but was structural material related to support, herbivore defense, and other factors (Poorter 1989; Poorter and Remkes 1990; Poorter and Lambers 1991). Leaf-area ratio may thus be a better measure of allocation to photosynthesis than percentage leaf mass. Poorter and Lambers (1991) also questioned the validity of Shipley and Peters's measured RGR_{max} because larger plants likely became nutrient-limited in their small pots and because of the large variance in RGR_{max} resulting from poor replication.

Shipley and Peters correctly note that I applied my model to a wide range of species (from algae to trees) that were unlikely to be physiologically identical. When I did this, I stated (Tilman 1988, p. 60) that I was assuming that species-to-species differences in morphology were much greater than species-to-species differences in physiology. I asserted that this was probably a valid approximation when comparing terrestrial plants with large differences in morphology but said that, "after morphology, the next major determinant of maximal growth rates is likely to be maximal rates of photosynthesis" (Tilman 1988, p. 60). Poorter's (1989) review supports this assumption, although Shipley and Peters's work calls it into question. More experimental work is clearly needed.

In attempting to understand what might have caused the RGR_{max} 's that Shipley and Peters observed, I classified the 68 species they studied as to the type of habitat in which each is most commonly found (see Appendix). This classification was based on discussions with colleagues who work in wetlands and on the habitat affinities given in Gleason and Cronquist (1963).

One simple classification was to divide the 68 species into those that mainly live rooted in mineral soil ($n = 54$) versus in peat ($n = 14$). An ANOVA, per-

formed with the general-linear-model (GLM) approach on SAS, revealed a highly significant effect of mineral soil versus peat on the RGRs reported by Shipley and Peters ($F = 21.3$, $df = 1, 66$, $P < .0001$). Peat-land plants had significantly lower RGR_{max} (mean of 0.15 d^{-1}) than plants of mineral soil (0.23 d^{-1}).

The plants were further classified as reaching their peak abundance in one of seven habitat types: uplands (five species), meadows and moist soils (14 species), shores and stream banks (seven species), marshes (14 species), fens (13 species), standing water (submerged or emergent plants, mainly of lake shores; 11 species), and bogs (four species). Clearly, many of these species have wider distributions than this, but their traits are likely to have been molded most by the habitat in which they were most common. A GLM ANOVA of Shipley and Peters's RGR_{max} values with these seven categories as factors explained 34% of the variance in RGR_{max} ($F = 5.35$, $df = 6, 61$, $P < .001$). In contrast, the strongest correlation that Shipley and Peters found between RGR_{max} and root-shoot ratio explained only 9.6% of the variance. There was no significant relationship between the seven habitat classes and root-shoot ratios on either day 10 ($F = 0.92$, $df = 6, 61$, $P = .48$) or day 30 ($F = 1.32$, $df = 6, 61$, $P = .26$). Further GLM analysis showed that the root-shoot dependence of RGR_{max} depended on habitat class ($F = 2.55$, $df = 7, 54$, $P = .02$) and was never significantly positive within a habitat class.

This reanalysis of the data collected by Shipley and Peters (1990) shows that RGR_{max} of 30-d-old herbaceous seedlings was more strongly associated with habitat affinity than with root-shoot ratio (fig. 1). This may just reflect the confounding effects of lumping leaf and stem into the shoot category. However, habitats as different as bogs, fens, marshes, and uplands place different constraints on plants that lead to physiological differences (e.g., Hutchinson 1975; Spence 1982; Chapin and Shaver 1985; Oechel and Lawrence 1985). The most slowly growing plants were bog plants and plants of standing water (fig. 1). This is consistent with Chapin's (1980) generalization that plants of nutrient-poor and stressed habitats have lower RGR_{max} and lower tissue nutrient concentrations (and thus lower photosynthetic rates; Field and Mooney 1986) than plants of more nutrient-rich habitats. Plants of shores and streambanks, which are highly disturbed habitats (e.g., Wilson and Keddy 1986), had the highest maximal growth rates.

This reanalysis of Shipley and Peters's data suggests that some correlate of habitat type, such as physiology, may be a more important determinant of these RGR_{max} 's than root-shoot ratios. However, this reanalysis cannot address the issue of the relative importance of leaf allocation (or leaf-area ratio; Poorter 1989) versus habitat affinity because Shipley and Peters did not report leaf allocation.

The purpose of my book (Tilman 1988) was to explore some of the population and community implications of the unavoidable, allocation-based trade-offs that all plants face in dealing with major environmental constraints. In that book, I focused on the allocation of biomass to major plant structures (leaves, stems, and roots) but did not deal with the equally interesting and important trade-offs that plants face in allocating protein (i.e., nitrogen) to alternative physiological functions. There are many other ways in which Allocate, the model presented in Tilman (1988), could be improved. The results of Shipley and Peters (1990) sug-

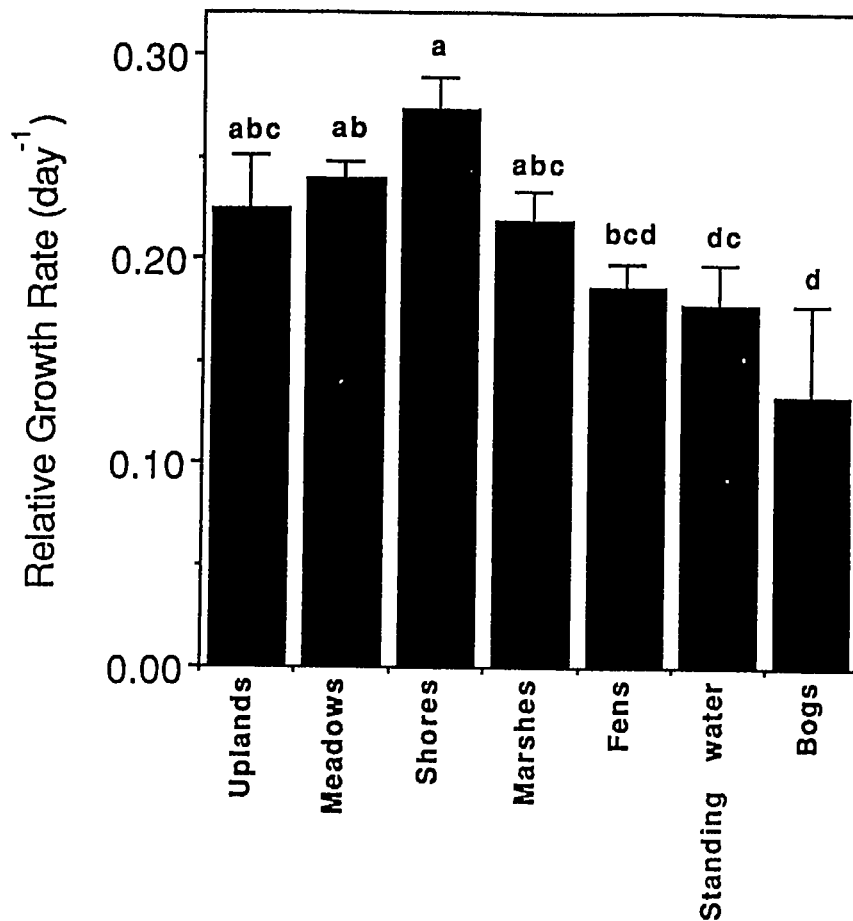


FIG. 1.—The 68 wetland species studied by Shipley and Peters (1990) were classified as having their peak abundance in one of seven habitat types. The mean RGR_{max} and SE for each class are shown, as are results of contrasts using Duncan's multiple-range test. Means that differ significantly ($P \leq .05$) do not share the same lowercase letter (ANOVA, $F = 5.35$, $df = 6, 61$, $P < .001$).

gest that it may be just as important to include physiological as morphological trade-offs in such models. My goal, though, was not to develop ever more complex and realistic models but to explore how environmental constraints and organismal trade-offs might interact to explain major patterns in plant communities. Recent work suggests that it may be unnecessary to measure all the morphological and physiological parameters in such models to predict the outcome of nutrient competition. Rather, a single number, R^* (the concentration of a limiting nutrient in an equilibrational monoculture of a species), may integrate the effects of morphology and physiology on nutrient competitive ability (Tilman 1990). Complex models like *Allocate* (Tilman 1988) are most useful in exploring the logical links between plant morphology and community ecology and illustrating how trade-offs influence competitive ability.

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APPENDIX

APPROXIMATE HABITAT AFFINITIES FOR THE SPECIES STUDIED BY SHIPLEY AND PETERS (1990)

Species	Habitat Affinity
<i>Hypericum ellipticum</i>	Shores and streambanks
<i>Penthorum sedoides</i>	Marshes
<i>Echinochloa wiegandii</i>	Shores and streambanks
<i>Epilobium ciliatum</i>	Meadows and moist soil
<i>Gnaphalium uliginosum</i>	Uplands
<i>Agrostis stolonifera</i>	Shores and streambanks
<i>Juncus brevicaudatus</i>	Shores and streambanks
<i>Leersia oryzoides</i>	Marshes
<i>Plantago major</i>	Uplands
<i>Polygonum lapathifolium</i>	Meadows and moist soil
<i>Juncus effusus</i>	Marshes
<i>Polygonum coccineum</i>	Standing water
<i>Bidens cernua</i>	Meadows and moist soil
<i>Coreopsis rosea</i>	Standing water
<i>Euthemia graminifolia</i>	Meadows and moist soil
<i>Lycopus americanus</i>	Meadows and moist soil
<i>Lythrum salicaria</i>	Marshes
<i>Mimulus ringens</i>	Marshes
<i>Verbana hastata</i>	Meadows and moist soil
<i>Eupatorium perfoliatum</i>	Meadows and moist soil
<i>Cyperus rivularis</i>	Shores and streambanks
<i>Galium obtusum</i>	Meadows and moist soil
<i>Typha latifolia</i>	Marshes
<i>Eleocharis obtusa</i>	Standing water
<i>Eupatorium maculatum</i>	Shores and streambanks
<i>Viola lanceolata</i>	Fens
<i>Scutellaria lateriflora</i>	Meadows and moist soil
<i>Aster nemoralis</i>	Bogs
<i>Hypericum majus</i>	Meadows and moist soil
<i>Juncus canadensis</i>	Fens
<i>Potentilla anserina</i>	Shores and streambanks
<i>Sium suave</i>	Fens
<i>Spartina pectinata</i>	Marshes
<i>Artemisia campestris</i>	Uplands
<i>Cyperus aristatus</i>	Meadows and moist soil
<i>Eleocharis erythropoda</i>	Standing water
<i>Lysimachia ciliata</i>	Marshes
<i>Sparganium eurycarpum</i>	Standing water

APPENDIX (*Continued*)

Species	Habitat Affinity
<i>Triadenum fraseri</i>	Fens
<i>Typha angustifolia</i>	Marshes
<i>Asclepias incarnata</i>	Fens
<i>Carex rostrata</i>	Fens
<i>Rumex verticillatus</i>	Fens
<i>Scirpus validus</i>	Fens
<i>Juncus bufonius</i>	Meadows and moist soil
<i>Scirpus cyperinus</i>	Fens
<i>Carex crinita</i>	Meadows and moist soil
<i>Dulichium aurundinaceum</i>	Marshes
<i>Glyceria canadensis</i>	Marshes
<i>Panicum longifolium</i>	Meadows and moist soil
<i>Houstonia canadensis</i>	Uplands
<i>Juncus filiformis</i>	Fens
<i>Acorus calamus</i>	Standing water
<i>Rhynchospora capitellata</i>	Bogs
<i>Sabatia kennedyana</i> fern	Marshes
<i>Xanthium strumarium</i>	Uplands
<i>Cladium mariscoides</i>	Fens
<i>Drosera intermedia</i>	Bogs
<i>Iris versicolor</i>	Fens
<i>Carex folliculata</i>	Marshes
<i>Scirpus acutus</i>	Standing water
<i>Scirpus americanus</i>	Standing water
<i>Scirpus torreyi</i>	Marshes
<i>Juncus militaris</i>	Standing water
<i>Eleocharis smallii</i>	Standing water
<i>Lobelia dortmanna</i>	Standing water
<i>Rhynchospora capillacea</i>	Fens
<i>Eriocaulon septangulare</i>	Bogs

NOTE.—Data are based on Gleason and Cronquist (1963) and the opinions of several wetland ecologists.

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