NOTES AND COMMENTS

IS INTERSPECIFIC VARIATION IN RELATIVE GROWTH RATE POSITIVELY CORRELATED WITH BIOMASS ALLOCATION TO THE LEAVES?

Recently, Shipley and Peters (1990) have made an attempt to test an important aspect of Tilman's (1988) contentions, namely, that "allocation to roots or stems comes at a cost—a decreased maximal rate of vegetative growth" (Tilman 1988, p. 98). That is, plants that invest more biomass in their roots must produce less biomass than those that invest relatively more in aboveground biomass. Shipley and Peters (1990) tested this hypothesis using 68 species from wetland regions. They did not find a negative relation between growth of seedlings, measured as the relative growth rate (RGR), and allocation to roots, measured as the root-shoot ratio. Rather, a positive correlation was found, at least for plants 30 d after germination. They therefore concluded that Tilman's contentions are incorrect.

SHIPLEY AND PETERS'S EXPERIMENT

In our opinion Shipley and Peters's experimental approach contains some flaws, and, hence, their work cannot yield conclusive evidence. We wish to comment on three aspects of their experimental design and contribute further to the discussion by presenting some of our recent data. In addition we use these data to comment on a second assumption in Tilman's hypothesis.

1. *Harvest Schedule*

Shipley and Peters determined weights of a number of plants, 10 and 30 d after germination, from which they calculated a RGR for each species over this period. However, plants do not necessarily grow exponentially for such a long time. In experiments such as those of Shipley and Peters, RGR may decrease by as much as 50% between day 10 and day 30 (Hunt and Lloyd 1987; J. Coleman, personal communication). At least part of this ontogenetic drift, which is especially evident in fast-growing species, is due to the increasing size of the plants, which results in self-shading (see, e.g., Poorter et al. 1988) and requires extra investment in support tissue (see, e.g., Konings et al. 1989). Comparisons of different species or treatments can thus best be done at a common biomass trajectory (Rice and Bazzaz 1989). Overlooking ontogenetic drift in RGR or allocation, as done by

Shipley and Peters, may seriously affect the relationship between these two variables.

2. *Number of Replicates*

At each harvest, Shipley and Peters determined weights of two to six plants. As a result of plant-to-plant variation in dry weight, which was considerable in their experiment, the determination of RGR using so few plants may lead to quite large errors. Given a true RGR value of 200 mg g^{-1} d^{-1}, two harvests of six plants, and a mean SD in natural-log-transformed dry weight of 1.0 (SD ranges from 0.4 to 1.8 in table 3 of Shipley and Peters [1990]), a simple simulation shows that RGR deviates by more than 15% in 30 out of 100 of such experiments. These deviations increase progressively when less than six plants are harvested, as frequently occurred in Shipley and Peters's experiment. Moreover, in some cases mean total plant weight at their first harvest was less than 0.05 mg. Assuming that plant weight was determined with a balance accurate up to 0.01 mg, a deviation of one unit in total plant weight already causes a difference in RGR of 15%.

Although errors in the determination of RGR will not systematically alter the relation between RGR and allocation, it may mask a possible connection. Hence we cannot exclude the possibility that the nonsignificant $(.05 < P < .06)$ negative correlation between RGR and root-shoot ratio at day 10 of Shipley and Peters's experiment would turn out to be significant in a more carefully designed experiment. However, reasoning along the same lines, the slightly positive correlation between RGR and root-shoot ratio at day 30 would become even more significant. How could such a shift in root-shoot ratio occur?

3. *Growth Conditions*

All plants were grown in 480-mL pots, filled with a commercial potting soil and with a single addition of NPK fertilizer before sowing. Such small pots may not invariably allow maximum growth of plants during as much as 1 mo. Assuming (1) that even the largest plants in their experiment (4 g) did not exhaust more than 50% of the total amount of N, and (2) a concentration of 4% N in the plant material, these pots should have contained 23 mmol of available N. From the data of Shipley and Peters we cannot derive the total amount of N in the pots available for the plant. However, they state that addition of 2.7 mmol N in their fertilizer experiment decreased the root-shoot ratio. This is a strong indication that nitrogen availability was actually limiting growth. Their experiment in which the nutrient level was varied cannot support their contention that submaximal RGRs could not occur, since the weights of the largest plants in their fertilizer experiment were only 10% of those of the largest plants in their broad comparison. It is mainly when plants become bigger that total biomass increases sharply. Because of the high absolute growth rate at that stage, nutrient demand may easily exceed nutrient availability (cf. Ingestad 1970), especially if fertilizer is not applied regularly during the experiment. Shipley and Peters cite Grime and Hunt (1975) as additional evidence that nutrient availability did not limit growth, but the Grime and Hunt data cannot lend support to Shipley and Peters's claim; in the experiment of Grime and Hunt, plants received a very high supply of nutrients

every other day. Moreover, those plants were grown at a relatively low light intensity and thus showed a much lower root-shoot ratio and a lower RGR.

A second consequence of the use of such small plots (height 9 cm) during as much as 1 mo, is that roots will easily get pot-bound. This implies that a small part of the pot volume will be densely rooted with all nutrients soon taken up, whereas in less densely rooted parts nutrients are still available.

Thus, it is likely that (localized) depletion may have occurred, at first for the larger plants, which are the ones that also grow inherently fastest *(P < .05* in a linear regression of Shipley and Peters's data of final weights and RGR). These plants will respond to the (partial) depletion by enlarging investment in the roots (Brouwer 1963). Indeed, in Shipley and Peters's experiment, the correlation between RGR and root-shoot ratio changes from negative at day 10 to positive at day 30. Therefore, the positive correlation between RGR and allocation to the roots for the 30-d-old seedlings can be the result of nutrient depletion in the pots of the fastest-growing plants.

TILMAN'S HYPOTHESIS

Based on the shortcomings in the experimental design, we conclude that Shipley and Peters's data do not allow any evaluation of Tilman's hypothesis. How then can this hypothesis be tested?

1. *Allocation*

In our opinion the best way to avoid an interaction between potential RGR and nutrient depletion is by growing plants in a nutrient solution that is replenished well before depletion might occur, rather than in small pots containing a soil mixture. We have carried out such a comparative experiment with 24 herbaceous C_3-species (Poorter and Remkes 1990), harvesting 56 plants per species in a period of 17 d. In this experiment, in which we corrected for ontogenetic drift by calculating parameters for all species on a common dry-weight trajectory, we determined the fraction of biomass allocated to the leaves (leaf-weight ratio, LWR), rather than the root-shoot ratio, since the LWR is actually the measure used in Tilman's approach. We have found a positive correlation between LWR and RGR *(P < .05)*. This agrees qualitatively with Tilman's contention that a larger investment in leaves is associated with a higher growth rate. However, an increase in RGR of 100% is associated with an increase in LWR of only 22%. Therefore, LWR cannot explain the variation in RGR quantitatively. Which physiological or morphological factor then determines the interspecific variation in RGR?

In our opinion it is not the proportion of biomass invested in leaves (LWR) that determines the RGR of a plant, but rather the amount of leaf area per unit total plant weight (leaf-area ratio, LAR). In the above-mentioned experiment with 24 species (Poorter and Remkes 1990), an increase in RGR of 100% was associated with an increase in LAR of 82%. These differences could, to a small extent, be explained by differences in LWR but were mainly due to differences in the specific leaf area (SLA), the amount of leaf area per unit leaf weight. The same

conclusions were reached in a comparison of literature sources on interspecific variation in RGR (Poorter 1989).

2. *Physiology*

Tilman's contention on the positive relation between LWR and RGR is closely connected with a second one, in which he assumes the rates of photosynthesis and respiration per unit shoot weight and root weight, respectively, to be the same for all species. However, we found the rates of photosynthesis and respiration per unit shoot and root biomass to be correlated positively with RGR (Poorter et al. 1990). No relationship was found between RGR and the rate of photosynthesis per unit leaf area, as a result of the higher SLA of the faster-growing species. We therefore conclude that our data do not support Tilman's second assumption.

FINAL CONCLUSIONS

The allocation experiment of Shipley and Peters (1990) was inspired by the central role allocation plays in the theory of Tilman (1988) in explaining interspecific differences in RGR. They rejected this theory on the basis of an experiment that cannot be conclusive since it is flawed by a poor experimental approach. However, our own data do not support Tilman's theory either. Although biomass allocation to leaves could explain some variation in RGR, the growth parameter SLA is much more important.

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