Plant allocation, growth rate and successional status

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Summary

1. Theory predicts a negative correlation between root (and stem) allocation and growth rate in enriched environments (RGR_max), but evidence does not consistently support this. There is one possible supporting example from previous research in which root allocation in the field increases during old-field succession at the Cedar Creek Natural History Area, both community wide and for individual species samples, and RGR_max declines for some important species.

2. In this study, we confirm that late successional species have lower RGR_max for a larger sample of species (n = 28) as well as higher field root allocation. However, root allocation by seedlings does not increase for the late successional species for those same species in the greenhouse in enriched conditions; indeed it declines.

3. These results suggest that seedlings may have markedly different allocation than adults and that observed allocation patterns may be better viewed as adaptively plastic responses to resource gradients, rather than fixed species attributes that determine growth rates. Other, presumably less plastic characters (e.g. nitrogen- or water-use efficiency) may control growth rate, optimal allocation, and potentially competition and succession in this sample of plant types.

4. Leaf and stem allocation show no strong successional trend in the field or greenhouse, but do show a negative correlation with each other. Seed size is negatively correlated with growth rate, but shows no trend in relation to successional status.

Key-words: Balanced growth, competition, RGR_max, root–shoot ratio, seed size, succession


Introduction

The relationship between allocation (particularly the root–shoot ratio) and relative growth rate (RGR; biomass increment per unit total biomass) has been predicted to be close and causal. Monsi (1968) and Mooney (1972) assert that, all else being equal, plants that allocate more to shoot will have higher maximal growth rates (RGR_max) than those that allocate less. This idea is a special case of optimal root–shoot ratio (Davidson 1969; Thornley 1972; Wilson 1988a; Gleeson & Tilman 1992) when it is assumed that root resources are not limiting. Tilman (1988) used this idea to illustrate the relation between allocation and growth, and developed a simulation model based on allocation differences to help explain broad patterns of vegetation structure and dynamics resulting from simultaneous above- and below-ground competition. While the principle itself is almost a necessary truism, attempts to demonstrate this relationship through comparisons of species have produced mixed results (Hunt & Lloyd 1987; Hunt, Nicholls & Fathy 1987; Poorter 1989; Shipley & Peters 1990a; Garnier 1991). One obvious problem with the hypothesis is that other aspects of plants vary and have been shown to relate to growth rate, e.g. tissue nitrogen (Ingestad 1982) and specific leaf area (Poorter 1989; Poorter & Remkes 1990). While these factors should increase the amount of variation found in species comparisons, it remains disturbing that there seems to be no general underlying pattern consistent with the allocation prediction (Poorter & Lambers 1991; Shipley & Peters 1991; Tilman 1991a,b). Does this mean that growth rate and allocation are unrelated characters?

This study reports a greenhouse comparison of species that derive from a well-studied old-field successional sequence (Inouye et al. 1987; Tilman 1988). In particular, previous data have shown that late successional species have lower RGR (Tilman & Cowan 1989) in pots and higher root allocation in the field (Gleeson & Tilman 1990). These trends appear to be consistent with the hypothesis, but the results of the present study fail to reaffirm it when RGR and allocation are measured in the same experiment. However,
Table 1. Species grown in the greenhouse (a = annual, b = biennial, p = perennial). ‘Field age’ is the mean of relative cover distribution through time of each species

<table>
<thead>
<tr>
<th>Life history</th>
<th>Field age</th>
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<tbody>
<tr>
<td>Grasses and sedges</td>
<td></td>
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<tr>
<td>Agropyron repens</td>
<td>p</td>
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<td>Agrostis scabra</td>
<td>p</td>
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<tr>
<td>Andropogon gerardii</td>
<td>p</td>
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<tr>
<td>Bromus inermis</td>
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<tr>
<td>Cenchrus longispinus</td>
<td>a</td>
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<tr>
<td>Eragrostis spectabilis</td>
<td>p</td>
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<tr>
<td>Poa pratensis</td>
<td>p</td>
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<tr>
<td>Schizachyrium scoparium</td>
<td>p</td>
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<tr>
<td>Setaria glauca</td>
<td>a</td>
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<tr>
<td>Cyperus filiculmis</td>
<td>p</td>
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<tr>
<td>Forbs</td>
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<tr>
<td>Ambrosia artemisiifolia</td>
<td>a</td>
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<tr>
<td>Anemone cylindrica</td>
<td>p</td>
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<tr>
<td>Asclepias syriaca</td>
<td>p</td>
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<td>Asclepias tuberosa</td>
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<tr>
<td>Berteroa incana</td>
<td>b</td>
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<tr>
<td>Chenopodium album</td>
<td>a</td>
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<tr>
<td>Hedeoma hispida</td>
<td>a</td>
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<tr>
<td>Laurus aspera</td>
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<td>Lycnhes alba</td>
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<td>Rudbeckia serotina</td>
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<td>Rumex acetosella</td>
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<td>Solidago nemoralis</td>
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<tr>
<td>Tragopogon dubius</td>
<td>b</td>
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<tr>
<td>Verbascum thapsus</td>
<td>b</td>
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<tr>
<td>Vicia villosa</td>
<td>a</td>
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<tr>
<td>Woody</td>
<td></td>
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<tr>
<td>Quercus rubra</td>
<td>p</td>
</tr>
<tr>
<td>Ulmus americana</td>
<td>p</td>
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<tr>
<td>Pinus banksiana</td>
<td>p</td>
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All nomenclature follows Gleason & Cronquist (1963).
* NA, not available.

because of the contrast in field and greenhouse allocation patterns found here, an alternative view is suggested which implies a more indirect relationship between growth rate and allocation.

Materials and methods

GREENHOUSE EXPERIMENT

Twenty-eight species grown from seed collected at the Cedar Creek Natural History Area of the University of Minnesota were measured for growth rate and biomass allocation under resource-enriched conditions in a greenhouse in the spring of 1987. The species are listed in Table 1. Two samples of Ambrosia artemisiifolia were included separately because they differed in seed size (0.0017 vs 0.0032 g), a size difference which persisted throughout the experiment [mean final biomass ± SD 3.31 ± 0.64 vs 5.63 ± 0.81 g, Student’s t-test, n = 17, P < 0.001]. An initial germination trial established levels of germination which were used to gauge the planting density. The experiment consisted of plants grown individually in well-watered and fertilized soil for 6 weeks with harvests of 1/3 of the individuals after 2, 4 and 6 weeks of growth after germination.

All herbaceous species were grown in super-cell Cone-Tainers (175 ml), which are conical–cylindrical plastic containers designed for mass seedling rearing. They are supported in racks by their upper margin in close arrays (maximum of 98 pots per filled rack). Racks were half-filled at the start of this experiment. Tree seedlings were grown in larger plastic pots, Ulmus and Pinus in small pots (525 ml) and Quercus in larger pots (1800 ml). Pots were filled with a mixture of 8 parts field soil, 3 parts peat moss and 3 parts perlite. After 2 weeks, all pots received a weekly watering with a soluble commercial fertilizer solution (Peter’s General Purpose Special, 20-20-20 plus trace elements, Grace-Sierra Horticultural Products, Milpitas, California). Plants were watered as required (up to twice per day at the end of the experiment). Plants received daylight supplemented by sodium vapour lamps set at 16:8 L:D. The greenhouse was heated and temperature varied from 15 to 27°C. The experiment was planted on 22 March 1987, first germination was on 29 March 1987 and the final plant was harvested on 31 May 1987.

Date of first germination was recorded (at 2-day intervals) for each pot and each pot thinned to one individual per pot. Racks were set up on four greenhouse tables and each rack divided into two sections each containing one pot of each herbaceous species located randomly within each section. Each species (including trees) had approximately 50 total pots, so that each harvest involved at least 15 plants per species chosen randomly from the total sample. The data for harvest at week 4 were deleted for Asclepias tuberosa because of insufficient plants. The larger pots for the tree species could not be included in the herbaceous racks. Ulmus and Pinus pots were randomized on top of separate racks dispersed among the herbaceous racks. The larger Quercus pots were kept together in the centre of the greenhouse. At harvest plants were removed from pots, roots rinsed with a fine water spray over a 2-mm mesh screen, plants dried, separated into root, stem and leaf, and weighed to the nearest 0.0001 g. Seed samples of each species were dried and weighed in lots of 25–100, seeds were removed from pods (e.g. Vicia villosa, Cenchrus longispinus), but other seed structures were not removed.

ANALYSIS

These data were used to calculate allocation pattern and growth rate. Relative growth rate was calculated from biomass M for each of the three intervals Δt (seed to total biomass at 2, 2–4 and 4–6 weeks) using the formula \( \ln(M_{t+1} - \ln M_t)/\Delta t \), and for the growth curve of the four data points together by regression of
In M vs time (Hunt 1990). As described in the Results, this last measure was used as the overall estimate of $RGR_{\text{max}}$. In addition, the rate of change of $RGR$ with age for each species was defined as the slope of the regression of 2-week $RGR$ against harvest date for each species.

Allocation pattern was determined as per cent root, leaf and stem at each harvest (for a comparison of allocation at the same age) and for the experiment as a whole by averaging. Per cent root was averaged for the three harvest dates, and for per cent leaf and stem by averaging harvests of weeks 4 and 6 only (because of the small plant size, leaf and stem were not separated at week 2). These are referred to as ‘mean per cent’ root, leaf and stem. In addition, an estimate of change in per cent root was obtained by regression using the allometric equation, $y = ax^b$. The parameter $a$ is equal to $y/\lambda$, and is equivalent to comparing allocation ($y$) at the same value of $x$ (=1). If $x =$ plant biomass, then $a$ allows a comparison of plants at the same total size (1 g; note that this method can result in comparison of plants at sizes they may not actually attain). A value of the exponent $b$ not equal to 1 means that the allocation pattern is changing with size. If $y =$ root biomass, this exponent is the per cent root analogue of $k$ (Hunt 1990) for root–shoot ratio.

In the analysis, we were concerned with three possible artefacts. First, use of seed size as the initial weight could cause bias in estimates of $RGR$. As seed biomass includes various structures for preservation, defence and dispersal, growth rates would be underestimated by a species-specific amount. Second, resource stress at larger sizes might confound intrinsic effects of size and age on growth. Third, statistical artefacts due to lack of independence of variables can occur with composite variables such as RGR and per cent root, particularly through correlations with biomass. For the relation between $RGR$ and biomass, $\ln(\text{biomass})$ is defined as the mean of the natural logs of the initial and final size of each interval (equivalent to the natural log of the geometric mean of the sizes). This definition reduces the dependence of the size–growth rate relationship on statistical artefact, as $RGR$ is positively correlated with final size and negatively correlated with the initial size. Analyses were performed using STATGRAPH and PC SAS.

FIELD DATA
The field allocation patterns and successional status are described elsewhere (Gleeson & Tilman 1990). In 1987, individual plants were extracted from field-collected soil cores 20 cm wide $\times$ 30 cm deep when in reproductive growth form and dry weights of tissues obtained. Root biomass is clearly underestimated by this method, particularly for larger root systems. Also, the age of individual perennial plants is unknown. Successional status derives from field abundance surveys (Tilman 1988) and is defined as the mean of the distribution of relative cover against field age for each species in the chronosequence and so has units of ‘field age’. This distribution is necessarily truncated at the age of the oldest field (60 years) and thus the truncation is most severe for the later species. Ulmus and Pinus were not harvested in the field, nor were they, along with Quercus, encountered in the field censuses, and consequently they are not included in any analyses of successional trends.

Results
We will describe the patterns in growth rate and allocation and then relate these results to each other and to field patterns. One feature of the results complicates the analysis; both growth rate and allocation pattern change with time even over the short period of this experiment. Thus trends also need to be considered.

GROWTH RATE
The mean $\pm$ SD overall $RGR$ was $0.175 \pm 0.042$ g g$^{-1}$ day$^{-1}$. When compared to each of the 2-week $RGR$, the overall $RGR$ was highly correlated to growth in the first interval ($r = 0.88$, df = 27, $P < 0.001$) and second interval ($r = 0.83$, df = 28, $P < 0.001$) and also significantly related to growth in the third ($r = 0.50$, df = 28, $P = 0.007$). Overall $RGR$ will be used as the estimate of $RGR_{\text{max}}$.

Overall, relative growth rates (2-week $RGR$) declined as growth progressed (Fig. 1a). This downturn could be due to intrinsic age-dependent factors (developmental, ontogenetic), intrinsic size-dependent factors (scaling constraints), or extrinsic size-dependent factors such as resource depletion. Over all three harvests, there is a strong relationship between size and growth rate (Fig. 1b, $r = -0.69$, df = 84, $P < 0.001$), where size is defined as the mean of the natural logs of the initial and final size of each interval (see Materials and methods). However, when looking at the correlation of $RGR$ and size at each age, the size effect is not significant at any age. ANCOVA of 2-week $RGR$ on age with size as a covariate shows a highly significant effect of age ($F = 88.3$, $P < 0.001$) and no effect of size ($F = 0.2$, NS). We conclude from this that declines in RGR throughout the experiment are primarily due to age-related factors, rather than intrinsic or extrinsic size-related factors. The use of seed size may create additional variance in RGR. There is a correlation of seed size and RGR in the first interval [using $\ln($seed biomass$)$, $r = -0.68$, df = 27, $P < 0.001$]. However, seed size is also negatively correlated to RGR in the second interval ($r = -0.56$, df = 27, $P = 0.002$), which would not be expected if it were an artefact, as well as with overall $RGR_{\text{max}}$ ($r = -0.69$, df = 27, $P < 0.001$). Quercus was excluded from these analyses as an extreme point in seed size (if included it improves the correlations).
There is a negative correlation between seed size (log transformed) and RGR\textsubscript{max} (Fig. 1c) whether trees are included \((r = -0.78, df = 28, P < 0.001)\) or not \((r = -0.71, df = 25, P < 0.001)\). The regression line was similar with trees (slope \(-0.015, intercept 0.058\)) or without (slope \(-0.015, intercept 0.057\)). For comparison with Shipley & Peters (1990b) we also report here the log\textsubscript{10}-log\textsubscript{10} regression with trees \((r = -0.79, df = 29, P < 0.001, slope -0.122, intercept -1.18)\) and without \((r = -0.65, df = 26, P < 0.001, slope -0.09, intercept -1.07)\). We conclude that only a relatively small portion of the variation in 2-week RGR explained by seed size is due to artefacts of non-growth structures and that there appears to be a genuine relationship between seed size and growth rate.

The decline in growth rate with age is given by the slope of the relationship of 2-week RGR against age. It varies between species from \(-0.0132\) to \(0.00172\) with a mean SD of \(-0.00527\pm0.00342\). This slope is positively correlated with RGR\textsubscript{max} \((r = -0.72, df = 28, P < 0.001)\), indicating that higher RGR decline faster.

In summary, there is a decline in the growth rates with time and rankings remain consistent with some variation. Biomass does not appear to be a strong determinant of RGR when effects of age are excluded, suggesting that the main cause for declining growth rates are developmental.

Grasses and forbs were not significantly different in RGR\textsubscript{max} \((0.177\pm0.03 vs 0.157\pm0.04, NS)\), but woody species were lower \((0.091\pm0.05, ANOVA P=0.004)\). Among the herbs, perennials are not significantly different than annuals \((0.149\pm0.046 vs 0.167\pm0.027)\) and biennials \((0.192\pm0.052)\), nor are mean seed sizes different. Rates of decline in RGR are significantly lower for perennials \((-0.0039\pm0.003)\) relative to annuals \((-0.0075\pm0.002)\) and biennials \((-0.0090\pm0.006, ANOVA P=0.008)\).

**ALLOCATION PATTERNS**

While there are several measures of allocation, correlation between them is generally good. Per cent root estimates are highly correlated from harvest to harvest and with the means \((0.57 < r < 0.95, df = 28, P < 0.002\) for all), as are estimates of per cent leaf \((0.90 < r < 0.98, df = 28, P < 0.001\) for all) and per cent stem \((0.88 < r < 0.98, df = 28, r < 0.001\) for all). The mean allocation will be used to define allocation pattern.

In general, per cent leaf, stem and root are expected to be negatively correlated by the null hypothesis as they are not independent. However, per cent stem and per cent leaf are much more strongly negatively correlated (using mean allocation, \(r = -0.85, df = 28, P < 0.001\)) than root and stem \((r = -0.21, NS)\) or leaf and root \((r = -0.32, df = 28, NS)\). One interpretation of this might be that the combination of stem and leaf (i.e. ‘shoot’) is a more meaningful index of productive potential than per cent leaf. We use per cent root
as the main index of allocation because it implies both per cent shoot (% shoot = 100 - % root) and root-shoot ratio [root/shoot = (% root/100)^{-1} - 1].

Allocation patterns varied with age and size, but not dramatically. Per cent root declined from the first to second harvest. Per cent stem increased and per cent leaf declined from the second to third harvest. There is no correlation between size and per cent root at any age. We conclude that there are no strong effects of size on allocation in this experiment. In particular, there is no suggestion that root allocation of large plants is affected by depletion.

Grasses show higher mean per cent stem than forbs (0.325 ± 0.056 vs 0.081 ± 0.102, ANOVA P < 0.001), lower per cent leaf (0.395 ± 0.053 vs 0.609 ± 0.141, P < 0.001), and lower per cent root (0.309 ± 0.04 vs 0.341 ± 0.09, P = 0.019). The woody species were not distinguishable from grasses or forbs in root (0.208 ± 0.03, NS), leaf (0.587 ± 0.02, NS), or stem (0.205 ± 0.04, NS). These relationships are maintained if rosettes are eliminated. There are no differences in the root trend parameter.

Mean per cent leaf and stem of annuals (0.487 ± 0.118, 0.196 ± 0.133), biennials (0.622 ± 0.224, 0.0 — both are rosettes), and perennials (0.540 ± 0.156, 0.196 ± 0.144) are not significantly different. Perennials have lower mean per cent root (0.287 ± 0.064) than annuals (0.355 ± 0.055) and biennials (0.384 ± 0.239, ANOVA P = 0.016). There are no differences in the root trend parameter.

**ALLOCATION AND GROWTH RATE**

There are no significant correlations between RGR\text{max} and mean per cent root, stem or leaf. There is a negative correlation of the root trend parameter (allometric exponent ‘b’) and RGR\text{max} (r = -0.41, df = 28, P = 0.029). In addition, there is a positive correlation of the root trend parameter (exponent) and the rate of decline in RGR (r = 0.40, df = 28, P = 0.033). We conclude that there is no strong evidence for a direct relation between allocation and growth rate in these seedlings. We have no interpretation for the relationships involving trends.

**RELATIONSHIP TO FIELD PARAMETERS**

For the species in this study, as previously reported for a larger sample of species (Gleeson & Tilman 1990), late successional species had higher per cent root in the field (r = 0.41, df = 25, P = 0.038; Fig. 2a). Note that the age of these field plants was not known.

In the greenhouse, late successional species have lower RGR\text{max} (r = -0.61, df = 25, P = 0.001; Fig. 2b) and lower final biomass (r = -0.52, df = 25, P = 0.008).

Per cent root in the greenhouse is lower for late successional species (r = -0.42, df = 25, P = 0.038; Fig. 2c). The greenhouse trend in root allocation (allometric exponent ‘b’) increases with per cent root in the field (r = 0.48, df = 25, P = 0.015), but not with successional status. Later successional species have higher mean per cent leaf in the greenhouse than early species (r = 0.47, df = 25, P = 0.019).

There are no significant relations of per cent stem or seed size (Fig. 2d) with either field allocation or successional status. However, if rosette species are removed (as they are harvested in the field in reproductive state), the stem/leaf ratio (although not for per cent stem or leaf alone) is positively correlated between the greenhouse and field (r = 0.521, df = 18, P = 0.022).

**Discussion**

The strongest impression produced by these results is the contrast between the coherence of the greenhouse data with respect to measurements of both growth rate and allocation separately, and the distinct lack of a coherent relation between the two when considering the greenhouse results alone. It would be logical to conclude that the characters of growth rate and allocation are essentially functionally decoupled. However, when considered in relation to field allocation and successional status, a more integrated view emerges that suggests an indirect relationship rather than functional independence.

The most surprising result is that successional allocation trends are reversed from the field to the greenhouse. Later successional species have higher root allocation in the field (Gleeson & Tilman 1990) and common garden monocultures (Tilman & Wedin 1991). In contrast in the greenhouse, when grown individually in enriched conditions, later successional species showed no greater per cent root and in fact showed less. Earlier studies indicated that later successional species at Cedar Creek have lower growth rates than earlier successional species when grown in monocultures at a range of soil qualities (Tilman & Cowan 1989; Tilman & Wedin 1991). This result is confirmed in this study for a larger set of species in enriched conditions (RGR\text{max}). These results taken together suggest several conclusions. First, the growth rate trends in relation to successional status appear to be consistent across growth conditions, suggesting that comparative RGR rank is a relatively stable species character. Second, the variation in allocation implies that root-shoot allocation is very plastic and is not strongly distinct between these species as seedlings. Indeed, it would be difficult to distinguish between grasses, forbs and trees on allocation alone in this short-term study. Thirdly, the reversal of successional allocation trends from the field to the greenhouse is an unexpected and distinctive pattern requiring an explanation.
LIMITS TO PLASTICITY

One interpretation consistent with these results is that the species from later successional fields are superior competitors because they have higher nitrogen- (or water-) use efficiency (Chapin 1980; Wedin & Tilman 1993), and thus generally require less N (or water) per unit biomass of growth. As a result, the demand for root resources relative to shoot would be less than for early successional species, and late successional species would have lower per cent root under enriched conditions (Davidson 1969; Thornley 1972; Wilson 1988a; Gleeson & Tilman 1992), but still could have higher per cent root in the field due to extreme depletion (Tilman & Wedin 1991) under the intense root competition (rather than shoot competition) that is apparent in later successional stages (Gleeson & Tilman 1990; Zak et al. 1990; Wilson & Tilman 1991). Lower maximal growth rates might be a necessary cost of nitrogen-use efficiency (Ingestad 1982; Field & Mooney 1986) and thus would be correlated with, rather than caused by, these allocation differences. Consistent with this interpretation, late successional plants are relatively smaller than early successional species in the greenhouse after equal periods of growth, but relatively larger in the field (Gleeson & Tilman 1990) and common garden after 2 or more years of growth (Tilman & Wedin 1991). In addition, tissue nitrogen declines in older fields (Gleeson & Tilman 1990).

This interpretation makes the assumption that tissue nitrogen is a relatively fixed character and that allocation is relatively plastic and adjusted to maximize growth rate for given resource levels. However, there must be limits to plasticity, especially in adult plants, because Tilman & Wedin (1991) never observed early successional species with as high an allocation to root on low nitrogen soils as occurred for late successional species on those same low nitrogen soils. If tissue nitrogen and allocation showed equivalent plasticity, plants would be expected to adjust both
characters in response to the environment (Mooney & Gulmon 1979; Hilbert 1990; Gleeson 1993). Ecologically, the characters that are the least plastic can potentially control the distribution of the species, while the more plastic ones would be predicted to adjust to the environment (and different species would be predicted to converge on the same character values, all else being equal). Improved knowledge of the relative plasticities of characters will enhance our understanding of species interactions and improve our ability to construct predictive models.

SEED SIZE

Species with larger seeds have lower growth rates, but seed size is unrelated to successional status. Lower growth rates for larger-seeded species do not appear to be an artefact of non-resource seed biomass as this relationship persists for estimates of RGR that exclude seed biomass. As late successional species do not have larger seeds, successional status cannot explain the pattern. The additional resources in larger seeds would seem likely to increase rather than decrease RGR, so the pattern seems difficult to explain and may not be general (Tilman 1988; Shipley & Peters 1990b).

The lack of correlation between seed size and successional status is consistent with the model of Tilman (1988), which predicts that the selective advantage of large seeds requires rich soils. On poor soils, there is no advantage to increasing seed size over increasing number because there is no differential size advantage in root competition (Wilson 1988b). This is consistent with the field allocation (Gleeson & Tilman 1990) and a competition experiment (Wilson & Tilman 1991) at Cedar Creek, which suggest that these fields show little evidence of light competition in the first 60 years.

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