A Meta-analysis of Studies on Plant Growth Rate and Allocation to Roots vs. Shoots.

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Introduction

Differences in soil mineral availability among locations are one of the most important factors in determining the distributions of plant species. If we are to be able to understand current controls over species abundances and predict their responses to continuing anthropogenic changes in mineral supply (Aber 1992; Jefferies and Maron 1997), it is essential that we understand the plant characteristics responsible for adaptation to different levels of fertility (Grime 1991). Plant growth rate and gross allocation patterns are two factors that have often been suggested to provide important elements of adaptation to soils of high or low fertility. The maximum relative growth rate a species can achieve (RGR_{max}; change in mass mass^{-1} time$^{-1)}$ varies greatly, and various authors have suggested that a high RGR_{max} is characteristic of species adapted to highly fertile environments (Chapin 1980; Grime 1979; Lambers and Poorter 1992).

As with relative growth rate, plant allocation to roots and shoots has received a great deal of attention in discussions of plant adaptation and acclimation to environments differing in fertility. The proportion of plant mass allocated to root, often called the root weight ratio (RWR), is an expression of a basic foraging tradeoff that plants face. The essential resources required by plants are acquired by different organs; light and carbon by the above-ground photosynthetic organs (shoots) while water and mineral ions are acquired by roots. Use of a given molecule (of sugar, lipid, amino acid, etc.) in the construction of one organ necessarily means that the same molecule cannot simultaneously be used in construction of another organ. Plants must therefore balance their needs to acquire light and soil resources by allocating materials to the production of roots and shoots in appropriate proportions. Extensive modelling efforts have been undertaken to assess how optimum allocation changes for plants under different conditions. These efforts universally find that increased allocation to roots is favored as soil resource availability declines relative to the availability of light (Gleeson 1993; Hilbert 1990; Johnson & Thornley 1987; Kachi & Rorison 1989), a pattern also found empirically by Wilson (1988) in a review of experimental studies on allocation.

Important generalizations about growth rate and allocation have emerged from studies that have quantitatively synthesized research in this area. Poorter (1990) examined the results of 69 studies to determine which plant traits were most closely associated with interspecific variation in RGR. He found that RGR was correlated most strongly (positively) with specific leaf area (leaf area/leaf weight), and leaf area ratio (LAR; leaf weight/total plant weight) but was also positively associated with mass allocation to leaves, and net assimilation rate (NAR; change in plant weight per leaf area per time). Reynolds and D'Antonio (1996) examined 77 studies

incorporating more than 206 comparisons of root weight ratio (RWR) of plants at more than one level of nitrogen availability. A plastic increase in root allocation as nutrient availability decreased was common. For 172 instances of plants grown alone or in monoculture they found that in 133 RWR decreased significantly as nitrogen availability increased, while in 6 instances RWR increased significantly and in 33 there was no statistically significant change.

These studies have provided important generalizations about plant growth and allocation, but many important questions have remained unanswered. In many cases this is not so much for a lack of relevant data, but because no attempts at synthesizing the literature (such as Poorter's or that of Reynolds and D'Antonio) have been performed. The present work attempts a quantitative synthesis of studies which address five hypotheses concerning interspecific comparisons of relative growth rate and allocation to roots vs. shoots. While some authors have regarded these patterns as established facts, they will be regarded here as hypotheses to be tested empirically. The five hypotheses, to be discussed in greater detail below, are:

1) Species adapted to fertile environments have a higher RGR_{max} than species from infertile environments.

2) Species with high RGR_{max} also grow the fastest at any level of soil nutrient availability.

3) Species adapted to fertile environments allocate less to roots than species from infertile environments.

4) Root allocation is so highly plastic that there is no correlation between the RWR of species when grown in high nutrient vs. low nutrient conditions,
or alternatively,
Root allocation is highly plastic in some species and relatively invariant in others, so that there is a negative correlation between the RWR of species when grown in high nutrient vs. low nutrient conditions.

5) Species with high RGR_{max} have relatively low mass allocation to roots.

The Hypotheses

1) RGR_{max} vs. fertility of habitat:

An ability to grow rapidly under high resource conditions is considered by many authors to be a hallmark of plant strategy for living in fertile soils (Chapin 1980; Lambers and Poorter 1992). Relative growth rate occupies a central place in the CSR theory of J.P. Grime (1979) as an essential element delimiting the principal plant strategies. A high RGR_{max} is an important component of what he refers to as the competitive and ruderal plant strategies, while a low RGR_{max} is characteristic of plants adapted to low fertility, high stress environments (Grime 1979).

2) The consistency of species rankings in RGR across fertility gradients.

One possible explanation for the replacement of species across fertility gradients is that there is a tradeoff in growth rate at high vs. low nutrient availability, so that different species dominate portions of the fertility gradient by being able to outgrow (and outcompete) at particular fertility levels. Schulze and Chapin (1987) refer to this idea as the Orians-Solbrig hypothesis, after the authors who suggested a similar pattern for water availability gradients.

However, several authors have suggested that the Orians-Solbrig hypothesis is not empirically supported, and that species with high maximum relative growth rate (i.e. at high resource availability) also tend to have high relative growth rates under low nutrient conditions (Chapin 1980; Chapin 1988; Lambers and Poorter 1992; van der Werf *et al.* 1993).

3) RWR and habitat fertility

Patterns of allocation may play an important role in determining species distributions along natural nutrient gradients. Along with the near-ubiquitous plastic increase of root weight ratio with decreasing nutrient availability (Reynolds and D'Antonio 1996; Wilson 1988), it has been suggested that plants adapted to low fertility environments have a higher RWR than those adapted to more fertile environments when grown under identical conditions (Field & Chapin 1992). In poor soils, plants with large root systems relative to their size might have an advantage in acquisition of scarce mineral resources. Conversely, in high nutrient soils, a large root system might be a superfluous expense for a plant, which could invest its resources more profitably elsewhere.

4) The consistency of species rankings in RWR across fertility gradients.

Chapin (1980) suggested that species adapted to fertile environments have high RWR when grown under conditions of low nutrient availability, but low RWR when grown at high levels of nutrients. In contrast, species adapted to infertile sites have a fairly fixed RWR at any nutrient level. The RWRs of a set of plant species grown at high and at low nutrient availability would be expected to be negatively correlated. In contrast, Gleeson & Tilman (1994) suggested that RWR is so plastic that it can not be regarded as characteristic of a plant species; the RWRs of a set of species under one environmental condition might be uncorrelated with those under a different set of conditions.

5) Relative growth rate in relation to Root Weight Ratio

Since plants are composed largely of material derived from photosynthesis, increased allocation to non-photosynthetic organs should in general reduce plant growth rate (Mooney 1972), and one might predict that species with high allocation to roots would have low RGR (Lambers and Poorter 1992, p 201, 237). In the early 1990s there was a vigorous debate over whether a negative correlation is generally found between the RWR and the RGR_{max} of a sample of plant species (Poorter & Lambers 1991; Shipley & Peters 1990; Shipley & Peters 1991; Tilman 1991a; Tilman 1991b). Both sides in this debate were able to cite various studies in defense of their positions, including ones that actually found a *positive* correlation between root allocation and growth rate (Hunt & Lloyd 1987).

Materials and Methods

Meta-analysis

A great deal of empirical information is available to address each of these hypotheses. Studies can be cited in support of each; studies can also be cited which refute them. Our interest is in the generality of these patterns, and to address this we need to assess the results of available data in an unbiased fashion. This paper uses the techniques of meta-analysis to synthesize the

results across multiple studies. Meta-analysis has become important in the field of ecology since the early 1990s (Gurevitch, Curtis and Jones 2001; Gurevitch & Hedges 1993; Gurevitch *et al.* 1992), although it has been widely used in fields including medicine and education since the 1970s (Cooper & Hedges 1994). Meta-analysis consists in the application of statistical approaches to combine the results of studies that shed light on the same question. This approach is suited for the analysis of highly focused questions that lend themselves to standardized quantitation, such as the five questions listed above.

Meta-analysis as practiced here involves four steps. The first is to identify studies from the published literature that contain data relevant to the questions being addressed. In the second step, a measure of "effect size" is calculated for each study. There are a number of effect size measurements that have been used in meta-analysis, depending on the nature of the data to be analyzed. The standard correlation coefficient r is a widely known example of an effect size metric used in meta-analysis.

The third step in meta-analysis is to calculate mean effect sizes across groups of studies. This is the mean of the effect sizes for a number of studies, generally weighted by the sample size and variance of the studies. These means are typically calculated for all the studies in a sample considered together (the grand mean effect size) and for subsets of data that share some meaningful distinction (such as studies involving herbaceous species, and studies involving woody species).

The fourth step in a meta-analysis is to test for significant deviations from various null hypotheses of interest. Techniques exist to derive confidence intervals for a mean effect size. Using these, one may test whether a mean effect size differs from zero (that is whether there is a significant effect across all studies). Additionally one can test whether the mean effect size differs among classes of the data (e.g. between studies on woody plants and studies on herbs). This step uses sampling theory and techniques developed especially for meta-analysis, as effect sizes do not conform to the distributions required for use of familiar techniques such as the ANOVA or t-test. Probability statements arising out of meta-analysis are interpreted just as are those arising from more familiar statistics, and a significance level of $p < 0.05$ is conventionally used.

Literature surveyed

Although it would be desirable in principle to examine every study that had ever published data relevant to the questions asked in this analysis, this would be impossible in practice, so that a sample of the relevant literature must be used instead. In order to avoid potential sources of bias in article identification, I did not use methods such as keyword searches in bibliographic databases (Reed & Baxter 1994), to identify studies for inclusion. Instead, I exhaustively examined every issue of the journals *Ecology, Functional Ecology, The Journal of Ecology, The New Phytologist, Oecologia* and *Oikos,* published from 1987 through 1996. These journals were chosen as leading journals publishing research in plant ecology; experience with the literature suggested these journals would contain numerous studies relevant to the questions being asked. The starting date of 1987 was chosen as it was the first date of publication for *Functional Ecology*, and therefore allowed a comparable sample for each journal used.

A priori criteria were used to determine whether to include articles, to avoid potential bias in determining their suitability. Every study chosen had to present data allowing for the

comparison of two or more wild plant species. Data for domesticated species or cultivars were not used. All plants had to be grown either as isolated individuals or in monoculture, and all species within a study had to be grown under identical conditions.

Many of the studies presented several comparisons on the same species that could potentially be used for this analysis. For example, a study might present RGR data for several species at both ambient and doubled CO_2 levels. It would have been inadvisable to include more than one such comparison from a given experiment in the meta-analysis, as separate comparisons could not be regarded as independent observations. A set of a priori criteria were therefore used to choose one set of experimental conditions to represent each study. Several of the hypotheses to be examined refer to plants growing under optimal conditions, or conditions in which growth is limited solely by nutrient availability. Given a choice of data obtained under various experimental conditions to use for this analysis, I therefore chose the highest light, most optimal watering conditions (neither flooded nor droughted), most favorable growth temperature and the lowest level of herbivores, pathogens and toxic substances from each experiment. There were two exceptions to the principal that plants grown under the most favorable conditions were used. All data used was for plants grown at ambient CO_2 levels, as the great majority of studies included only plants grown under these conditions, and this made the conditions across studies more comparable. Similarly, non-mycorrhizal plants were used when both mycorrhizal and non-mycorrhizal treatments were included, as many experiments were performed in pots with non-inoculated plants, and data for non-mycorrhizal plants was therefore more comparable across studies. For hypotheses 1 (RGR_{max} and fertility) and 3 (RWR and fertility) the highest nutrient level treatment of each study was used, as the closest approximation of optimal growth conditions. For hypotheses 2 (hierarchy of RGR) and 4 (hierarchy of RWR) the highest and lowest nutrient levels from each study were used.

Determination of the relative fertility of habitats from which species derive

To address several of the hypotheses, it was necessary to rank species according to the fertility of the habitats in which they typically occur. Depending on the information available for a particular study, this was done in either of two ways: evaluation by the authors of a study (e.g. "*Holcus lanatus* (L.) and *Deschampsia flexuosa* (L.) Trin., associated with fertile and infertile habitats respectively" (Van de Vijver *et al*. 1993), or by use of Ellenberg N numbers.

Ellenberg numbers derive from the work of the late German botanist and ecologist Heinz Ellenberg, and have gained a widespread use in plant ecology as indicators of the typical habitats of numerous European plant species. Ellenberg published extensive tables that rank several thousand European plant species according the locations in which they are found across a number of environmental gradients (Ellenberg 1979). His N values range from 1, for species found "only in soils *very* poor in mineral nitrogen" to 9 for species found "only in soils *very* rich in mineral nitrogen" (Ellenberg 1979) p. 109, italics his). The Ellenberg numbers of plants at a given site have proven to be a good index of soil characteristics (Gebauer, Rehder & Wollenweber 1988; Hawkes 1997) and have been found to correspond with the characteristics of plants collected in sites as far removed from central Europe as Britain (Thompson *et al*. 1993) and the United States (Taub 2002).

For analyses comparing species from more and less fertile habitats, only studies which compared species that differed by at least four in Ellenberg N number were used. This corresponds for example to a comparison of species found "mostly in *poor* soils" (N#=3) with ones that are found "mostly in soils *rich* in mineral nitrogen" (N#=7, Ellenberg 1979 p. 109, italics his).

Experimental nutrient gradients

Several of the hypotheses involve comparisons of the properties of plants grown under high vs. low nutrient conditions. For these questions, each study used in the meta-analysis had data for either RWR or RGR (depending on the hypothesis) for four or more species at two or more levels of a macronutrient (N, P, K, Ca, S, Mg). This included studies in which species were grown in two or more natural soils, so long as the relative fertility of the soils was clearly stated by the authors of the study. It was not possible to analyze data across gradients of each macronutrient separately, as sample sizes of studies that varied the same nutrients were too low to be meaningfully analyzed. Data across all types of macronutrient gradients are therefore combined for analysis.

Statistical methods

Two types of effect size metrics were used in this meta-analysis, depending on the form of the data available. When possible, both types of analyses were performed to address the same hypothesis. For studies that included data for four or more species and allowed two continuous variables to be compared (hereafter referred to as correlational studies), Z-transformed correlation coefficients were used as the effect metric (effect metrics for each hypothesis detailed in Table 3). Transformation of the r values was necessary, as the theoretical distribution of Z is more normal than that of r (Rosenthal 1994). Studies were weighted by the reciprocal of their conditional variance, with the conditional variance of effect size for each study estimated as

$$\frac{1}{n-3}$$

where n is the number of species included in the study (Shadish & Haddock 1994). This procedure weights studies according to the number of species included (and hence the confidence in the r values). The grand mean effect size estimate across all studies that is derived from this analysis is simply the weighted average Z score. As r values are more readily understandable than z values for most ecologists, I have backtransformed the data into r for the purposes of presentation. Confidence limits for the mean effect size was determined using parametric mixed models with differences among individual species treated as random variation, and differences between groups (i.e. woody vs. herbaceous) treated as fixed variation as per Gurevitch and Hedges (1993) and Rosenberg, Adams & Gurevitch (1997).

Studies that included less than four studies, or used a non-continuous independent variable (e.g. "fertile vs. "infertile") were analyzed separately, as a correlation approach cannot be applied. The effect size used is the natural log of the ratio of a measured variable (either RWR or RGR in the various analyses) (Hedges, Gurevitch & Curtis 1999).

$$\ln\left(\frac{\text{variable}_1}{\text{variable}_2}\right)$$

where the subscripts 1 and 2 indicate the mean value of the variable for species from fertile and infertile sites (for hypotheses 1 and 3) or the faster and slower growing of two species (for hypothesis 5). As this involves a categorical distinction among species, these studies will be called "categorical studies". Effects metrics for each hypothesis are detailed in Table 4. As many of the papers from which the data was drawn did not indicate sample sizes or standard errors, weighting by these factors was impossible, and an unweighted analysis was performed. This did not allow for application of a parametric model to the analysis, and confidence limits for the mean effect size were instead determined using a bootstrap procedure (Rosenberg *et al*. 1997).

Results:

Studies included

In all, 64 studies were found which met the criteria for inclusion and provided information for one or another of the hypotheses (Appendix 1). Many studies provided data relevant to more than one hypothesis; the number of studies addressing each hypothesis (Table 1) ranged from 8, for hypothesis 2 (hierarchy of RGR across nutrient gradients) to 41 for hypothesis 5 (correlation between RGR and RWR). The sampling of plant lifeforms was quite different for studies addressing each of the hypotheses. There were few studies on woody plants that provided information on the RGR or RWR of species adapted to different levels of fertility (Table 1, lines), while a considerable number of studies on woody plants compared RGR and RWR (Table 1). The majority of studies were performed on European and North American accessions of temperate species (Table 2). European researchers favored growth chambers far more than North American researchers (Table 2). Most correlational studies that compared plants from different habitats used Ellenberg N numbers as the index of the fertility of the sites from which species derive. For most categorical studies comparing different habitats, the fertility was based on the judgment of the author(s). For all studies, mean effects values for woody and herbaceous plants are reported separately only when these were found to differ significantly, otherwise a single overall effect is reported.

Table 1: Species included in the meta-analyses grouped by plant type.

Hypothesis	Graminoids	Forbs	Both forbs and grasses	Woody species	Both woody and herbaceous
1) RGR vs habitat	14	1	5	1	1
2) RGR hierarchy	1	1	2	4	0
3) RWR vs habitat	14	1	6	2	2
4) RWR hierarchy	4	0	3	6	0
5) RGR vs. RWR	13	4	5	17	3

Table 2: Species included in the meta-analysis by origin of plant accessions and experimental setting.

	Tropical				Temperate				Boreal	Other
	Africa	Asia	Australia	North America	Africa	Australia	North America	Europe	North America	
Growth chamber				1	1		5	18	2	1
Greenhouse				3		1	9	3		
Outdoors in pots	2	1	1				4	6		1
Outdoors in soil				1			3	1		

Hypothesis one

Across all studies, species from more fertile habitats grew faster than those from less fertile environments (Table 3, Table 4, Figure 1), with a mean correlation between habitat fertility and the RGR_{max} of species in correlational studies of r=0.47 (Table 3). For categorical studies there was also a significant relationship between fertility of the habitat of origins and RGR_{max}. The back-transformed effect size indicates that species from more fertile habitats had RGRs 1.64 times as high as those from less fertile habitats to which they were compared (Table 4), however the confidence limits for this value are very wide.

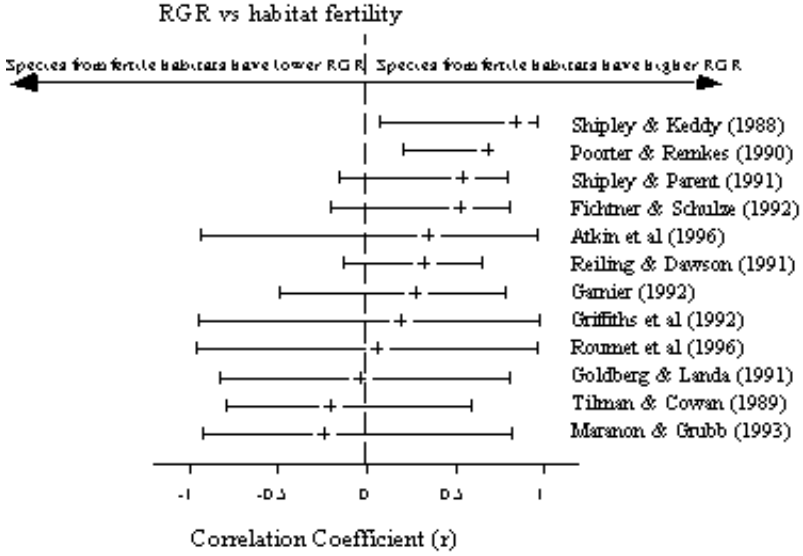


Figure 1. Correlation coefficients with confidence limits for studies examining the correlation of RGR and fertility of species' typical habitat.

Table 3: Mean effect sizes for correlational studies. Mean r and confidence limits are backtransformed from Z values.

Hypothesis	Correlation examined	Subset of Studies	number of studies	mean r	95% confidence limits to r
1)	RGR with fertility of habitat of origin	all	12	0.47	0.28 to 0.62
2)	RGR at high nutrients with RGR at low nutrients	Herbaceous species	4	0.40	0.11 to 0.63
2)	RGR at high nutrients with RGR at low nutrients	Woody species	4	0.90	0.82 to 0.94
3)	RWR with fertility of habitat of origin	all	12	0.10	-0.27 to 0.44
4)	RWR at high nutrients with RGR at low nutrients	Herbaceous species	7	0.92	0.81 to 0.96
4)	RWR at high nutrients with RGR at low nutrients	Woody species	6	0.77	0.62 to 0.86
5)	RGR with RWR	Herbaceous species	9	-0.29	-0.46 to 0.10
5)	RGR with RWR	Woody species	8	0.029	-0.21 to 0.27

Hypothesis two

The relative rankings of species in RGR was fairly consistent across nutrient gradients (Table 3, Figure 2), though to a degree that differed for herbs and woody plants ($Q=22.0, df=1, p<0.001$). For woody plants, the rankings of species in RGR were extremely consistent at high and low fertility, with the correlation between RGR averaging $r=0.90$, with fairly tight confidence limits (Table 3). For herbaceous plants, growth rate was significantly correlated across the nutrient gradients, but the correlation was weaker; with $r = 0.40$ (Table 3).

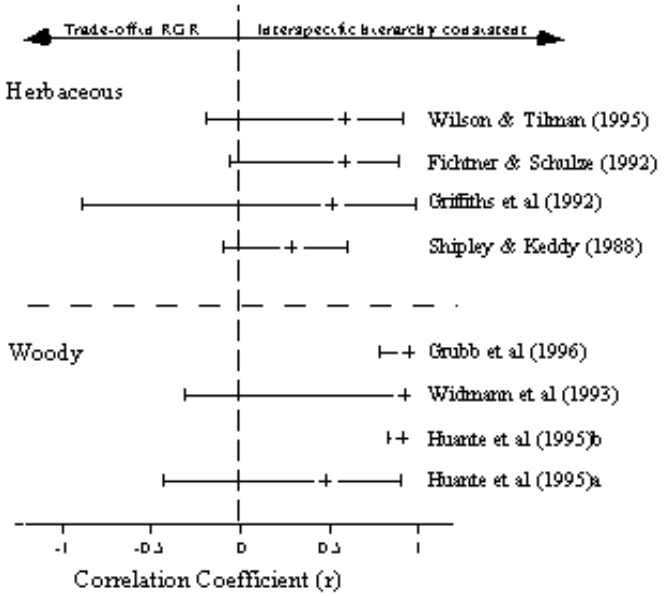


Figure 2. Correlation coefficients with confidence limits for studies examining the correlation of RGR across species at two nutrient levels.

Hypothesis three

Species from more fertile habitats showed no consistent tendency to allocate either more or less to roots than species from less fertile habitats, with a nonsignificant correlation for correlational studies of r= 0.052 (Tables 3 & 4, Figure 3). For categorical studies, there was a non-significant difference between species from more and less fertile sites, with a ratio of 0.93.

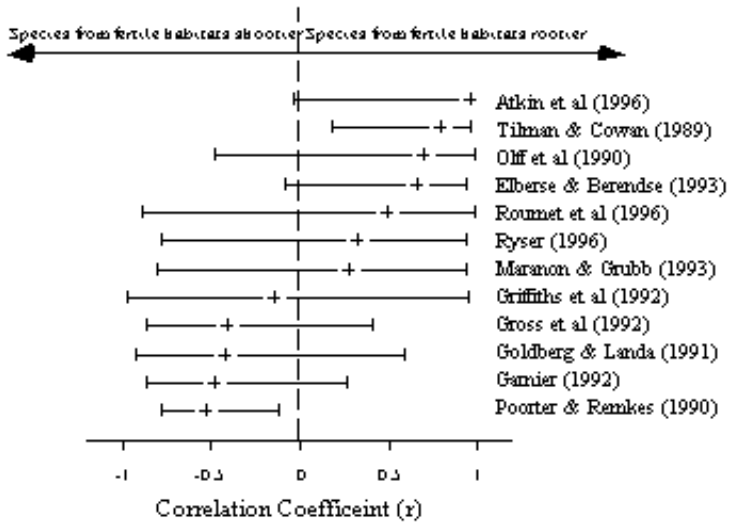


Figure 3. Correlation coefficients with confidence limits for studies examining the correlation of RWR and fertility of species' typical habitat.

Table 4: Mean effect sizes for analyses based on ln ratios. Ratios and confidence limits are backtransformed using antilogarithms.

Hypothesis	Effect size is ln of the ratio:	Subset of studies	# of studies	Ratio	95% confidence limits to ratio
1) RGR and fertility of usual habitat	Mean RGR of species from more fertile habitat / Mean RGR of species from less fertile habitats	all	11	1.64	1.09 to 3.12
3) RWR and fertility of usual habitat	Mean RWR of species from more fertile habitat / Mean RWR of species from less fertile habitat	all	14	0.93	0.72 to 1.18
5) RWR vs RGR	RWR of faster growing species / RWR of slower growing species	herbs	13	1.26	1.02 to 1.63
5) RWR vs RGR	RWR of faster growing species / RWR of slower growing species	woody	9	0.74	0.51 to 1.42

Hypothesis four

While most species showed a plastic response of RWR to nutrient availability, the relative value of RWR was a reliable characteristic of species, with individual species being consistently "rooty" or "shooty". This is shown by the large effect sizes for the correlation between RWR at high and low nutrient availability (Table 3, Figure 4). These effect sizes differed between herbs and woody plants (Q_b=4.22,df=1,p<0.05) and when backtransformed suggest for herbaceous species a correlation of r=0.92 for RWR at high and low nutrients, and for woody plants a correlation of r=0.77 (Table 3).

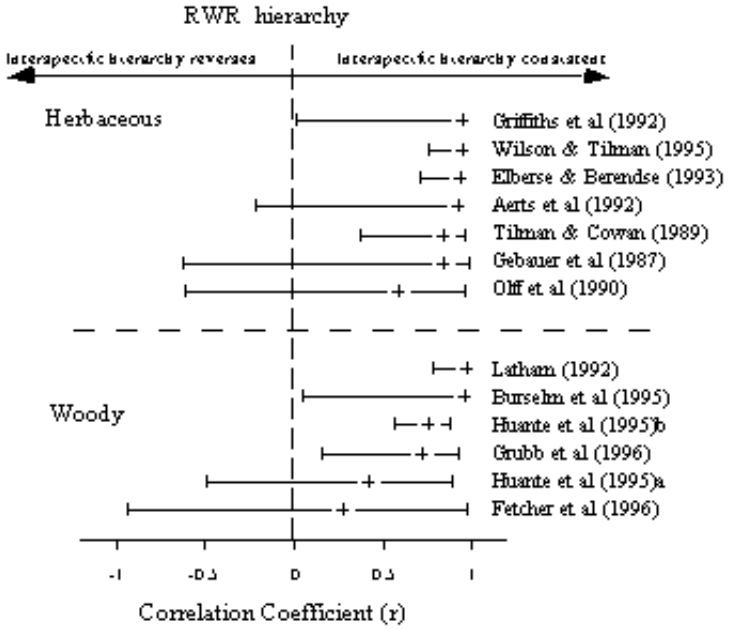


Figure 4. Correlation coefficients with confidence limits for studies examining the correlation of RWR across species at two nutrient levels.

Hypothesis five

The relationship between RGR_{max} and RWR differed between correlational and categorical studies. For both types of studies there were differences between herbs and woody plants; these were significant for categorical studies (Q=1.51, df =1, p = 0.02) and approached significance for correlational studies (Table 3, figure 5; for correlational studies Q= 3.55, df =1, p = 0.059). However the direction of the difference was not the same for correlational and categorical studies. In correlational studies on herbs, there was a significant negative correlation between RGR and RWR, while for categorical studies, there was a positive relationship between them. For both types of studies woody species did not show any significant pattern.

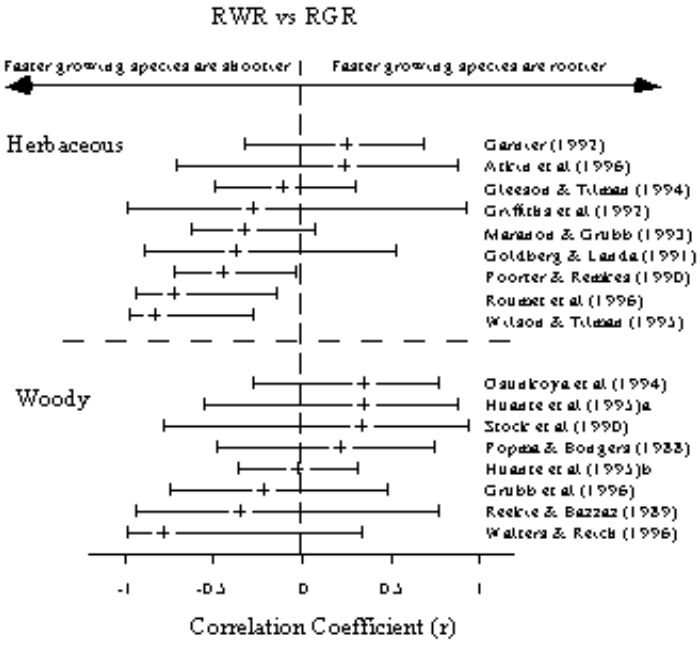


Figure 5. Correlation coefficients with confidence limits for studies examining the correlation of RWR and RGR.

Discussion

Hypothesis 1

Significant positive relationships between the fertility of habitats and the RGR_{max} of the species found in them were found in both correlational and categorical studies. This strongly supports the notion of a general relationship between these variables (Grime & Hunt 1975; Lambers and Poorter 1992) for herbaceous species. Whether this pattern also holds for woody species is less certain, as only two studies compared the RGR of woody plant species adapted to different level of fertility (Table 2). Evidence for a positive relationship between RGR and the fertility of the habitats from which species derive is difficult to come by for woody species. Grime and Hunt's (1975) massive comparison of 135 British plant species included only 14

woody species, and while it is clear that woody species in that study grew slower as a group than the herbaceous species, it is not clear that there was any relationship between habitat fertility and RGR_{max} among the woody species. Most discussions of RGR in woody species (particularly trees) discuss growth rate differences as components of strategies pertaining to the light requirement for regeneration (Swaine & Whitmore 1988), and it may be that most variation in RGR_{max} among woody plants is associated with adaptation to different light regimes, obscuring any differences that are due to adaptation to habitats of different fertility.

Hypothesis 2

The positive correlation between growth rates at high and low nutrients found here suggests that the Orians and Solbrig hypothesis (Schulze and Chapin 1987) does not apply across nutrient gradients; there is no trade off between growth rate at high and low. There are, however, several reasons to believe that the estimated correlation between growth rates at high and low nutrient availability is an overestimate. The first reason is that the differences between the high and low nutrient condition treatments in these experiments may not have been large enough for the hypothesized tradeoff in growth rate to occur. A study by Raiimakers and Lambers (1996) illustrates this possibility. This study compared the growth of two neo-tropical tree species at 10 levels of phosphorus. At phosphorus levels ranging from 16 to 4096 mg of P per pot one species, *Taphira obtusa,* had the higher RGR. At the lowest levels of phosphorus (0-8 mg. per pot), the second species, *Lecythis corrugata* had the higher RGR. A crossover point in RGR between the two species was only observed because of the extremely broad (256-fold) gradient in nutrient levels that was used in this experiment. With two exceptions (Fichtner and Schulze 1992; Huante *et al.* 1995a) the experiments included in this meta-analysis had a ratio of fertilization rates between the high and low nutrient treatments of ten or less. This may well be too small a range to observe a trade-off in growth rates.

Additional evidence that the nutrient gradients used in these experiments were not sufficient to see a trade-off in growth at high and low RGR can be gained by examining the results of RGR hierarchy experiments involving less than four species. There were 14 such experiments in the sample of journals used for the meta-analysis. Although suitable methods could not be found to incorporate these studies into a formal meta-analysis, it is instructive to examine these results, as these studies were performed across both broad and narrow ranges of nutrient availability. Table 5 divides these studies into those in which the ratio of fertilization rates between high and low nutrient treatments was either greater than or less than 100. For most of the studies across narrow nutrient gradients, one species had consistently higher RGR. On the other hand, in those studies which had a broad nutrient gradient, the ranking of species in RGR switched in most cases.

Table 5: The number of two-species studies consistent and inconsistent hierarchies of RGR across small and large nutrient gradients.

	Nutrient gradients < 100 X	Nutrient gradients > 100 X
Same species has higher RGR at both nutrient levels	6	2
Different species with higher RGR at high vs. low nutrients	1	5

There is no simple answer to the question of how broad a gradient in nutrient availability would be sufficient to detect any trade-off in RGR at high vs. low nutrition; ideally the experimental gradient should reflect that found in natural soils. Unfortunately it is difficult in practice to exactly relate experimental conditions to natural ones. The various techniques used for measuring soil nutrient status, including total elemental composition, mineralization and various extraction techniques have both strengths and limitations (Binkley & Vitousek 1989), and may not always reflect the soil nutrient status that is relevant to the plant.

Another factor that could potentially inflate the correlation seen for RGR between high and low nutrient supply treatments is that many plant growth experiments are conducted on seedlings, which may be heavily dependent on seed reserves, and relatively unaffected by soil conditions. Evidence that this is the case may be found in the high growth rates achieved in some experiments by plants in even the lowest nutrient conditions. For example, Huante et al (1995a) grew seven neotropical tree species at four levels of phosphorus fertilization. Even with zero added phosphorus (plants were grown in pure silica sand, which would have contained very little nutrients of its own), all species had positive RGRs, averaging 64% of the RGR attained at the highest P level. Similarly, species at the lowest nitrogen level in Fichtner and Schulze (1992) had very high relative growth rates of approximately 0.2 gm gm^{-1} day^{-1}.

A third factor that would inflate the correlation between RGR at high and low nutrient availability in these experiments is that some species may do poorly in a particular set of experimental conditions for reasons unrelated to their normal response to nutrients. The temperature, pH of the soil or other environmental conditions in an experiment may be unsuitable for some of the species used, or they may suffer from pathogens. For these species RGR may be low at any experimental nutrient level, but will not reflect the growth rates the species is capable of under suitable conditions. Although these arguments suggest the observed correlation between RGR at high and low nutrient availability may be an overestimate, no study has found a negative correlation, and it seems likely that there is overall either a slight positive correlation, or no correlation between RGR at high and low nutrient availability along natural nutrient gradients.

Many authors have viewed the fairly high positive correlations seen for growth rate between plants grown in high and low nutrient conditions at face value and have asked: If some species are simply slow-growing in any environment, what advantage might there be to being an

inherently slow growing plant? (Chapin 1988). All else being equal, slow growing plants can be expected to attain a small size, have a low reproductive output (Harper 1977) and be at a competitive disadvantage (Goldberg 1990). Most current explanations for the inherently slow growth rates of some plant species emphasize a trade-off between growth (that is the ability to add tissue) and the ability to resist tissue loss (Aerts and van der Peijl 1993; Lambers and Poorter 1992).

Hypothesis 3

There is a near-ubiquitous response of plants to allocate a greater fraction of plant mass to roots as soil nutrients decrease (Reynolds and D'Antonio 1996; Wilson 1988), and it is tempting to predict that species that typically inhabit infertile environments will have a high allocation to roots as well (Field and Chapin 1992). Examination of a simple partitioning model suggests that this may not be a reasonable expectation. We can express a plant's need to maintain a functional balance between acquisition of carbon and soil nutrients as a proportionality between the activities of roots and shoots c.f. (Davidson 1969):

root weight X rate of absorption $\propto$ shoot weight X rate of photosynthesis

This can be rearranged to express the optimal root-shoot ratio c.f. (Hunt & Burnett 1973):

$$\frac{\text{root weight}}{\text{shoot weight}} \propto \frac{\text{rate of photosynthesis}}{\text{rate of absorption}}$$

As soil nutrient concentration increases, roots take up nutrients at an increased rate (Barber 1984), lowering the value of the right side of the proportionality. The optimal root: shoot ratio expressed on the left side is therefore be reduced as well, as nutrient availability increases. This is of course the pattern that is commonly seen empirically within species (Reynolds and D'Antonio 1996). Considered on an interspecific basis, however, it is not clear whether to expect a higher root allocation in plants from infertile sites.

There are three factors in the proportionality which might vary among species, with consequent variation in the optimal allocation pattern. Species might differ in photosynthetic rate (per weight of shoot), root absorption (per rate of root), and they might also differ in the scaling factor implied by the proportionality. This scaling factor reflects relative requirements for soil nutrients and photosynthate. Each of these three factors may differ in predictable ways among species adapted to different fertility levels, or with different growth rates.

There is evidence that species from fertile habitats typically have relatively high rates of photosynthesis per unit weight of leaf or shoot, due in large part to a greater specific leaf area (Lambers and Poorter 1992; Poorter *et al.* 1990). As this increases the ratio on the right hand side, we expect a corresponding increase in the ratio on the left side of the proportionality as well; on this basis species from fertile sites should have *higher* root allocation than those from infertile sites.

Counteracting this effect, fast-growing species, and species from fertile sites may have high root activity as well as shoot activity (Chapin 1980; Garnier *et al.* 1989). This pattern

would be in accord with Grime's (1979) hypothesis that resource acquisition ability above and belowground are positively correlated.

It is not clear whether there are consistent differences among species from fertile and infertile sites in relative requirements for carbon and soil derived nutrients such as nitrogen. Chapin (1980) suggested that plants from infertile habitats generally have higher tissue concentrations of various nutrients than species from fertile sites. However Poorter *et al.* (1990) and Garnier and Vancaeyzeele (1994) both found that fast-growing species (and by extension species from fertile sites) had higher tissue concentrations of nitrogen than slower-growing (infertile site) species.

Whether species from fertile habitats will generally have high or low allocation to shoots depends on the relative importance of these three factors, which have effects in contrary directions. The lack of any relationship between habitat fertility and RWR found in this analysis may indicate that these influences on RWR effectively cancel one another out.

Hypothesis 4

Based on the results of this analysis, the proportional mass allocation to roots appears to be a consistent characteristic of a species, relative to that of other species. This is in spite of the fact that the RWR values of nearly all species decrease as nutrients increase (Reynolds and D'Antonio 1996). Unlike with the RGR gradient experiments, there is no reason to think that the gradients used here were too small; the correlation between RWR at high and low nutrient levels was highly consistent across both large and small nutrient gradients (data not shown).

This contradicts both the expectation of a negative correlation between RWR at high and low nutrient availability (Chapin 1980), and the expectation of no correlation (Gleeson and Tilman 1994). Reynolds and D'Antonio (1996) in a survey of studies on the plastic response of RWR to nitrogen found no identifiable patterns in intraspecific differences in the magnitude of the plastic response in RWR. There was no relationship in their literature survey between the magnitude of the plastic response to nitrogen availability and either the fertility of the habitats from which species derive, RGR_{max} or plant life form. Together with the results of the present analyses, this suggests that plastic responses in RWR with respect to nutrients are similar among species.

Hypothesis 5

It is difficult to reconcile the results from the correlational and categorical analyses. For herbaceous species, results from the two analyses were diametrically opposed, with high RGR associated with low allocation to roots in correlational studies, and with low allocation to roots in categorical studies. The two analyses necessarily used different effect metrics, but it is difficult to see how this could lead to such divergent results. There are no obvious general differences among studies included in the two analyses in terms of the species used, the conditions under which plants were grown, or other aspects of the experimental designs.

It is tempting to ascribe the results of one or both analyses to Type 1 error. Neither result is profoundly significant; for each the confidence limits nearly overlap zero. The results from either study alone would suggest a rather weak relationship between RGR and RWR (in opposite directions of course), and the two taken together certainly suggest that, if there is a general

relationship, it must be rather modest in magnitude. In both analyses there was no significant relationship between growth rate and root allocation for woody species.

General Considerations

The use of meta-analytic techniques is often able to reveal significant patterns that would be missed in individual studies, due to low sample sizes and a lack of statistical power. Consider, for example, the studies included in the analysis of the correlation between RGR_{max} and the fertility of the habitats from which species derive. Of the 12 studies, only two showed a significant relationship between habitat fertility and RGR. The authors of these individual studies would have been justified in concluding that there was no relationship, or limited to discussing non significant trends (e..g "RGR was independent of the species nitrophily... however at high N-supply there was a general tendency that RGR was higher in nitrophilic...species" (Fichtner and Schulze 1992).

A meta-analysis cannot, however, give the ultimate answers to the hypotheses it addresses, as it shares the limitations of the separate studies of which it is comprised. The species in the various studies synthesized here are far from a representative set of all plant species, with strong biases toward temperate North American and European species, and graminoids (grasses and sedges). We must be cautious in extrapolating the findings from this study to other types of plants. The differences found in several of the analyses between woody and herbaceous species underscore the fact that different functional groups of plants exist, and that patterns of growth or allocation that are true for one group may not be universal.

Just as meta-analysis can make use only of the range of species and systems actually studied by authors, meta-analysis can only synthesize studies as they have been performed, not as they perhaps could or should have been done. The interpretation of these studies is therefore limited by any problems in the design or analysis of these experiments that are common to the various studies. There has been much discussion in the ecological literature of the use of techniques such as phylogenetically independent contrasts (Felsenstein 1985) to correct for possible problems of phylogenetic non-independence in comparative studies (Harvey, Read & Nee 1995). Application of these techniques to meta-analysis would be almost impossible unless the authors of the individual studies had already performed their analyses on this basis. To utilize independent contrasts methods in a meta-analysis, one would have to derive a separate phylogeny, including branch lengths, for every study included in the meta-analysis. While use of such techniques might be desirable, the findings of this analysis might well remain unchanged. It is not obvious from examination of the individual studies that make up these meta-analyses that there is any tendency for related species to have similar RGR or RWR. In general when patterns are strong, phylogenetically independent contrasts and simple correlation techniques lead to similar conclusions (Ricklefs 1996).

Despite its possible limitations, this study has found some clear patterns, and turned up several questions for future study. For temperate herbs, there is a clear and reliable relationship between RGR_{max} and the fertility of the habitats in which a species is typically found. Further studies are needed to establish if the same pattern is true for woody plants and for species in other regions of the globe. New studies are also needed which examine the growth of species across wider gradients of nutrient availability, to clarify whether there is a trade-off between

growth rate at very low and very high levels of nutrients. This study has also failed to find several predicted patterns. There appears to be no relationship between the RWR of a species and the fertility of the habitats in which it is found. There also does not appear to be any tendency for species rankings in RWR to reverse from high to low nutrient availability.

The ability of this meta-analysis to detect these patterns illustrates both the level of recent activity of research into the ecology of plant nutrition, and the value of a meta-analytical approach. There has been, as Grime (1991) predicted "a revival of research activity in mineral nutrition", particularly of multispecies comparative studies. However, without formal synthesis, reaching reliable conclusions about the findings of the data generated by this research would be quite difficult. A combination of continued empirical research and careful synthesis is most likely to keep knowledge of the ecology of plant nutrition moving forward in the future.

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Appendix 1: Studies included in the meta-analysis:

Study	RGR vs habitat	RGR hierarchy	RWR vs. habitat	RWR hierarchy	RGR vs. RWR
Aerts, Boot & van der Aart 1991			Categ.		
Aerts, De Caluwe & Konings 1992			Categ.	Corr.	
Alward & Joern 1993			Categ.		
Atkin & Cummins 1994	Categ.		Categ.		Categ.
Atkin, Botman & Lambers 1996	Corr.		Corr.		Corr.
Bazzaz et al. 1989					Categ.
Boot & den Dubbelden 1990					Categ.
Bowler & Press 1993	Categ.				
Burselm, Grubb & Turner 1995				Corr.	
Campbell & Grime 1989	Categ.				
Chambers & Kalff 1987					Categ.
Chapin, Groves & Evans 1989	Categ.		Categ.		Categ.
Crick & Grime 1987	Categ.		Categ.		Categ.
DeLucia, Schlesinger & Billings 1989					Categ.
DeLucia, Schlesinger & Billings 1989	Categ.		Categ.		Categ.
Dippery et al. 1995					Categ.
Elberse & Berendse 1993			Corr.	Corr.	
Fetcher et al. 1996				Corr.	
Fichtner & Schulze 1992	Corr.	Corr.			
Freijsen & Otten 1987					Categ.
Garnier et al 1989					Categ.
Garnier 1992	Corr.		Corr.		Corr.
Gebauer et al. 1987				Corr.	
Gleeson & Tilman 1994					Corr.
Goldberg & Landa 1991	Corr.		Corr.		Corr.
Griffin, Winner & Strain 1995					Categ.
Griffiths et al. 1992	Corr.	Corr.	Corr.	Corr.	Corr.
Gross, Maruca & Pregitzer 1992			Corr.		
Grubb et al. 1996		Corr.		Corr.	Corr.
Halvorson et al. 1991					Categ.
Hatcher et al. 1994			Categ.		
Huante, RIncon & Chapin 1995	Categ.	Corr.	Categ.	Corr.	Corr.
Huante, Rincon & Acosta 1995		Corr.		Corr.	Corr.
Kachi & Rorison 1989					Categ.
Kachi & Rorison 1990	Categ.		Categ.		Categ.
Konings, Koot & Tijman-de Wolf 1989	Categ.		Categ.		Categ.
Latham 1992				Corr.	
Lindroth, Kinney & Platz 1993					Categ.
Maranon & Grubb 1993	Corr.		Corr.		Corr.

McGraw & Chapin 1989			Categ.		
Muller & Garnier 1990					Categ.
Olff, Van Andel & Bakker 1990			Corr.	Corr.	
Osunkoya et al. 1994					Corr.
Poorter & Remkes 1990	Corr.		Corr.		Corr.
Popma & Bongers 1988					Corr.
Reekie & Bazzaz 1989					Corr.
Reiling & Davison 1992	Corr.				
Richards, Stock & Cowling 1995					Categ.
Robinson & Rorison 1987	Categ.				
Roumet et al. 1996	Corr.		Corr.		Corr.
Ryser 1996			Corr.		
Schierenbeck, Mack & Sharitz 1994					Categ.
Schlapfer & Ryser 1996	Categ.		Categ.		Categ.
Shipley & Keddy 1988	Corr.	Corr.			
Shipley & Parent 1991	Corr.				
Stock, Pate & Delfs 1990					Corr.
Tilman & Cowan 1989	Corr.		Corr.	Corr.	
Tjoelker et al. 1993					Categ.
Tschaplinski et al. 1995					Categ.
Van de Vijver et al. 1993			Categ.		
Veenendaal et al. 1996					Categ.
Walters & Reich 1996					Corr.
Widmann et al. 1993		Corr.			
Wilson & Tilman 1995		Corr.		Corr.	Corr.