ESSAY REVIEW

Why do species of woody seedlings change rank in relative growth rate between low and high irradiance?

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Introduction

It is often assumed that if a plant species has a higher relative growth rate (RGR) than another species in deep shade, it will have a lower RGR at high irradiance (Spurr & Barnes 1980; Thomas & Bazzaz 1999; Walter 1973). In other words, species change rank (crossover) between low and high irradiance. This idea was suggested chiefly by the finding that in deep shade the mass-based net photosynthetic rates of the leaves of shade plants exceed those of sun plants, while at high irradiance the reverse is true (Björkman & Holmgren 1963; Boardman 1977; Givnish 1988). This finding has been assumed to scale up to the level of whole-plant RGR (Shugart 1984). In the past decade, however, a contrary view concerning RGRs has emerged, the idea that if a plant grows faster than another at high irradiance it will also do so in the shade (Kitajima 1994; Poorter 1999).

According to this later view, light plays a role in maintaining the mixture of forest species only through the well established trade-off between survival rate in deep shade and RGR in bright light (Kitajima 1994, 1996).

Similar experimental studies of RGR responses to irradiance for woody seedlings report surprisingly different results. Here we indicate why such disparate results have been produced. We provide a simple analytical approach to understanding why crossovers should occur among particular species at particular stages of ontogeny. This approach is useful for understanding the maintenance of forest species richness, as well as for interpreting plant specialization in physiology and morphology to contrasting irradiance regimes.

Conflicts among studies

We reconsider here seven studies (Table 1) that focused on the dry-mass RGRs of five to 15 species of woody seedlings from temperate or tropical systems, at two or more irradiances (comprising at least understory shade, i.e. ≤2% daylight, and tree-fall gap irradiance, i.e. 10–25% daylight); in each study the species spanned a wide spectrum of shade tolerance/light demand. The results can be summarized by the correlation coefficients of RGR$_{gap}$ and RGR$_{under}$ calculated from the final harvests of all species in each study (Kitajima 1994). The extreme opposite results are shown in Fig. 1: an almost complete positive correlation (Kitajima 1994), and a nearly significant negative one (Agyeman, Swaine & Thompson 1999). While most studies show an overall positive correlation, its strength varies (Table 1, iii).

How do such different patterns arise from the same type of experiment? We suggest that a major cause is the different methods used to grow seedlings, and the harvest intervals chosen. For instance, we suppose that harvesting seedlings after a short time will produce rank retentions that would not be found in longer studies, and that do not represent the relative performances of seedlings during longer periods of growth in the wild. For example, while a certain small-seeded, light-demanding species may grow more quickly than a certain large-seeded shade-tolerator, both in deep shade and at high irradiance immediately after emergence, we suggest that the advantage in deep shade may well be temporary. After a year or two (assuming it survives), it may well be outranked in the shade by the shade-tolerator. This is expected from what is known of seedling physiology. The small-seeded seedling will have an initial burst of relative growth consistent with its initially very high specific leaf area (lamina area/lamina dry mass, SLA), which gives it a relatively high leaf area ratio (lamina area/plant dry mass, LAR; Grubb 1998a; Grubb et al. 1996; Marañón & Grubb 1993; Wright & Westoby 1999). As a result, it will have the superior RGR at both gap and understory irradiances. However as the seedlings grow larger, differences among species’ SLAs diminish (Grubb et al. 1996; Veneklaas & Poorter 1998), lose their correlation with seed size (Grubb et al. 1996), and cease to be the chief determinant of RGR (Grubb et al. 1996), a point further explained in the following section.

Once other factors influence RGR, the large-seeded shade-tolerator may outrank the small-seeded light-demander at understory irradiance, although not at gap irradiance (indicated by the trends of RGR over time in Walters, Kruger & Reich 1993). A longer study will therefore produce more rank changes between gap and understory irradiance than a shorter study. We
Table 1. Results of seven studies focusing on growth of woody seedlings at low and high irradiance. Relative growth rates (RGRs) were recalculated from raw data, when these were provided, for greater accuracy than reading values from graphs.

<table>
<thead>
<tr>
<th>(i) Number of species and life form at maturity (RF = rainforest)</th>
<th>(ii) Irradiance (% daylight)</th>
<th>(iii) General across-species correlation between RGRs at irradiances shown in bold in (ii)</th>
<th>(iv) Percentage of species pairs' CPs occurring between 2 and 10% daylight</th>
<th>(v) Species pairs' CPIs (% daylight): 1st quartile/median/3rd quartile</th>
<th>(vi) Fit of (L) vs. (R) line: (r) and (P) value</th>
<th>(vii) Regression coefficient of (L) vs. (R) line ((\alpha))</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 tropical RF trees</td>
<td>2</td>
<td>6, 10, 28, 44, 66</td>
<td>Negative trend (r = -0.46; P = 0.082)</td>
<td>68</td>
<td>2.1</td>
<td>(r = -0.96; P &lt; 0.001)</td>
<td>1 6</td>
</tr>
<tr>
<td>10 tropical RF trees</td>
<td>-1•6</td>
<td>-4.1, -46</td>
<td>No pattern* (r = 0.12; P = 0.74)</td>
<td>36</td>
<td>1.8</td>
<td>(r = -0.91; P &lt; 0.001)</td>
<td>1 6</td>
</tr>
<tr>
<td>Five temperate trees</td>
<td>2</td>
<td>8</td>
<td>No pattern (r = -0.17; P = 0.79)</td>
<td>50</td>
<td>1.3</td>
<td>(r = 0.08; P = 0.005)</td>
<td>1 2</td>
</tr>
<tr>
<td>13 tropical RF trees</td>
<td>2</td>
<td>23</td>
<td>Positive correlation (r = 0.94); (P &lt; 0.001)</td>
<td>12</td>
<td>-0.88</td>
<td>(r = 0.34; P &lt; 0.25)</td>
<td>-0.40</td>
</tr>
<tr>
<td>10 tropical RF trees†</td>
<td>2•5</td>
<td>10, 37</td>
<td>Positive correlation (r = 0.85; P = 0.002)</td>
<td>22</td>
<td>-0.04</td>
<td>(r = -0.58; P = 0.078)</td>
<td>1 4</td>
</tr>
<tr>
<td>Nine temperate shrubs, one temperate tree</td>
<td>0–3, 1•6</td>
<td>11, 63</td>
<td>Positive correlation (r = 0.91; P &lt; 0.001)</td>
<td>11</td>
<td>-0.44</td>
<td>(r = 0.24; P = 0.17)</td>
<td>-0.44</td>
</tr>
<tr>
<td>15 tropical RF trees</td>
<td>3</td>
<td>6, 12, 25, 50, 100</td>
<td>Positive correlation (r = 0.82; P &lt; 0.001)</td>
<td>26</td>
<td>0.43</td>
<td>(r = 0.83; P &lt; 0.001)</td>
<td>1 1</td>
</tr>
</tbody>
</table>

RGR = Dry mass relative growth rate; CPs = crossover-points; CPIs = crossover-point irradiances. See text for definitions of dark loss rate (\(L\)) and responsiveness (\(R\)).

*Positive correlation results if \(Cecropia obtusifolia\) is excluded from the analysis; then \(r = 0.81, P = 0.008\).

†12 tree species were grown in this study, but for two species no data were available at the irradiances considered, due to high seedling mortality.

‡RGRs were read from a graph for those values that conflicted with those recalculated from raw data.
Very frequently the fit is significant \((P < 0.05)\), even when only three data points are available. We are concerned here only with the range of irradiance over which species show increasing RGRs, and therefore we exclude growth data for photoinhibitory irradiances or limitation, by nitrogen for example (for these studies we excluded data for irradiances above 23% daylight). As data are scarce, methods of less than ideal exactitude must suffice; we fitted the function to only two data points when the absence of other data made this necessary. While the logarithmic function is adequate, other models such as the Michaelis–Menten function may have advantages when more data are available (see sapling studies below).

A major advantage of using a two-parameter function such as the logarithmic is that we can easily estimate the irradiance at which the crossover of any two species’ RGR functions occurs, the crossover point irradiance (CPI):

\[
CPI = e^{\frac{L_{speciesA} - L_{speciesB}}{R_{speciesA} - R_{speciesB}} - 1}
\]

Equation 2 emphasizes that just as any two non-parallel lines must cross, any two species’ RGR functions must cross over. Therefore two species must switch rank at a particular irradiance if their \(R\) values differ. When the difference between two species’ \(R\) values is small, relative to the difference between their \(L\) values, the CPI may become wholly theoretical, occurring above 100% or below 0% daylight. Otherwise the CPI is likely to occur between 0 and 100% daylight. The CPI may be calculated for each species pair; it then allows prediction of which of the pair grows more quickly at any irradiance. The estimated \(R\) and \(L\) values may be used to calculate the difference between the species’ RGRs at any irradiance.

We emphasize that \(R\) and \(L\) values are statistical quantities, and are subject to uncertainty—largely due to intraspecific variability in RGR response. For this reason, any study that quotes studies’ \(R\) and \(L\) values, or the derived CPI values, should also provide standard errors or confidence intervals (Sokal & Rohlf 1995). We do not offer here the parameters for prediction for any particular species or species pair. Below, when we refer to a species’ \(R\) value (or \(L\) value), we mean a central value for the species. In the following analysis of CPIs we are chiefly interested in comparing trends across studies; for the statistics we use (median and interquartile range) the standard errors of individual species’ values are not needed.

Once the CPIs are calculated for each species pair, the percentage occurring between understorey and gap irradiances can be determined (Table 1, iv). When a species pair’s CPI falls within this range, a rank-reversal between understorey and gap irradiance results. The percentage of species pairs’ CPIs that occurs between understorey and gap irradiance provides a more complete quantification of rank reversals for each study than is possible in a plot of \(\text{RGR}_{\text{understorey}}\) vs. \(\text{RGR}_{\text{gap}}\) (of the type shown in Fig. 1), or in considering correlation...
coefficients. Ultimately the information is the same: >50% indicates the emergence of a negative correlation across species between these irradiances, that is, the plot beginning to slope negatively. This analysis again highlights the disparity among the studies: the percentage of species pairs crossing over between gap and understorey irradiance ranges from 11 to 68%.

Just as species’ RGR functions change during ontogeny, species pairs’ CPIs will change with time. We predict that they will often increase, at least for many of those species pairs comprising a small-seeded light-demand and a large-seeded shade-tolerator. As we suggested earlier, when RGRs are determined primarily by seed size (through SLA), the light-demander will grow more quickly at both gap and understorey irradiance, and so the species pair’s CPI will at this stage be very low, well below understorey irradiance. However, as the seed-size effect diminishes, the shade-tolerator will often outperform the light-demander at understorey irradiance; the CPI will hence increase to a value above that irradiance.

We can test this hypothesis with the seven studies’ data. However, as the studies included different sets of species, we cannot compare their species pairs’ CPIs directly; instead we compare their CPI summary statistics. Most useful here are the median and interquartile range of the species pairs’ CPIs (Table 1, v). The variability of the studies’ medians is apparent. For the two studies showing strongest general rank retention (Grubb et al. 1996; Kitajima 1994), most of the species pairs’ crossovers occur at <2% daylight; the other studies show a range of higher median values. The studies used various pretreatments and growth periods (Table 2). Confirming our hypothesis, the range of CPI medians reflects the range of seedling growth periods; for the seven studies, median CPI is correlated strongly to experimental duration (Fig. 2; \( r^2 = 0.73; P = 0.014 \)). The longer the study, the greater the irradiance at which its species tend to change rank. The dispersion of the species pairs’ CPIs also increases: studies’ interquartile ranges increase linearly with seedling age \( (r^2 = 0.92; P < 0.001) \).

We note that the results of two other studies of species’ dry mass RGRs across irradiances (Boot 1996; Reich et al. 1998a) are consistent with these trends: including points for these species gives for the first trend \( r^2 = 0.73 \) \( (P = 0.002) \), and for the second trend \( r^2 = 0.90 \) \( (P < 0.001) \). We did not include these studies in the full analysis because they did not match the criteria met by the other seven studies – one covered too few species (Boot 1996), and for the other the lowest irradiance used was 5% daylight (Reich et al. 1998a).

### Table 2. Methodology of the seven studies the results of which are summarized in Table 1

<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Pretreatment, (weighted mean duration, weeks)</th>
<th>Experimental growth period, weeks (weighted mean duration, weeks)</th>
<th>Seedling growth period, weeks (pretreatment + experimental growth period)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agyeman et al. (1999)</td>
<td>2–6 weeks in 15% daylight, depending on species; (4*)</td>
<td>‘not exceeding’ 16 weeks for ‘fast-growing species’; 23 weeks for ‘slower-growing’ species; (21*)</td>
<td>25</td>
</tr>
<tr>
<td>Popma &amp; Bongers (1988)</td>
<td>Grown in ‘moderate shade’ until two post-cotyledonous leaves developed (ex: two species, grown in sunny greenhouse); (4*)</td>
<td>~14–39 weeks, depending on species; (32)</td>
<td>36</td>
</tr>
<tr>
<td>Walters &amp; Reich (1996)</td>
<td>~7 weeks in 20% daylight</td>
<td>~13</td>
<td>20</td>
</tr>
<tr>
<td>Osunkoya et al. (1994)</td>
<td>4 weeks in 37% daylight</td>
<td>~61</td>
<td>65</td>
</tr>
<tr>
<td>Grubb et al. (1996)</td>
<td>2 weeks in 60–70% daylight</td>
<td>~16</td>
<td>18</td>
</tr>
<tr>
<td>Poorter (1999)</td>
<td>5 species transplanted from wild - these planted in 3% light and ‘gradually moved to higher irradiance levels’, 10 species grown from seed; pretreatment depending on species, 2–36 weeks (15)</td>
<td>~12 to ~28; (23)</td>
<td>38</td>
</tr>
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</table>

*Value approximate; not enough information available for a true weighted mean.
Woody seedling relative growth rate rank changes

The trends described above ensure that short studies of species that vary in seed size produce low CPIs (<2% daylight), with minimal scatter, while longer studies produce crossover points scattering widely, with their medians occurring between gap and understorey irradiances. Most of the studies were long enough to result in >20% of the crossover points occurring between gap and understorey irradiance. This finding illustrates the principle that very short studies do not adequately represent the processes of long-term natural establishment, unless one can competently scale up. The finding that median CPI increases stably with time suggests that scaling up is possible.

This analysis is only roughly quantitative; we compare studies of different species, grown in different locations, in different ambient conditions. Further, many of the studies used imperfect methodologies, including problematic calculations of RGRs (e.g. weighing for ‘initial biomass’ of the ungerminated embryo-cum-endosperm, or weighing young seedlings after removal of cotyledons or still-attached seeds), pretreating species differently, growing species for different lengths of time and/or in differently sized pots, and fertilizing and watering on an ad hoc basis. These are confounding influences, and future experiments will presumably achieve greater rigour. The robust and systematic trends we demonstrate suggest that once such rigour is achieved in several long, multiple-harvest experiments on identical groups of species, quantitative trends may emerge which will allow prediction of rank reversals and rank reten-
tions over different growth periods.

Morphological and physiological basis

Why should so many species’ CPIs increase as seedlings mature? We have suggested that seed size is a major factor. Because most researchers select mainly small-seeded light-demanders and large-seeded shade-tolerators, this effect is common. For light-demanders and shade-tolerators of similar seed size, we might expect a smaller CPI shift. The importance of such seed size effects on CPI shifts in nature requires study. Why should so many species pairs’ CPIs increase as seedlings mature? We have suggested that seed size is a major factor. Because most researchers select mainly small-seeded light-demanders and large-seeded shade-tolerators, this effect is common. For light-demanders and shade-tolerators of similar seed size, we might expect a smaller CPI shift. The importance of such seed size effects on CPI shifts in nature requires study.

While seed size correlates strongly with shade tolerance for certain species sets, for others there is only a weak correlation, or none, as light demand is only one of a host of potentially strong evolutionary influences on seed traits (Grubb 1996; Grubb 1998b; Grubb & Metcalfe 1996). A completely different reason for the CPI shift may be the fact that plants become increasingly pot-bound, chiefly due to increasing nutrient limitation (cf. Ingstad 1982), but perhaps also to space limitation (Cresswell & Causton 1988; McConnaughay & Bazzaz 1992). This issue also requires study.

Leaving such questions aside for the moment, we can use the parameters of the species’ RGR to further investigate the CPI shift. As described earlier, L and R determine each species pair’s CPI by equation 2. We ask to what degree this equation constrains the possible CPI’s: is there a general relationship between L and R?

The slopes of regression for each study vary greatly (Table 1, vii); as expected (Sokal & Rohlf 1995) the slopes show no correlation. The L vs. R trade-off described is a new example of a quantifiable trade-off between resource acquisitive-ness and retentiveness (cf. Grime 1974). Mechanistically, the species that increase their RGR most when given a larger resource supply often pay a price in high respira-
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Classical theory suggests a negative correlation. For leaves, mass-based dark respiration rate is positively correlated across species with light compensation point and maximum mass-based photosynthetic rate (Givnish 1988). If modelled logarithmically, this relation becomes a negative L vs. R-type correlation (with dark respiration rate analogous to –L, and photosynthetic rate analogou-
s to RGR). For whole plants, a species’ R value will be determined not only by photosynthetic responsive-
ness, but also by morphology; and a species’ L value will reflect not only dark respiration rate but also loss of parts. Remarkably, there is a significant whole-plant L vs. R correlation for four of the seven studies at P < 0.05, and for a fifth at P = 0.078 (Table 1, vi; Fig. 3).

The trends described above ensure that short studies of species that vary in seed size produce low CPIs (<2% daylight), with minimal scatter, while longer studies produce crossover points scattering widely, with their medians occurring between gap and understorey irradiances. Most of the studies were long enough to result in >20% of the crossover points occurring between gap and understorey irradiance. This finding illustrates the principle that very short studies do not adequately represent the processes of long-term natural establishment, unless one can competently scale up. The finding that median CPI increases stably with time suggests that scaling up is possible.

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tion rate (Reich et al. 1998a; Reich et al. 1998b) and/or short-lived parts (Walters & Reich 1999). The trade-off has further relevance as a tool for investigating the physiological and morphological bases for species pairs’ crossovers.

Firstly, for most studies the tightness of the line’s fit (Figure 3) means that we can predict each species’ L value from its R value from the regression:

$$L = -\alpha R + \beta + \epsilon,$$

where $\epsilon$ represents the error, the deviation of species’ L value from that predicted by the line. This equation must constrain the CPI for each species pair, as it correlates L and R, the parameters used for the CPI calculation. The variation among the studies’ L vs. R slopes (see Table 1, vii) indicates that a separate equation holds for each study; therefore, a study’s $\alpha$ value can play a major role in determining the CPI values of its species.
pairs. This is clarified if equation 3 is substituted into equation 2:

$$\text{CPI} = e^{\alpha - \frac{\ln(\text{growth})}{\ln(\text{mass})}}$$

If there were no scatter about a study's L vs. R regression (and therefore for each species pair $e^{\alpha} = e^{\beta} = 0$), all the species' RGR functions would cross over at $e^{\alpha} = 1$, that is, the steeper the slope of the study's L vs. R line, the higher will be the study's median CPI (studies' median CPIs and $\alpha$ values are positively correlated, $r = 0.84$, $P = 0.018$).

That $\alpha$ should vary with median CPI across the studies is not surprising. As we have seen, the studies span a range of seedling growth periods: the enormous differences in morphology among a group of young seedlings of species originating from a wide range of seed sizes, and the rapid changes in morphology of each species during early ontogeny, will affect the slope of the L vs. R line. Elucidation of the precise effects will require explicit investigation; however, we suggest that initially small $\alpha$ values can arise from the coincidence of initially high SLA values for small-seeded light-demanders and initially low SLA values for large-seeded (epigeal) shade-tolerators, as described above. Because of the morphological differences among seedlings, species differing slightly in L may differ hugely in R during early establishment.

For instance, suppose that during early establishment one species has a marginally more negative L than another, and therefore a marginally stronger irradiance response, as a result of its gas-exchange properties. If this species also has smaller seeds than the other (i.e., it is a small-seeded light-demanders), and so a higher LAR, it can have a dramatically larger R as R is related both inversely to L, for physiological reasons, and positively to LAR. This ensures a shallow L vs. R slope (Fig. 4a). The species with the more negative L may, however, have larger seeds, and therefore have the lower initial LAR (for instance, if it is a larger-seeded light-demanders). If this is the case, the species with the more negative L may also have the smaller R. Such a plant will produce scatter about the study's L vs. R line, weakening the slope further.

A shallow slope may also result when the shade-tolerators are hypogeal species (i.e., their cotyledons remain in the seed coat). Such species will probably take longer than epigeal species to reach the stage of positive RGR (Grubb 1996a). Hypogeal shade-tolerators in the understory will take a long time to catch up with small-seeded epigeal light-demanders in dry mass and leaf area: in effect, their LAR will remain zero for a longer period. As a result, R is very small. This is another mechanism by which two species differing marginally in L can differ hugely in R (Fig. 4a).

At a given irradiance, the species' LARs become more uniform during growth (Grubb et al. 1996; Veneklaas & Poorter 1999), and acclimate across irradiances (Veneklaas & Poorter 1998). If we consider a group of species varying widely in seed size, as do the seven studies, we are likely to find that over time the effect of the impressive initial divergence of the species' LARs at each irradiance will become weakened by species differences in other traits that affect onward growth. Morphology now confounds the L vs. R relationship much less, and the L vs. R slope will steepen ($\alpha$ will increase) (Fig. 4b).

From this stage on, possible major determinants of species ranking in RGR include, in addition to LAR, respiratory costs and leaf lifetime (especially in deep shade; Agymen et al. 1999; Setia & Kikuzawa 1991; Walters & Reich 1999), net photosynthetic rates (Strauss-Debenedetti & Bazzaz 1996; Walters & Reich 2000a; but see Beaudet et al. 2000); and whole-plant architecture (King 1991; Kohyama & Grubb 1994; Kohyama & Hotta 1990). All these traits influence the unit leaf rate (dry mass gain per lamina area, ULR), which is the other component of RGR besides LAR (RGR = LAR × ULR). Evans (1972). At high irradiance the fastest-growing species will be those with highest ULRs and LARs. At low irradiance, for species' ULRs, and not their LAR values, often determine their relative performances (Agymen et al. 1999; Osunkoya et al. 1994; Popma & Bongers 1988). In fact, at low irradiance LAR may show a weak negative correlation with RGR (Agymen et al. 1999; Popma & Bongers 1988), as it is those species with highest LAR values (the light-demanders) that eventually tend to have the lowest ULRs in the shade, due to high respiratory costs and short leaf lifetimes (Walters & Reich 1999).

These effects indicate the non-genericity of the paradigm asserted by Veneklaas & Poorter (1998), that LAR determines RGR differences at low irradiance, while ULR determines differences at high irradiance. Such a paradigm does not apply to very young seedlings, whose RGR ranking at both low and high irradiance is determined by seed size-linked differences in SLA and therefore LAR, as found by Kitajima (1994). The leaf mass fraction (LMF), the other component of LAR, generally does not drive RGR in young seedlings of...
Maintenance of species richness

Contention surrounds the issue of whether species differences in seedling RGRs across irradiance regimes contribute to the maintenance of forest species richness. The contention has arisen in part from the seemingly conflicting evidence in the seven studies, and in related work (Kobe 1999; Walters & Reich 2000b). A result from a very short study, such as that of Kitajima (1994), will suggest that in nearly every case a plant that grows most quickly at low irradiance also grows most quickly at high irradiance, and so the forest’s heterogeneous light environment cannot maintain species richness through species differences in RGR responses to light. There are other ways in which light environment can play a role: as mentioned in the Introduction, there is ample evidence for a trade-off between survival rate and growth rate at high irradiance for seedlings and saplings (Grubb et al. 1996; Hubbell & Foster 1992; Kitajima 1994; Kobe et al. 1995; Kobe 1996; Kobe 1999).

However, the results of short studies do not reflect long-term processes in the field. When we consider the five longest studies of the seven, >20% of the total species pairs in each study show rank reversal in RGR between gap and understorey irradiance (Table 1, iv). Such changes to RGR hierarchies with changing resource supply rates can potentially contribute importantly to the maintenance of species richness (Latham 1992). Sorting the species pairs into functional type categories increases resolution. We have used convenient categories following Whitmore (1999) (and stress that these categories are qualitative and defined arbitrarily): pioneer (P); light-demanding non-pioneer (LD), and shade-tolerating non-pioneer (ST). In general, for the five studies in which >20% of species pairs’ CPIs occurred between 2 and 10% daylight, substantial proportions of species pairs of all combinations of functional types have crossovers between 2 and 10% daylight (Table 3).

Table 3. Percentage (and proportion) of species pairs’ crossover points occurring between understorey and single treefall gap conditions (2% and 10% daylight) in five studies

<table>
<thead>
<tr>
<th>Number of species and life form at maturity</th>
<th>Percentage of species pairs’ CPs occurring between 2% and 10% daylight</th>
<th>Author/s</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 tropical rainforest trees</td>
<td>68 (72/105) (5% of total)</td>
<td>Agyeman et al. (1999)</td>
</tr>
<tr>
<td>10 tropical rainforest trees</td>
<td>36 (16/45) (0% of total)</td>
<td>Popma &amp; Bongers (1988)</td>
</tr>
<tr>
<td>Five temperate trees</td>
<td>22 (10/45) (0% of total)</td>
<td>Osunkoya et al. (1994)</td>
</tr>
<tr>
<td>15 tropical rainforest trees</td>
<td>26 (27/105) (3% of total)</td>
<td>Poorter (1999)</td>
</tr>
<tr>
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</tbody>
</table>
approach used on seedlings see Kobe 1999). This approach has the potential to be admirably non-destructive, but it does not immediately permit estimation of whole-plant (mass-based) relative growth, as height- or diameter-based allometries for a given species are susceptible to ontogenetic drift and environmental variation, not at present well understood (Henry & Aarsen 1999; Kobayama & Grubb 1994).

In the several studies of sapling RGRs cited above, data were gathered at many irradiances, and a Michaelis–Menten (MM) response fitted to the increase of RGR with irradiance. The MM model has been used to test for a trade-off between `high-light growth’ and `low-light growth’, where the former is defined as one parameter of the model, the maximum RGR at high irradiance (the asymptote of the MM line), and the latter is defined as the second parameter, the estimated slope of the growth function at zero irradiance, which indicates the RGR forecast for very deep shade (Pacala et al. 1994).

These studies have demonstrated variously a weak trade-off (Pacala et al. 1994; Wright et al. 1998), or no relationship (Wright et al. 1998) between high- and low-light growth, depending on the group of species tested. Such findings do not imply a strict rank retention of species’ RGRs across irradiances. For instance, in a study of the radial RGRs of 10 species of saplings from a wide range of natural light environments (Pacala et al. 1994), 31% of species pairs crossed over between 2 and 10% daylight. The median CPI in this study is 8.2% daylight – a value exceeding any of those for the seedling studies (Table 1, v), consistent with the finding for seedlings that median CPI for a group of species changes are smooth. Long-term studies will be useful in testing this assumption.

Suggestions for new research

When designing an experiment, the length of the seedling growth period and the initial sizes of seedlings used must be considered. As the median CPI of a study’s species pairs, and the CPI interquartile range, increase as plants grow, the estimation of species pairs’ rank reversals will be greatly affected. In future studies it will be important to determine the length of time one wishes to model in nature, and to grow species either for that length of time, or for a shorter period, over which time progressive harvests are made. RGRs calculated from later harvest intervals will better represent long-term trends than RGRs calculated from early intervals. Our analysis indicates that time- and/or size-based trends may be quantitatively established, and natural processes occurring over longer periods may be extrapolated realistically. This proposition assumes that as species’ RGR functions change during ontogeny, the changes are smooth. Long-term studies will be useful in testing this assumption.

The L vs. R trade-off described above allows investigation of the morphological and physiological factors underlying a species pair’s rank reversal or rank retention at a given irradiance. Further study of the slope of this relationship, and how it relates to species choice and length of study, may lead to the prediction of species’ relative performances at specific irradiances from physiological and morphological metrics.

The studies made so far collectively support the idea that species differences in RGR across irradiance regimes do constitute a basis for the maintenance of species richness in forests. This evidence assumed that species’ RGRs, as determined from isolated plants in pot experiments, reflect their relative performance in natural communities. This assumption requires detailed testing.

Not considered above, but potentially very important, is interspecific variation in response to sunlight as opposed to the diffuse light experienced in all of the studies we have analysed (Walling, Ball & Woodrow 1997).

Do species cross over in response to other resources? The CPI approach can, in theory, be extended to determining crossovers in response to, for instance, low- and high-nutrient supply rates. Such crossovers may also change with time: one study reports that when five grass species from contrasted sites were grown on nutrient-poor soil, the three species from primarily nutrient-rich sites outperformed the two from nutrient-poor sites, but only for one season – by the second season the rank- ing had switched (Ryser 1996). The eventual crossovers were attributed to a trade-off between carbon assimilation rates and leaf longevity (Ryser 1996), the same principle that we have argued is one basis for crossovers in response to irradiance. In nutrient studies the principle has also been framed in terms of the assimilation and loss rates of nitrogen, rather than carbon (Aerts & van der Peijl 1993). If woody species cross over in RGR predictably in response to multiple resources, and further, their crossovers change predictably over time, the resulting patterns may determine an important part of forest function.

Much work lies ahead. The final objective, however, is undeniably compelling. With this research we move toward a technical basis for the conservation and management, even the gardening of forest systems, of any type, at least at the small scale. Coincident with the development of this knowledge – and of complementary knowledge also being actively sought (for instance the understanding of seed dispersal patterns and the roles of herbivores and pathogens) – will be a minimum theoretical and empirical framework for understanding how forests persist and function, from the level of species physiology, to the co-existence of dominant species, to succession.

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