

Testing performance rank reversals among coexisting species: crossover point irradiance analysis by Sack & Grubb (2001) and alternatives

INTRODUCTION

Two potentially competing species can coexist when their relative fitness ranks reverse at different points in a spatially or temporally heterogeneous landscape (Chesson 1985). Trade-offs between components of fitness, such as between survival and growth rates, or between fecundity and survival, may lead to rank reversals in relative fitness even when individual fitness components do not exhibit rank reversals. Alternatively, fitness rank reversals can be driven by rank reversals of a key performance trait, such as growth rate, between contrasting environments. Detecting such rank reversals in any competitive community is thus of interest. In particular, comparative studies of tree seedlings along a light gradient provide a rich arena for testing the relative importance of the rank-reversal hypothesis in community organization, and for exploring the physiological bases of rank reversals. Givnish (1988) and Latham (1992) proposed a hypothesis of rank reversal in relative growth rates (RGR) as the mechanism of niche differentiation and species coexistence along light gradients, and presented supporting evidence from comparative studies using a small number of species. In terms of whole-plant growth rates, more recent comparative studies of a larger number of species have failed to detect substantial rank reversals between gap and shade irradiance (Kitajima 1994; Veneklaas & Poorter 1998; Poorter 1999; Walters & Reich 1999). Sack & Grubb (2001; hereafter SG) introduced a new analytical approach to this problem – the crossover-point irradiance (CPI) method summarized in the next section – and analysed seven published studies to evaluate patterns of rank reversals in tree seedling RGR. Below, we compare statistical properties of the CPI method and two other statistical tests for evaluating the significance of rank reversals, and discuss SG's interpretation of the patterns they found.

STATISTICAL CONCERNS – WHAT IS THE NULL MODEL?

Sack & Grubb (2001) begin with the idea that mass-based photosynthetic rates of leaves of shade species exceed those of sun species in shade (e.g. Björkman & Holmgren 1963, comparing quantum yields for ecotypes of a herbaceous species; Givnish 1988, comparing sun- and shade-phenotypes of a single genotype; but see Osmond *et al.* 1999 and Walters & Reich 1999). Regardless of the generality of leaf-level physiological

trade-offs, the critical question is how to detect the signature of physiological trade-offs at the levels of whole-plant function and community structure.

These two higher levels of inquiry – the organismal and the community – suggest two different null hypotheses. If one wants to test whether lower-level trade-offs scale up to the whole-plant level, a sensible null model is that species maintain the same performance rank in all environments. One does need to ensure that apparent rank reversals are not simply the effect of measurement error, but even a single rank reversal that can be distinguished from measurement error will falsify the model. That SG consider even a small number of rank reversals to be significant suggests that this performance-maintenance model underlies their argument. An alternative null model, useful for testing whether leaf- and organism-level trade-offs scale up to affect community structure, states that the performance rank of a species in two different environments is uncorrelated. Under this model, half the species pairs in a community are expected to show rank reversals by chance; showing that the proportion of rank reversals is significantly different from half falsifies the null hypothesis. Finding fewer rank reversals than expected by chance (positive correlation) suggests that all species are physiologically or phylogenetically constrained to show similar (parallel) reaction norms. Finding more rank reversals than expected by chance (negative correlation) suggests that physiological trade-offs are important in structuring the community; this is the pattern one would see if communities are initially assembled at random, but thereafter stronger species outcompete weaker species in non-reversing pairs. If rank reversals are not more common than expected by chance, one should seek alternative mechanisms for species coexistence. (As with all statistical tests, one can fail to reject the null hypothesis either because the hypothesis is true – in this case, that physiological trade-offs in a single trait do not drive community structure – or because of bias or lack of power.)

A standard parametric test for rank reversals quantifies the direction and strength of correlation of performance measured in two different environments by plotting each species' performance score in one environment against that in another environment (Kitajima 1994). A negative correlation implies more rank reversals than expected by chance, while a positive correlation implies significant rank retention among species. Less positive or more negative correlation in one data set than in another indicates more frequent rank reversals in the former. Rank reversal frequency can also be tested non-parametrically with Kendall's test for rank concordance (Sokal & Rohlf 1981). Sack & Grubb (2001) developed a new parametric approach of calculating CPI, the irradiance (percentage of full

daylight) at which the reaction norms of RGR of a species pair would intersect along a light gradient. The frequency of rank reversals is evaluated by the proportion of CPI that falls within an arbitrary selected range of irradiance, for which SG selected 2–10% to represent commonly encountered light availability in forest understories. Typical forms of the RGR reaction norm show an asymptotic increase, often with a drop at the highest irradiance (Poorter 1999; Valladares *et al.* 2000). Thus, up to 15–20% irradiance several functions, including logarithmic, Michaelis–Menten and non-rectangular hyperbola, may fit equally well to observed reaction norms that have multiple data points in this range (Poorter 1999). Sack & Grubb (2001) chose a semilog plot to linearize the reaction norm:

$$\text{RGR} = R \ln(\text{irradiance} + 1) + L \quad \text{eqn 1}$$

Any two non-parallel lines in a two-dimensional space must intersect; the irradiance at which the reaction norms for species A and B are predicted to cross (CPI) may be calculated according to equation 2 of SG. The CPI method has several advantages. Crossover-point irradiance directly infers the irradiance at which two species switch their performance ranks, and can be compared across experiments that have used different light treatments. It can also be calculated when performance data are collected in only two light environments; this feature is convenient because having more than two light treatments may be logistically difficult in a comparative study of many species. Crossover-point irradiance has the potential to extrapolate results for experiments that measure performance in too narrow a range of light environments, which would otherwise bias results against detecting rank reversals in a single performance trait. This is perhaps the most attractive feature of the CPI which, as shown by SG's analysis, often occurs at irradiances below the minimum used in typical experiments.

However, the CPI method has several drawbacks. First, SG apparently aim to test the null hypothesis of RGR rank maintenance rather than of random assembly; we do not know what fraction of CPI is expected to fall within a given range of irradiance by chance. Second, the calculated CPI values may be biased by structural error – mis-specification of the underlying function for the true reaction norm. Third, the CPI method as implemented by SG does not take into account the potential effects of measurement error. If measurement errors are large, the estimated fraction of CPI cannot contain much true information. In order to compute appropriate confidence intervals to falsify the null hypothesis of rank maintenance, one would require additional statistical techniques that incorporate measurement error. Below, we use simulations to explore the sensitivity of CPI and other methods to measurement and structural error. All simulation analyses were done using the R language (Ihaka & Gentleman 1996).

EVALUATION OF STRUCTURAL AND MEASUREMENT ERRORS

We estimated reaction norms for 15 species from the data of Poorter (1999) at irradiances of 3, 6, 12 and 25% of daylight (excluding the highest light treatment of 50%, as done by SG), using either logarithmic functions (as did SG) or vertically offset Michaelis–Menten curves, which can have a positive or negative y intercept (non-zero RGR at zero irradiance). We also did the analysis by fitting non-rectangular hyperbolas that have been widely used to fit the light response of instantaneous photosynthetic rates (Lieth & Reynolds 1987); the results are similar to those for the Michaelis–Menten curves and are not discussed further.

The Michaelis–Menten curves fit the RGR reaction norms of Poorter (1999) better than SG's logarithmic curves, as expected since Michaelis–Menten curves have one more parameter than logarithmic curves. Median r^2 for Michaelis–Menten fits was 0.83 (range 0–0.99), while the median r^2 for logarithmic fits was 0.67 (range 0.004–0.96). We then took either function to be the 'true' reaction norm, and explored the effects of measurement and structural errors on the estimated fraction of CPI that occurs between 2 and 10% daylight (= range used by SG). We evaluated measurement error by adding truncated normal deviates to RGR estimates. We evaluated structural error by mis-specifying the parametric function for calculation of CPI – for example, using a logarithmic function when the true function for the simulation was Michaelis–Menten, and *vice versa*. The CPI values were calculated for logarithmic curves using SG's equations 1 and 2; standard numerical methods (Brent's method; Press *et al.* 1994) were used to find the CPI for Michaelis–Menten curves.

The true CPI fraction is always correctly estimated if no noise is added to the reaction norm and if CPI is estimated with a parametric form that matches the true form. If the true reaction norms are Michaelis–Menten (Fig. 1a), the estimates are relatively unaffected by noise if the correct function (Michaelis–Menten) is specified. However, incorrectly using a logarithmic function to fit the reaction norms predicts a significantly smaller fraction of CPI in the 2–10% daylight range (0.15) than the true estimate (0.23 with Michaelis–Menten) with little noise, and estimates increase with noise. In contrast, if the true reaction norms are logarithmic (Fig. 1b), CPI estimates using the true function increase with increasing noise, while CPI estimates using Michaelis–Menten are biased downward from the true fraction when measurement error is low, and increase to approach the true estimate (0.16) at the higher noise levels.

We conclude that the estimation of CPI can be sensitive to both measurement and structural error. The assumption of a logarithmic relationship adopted by SG tends to bias the estimated fraction of CPI upward with increasing measurement error (Fig. 1).

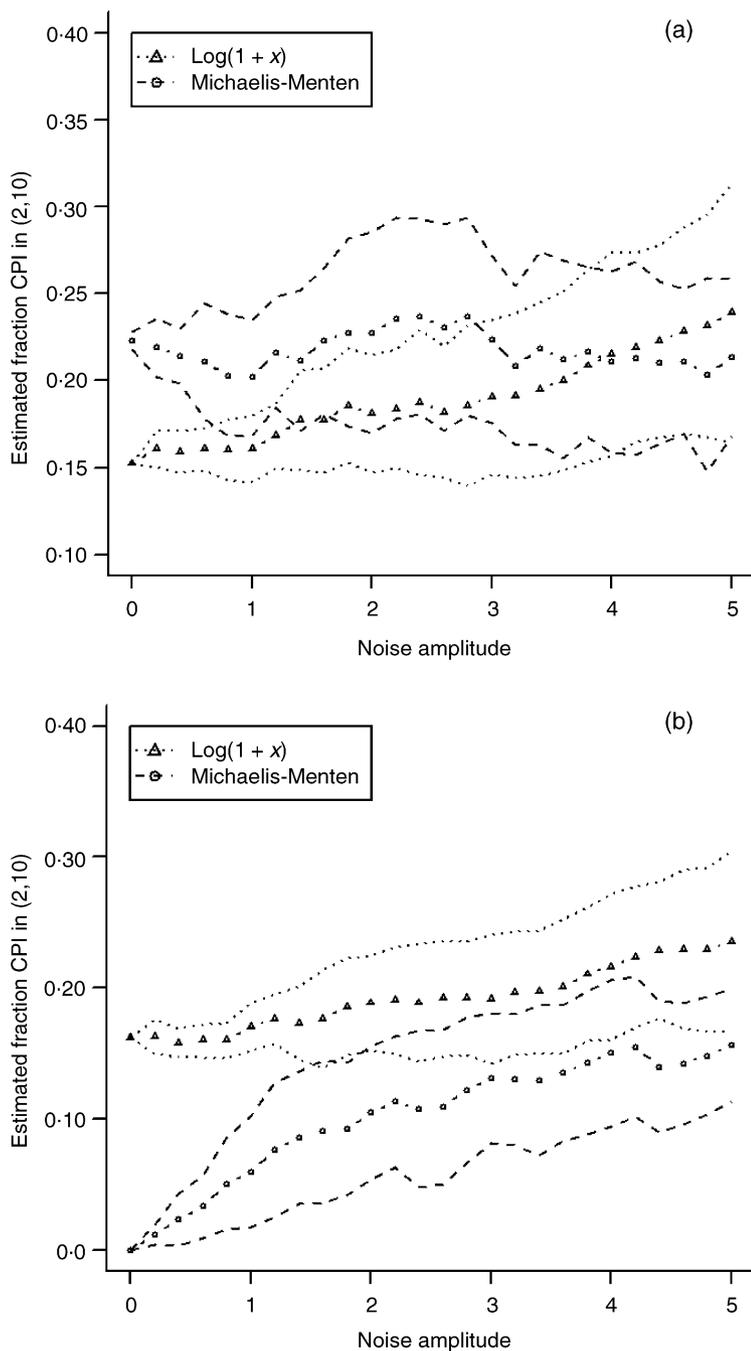


Fig. 1. Estimated fraction of crossover points falling between 2 and 10% irradiance as a function of estimated phenotypic reaction norm shape and measurement error. Simulations use reaction norms fitted to RGR data for the 15 tree species of Poorter (1999); measurement error is added from a truncated normal distribution with mean parameter zero and standard deviation (in RGR units) as shown on the horizontal axis. True reaction norms are (a) Michaelis–Menten; (b) logarithmic. Dashed and dotted lines show 95% confidence limits from 10 simulations at each noise level.

Fortunately, if that assumption is wrong (if the true reaction norms are Michaelis–Menten), the estimated fraction of CPI is biased in a conservative direction (underestimates the fraction of CPI in the specified range of irradiance; Fig. 1a). We do not have a good mechanistic argument to derive correct functions for RGR reaction norms, so that any function is necessarily an approximation.

The asymptotic shape of reaction norms of RGR as a function of percentage daylight may resemble that of instantaneous photosynthetic light response curves for a leaf, but this coincidence does not imply common mechanisms. Sack & Grubb (2001) argue that the slope (R) of the RGR reaction norm is analogous to photosynthetic light-use efficiency, whereas the intercept (L) is a function of dark respiration. However, both parameters (L and R) reflect morphological as well as physiological traits of the species. The slope R is not analogous to the ‘quantum yield’ determined as the initial slope of the photosynthetic light-response curve, but rather is an indicator of morphological and physiological plasticity (Valladares *et al.* 2000). The intercept, L , of the reaction norm is a statistical extrapolation, unlike the dark respiration in the photosynthetic light-response curve. Estimated intercepts and slopes are unlikely to be independent of each other for a simple reason, without a need to invoke biological mechanisms proposed by SG; under a null model of a common light compensation for all species, intercepts and slope should be negatively correlated with each other.

CPI COMPARED WITH ALTERNATIVE STATISTICAL TESTS

We used Poorter’s data of RGR at 3 and 12% daylight (corresponding roughly to understorey *vs* gap irradiance) to simulate how correlation analysis may be affected by measurement error. Parametric correlation analysis does not assume a particular parametric function for the shape of reaction norms. It is also easy to calculate significance levels for correlation, and adding noise simply dilutes the significance of the results, rather than biasing them (Fig. 2a). Correlation analysis does have the disadvantage that it can use only actual data at two different irradiances, which must be assumed to represent the irradiance extremes experienced by plants in the field (a potentially dangerous assumption; cf. Montgomery & Chazdon 2002).

Next we examined a non-parametric test for the number of observed rank reversals against a null model of random rank shuffling, which is mathematically equivalent to Kendall’s τ statistic for rank retention (Sokal & Rohlf 1981). Kendall’s τ gives the significance level of an observed number of crossovers as the probability that the same number or more (or fewer) crossovers occur for a random permutation of the species performances in the second environment. This non-parametric crossover analysis (Fig. 2b) gives results similar to those from parametric correlation analysis. A small number of crossovers corresponds to a positive correlation, and the estimated number of crossovers increases with increasing noise amplitude (Fig. 2b), corresponding with the decreasing positive correlation in Fig. 2(a). The estimated number of crossovers becomes non-significant at a lower noise level than does the estimated correlation, because non-parametric analysis trades off statistical power for robustness to outliers.

In summary, the three statistical methods have pros and cons that stem from different assumptions (Table 1). The main disadvantages of the CPI method are that we do not know how many crossovers characterize

confidence limits for the null case, nor can we distinguish the effects of high noise levels from a true community signal of rank reversals. One may argue that even a few rank reversals contribute significantly to species coexistence, but unless rank reversals are observed more frequently than expected by random permutation, rank reversals in a given performance trait cannot be the main reason for observed microsite preferences. The true value of the CPI method will emerge when there are sufficient data (accurate measurements at sufficiently different irradiances) to make statistically strong conclusions about the true shape of the reaction norms.

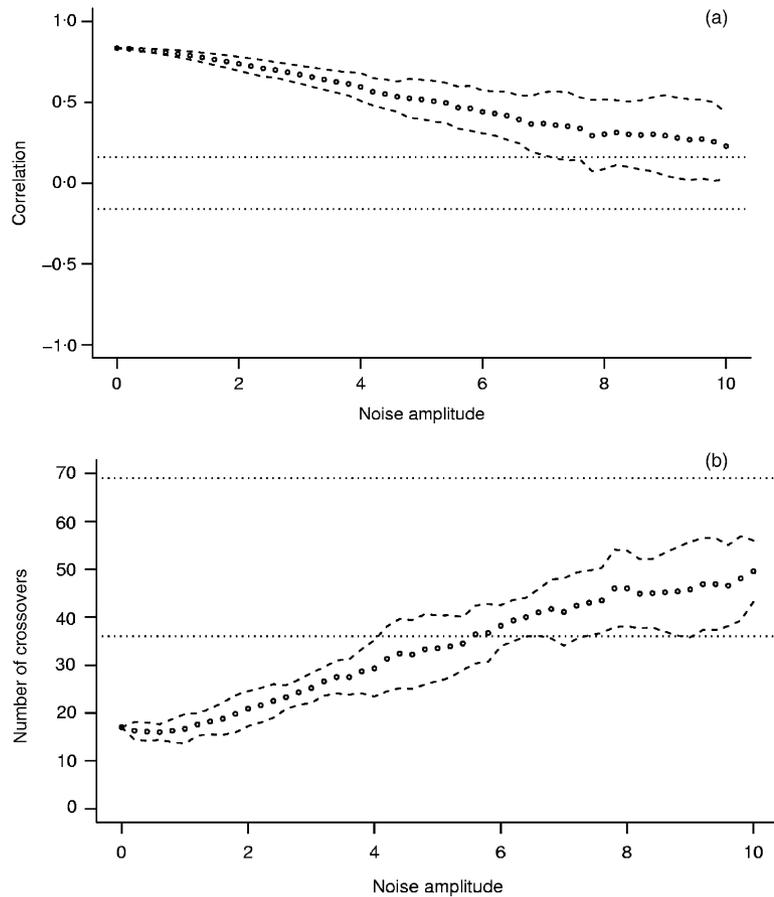


Fig. 2. Pearson correlations (a) and number of crossovers (b) between RGR at low (3%) and high (12%) irradiances as a function of noise added to RGR data for the 15 tree species of Poorter (1999). Dashed lines show 95% confidence intervals on correlations from 10 simulations at each noise level; horizontal dotted lines show 95% significance levels for non-zero correlations.

INTERPRETATIONS OF CROSSOVER PATTERNS

The title of Sack & Grubb (2001), ‘Why do species of woody seedlings change rank in relative growth rate between low and high irradiance?’, does not match the results of their analysis. Only one of the seven studies examined by SG showed a negative correlation – and even this correlation was only suggestive and not statistically significant ($P = 0.083$). Accordingly, we suggest that future searches for mechanisms of species coexistence should be directed toward testing alternatives to the rank-reversal hypothesis, such as allocation-based trade-offs in life-history traits (e.g. negative correlation between growth rates and survival; Brokaw 1987; Kitajima 1994; Dalling & Hubbell 2002; Kitajima 2002; Wright 2002) and ontogenetic crossovers (e.g. species that are shade tolerant as juveniles becoming shade intolerant with age and *vice versa*; Grubb 1996; Svenning 2000).

Because median CPIs for the seven studies cited by SG increase with duration of growth period, SG suggest simply that future studies should use longer durations. However, higher CPIs do not necessarily mean an increase in the frequency of rank reversals. If all species exhibit parallel shifts in RGR reaction norms to higher irradiance (perhaps caused by a growth-associated increase in respiratory tissue relative to photosynthetic

Table 1. Three approaches evaluating the rank reversals of performance (reaction norm crossovers) at different irradiance levels

	Null model	Test	Assumptions	Pros	Cons
CPI	Performance rank maintenance?	Parametric (logarithmic function)	Chosen non-linear function matches true reaction norm	Ease of biological interpretation Extrapolation and standardization of data Logarithmic function requires measurements at only two irradiances	Questionable null model Difficult to quantify effects of measurement error Potential bias from mis-specification of reaction norm shape
Correlation	Random rank associations	Parametric (normal errors)	Two irradiance treatments selected for comparison are appropriate	Ease of statistical interpretation Incorporates normally distributed intraspecific variation and measurement error Independent of reaction norm shape	Dependent on choice of irradiance treatments used in analysis Allows for only two irradiance treatments
Rank test	(same as above)	Non-parametric	(same as above)	Robust against non-normal variation	(same as above)

leaf area), then median CPI will increase without an increase in the number of rank reversals. Median CPIs are not correlated with either cross-species correlation of RGRs, or fraction of CPI in the 2–10% range for the seven studies examined by SG ($P = 0.47$ and 0.38 , respectively). Their suggestion that frequency of rank reversals increases with study duration is not supported statistically. The observed increase in scatter of CPI, on the other hand, may suggest an increase in measurement errors with experimental duration. Further, a proper test of the relationship between experimental duration and CPI distribution patterns should be done within the same study, rather than using means from studies that differ greatly in many other aspects of experimental design.

A better title for SG's paper would be: 'Why don't young woody seedlings change their RGR ranks between high and low irradiance in short-term studies?', which better represents the physiological hypotheses that they propose: (1) seed mass is the main initial determinant of specific leaf area (SLA); (2) SLA determines RGR initially in both high and low irradiance; (3) SLA becomes independent of seed mass as seedlings grow; (4) SLA remains a main determinant of species differences in RGR in shade, but unit leaf rate (ULR) becomes the main determinant of species differences in RGR in sun; and (5) cross-species correlation between RGR at high and low irradiance is initially high, but weakens with seedling age. We agree these are reasonable hypotheses that deserve more explicit tests, but we would add some qualifiers. Cross-species correlation between SLA and seed mass is not necessarily caused by physical constraints, but may be largely caused by life-history correlates and phylogenetic inertia. High SLA for the first seedling leaf reflects not merely 'seed size-linked differences' (SG), but is better viewed as a physiological strategy to maximize initial RGR.

Sack & Grubb (2001) emphasize that 'very short studies do not adequately represent the processes of long-term natural establishment'. We agree in principle. If some crossovers are undetectable because species differ little in their absolute growth in shade, longer studies may help detect species differences via increased signal-to-noise ratio. However, whether a short- or long-term study is appropriate depends on the research objective. If the main objective is to understand the physiological and morphological reasons why species differ in their survivorship during the first few months after establishment (Kitajima 1994), then a short-term study is adequate. Short-term growth analysis at standardized ontogenetic stages yields meaningful physiological information because the theoretical relationship $RGR = LAR \times ULR$ assumes short harvest intervals (Hunt 1982). Longer-term greenhouse studies also have many potential pitfalls. Longer-term studies may compare a fast-growing species at an advanced ontogenetic stage with a slower-growing species at an early ontogenetic stage. The roots of fast-growing species are also likely to experience pot

limitation earlier than those of slower-growing species. Moreover, long-term greenhouse studies may not adequately predict field performance. Growth and survival in the field are influenced by numerous factors, including herbivory, pathogens, drought, etc. (Kitajima 1996; Dalling & Hubbell 2002; Montgomery & Chazdon 2002). We therefore propose that short- and long-term studies in greenhouse and field, respectively, should be viewed as complementary.

Effects of pretreatment light conditions deserve even more attention than asserted by SG. Typically, plants are raised in moderately high light before transfer to shade. Acclimation from sun to shade often involves abscission of sun-phenotype leaves, which occurs rapidly for species with inherently faster growth rates and tissue turnover rates. These acclimation responses tend to penalize inherently fast-growing species and favour detection of crossovers, especially if the study is relatively short. Unless the intention of the experiment is to examine the responses of gap-established seedlings to canopy closure, use of different pretreatment light conditions should be avoided.

CONCLUSIONS

Determining whether or not species switch performance ranks between contrasting environments is important in developing a mechanistic understanding of species coexistence. Although CPI is a biologically meaningful concept, it uses a null hypothesis that does not address the importance of rank reversals in maintaining coexistence. Furthermore, its application is questionable because of structural and measurement errors unless the shape of the reaction norm can be estimated reliably. Hence the design shortfall of measuring performance in an inadequate range of environments cannot be overcome by the CPI method applied to two-point reaction norms. It is important that experiments aiming to examine patterns of reaction norms should employ appropriate light treatments, and avoid artefacts from pretreatment conditions and ontogenetic heterogeneity.

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Crossovers in seedling relative growth rates between low and high irradiance: analyses and ecological potential (reply to Kitajima & Bolker 2003)

Species differences in relative performance in response to irradiance contribute to the maintenance of forest species diversity (Schnitzer & Carson 2001; Wright 2002). In Sack & Grubb (2001; henceforth ‘SG’), we introduced a crossover analysis, (i) to quantify approximately the crossover-point irradiances (CPIs) – the irradiances at which species-pairs change rank (crossover) in dry mass relative growth rates (RGRs); and (ii) to establish the percentage of species-pairs that crossover between 2 and 10% daylight (understorey *vs* gap irradiance). The reply of Kitajima & Bolker (2003; henceforth ‘KB’) is stimulating but, contrary to what they assert, the available evidence indicates that RGR crossovers are in fact frequent and potentially important. Crossover analysis, carefully applied, allows a resolution of species hierarchies impossible using the decade-old correlation analysis, thus providing higher power for interpretation.

FREQUENCY OF RGR CROSSOVERS

KB state that ‘recent comparative studies ... have failed to detect substantial rank-reversals’ in species RGRs between low and high irradiance. However, the data from the available comparative studies show a wide range in the reported frequency of rank changes (‘crossovers’). For 12 studies (the seven reviewed by SG and five others in Table 1), between 8 and 68% of species-pairs crossed over in RGR between 2 and 10% daylight. Averaging the 12 studies, 27% of species-pairs crossed over from low to high irradiance – a minority, but a substantial one.

Further, as emphasized by SG, longer-running studies are more reliable in showing crossovers that are

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Table 1. Results of five recent short-running studies focusing on growth of woody seedlings at low and high irradiance, similar in design to the seven reviewed by Sack & Grubb (2001). Three of these studies became available after Sack & Grubb (2001) was complete; two have 'low irradiance' higher than in the seven studies initially used. Seedling growth period includes approximate pre-experiment growth time plus experimental duration

Number of species and life form at maturity	Irradiance (% daylight)		Seedling growth period (weeks)	Percentage of species pairs' CPs between 2 and 10% daylight	Species pairs' CPIs (% daylight): 1st quartile/median/3rd quartile	Author/s
	'Understorey'	'Gap' or 'Clearing'				
Nine boreal trees	5	25	9	11	-0.68 -0.19 0.98	Reich <i>et al.</i> (1998)
10 temperate trees	0.6, 1.4, 2.8	7.3	9	13	0.22 0.88 1.67	Walters & Reich (2000)
13 temperate trees and shrubs	3	30	18	8	-0.81 0.12 3.77	Sack (2000)
Six tropical rainforest trees and shrubs‡	5	31	21	33	0.84 2.43 6.41	Pattison <i>et al.</i> (1998)
12 cool temperate rainforest trees	1.2	15	>26*	32	0.04 2.12 6.40	Lusk & Del Pozo (2002)

*Study that considered wild seedlings initially similar in size, grown experimentally 26 weeks.

‡Six of the nine species in this study survived in the low irradiance treatment.

CP, crossover point; CPI, crossover-point irradiance.

likely to occur during establishment in the wild. Young seedlings tend to cross over in RGR at very low irradiances, but as the seedlings grow the CPIs tend to increase, often into the ecologically relevant range of irradiances (SG). To test this prediction, we plotted the seven studies' median CPIs *vs* seedling growth time. The positive correlation was significant. Adding four additional studies for which total seedling growth time is available (Table 1) increases the significance (Pearson's $r = 0.87$, $P = 0.001$; all statistics performed with MINITAB RELEASE 13.32). KB argued that increases in median CPI are not relevant to crossovers – in fact, increasing CPIs *directly represent* the shifting upward of crossovers, and inevitably many crossovers move into the zone of interest, here the arbitrarily chosen range of 2–10% daylight irradiance. Some crossovers are bound to move upward out of this zone. KB questioned whether there was a relationship between percentage crossovers in the range 2–10% irradiance and median CPI. For the set of 12 studies, the percentage crossovers between 2 and 10% daylight irradiance were rank correlated with median CPIs (Spearman's $r = 0.77$, $P = 0.003$). Further, for the 11 studies for which total growth times are available, percentage crossovers between 2 and 10% daylight irradiance were rank-correlated with total growth times (Spearman's $r = 0.62$, $P = 0.04$). As another test, we compared the percentage crossovers between 2 and 10% daylight irradiance for the six studies that ran < 20 weeks with that for the six studies that ran \geq 20 weeks. The shorter-running studies had a median of 12% crossovers, the longer-running studies 32% ($P = 0.04$, Mann–Whitney test). As described by SG, these studies concern diverse species; there is thus a robust tendency for longer-

running studies to reveal more RGR crossovers in the ecologically relevant range of irradiances. We expect studies to show the same trend for given species in given conditions, harvested at different times (cf. Bloor 2001).

As in controlled studies, in the wild species of seedlings frequently cross over in RGRs between understorey and gaps (Kaelke *et al.* 2001; Lusk 2002; Montgomery & Chazdon 2002). Species of saplings in deeply shading forests also frequently cross over between 2 and 10% daylight irradiance, in relative or absolute radial growth rates (31% of species-pairs cross over in Pacala *et al.* 1994; 57% in Lin *et al.* 2002).

We hypothesized that a major reason for more crossovers in longer-running studies is the negative correlation between RGR and seed size, coupled with a tendency for smaller-seeded species to be more light-demanding. This pattern leads to small-seeded light-demanders growing rapidly in both low and high irradiance initially, due to their initially high specific leaf areas (SLAs), but less so in later growth. Other mechanisms are also likely to be partially responsible. KB recognize that our hypotheses are reasonable; they suggest, however, that the linkage between small seed size and high SLA is a 'physiological strategy' to ensure a high RGR early on. The evidence instead suggests that the linkage between small seed size and high SLA is primarily due to allometric scaling and biomechanics. Notably, the linkage occurs even in the absence of selection for high maximum RGR, e.g. in tiny-seeded, shade-tolerant rainforest species (seed mass \ll 1 mg), and in tiny-seeded, short-lived plants of nutrient-poor soils in the Mediterranean and further north in Europe

ECOLOGICAL POTENTIAL OF RGR CROSSOVERS

KB propose that for crossovers to be 'significant', more than 50% crossovers are needed. However, such a 50% null model has no foundation in physiology, and it offers little of value for community ecology. Suppose we have a set of species in which 25% of species pairs cross over in RGR between low and high irradiance. We set up two large grids, one in understorey and one in a clearing. We plant the two grids identically, with a randomly selected pair of species in each grid square. Assuming that RGR determines eventual competitive outcomes (or, at least, that it is an index of effectiveness for establishment), and excluding interactions with other factors, the species distributions in the grids in understorey and clearing will eventually differ by $\approx 25\%$. A proportion this high suggests that shifts in RGR hierarchies across irradiances play a potentially large role in determining sun-shade population differences. Even if only 10% of species-pairs cross over in RGR from low to high irradiance, that feature must contribute to the maintenance of species richness in forest, unless the performance in low or high irradiance is negated in the field by the effects of other resources, herbivores or pathogens.

NEGATIVE CORRELATION OF L AND R – THE UNDERLYING BASIS FOR RGR CROSSOVERS

SG proposed that RGR crossovers arise from species differences in *resource retentiveness* and *resource acquisitiveness*. We showed how the intercepts and slopes of the species' regressions for RGR vs ln-transformed irradiance represent resource retentiveness and resource acquisitiveness in respect of irradiance – we refer to them, respectively, as dark loss rate (L) and light-responsiveness (R). We found a typical negative relationship between species' L and R , a relationship which for given species sets determines the range of irradiances in which species-pair crossovers tend to occur. KB seem to question whether the L vs R relationship arises mechanistically, because intercepts and slopes for a set of regressions (such as L and R for species' regressions of RGR vs ln-transformed irradiance) are in general 'unlikely to be independent of each other' – they are often negatively correlated. However, we note that the exact relationship between intercepts and slopes of a set of regressions is not predetermined; it depends where the regressions cross over each other in relation to the y axis, which in our case is fixed, non-arbitrarily, at irradiance = 0% daylight. For instance, if many regressions cross over at above 0% irradiance, there will arise a negative relationship between L and R ; on the other hand, if many regressions cross over below 0% irradiance, there may be no relationship

between L and R – or even a positive relationship. Thus the direction and the slope of the L vs R relationship for a species set depends on how many regression crossovers occur, and at how high an irradiance, as discussed in SG. In the hypothetical scenario proposed by KB, in which species share a light compensation point, the species' regressions all cross over at that point, above 0% irradiance. As noted above, a negative L vs R relationship should be expected. The commonly found negative L vs R relationship holds as a corollary of the fact that log-linear regressions hold approximately for RGR vs irradiance data sets below saturation irradiance, and that the species' regressions cross over where they do.

SG hypothesized a mechanistic basis for the species differences in RGR responses to irradiances, and thus for the L vs R trade-off and the crossover patterns that follow. KB agree that species differences in RGR responses to irradiance (according to the log-linear model, species differences in L and R) arise from species differences in crucial morphological and physiological traits, and from the plasticity of these traits across irradiances (Walters & Reich 1999; SG). Some traits would especially increase L in magnitude (make L more negative, e.g. high dark respiration rate, short leaf lifespan); others would especially increase R (e.g. high photosynthetic light responsiveness, high specific leaf area). Links between traits of these two kinds, singly or in combination, will contribute to an L vs R trade-off, and thus play a part in driving substantial RGR crossovers in the ecologically relevant range of irradiance.

SUGGESTIONS FOR FUTURE EXPERIMENTS

KB recapitulate some of the advice we gave for controlled studies of seedlings in different irradiances, especially that pretreatment should be considered carefully. In this context, KB assert that pretreatment in high irradiance especially penalises fast-growing plants placed in shade, due to abnormal leaf abscission, and favours detection of crossovers. However, there are no reports in the relevant literature of such abnormal abscission of post-cotyledonary leaves. Pretreatment in high irradiance might indeed favour the detection of crossovers, but not beyond those expected to occur in nature. Because the plants grow faster, they might escape more quickly from the period in which seed-size differences drive RGR hierarchies at both low and high irradiances – and thus show crossovers sooner than would otherwise develop in later establishment.

The advice of KB that differs most radically from ours concerns the suggested study length. KB encourage more short-term controlled experiments, considering longer-term controlled studies subject to such 'potential pitfalls' as the effects of ontogeny and pot-limitation. However, these effects in pot experiments are two of those that require further study for science

to progress. Both effects are potentially relevant in the field – changes in form occur naturally in the field (Kohyama & Hotta 1990; Sack *et al.* 2002). Also, competition may increasingly limit soil resource availability as seedlings establish in the forest, and studies are needed to determine whether this effect may parallel pot-limitation. Thus, longer-running controlled and field-based studies are needed to increase our understanding of RGR rank hierarchies under different irradiances, in longer-term establishment.

CROSSOVER ANALYSIS: LINE-FITTING AND CPI DETERMINATION

Crossover analysis relies on solving for the intersections of regressed lines, a standard statistical approach (Zar 1999) with current empirical applications in chemistry, economics and engineering (Kupka & Meloun 2001; Ladany & David 2001). Despite its usefulness this analysis, like any other, should not be applied as a black box. By taking due care and investigating and dealing with any problems that arise, such ‘drawbacks’ as those claimed by KB are resolvable. First, KB assert that crossover analysis does not apply the ‘50% null model’ described above. One could certainly apply that model by simply testing whether the determined percentage crossovers differ from 50%; however, this null model allows only low interpretive power, as discussed above. Second, KB state that crossover analysis might be ‘biased by structural error’ when the ‘true’ shape of the RGR light response is unknown. As part of their test simulation, KB generate artificial Michaelis–Menten (MM)-type data sets and artificial log-linear (LL) type data sets. KB then correctly show that CPIs differ when LL lines are applied to the MM-type data sets, and when MM lines are applied to the LL-type data sets. We concede that fitting such different types of line to data sets can produce different crossover patterns; the LL and MM curves fit the data differently because they are of distinct shapes, especially toward the upper end of the range of irradiances. However, these KB simulations do not replicate the careful use of crossover analysis as we described it. We advised fitting lines that empirically suit the data well – we suggested using LL for data sets that include RGRs below saturation irradiance, and MM when more data are available, including RGRs above saturation irradiance. In the other part of their simulation, KB apply the LL and MM lines to the original data of Poorter (1999) for RGRs ranging up to 25% daylight. These data sets are saturation responses, and are thus typically well approximated by the MM but not the LL (for eight out of 15 species RGR plateaus or decreases between 12 and 25% daylight); using the LL leads to bad fits. In SG we used the LL for data up to only 12% daylight in Poorter (1999); in this range the LL plots fit the data well. Notably, when KB used the MM plot for the MM-like data (up to 25% daylight) of Poorter (1999), they found 23% crossovers, close to 26%, the

value we found using the LL plot for data up to 12% daylight (SG). Thus any ambiguity about crossover patterns can be minimized by fitting lines to the RGR response data that suit the shape of the plotted data. If there is a question about whether a non-linear function approximates the obvious shape of the data, transformed residuals can be used to test its appropriateness (Seber & Wild 1989).

The third ‘drawback’ claimed for crossover analysis is that it is sensitive to measurement error. Measurement error is a potential problem in all analyses. KB show that adding noise can aggravate the problems created by fitting lines that do not match the data. In the KB simulations, however, the added error is excessive – we calculate for the RGR data of Poorter (1999) that the measurement error which, at very worst, one strives to achieve, $\pm 5\%$ error, in fact falls below 1 on the ‘noise amplitude’ axes for KB’s Fig. 1(a,b). Despite the excessive noise added, the CPI findings were remarkably robust in the one case in KB’s simulation in which lines were well fitted, i.e. when the MM lines were fitted to MM data (their Fig. 1a). Using confidence intervals for the CPIs (Kastenbaum 1959; Robison 1964; Carter *et al.* 1991) will ensure further robustness to measurement error. We note that not every data set may be amenable to determining narrow CPI confidence intervals; data for numerous irradiances may be required, especially before saturation or inhibition. Properties of the crossover analysis are summarized in Table 2.

PARAMETRIC CORRELATION AND RANK CORRELATION

KB discuss two other analyses, but these are not alternatives to crossover analysis. These analyses, as applied for nearly a decade, involve simply testing for parametric correlation or rank correlation of RGRs at low and high irradiances. The parametric correlation coefficient is most problematic: it conflates the frequency of crossovers with the intensity of given crossovers. Also, the parametric correlation cannot account for intraspecific variability of RGR (i.e. in the plot of RGR at high *vs* at low irradiance, the error bars around each species’ point). The rank-correlation between RGRs at high and low irradiance can at least take account of ties, which often occur among species’ RGRs at low or high irradiance (Sokal & Rohlf 1995). A positive correlation between species’ RGRs at low and high irradiance simply means that > 50% of species-pairs do not cross over; 49% might. Properties of the correlation analyses are summarized in Table 2.

SUMMARY OF OUTSTANDING DEBATE REGARDING IRRADIANCE AND SPECIES RICHNESS

We agree with KB that a trade-off between RGR at high irradiance and survival at low irradiance is a

Table 2. Properties of the crossover and correlation analyses; a revised version of the table of Kitajima & Bolker (2003) (KB), including additions for consistency. Analysis of relative growth rates (RGRs) is discussed, but the same analysis could be made of other performance variables such as survival rates. Note revised column headings: the contents of KB's 'Test' column are included in our 'Assumptions'; the 'Pros' column has become 'Purpose'; and 'Cons' has become 'Issues requiring care'. Measurement error is not included as an issue requiring care because it should be minimized in all experimental work, and the effects of random error are to some degree controlled via statistical analyses in all three methods. Points originally set out by KB are asterisked

Analysis	Purpose	Null model	Assumptions	Issues requiring care
Crossover and CPI analysis of species' RGR responses	<p>Estimation of:</p> <p>(a) Approximate irradiance at which crossovers in RGR occur for each species-pair, for plants of a given size, the 'crossover point irradiance' (CPI)</p> <p>(b) Species' RGRs at any irradiance in the measured range (using the parameters of RGR response functions)</p> <p>(c) RGR rank hierarchies at any irradiance within the measured range</p> <p>(d) Percentage crossovers for a set of species in any range of irradiance (arbitrarily set as 2–10% daylight in Sack & Grubb 2001)</p> <p>Investigation of underlying physiological and morphological bases for given crossovers (using the parameters of RGR response functions)</p>	<p>None assumed <i>a priori</i> (crossover analysis is not a statistical test in itself). Experimenter may choose one for interpretive purposes. We recommend considering > 5% crossovers as indicating that crossovers are potentially of ecological significance</p>	<p>As for typical linear and non-linear regression (Sokal & Rohlf 1995; Seber & Wild 1989)</p>	<p>Choosing a function to empirically fit the data well</p> <p>Presenting CPIs with narrow confidence intervals may require data for RGRs at many irradiances</p> <p>Allows only a rough approximation when RGRs available for only two irradiance levels</p>
Parametric correlation of species RGRs at low and high irradiance	<p>Tests for:</p> <p>(a) Association between RGRs at different irradiances</p> <p>(b) Whether percentage crossover is significantly > 50 or < 50%*</p>	<p>No association between RGR at the selected low and high irradiances 50% species-pairs crossover; 50% species-pairs retain ranks*</p>	<p>Assumptions of parametric correlation, including bivariate normality* (Sokal & Rohlf 1995)</p> <p>Two irradiance treatments selected for comparison are appropriate*</p>	<p>Considers RGRs at only two irradiance treatments. Dependent on choice of irradiance treatments used in analysis*</p> <p>Conflates frequency of crossovers with intensity of given crossovers</p> <p>Cannot include information of intraspecific variability in RGRs, i.e. RGR error bars</p> <p>Cannot take account of species 'ties' in RGR at low or high irradiance</p>
Rank correlation of species RGRs at low and high irradiance	<p>As for parametric correlation*</p>	<p>As for parametric correlation*</p>	<p>As for parametric correlation above, without assumption of bivariate normality*</p>	<p>As for parametric correlation above, but Kendall's test of rank concordance can be used to compare data for many irradiances (Sokal & Rohlf 1995). Ties are easily accounted for</p>

potentially prevalent mechanism for species coexistence (Kitajima 1994; Kitajima 1996; KB). However, it is too early to exclude other mechanisms, of which there are many that may function to maintain diversity (Grubb 1977). Species differences in survival rates at different irradiances are clearly important, caused by plant physiology and especially by interactions with pathogens and herbivores. Crossovers in RGR across irradiances also have major potential, given the high frequency of crossovers reported. Further, more studies are needed of the effects of irradiance combined with variation in the supply of other resources, and with the impacts of pathogens and herbivores (e.g. Howe 1990; Sack & Grubb 2002). It is important to keep this discussion in perspective. In most studies so far, species were chosen to span the full range of light demand. However, in species-rich forests most species are strongly shade-tolerant. For such groups, coexistence may depend more on differences in other properties than on irradiance responses (whether in RGR or survival rate), including, for example, annual variation in fruiting and dispersal (Grubb 1977).

It is worth asking whether variation in irradiance could promote species richness *only* through a trade-off between RGR at high irradiance and survival rate at low irradiance. KB hypothesize that some woody plants are 'fast growers' in any irradiance, and others 'hardy survivors'. In an extreme view of this 'grow vs live' trade-off, crossovers in performance across irradiances would not be a mechanism for irradiance to contribute to the maintenance of species richness. If such a 'grow vs live' trade-off does indeed shift dominance across irradiances, there must then be major differences across irradiances in the relative *importances* of RGR vs survival rate in determining dominance. For instance, survival rate should preferentially drive dominance in deeper shade, and RGR preferentially in higher irradiance. There is no experimental support for this hypothesis. Some have proposed that in the understorey, species differences among RGRs might be negligible, but even small RGR advantages can have dramatic consequences over several years. Further, rankings in RGR and survival rate at given irradiances are sometimes independent, and sometimes run in parallel (Walters & Reich 1996; Walters & Reich 2000; Lin *et al.* 2002; Lusk & Del Pozo 2002; Montgomery & Chazdon 2002; Wyckoff & Clark 2002; Bloor 2003). At a given irradiance, the two combined probably determine success (Kobe 1999).

As more data become available, crossover patterns can be investigated for RGR, for survival, and for their combined effects in plants of different sizes. It is clearly important to go beyond the simple correlation of performance at two irradiances. A thought experiment illustrates the resolution possible in principle through crossover analysis. Suppose we analyse RGR crossovers and determine the CPI for species A and B. It is, by its definition, the level at which to set a light 'dimmer switch' to equalize the species' RGRs at given sizes. If

one raises the dimmer switch above the CPI, both species increase their RGR, but of the two species, A grows fastest. If one lowers the switch below the CPI, both species slow their growth – but now species B grows fastest. CPIs for survival rates have similar implications. Changes to the dimmer switch for large sets of species could thus profoundly affect interspecies performance hierarchies. In a forest, irradiance varies hugely in space and time, as do soil resources and biotic factors. Given such variation, crossovers have a strong potential to drive patterns of species dynamics and coexistence.

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