

Determinants of whole-plant light requirements in Bornean rain forest tree saplings

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Abstract

1. Shade tolerance, defined as the ability to survive and grow under low light, varies markedly among tree species. However, the role of low-light growth responses in determining shade tolerance is unclear, as are the effects of non-light resources such as soil nutrients.

2. A conceptually simple field measure of shade tolerance is the whole-plant light compensation point (WPLCP), evaluated as the x -intercept of the relationship between growth and incident light integrated over a long time interval. Here we compare WPLCP for growth and survivorship of saplings of Bornean tree species differing in shade tolerance, and evaluate the importance of various physiological and morphological traits in predicting WPLCP. We also examine both phenotypic and evolved differences in WPLCP between tree saplings growing on two distinct soil types at Sepilok Forest Reserve, Sabah, Malaysia.

3. Growth-based estimates of WPLCP showed essentially a 1 : 1 correspondence to threshold light levels for survivorship. At higher light, more light-demanding species showed higher growth, resulting in a steeper slope of the relationship between relative growth rate (RGR) and light availability than in more shade-tolerant species. This resulted in significant crossovers in the RGR–light relationship among species.

4. Dark respiration (R_d) was the single best predictor of WPLCP; other leaf traits such as leaf nitrogen and photosynthetic capacity were correlated with, but excluded as predictors of, WPLCP in multiple regression analyses.

5. Although soil type had no consistent phenotypic effect on WPLCP, evolved responses among species were pronounced: species associated with the nutrient-poor, drought-prone, sandstone-derived soils had higher WPLCP values than alluvial soil specialists in phylogenetically controlled comparisons.

6. Our results indicate that minimum light levels for growth do not diverge from those for survivorship, and do not support the view that low-light survivorship solely determines shade tolerance. Our analyses also suggest that R_d is the strongest determinant of whole-plant light requirements in tropical tree saplings, and thus may be an easily measured surrogate of WPLCP and shade tolerance.

7. Prediction of tree species resource requirements is crucial for understanding forest dynamics and promoting ecology-based forest management and restoration, particularly in diverse tropical forests where data on the resource requirements of most species are not available. Easily measured surrogates of resource requirements (e.g. R_d as a predictor of shade tolerance) will contribute to this goal, as will an improved understanding of the interactive effects of multiple resources on tree performance.

Key-words: edaphic specialization, foliar dark respiration, habitat association, leaf traits, rank reversals, shade tolerance, trade-offs, tropical rain forest, whole-plant light compensation point

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Introduction

Wide variation exists in the light requirements of tropical trees. While commonly presented as the climax vs. pioneer dichotomy (Swaine & Whitmore 1988), the light requirements of species form a continuum between these two endpoints (e.g. King 1994; Poorter 1999; Valladares *et al.* 2000). Juvenile persistence and growth in the understorey is of central importance to forest structure and succession, impacting upon succession in forest gaps as well as under closed canopy (Connell 1989). The nature of species differences along the light response gradient, the mechanistic basis for such differences, and the impact of other resources on patterns of light response are thus all critical issues from both ecological and management perspectives.

The concept of shade tolerance generally encompasses both the ability to survive and to grow in light-limited environments. However, a number of studies have suggested that light-demanding species have greater growth potential than shade-tolerant species, regardless of the light environment, and that low-light survivorship is the key determinant of shade tolerance (Kitajima 1994; Kobe 1999; Poorter 1999; Walters & Reich 2000). Such a pattern is consistent with the idea that shade tolerance is achieved primarily through conservative patterns of carbohydrate storage leading to higher survival, which better enables saplings of shade-tolerant species to endure periods of negative carbon balance (e.g. Kobe 1997; Canham *et al.* 1999). A critique of this perspective derives from observations that continued carbon gain does require some level of growth as leaves and physiologically active roots have finite life spans and must be replaced (Chabot & Hicks 1982; Eissenstat & Yanai 2002). Although storage may buffer seedlings in the short term, particularly during periods of extreme stress (e.g. Myers & Kitajima 2007), negative carbon balance is expected to result in eventual mortality. Along these lines, many 'mechanistic' models of forest dynamics assume that tree growth is a main determinant of survivorship (e.g. Pacala *et al.* 1993). A key test of these alternatives is to explicitly examine minimum light requirements for growth and survivorship. If shade tolerance is based on low-light survivorship alone, shade-tolerant species should have lower light requirements for survival than for net growth.

A second central prediction of the hypothesis that light-demanding species show consistently higher growth across light levels is that there should be no occurrence of crossovers in the relationship between relative growth rate (RGR) and light availability among species (i.e. species ranks are maintained across light environments). Several previous studies suggest that the relationship between RGR and light availability in tropical tree seedlings is highly variable, with shade-tolerant species generally exhibiting more shallow responses to increased light availability than light-demanding species (Moad 1992; King 1994; Montgomery & Chazdon 2002; Makana & Thomas 2005). Assuming a linear relation-

ship between light availability and RGR at low to moderate light availability, differences in the slope of this relationship necessitate greater net growth at low light in more shade-tolerant species and a reversal in ranks with increasing light availability (Sack & Grubb 2001). However, there have been relatively few explicit tests for such crossovers, and there is continuing debate as to their frequency and importance on both conceptual and statistical grounds (Sack & Grubb 2001; Kitajima & Bolker 2003; Sack & Grubb 2003; Baraloto, Goldberg & Bonal 2005).

A conceptually simple measure of the light requirements of species takes advantage of the strong relationships between RGR and individual sapling light environment (King 1991; Moad 1992; Makana & Thomas 2005). The light level at which net growth is zero should in theory correspond to the point at which carbon gain balances metabolic costs of the plant in the long term, the 'whole-plant light compensation point' (WPLCP). A plant occurring at or below this light level is predicted to be incapable of long-term survival, although mortality may be delayed if patterns of carbohydrate utilization or storage are conservative. This growth-based measure of WPLCP integrates a number of physiological and morphological traits as well as ecological processes such as damage by herbivores, pathogens and stochastic events (e.g. damage from falling debris) that contribute to whole-plant carbon balance. Estimates of WPLCP have also previously been made on the basis of foliar photosynthetic and respiration measurements, making assumptions regarding respiratory costs of night-time leaf respiration, leaf construction costs, and allocation to stem and root tissue (Givnish 1988; Givnish, Montgomery & Goldstein 2004). However, a growth-based method of WPLCP determination should be preferable to physiology-derived measures due to biases associated with light acclimation, since gas-exchange parameters used to estimate WPLCP must generally be made under light conditions above the WPLCP itself. In particular, increases in foliar respiration and related parameters with increasing light (Boardman 1977; Strauss-DeBenedetti & Bazzaz 1991) are likely to result in an overestimation of WPLCP. Another advantage of the growth-based measure of WPLCP is that it is independent of physiological measurements, and thus suited to comparative analyses examining physiological and morphological traits as correlates of WPLCP.

An additional unresolved issue surrounding whole-plant light requirements is potential variation in WPLCP in response to soil resources. Such variation might be expected for both evolved responses of species and phenotypically plastic responses of individual plants. Explicit predictions can be made regarding the anticipated direction of such shifts under different scenarios of resource variation. For example, species occurring on drought-prone soils may commonly achieve greater water-use efficiency (WUE) at a cost of higher dark respiration rates at a given photosynthetic rate (Wright, Reich & Westoby 2001; Baltzer *et al.* 2005). The expected

result is an increase in WPLCP in species adapted to drought-prone soils, if dark respiration is an important determinant of light requirements at the whole-plant level. For species occurring on dry or nutrient-poor sites, root costs associated with uptake of the limiting resource(s) might similarly be predicted to result in increased WPLCP (Givnish 1984, 1988). Alternatively, species occurring on nutrient-poor soils might be predicted to have lower WPLCP due to reduced tissue nitrogen concentrations, since tissue nitrogen is closely related to tissue respiratory costs (Lambers *et al.* 1983; Ryan 1995). Phenotypic responses might be expected to result in a similar trade-off expressed at the level of individuals of a given species growing on different soil types.

To address these issues we quantified relationships describing net growth (and survivorship, where possible) as a function of incident light for saplings of 20 species of trees spanning a wide range of presumptive shade-tolerance in a Bornean rain forest on two distinct soil types. We focus on saplings, as differences in shade tolerance early in tree ontogeny are considered especially important as a determinant of tropical forest regeneration dynamics. Growth, physiological and morphological data were collected for edaphic specialist species pairs and generalist species to quantify WPLCP and identify various morphological and physiological traits relating to WPLCP. Study goals were: (i) to determine light levels required for survival and net growth for species varying in shade-tolerance; (ii) to test for rank reversals in growth among species across the light availability gradient; (iii) to assess the relationships between WPLCP, various physiological and morphological traits, and assess which traits contribute most to WPLCP; and (iv) to examine differences in WPLCP between species associated with two soil types differing in soil resource levels, and phenotypic responses of WPLCP to soil type.

Methods

STUDY SITE

Sepilok Forest Reserve (SFR) (5°10' N, 117°56' E) is a 4294-ha gazetted Virgin Forest Reserve managed by the Sabah Forestry Department and located in Sabah, Malaysian Borneo. The topography of SFR consists of sandstone ridges (30–90 m a.s.l.) separated by alluvial flats and gently undulating sandstone or mudstone hills. This results in two distinct floristic associations: sandstone hill and lowland dipterocarp forests (Fox 1973). Parent material and drainage varies between these soil types, resulting in differences in soil nutrient and water availability (see site description in Baltzer *et al.* 2005). The alluvial soil type has both higher nutrient availability and gravimetric water content than the sandstone soil type (Dent 2004; Baltzer *et al.* 2005). As a result of these resource gradients, forest structure differs with the alluvial forests having taller canopy and emergent trees, as well as lower stem density, but larger

average tree diameters; consequently the sandstone understorey receives greater direct radiation than that of the alluvial forest (Baltzer *et al.* 2005). This pattern is commonly observed in the region (e.g. Palmiotto *et al.* 2004) and may contribute to high Bornean tree species diversity (Potts *et al.* 2002).

STUDY SPECIES

Congeneric or confamilial species pairs were selected consisting of one species specialized to the sandstone soil type and the other to the alluvium with six pairs forming phylogenetically independent contrasts (i.e. each species pair shares a common ancestor that is different from that of any other pair; Harvey & Pagel 1991). Four generalists and other common unpaired specialists were also selected to obtain survey data on a wider range of species (Table 1). All taxa used in the study were common, distinctive species classified as edaphic generalists or edaphic specialists. This categorization was qualitatively based upon observation and numerous transects walked on each soil type searching for 'wrongly placed' individuals (specialists) or species that were fairly common on both sandstone and alluvial soil types (generalists). Our classifications corresponded closely with large-plot survey data available for the reserve (Nilus 2004) and corresponding analyses of habitat associations (R. Nilus, unpublished data).

Individuals were sampled along a wide light gradient provided by large gaps (400–600 m²; see reciprocal transplant experiment description in Baltzer *et al.* 2005; Fig. S1, Table S1). Saplings were sampled in all directions around each gap and 10–20 m into the forest understorey, thus resulting in a diffuse sampling area of *c.* 2000 m² at each focal point. As a consequence, saplings at any given 'site' often had no immediate study neighbours and experienced a broad variation in both above-ground and below-ground resource availability. The gap areas, where the highest light individuals were sampled, were maintained throughout the study by hand weeding and pruning branches growing into the plots, thereby preventing major changes in the light environment experienced by higher light individuals that would naturally occur through gap closure. We were thus able to obtain a wide range of light environments for all species regardless of successional status. The gaps were created one-and-a-half years prior to the initiation of this study through the augmentation of naturally occurring gaps; therefore study saplings had sufficient time to acclimate to their new light environment prior to measurement. Sapling selection was restricted to seemingly healthy individuals with unbroken stems and an initial sapling height of 0.5–1.5 m. Between 15 and 60 individuals of each species were selected and each individual uniquely tagged and measured for a number of morphological parameters including sapling height (along the stem from base to apical bud), basal diameter, leaf demography and leaf overlap (as a proxy for leaf display efficiency). For species occurring on both soil types at least 15 individuals

Table 1. Study species with families, authorities and habitat preferences (habitat). Asterisks following habitat type indicate pioneer species. Two habitats were examined in the present study: sandstone-derived ridges having both lower water and nutrient availability (sandstone) and moist, nutrient-rich alluvial valleys (alluvial). Species showing no preference with respect to habitat were classified as generalists. A representative voucher specimen for each species is indicated (numbers are the herbarium sheet numbers at the Forest Research Center, Sepilok)

Family	Species	Habitat	Voucher no.
Dipterocarpaceae	<i>Dipterocarpus grandiflorus</i> (Blco) Blco. (17)	Sandstone	125511
	<i>Dipterocarpus applanatus</i> V. Slooten (10)	Alluvial	141410
Dipterocarpaceae	<i>Shorea multiflora</i> (Burck) Sym. (9)	Sandstone	97997
	<i>Parashorea tomentella</i> (Sym.) Meijer (7)	Alluvial	136262
Dipterocarpaceae	<i>Hopea beccariana</i> Burck (6)	Sandstone	LSP 1144
	<i>Hopea nervosa</i> King (4)	Alluvial	–
Ebenaceae	<i>Diospyros euphlebia</i> Merr. (11)	Alluvial	136152
	<i>Diospyros fusiformis</i> Kosterm (16)	Sandstone	141525
Euphorbiaceae	<i>Mallotus griffithianus</i> (Muell. Arg) Hook (18)	Sandstone	99722
	<i>Mallotus miquelianus</i> (Scheff.) Boerl. (2)	Alluvial	97415
Fabaceae	<i>Sindora</i> cf. <i>coriacea</i> (3)	Sandstone	–
	<i>Cynometra inaequifolia</i> (5)	Alluvial	JBS 381
Dipterocarpaceae	<i>Dipterocarpus caudiferus</i> Merr. (13)	Generalist	102511
Euphorbiaceae	<i>Macaranga hypoleuca</i> (Rchb. F. & Zoll.) Muell. Arg. (19)	Generalist*	91284
Moraceae	<i>Ficus megaleia</i> Corner (15)	Generalist*	1704
Myristicaceae	<i>Knema laurina</i> (Blume) Warb. (8)	Generalist	102512
Euphorbiaceae	<i>Homolanthus populneus</i> (Giesl.) Pax. (20)	Alluvial*	129402
Lauraceae	<i>Eusideroxylon zwageri</i> Teijsm. Et. Binn. (1)	Alluvial	69481
Malvaceae	<i>Scaphium affine</i> Pierre (14)	Sandstone	119196
Simaroubaceae	<i>Eurycoma longifolia</i> (Jack.) (12)	Sandstone	87593

Numbers in parentheses following authorities correspond to those in Fig. 2.

were selected for sandstone and alluvial populations. Growth parameters and leaf turnover were monitored every two months from September 2001 to March 2002, and again in September and November 2002. Growth and leaf turnover were calculated for the entire study period (September 2001 to November 2002). To monitor leaf production, the three most recently expanded leaves on each branch were uniquely labelled with non-toxic permanent marker at the base of the leaf near the petiole. This was repeated at each subsequent sampling period. Aside from one extremely light-demanding species (*Homolanthus populneus*), there was never an instance when at least one of the three marked leaves could not be found on each branch. In the case of *H. populneus* leaf life span was recorded as less than 2 months and the conservative estimate of 2 months used in subsequent analyses. No apparent leaf damage resulted from the leaf labels. At each census, the number of leaves remaining from the previous census was tallied, as was the number of new leaves produced. Leaf longevity was estimated for individual saplings using a demographic approach (Jow *et al.* 1980) as follows:

$$L = \left(\frac{N_{t_2}}{d} + \frac{N_{t_1} - N_{t_2}}{b} \right) \times (t_2 - t_1)$$

Where L is expected leaf life span, b is overall leaf production between census dates, d is number of leaves dropped between census dates, N_{t_1} represents initial number of leaves present and N_{t_2} represents number of leaves present at t_1 plus number of leaves produced between t_1 and t_2 .

Basal diameter² × height was used as a non-destructive proxy for whole-plant biomass as the two have been shown to be highly correlated (e.g. Kohyama & Hotta 1990). Above-ground relative growth rate (RGR_{d^2h}) was calculated as:

$$RGR_{d^2h} = \frac{\ln(d_2^2 h_2) - \ln(d_1^2 h_1)}{(t_2 - t_1)}$$

Where d_1 and d_2 are basal diameter and h_1 and h_2 are height at the beginning (t_1) and end (t_2) of the measurement period, respectively. Height growth alone can be highly variable as a consequence of leader loss. The use of both diameter and height parameters in calculating growth provides a more robust growth rate measure. Since d^2h is linearly related to biomass (Kohyama 1991), RGR_{d^2h} will closely approximate RGR_{biomass} . Mean number of branches was low and did not differ systematically based upon soil type ($F_{1,620} = 2.05$, $P = 0.1531$; alluvial mean: 4.13 ± 0.58 ; sandstone mean: 5.29 ± 0.57), suggesting that allocation changes in relation to soil are unlikely to bias RGR_{d^2h} as a measure of whole-tree growth.

For each sapling, the length (L ; acumen to lamina base) and width (W ; widest point perpendicular to the midrib) of every leaf (or leaflet in compound leaved species) was measured to the nearest millimetre. The relationship between leaf length × width and leaf area ($LA = L \times W \times 0.697$) has been shown to be very strong (explaining approximately 99.6% of variation in leaf area) and independent of species for both African and Malaysian tree species (Thomas & Ickes 1995;

Makana & Thomas 2005). We therefore used this relationship to quantify leaf area based upon measured lengths and widths. Sapling leaf area was calculated as the sum of all measured leaf areas. Leaf herbivory was minimal and small amounts of damage were not incorporated into calculated leaf areas. However, in cases where a substantial proportion of the leaf was missing, due to herbivory or other damage, leaf area measures only included the remaining portion of the leaf.

We used leaf overlap as a surrogate for leaf display efficiency as it was necessary to develop a rapid method for measurement of leaf display efficiency in the field. Leaf overlap was estimated from photographs taken directly above the sapling crown in combination with leaf counts taken at the time of the photographs. Leaves in each photograph that were > 50% visible were counted (both leaf overlap and steep leaf angles reduced leaf exposure) and calculated as a proportion of the total number to determine leaf overlap. The relationship between this measure of leaf overlap and leaf display efficiency was determined by taking photographs above 20 glasshouse-grown saplings of species ranging widely in leaf overlap. The photographs were taken from a balcony 5 m above the saplings to avoid projection problems. Canopy leaf surface was measured from these photographs and scaled with an object of known dimensions within the photograph. Leaf area was determined and leaf display efficiency calculated as canopy area divided by total leaf area. Photographs were also taken directly above these saplings and leaf overlap determined using identical methods to those employed in the field. Leaf overlap was a good predictor of leaf display efficiency ($r^2 = 0.85$, $P < 0.0001$) in this subsample; therefore we employed the direct measures of leaf overlap made on study saplings in subsequent analyses. Additionally, we used the ratio of total leaf area to d^2h (where d is basal diameter and h is sapling height) as a surrogate for leaf area ratio (LAR*).

CHARACTERIZATION OF SAPLING LIGHT ENVIRONMENT

Individual sapling light environment was measured using hemispherical photographs taken directly above the crown of each sapling using a Nikon Coolpix 900 and FC-E8 fisheye converter (Nikon, Tokyo, Japan). Photographs were analysed using the program Winscanopy 2001 (Regent Instruments Inc., Québec, Canada), which predicts total, direct and diffuse radiation both above and below the canopy. Above-canopy direct radiation is a function of the latitude and longitude and the defined growing season while above-canopy diffuse radiation is estimated to be 15% of the direct radiation, or 13% of the total above-canopy radiation. This corresponds to model estimates of the diffuse fraction under clear conditions (Roderick 1999; Wang *et al.* 2006). Cloud cover and air pollution increase the diffuse fraction (Roderick *et al.* 2001), and therefore the value of 15% is a simplification of a complex, dynamic

process. The proportional changes in the direct and diffuse components as a consequence of canopy cover will be the same regardless of the diffuse fraction employed, assuming above canopy radiation is spatially constant within our study area; as study plots were within a relatively small area (*c.* 1 km²; Fig. S1) this assumption should be reasonable. Total above-canopy radiation corresponded very closely with quantum sensor measurements made in full sunlight using Hobo Weather Stations (Onset Instruments, Bourne, MA, USA) (data not shown).

SURVEY SPECIES GAS-EXCHANGE

Using a LI-6400 gas-exchange system (Licor, Inc., Lincoln, NE, USA), gas-exchange measurements were made on recent, fully expanded leaves developed in their ambient light environment. All measurements were made before noon with cuvette conditions maintained at 350 p.p.m. CO₂, 60–80% relative humidity and 25–30 °C leaf temperature. Gas-exchange measurements were made at 13 light levels: 0, 5, 10, 15, 20, 25, 50, 100, 300, 500, 1000, 1500 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Gas-exchange was not measured until the leaf was fully induced at that irradiance; often a single light response curve took at least 1 h to complete due to slow induction. Twelve saplings per species were selected from the extreme ends of the light gradient for physiological measurements (six high light and six low light). For generalist species, 12 saplings were sampled from sandstone and 12 saplings from alluvial populations. Measurements were made in October and November 2002 at the beginning of a wet spell.

Gas-exchange leaves were harvested, measured for area, dried at 60 °C and weighed. Leaf tissue, excluding primary and secondary veins, was finely ground using mortar and pestle. Leaf samples were digested using the sulphuric acid-hydrogen peroxide digest procedure. The digest was analysed for total nitrogen using the phenol blue (Berthlot) method in a continuous-flow analyser (Technicon Auto-analyser II, Technicon Instrument Corporation, Tarrytown, NY) (Schuman *et al.* 1973). Analyses were conducted in the Soil Science Laboratory, Faculty of Forestry, University of Toronto, ON. NBS standards (citrus leaf #1572) and duplicate samples were used to ensure accuracy of measurements. Stable carbon isotope ratios ($\delta^{13}\text{C}$) were measured for leaf samples of the three highest light replicates of closely related species pairs and generalists (individuals from both soil types) to estimate integrated WUE. Stomatal limitation increases the proportional uptake of the heavier carbon isotope (^{13}C) due to reduced discrimination between isotopes (Farquhar *et al.* 1982). Consequently, isotopic signatures indicate WUE integrated over the leaf lifetime (Farquhar *et al.* 1989). Analyses were performed at the Stable Isotope Facility, UC Davis, CA, USA, using a Hydra 20–20 stable isotope analyser combined with an ANCA_GSL (PDZ Europa Ltd, Cheshire, UK).

STATISTICAL ANALYSES

Estimates of WPLCP were made using either model I regression (for species incurring no mortality during the study) using PROC REG (SAS v. 8.1, SAS Institute Inc., Cary, NC) or censored regression (Schmid *et al.* 1994) using PROC LIFEREG (SAS v. 8.1) with relative growth rate (RGR) the dependent variable and individual sapling light environment the predictor variable. Assumptions of normally distributed, equal error variances were met for all growth–light relationships. Relationships between total, diffuse or direct radiation and sapling RGR were quantified. For estimation of WPLCP the relationship between total photosynthetic photon flux density (PPFD) and sapling RGR was used. The light environment corresponding to zero net growth was used as the WPLCP and corresponding standard errors calculated from the range of light environments in which zero growth was observed. Survivorship thresholds were determined using logistic regression (PROC LOGISTIC, SAS v. 8.1) with survivorship the dependent variable and individual sapling light environment (total PPFD) the predictor. The survivorship thresholds were calculated as the inflection point for the following function relating the probability of survivorship to log PPFD (Thomas 1996):

$$P = \frac{e^{a+b \ln S}}{1 + e^{a+b \ln S}}$$

where P is the probability of survivorship, $\ln S$ is natural logarithm of total PPFD, e is the base of natural logarithms, and a and b are constants. The inclusion of a logarithmic transformation of S means that as light levels approach zero, probability of survival also approaches zero. For this analysis two groups were examined. The first included only those species with sufficient dead individuals to run the analysis (five or more dead individuals). The second group included all species with five or more saplings that died or showed negative growth over the course of the year assuming that negative growth ultimately leads to death and that both resulted from light limitation.

The response of photosynthetic assimilation to photon flux density (PFDD) was fitted to a non-rectangular hyperbola (PROC NLIN, SAS v. 8.1) (Leverenz 1988; Ogren & Evans 1993):

$$P = R_d + \frac{\phi I + A_{\max} - \sqrt{(\phi I + A_{\max})^2 - 4\Theta\phi I A_{\max}}}{2\Theta}$$

where P is photosynthetic rate, R_d is leaf-level dark respiration, ϕ is apparent quantum yield of photosynthesis, I is the photosynthetic photon flux density, A_{\max} is the asymptotic light saturated photosynthetic rate and Θ is the convexity of the curve. Leaf-level light compensation point (LLCP) was estimated as the irradiance at which $P = 0$. The minimum LLCP was calculated as the average of the three lowest LLCP

values (these corresponded to the lowest low light environments). The remainder of measured physiological trait values used in the analyses were from highest light individuals of each species in order to capture potential physiological rates. Maximum stomatal conductance to water (g_s) corresponding to species high-light A_{\max} values was used to characterize stomatal response. Instantaneous WUE was calculated as A_{\max} in $\mu\text{mol m}^{-2} \text{s}^{-1}$ divided by transpiration in $\text{mol m}^{-2} \text{s}^{-1}$ thus providing a value indicating μmoles of carbon gained per mole of water lost. Photosynthetic nitrogen-use efficiency (PNUE) was calculated as the ratio of A_{\max} in $\mu\text{mol m}^{-2} \text{s}^{-1}$ to nitrogen content in g m^{-2} thus quantifying μmoles of carbon gained per g of N investment.

Bivariate relationships were examined between the following traits: WPLCP, minimum LLCP, area- and mass-based dark respiration (R_{area} , R_{mass}) and photosynthetic (A_{area} , A_{mass}) rates, apparent quantum efficiency (ϕ), area- and mass-based leaf nitrogen (N_{area} , %N), PNUE, g_s , WUE, $\delta^{13}\text{C}$, leaf overlap (LO), leaf life span (LL), leaf mass per area (LMA), and the above-ground biomass allocation proxy (LAR*) across species. (S)MATR (Falster, Warton & Wright 2003) was used to calculate type II regression parameters. Multiple regression analysis was conducted to examine the importance of physiological vs. morphological traits in predicting WPLCP. Model selection was based on the minimum Akaike Information Criterion (AIC) method (PROC REG, SAS v. 8.1). Specifically, lower AIC values indicate a more parsimonious model (Burnham & Anderson 1998) and therefore ΔAIC values were calculated for model selection. Physiological predictor variables included A_{area} or A_{mass} , LLCP, R_{area} or R_{mass} , %N or N_{area} , PNUE, g_s , WUE and LL, while morphological predictors included LO, LMA and LAR*. Separate analyses were conducted using mass- and area-based physiological parameters. $\delta^{13}\text{C}$ was not included as a model predictor as it was not measured for all species and would have reduced the species sample size substantially.

The relationship between the RGR vs. light availability regression coefficient and WPLCP was tested using type II regression with the regression coefficient as the y and WPLCP the x variable. (S)MATR was used to calculate regression parameters. A strong negative relationship existed between the slope and intercept of the relationship between RGR and light availability (data not shown). Only the slope parameter is considered here (c.f. Sack & Grubb 2001). Relationships between WPLCP_{survival} (calculated using both methods described above) and WPLCP_{growth} were also analysed using type II regression with WPLCP_{survival} as the x variable and WPLCP_{growth} the y variable. Only species with significant values for both WPLCP_{survival} and WPLCP_{growth} were included in the analyses.

To test for crossovers in growth rates as a function of light availability we used a nonparametric approach developed by Thomas & Bazzaz (1993) that tests for deviations of Spearman's rank correlation (r_s) from the

rank correlation equalling unity expected under the null hypothesis of zero crossover occurrences. The light gradient was binned into six categories (0–2, 2–2.5, 2.5–3, 3–4, 4–5 and 5–7 mol m⁻² day⁻¹) and mean species growth rate was calculated for each light environment category. Many of the WPLCP values occurred in the 2–3 mol m⁻² day⁻¹ range. We therefore decided to subdivide the light environment in this range. Values over 7 mol m⁻² day⁻¹ were not included in the highest light bin as a number of species were not present in these light environments. For *H. populneus* this meant the reduction of the sample size to below 15 individuals ($n = 13$ for this analysis only). The lowest light level encountered in the 0–2 bin was 0.49 mol m⁻² day⁻¹. The matrix rows and columns corresponded with species and binned light environments, respectively; the growth values in the original matrix were re-ordered within environment across species to create a null matrix in which r_s (rank correlation of mean species values across environments) equalled one. This null data set was resampled with replacement (across environments within species) and the resulting r_s values calculated 1000 times. This created a null distribution of rank correlations to which r_s values from the observed data matrix were compared. The proportion of simulated r_s that were below the observed r_s was used as the probability value for a one-tailed test (Thomas & Bazzaz 1993). Code was written in R (R v. 2.1; The R Foundation for Statistical Computing, Vienna, Austria).

Results

LIGHT GRADIENT EFFECTS ON PLANT TRAITS

With the exception of *Cynometra inaequifolia*, *Eusideroxylon zwageri*, *Knema laurina* (sandstone population) and *Sindora cf. coriacea*, all species showed significant positive above-ground growth responses to light availability within the range of light environments examined (Table 2). For the above-mentioned species, the relationship between sapling RGR and light environment was greatly improved when it was based on diffuse PPFD only. For *C. inaequifolia* and *E. zwageri* diffuse PPFD was a significant predictor of sapling RGR while neither total nor direct PPFD were (Table 2). Additionally, although *Eurycoma longifolia* and *K. laurina* (alluvial) showed significant positive growth responses to increased total and direct PPFD their growth responses were more strongly related to diffuse PPFD.

Species differed substantially in the relationship between PPFD and sapling RGR, with some species having much stronger growth response to increased light availability than others (Table 2). The most light-demanding species tended to have substantially steeper slopes in this relationship and exhibited negative growth or death at higher light levels than species that were less responsive to increasing light availability (Fig. 1, $r^2 = 0.76$, $P < 0.0001$), indicating that above-ground growth response to light availability is negatively related to

Table 2. Coefficients of determination for the censored or type I relationships between above-ground relative growth rate (mm³ month⁻¹) and total, direct or diffuse PPFD (mol m⁻² day⁻¹). Generalists are divided into responses for individuals on alluvial (a) and sandstone (s) soil (see habitat descriptions in Table 1). Statistical significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$; values without designation are not significant

Species	Total	Direct	Diffuse
<i>Dipterocarpus grandiflorus</i>	0.79***	0.79***	0.72***
<i>Dipterocarpus applanatus</i>	0.62***	0.61***	0.58***
<i>Diospyros euphlebica</i>	0.41**	0.41**	0.36**
<i>Diospyros fusiformis</i>	0.54***	0.54***	0.50***
<i>Mallotus miquelianus</i>	0.61***	0.61***	0.52***
<i>Mallotus griffithanus</i>	0.27*	0.25*	0.25*
<i>Hopea beccariana</i>	0.21***	0.21***	0.18***
<i>Hopea nervosa</i>	0.48***	0.48***	0.45***
<i>Shorea multiflora</i>	0.21***	0.21***	0.21***
<i>Parashorea tomentella</i>	0.68***	0.68***	0.69***
<i>Sindora cf. coriacea</i>	0.06	0.05	0.16
<i>Cynometra inaequifolia</i>	0.20	0.19	0.29*
<i>Eusideroxylon zwageri</i>	0.05	0.05	0.14*
<i>Homolanthus populneus</i>	0.49***	0.48***	0.49***
<i>Scaphium affine</i>	0.53***	0.52***	0.53***
<i>Eurycoma longifolia</i>	0.40**	0.39**	0.43***
<i>Knema laurina</i> (a)	0.19*	0.18*	0.30**
<i>Knema laurina</i> (s)	0.08	0.07	0.19
<i>Ficus megalala</i> (a)	0.62***	0.61***	0.69***
<i>Ficus megalala</i> (s)	0.52**	0.52**	0.51**
<i>Dipterocarpus caudiferus</i> (a)	0.25**	0.25**	0.16*
<i>Dipterocarpus caudiferus</i> (s)	0.25**	0.25**	0.20*
<i>Macaranga hypoleuca</i> (a)	0.53***	0.52***	0.50***
<i>Macaranga hypoleuca</i> (s)	0.35**	0.35**	0.23*

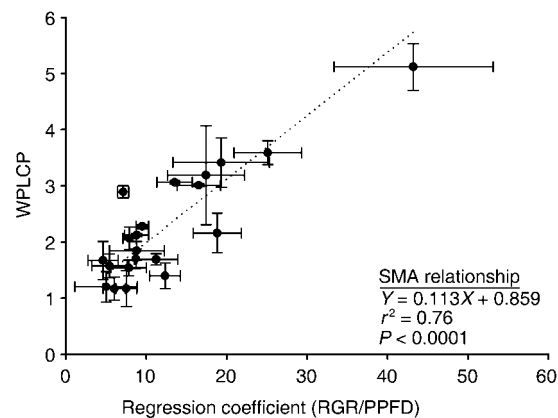


Fig. 1. Type II regression relationship between growth-based whole-plant light compensation point (WPLCP, mol m⁻² day⁻¹) and the slope of the relationship between relative growth rate (mm³ month⁻¹) and total PPFD (mol m⁻² day⁻¹). Each point represents a mean species value (\pm SE).

shade tolerance. This relationship is expected to result in growth rate crossover events between species of different shade tolerance abilities across the light availability gradient. Our bootstrap analyses document the occurrence of species rank reversals between light environments (Table 3; Fig. 2). In most cases, comparisons between immediately adjacent light environments (along the light availability gradient) showed strong similarity in

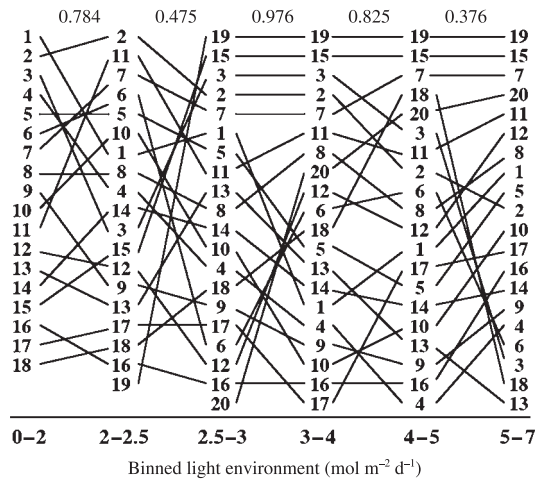


Fig. 2. Rank changes in above-ground relative growth rate between light environments for saplings of 20 tree species. Species 19 and 20 did not occur in the lowest light environments. Values above the figure correspond to Spearman's rank correlation values (r_s) between adjacent light environments. Species names with corresponding number can be found in Table 1.

Table 3. Tests of rank reversals of species above-ground growth rates across light environments. A matrix containing pair-wise Spearman rank correlations for species mean growth rates between all possible light environment comparisons. Significant deviations of the rank correlations from 1 correspond to changes in species ranks between light environments. Light environments in $\text{mol m}^{-2} \text{ day}^{-1}$ correspond to the following numbers: 1, 0–2; 2, 2–2.5; 3, 2.5–3; 4, 3–4; 5, 4–5; 6, 5–7

1	2	3	4	5	
2	0.784	–			
3	0.468	0.475	–		
4	0.504	0.468	0.976	–	
5	0.182**	0.304*	0.554	0.825	–
6	0.109**	0.434	0.312*	0.434	0.376

* $P < 0.1$; ** $P < 0.05$; values without designation are not significant.

species growth rate rankings (Table 3; Fig. 2). However, comparisons between lower light environments and the very highest light environments detected significant crossover events (Table 3).

Light environment was a significant predictor of both sapling RGR and survivorship. This was the case for the species examined regardless of shade tolerance. More light-demanding species had steeper relationships between RGR and total PPFD and also tended to show a more distinct survivorship threshold (higher logistic regression slope parameter), although the relationships for all included species were statistically significant. The relationship between the light environment at which zero net growth occurred (WPLCP) and the survivorship threshold light environment determined through logistic regression analysis was very strong and was not statistically different from the 1 : 1 relationship predicted under the assumption of identical light requirements for growth and survival (Fig. 3). This relationship held

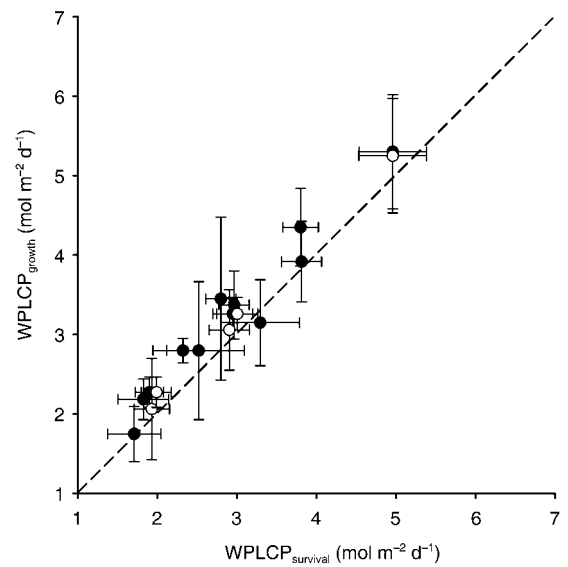


Fig. 3. Relationships between the minimum light levels required for survivorship ($\text{WPLCP}_{\text{survival}}$) and growth ($\text{WPLCP}_{\text{growth}}$). Closed circles correspond to survivorship estimates that consider negative growth as mortality (slope = 1.040 (0.900, 1.201); 95% CI); intercept = 0.1856 (–0.2608, 0.6320); $r^2 = 0.952$), while the open circles are estimates for those species having five or more dead individuals (not considering negative growth as mortality; slope = 1.030 (0.936, 1.134); intercept = 0.333 (–0.1755, 0.4420); $r^2 = 0.997$). Each point represents a species mean (\pm SE). The dashed line indicates the line of equality.

whether the analysis included only those species showing sufficiently high mortality (five species ranging in life histories) or when based upon both negative growth and mortality (assuming negative growth leads to death; 12 species).

PHYSIOLOGY VS. MORPHOLOGY AS PREDICTORS OF WHOLE-PLANT LIGHT COMPENSATION POINT

Strong relationships were found between WPLCP and a number of the physiological and morphological traits (Fig. 4; Table S2). LLCP , R_{mass} , R_{area} , A_{mass} , A_{area} , %N, PNUE, g_s and $\delta^{13}\text{C}$ were all positively correlated with WPLCP while LMA and LL were negatively correlated (Fig. 4). R_{mass} , A_{mass} and R_{area} were the best predictors of WPLCP, explaining 78%, 63% and 62% of variance in WPLCP, respectively (Fig. 4); %N and PNUE were also strong predictors (47% and 46% of the variance, respectively). LLCP correlated positively with WPLCP ($r^2 = 0.39$, $P = 0.019$). However, LLCP values were quantitatively only a fraction of the WPLCP values ($9.0 \pm 0.8\%$) and did not result in the same ranking of species as WPLCP (Spearman's rank correlation; $r_s = 0.31$, $P = 0.1641$). The lack of comparability of these two light compensation point metrics suggests that LLCP is not an adequate proxy for shade tolerance or species' light requirements. Neither leaf overlap nor the leaf allocation proxy (LAR^*) correlated significantly with WPLCP. Table S2 contains a correlation matrix of all measured traits.

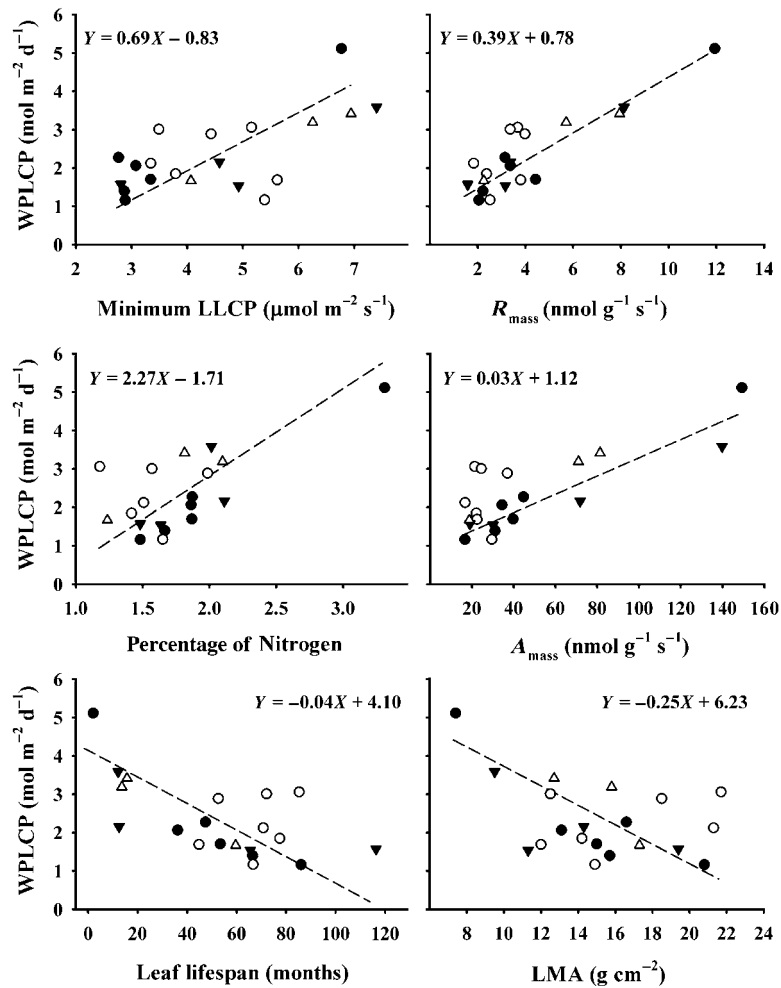


Fig. 4. Type II regression relationships between whole-plant light compensation point (WPLCP) and a number of physiological and morphological sapling traits including minimum leaf-level light compensation point (LLCP), mass-based dark respiration rates (R_{mass}), %N, mass-based photosynthetic rates (A_{mass}), leaf life span and leaf mass per area (LMA). Each data point corresponds to the average values for a single species. Closed/open symbols correspond with alluvial/sandstone populations while circles/triangles denote specialists/generalists (see habitat descriptions in Table 1; only species with significant WPLCP values are included). Type II coefficients of determination and significance levels for all trait combinations can be found in Table S2.

Multiple regression analysis of the morphological and physiological traits as predictors of WPLCP indicated that R_{mass} and R_{area} resulted in the best-fit mass- and area-based models, respectively, based upon the minimum AIC method (Table 4). Although a number of other traits significantly predicted WPLCP in bivariate relationships (Table S2), these traits were correlated with respiration, and were not included as predictors on the basis of minimum AIC.

PLASTIC RESPONSES OF WPLCP TO HABITAT

Plastic responses of growth-light relationships and WPLCP to soil resources were evaluated in three species (*K. laurina* did not show significant growth responses to total PPFD and therefore WPLCP could not be calculated). For the remaining species examined on both soil types, paired *t*-tests using WPLCP estimates for sandstone and alluvial populations indicated no systematic difference in WPLCP between populations ($t = 0.6521$, $P = 0.5812$).

HABITAT ASSOCIATIONS AND LIGHT REQUIREMENTS

This analysis was conducted on only five of the six phylogenetically independent pairs (the *Sindora*–*Cynometra* pair was excluded because neither of these species showed a significant growth response to increased total light availability and consequently WPLCP could not be estimated). Paired *t*-tests using closely related taxa from each soil type indicated that species naturally occurring on the sandstone soil type have higher whole-plant light requirements regardless of phylogeny (Fig. 5; $t = -7.10$, $P = 0.0021$). The sandstone specialist was higher in every pair. Results of *t*-tests indicated no difference between generalist species and either sandstone ($t = -0.158$, $P = 0.8796$) or alluvial specialists ($t = -0.0486$, $P = 0.9628$).

Discussion

The present study addresses four aspects of shade tolerance in tree saplings: (i) growth vs. survival as

Table 4 AIC-selected multiple regression model examining physiological and morphological traits as predictors of whole-plant light compensation point. Physiological predictor traits in the multiple regression model included area- or mass-based photosynthetic and respiration rates, leaf-level light compensation point, percentage or area-based foliar nitrogen, photosynthetic nitrogen-use efficiency, stomatal conductance, instantaneous water-use efficiency and leaf life span, while morphological predictors included leaf overlap, leaf mass per area and a leaf area ratio proxy (leaf area/(basal diameter² × height)). Separate analyses were conducted using mass- and area-based physiological parameters, where appropriate. Predictor variable abbreviations maintained in the minimum AIC model are as follows: area or mass based dark respiration rate (R_{area} or R_{mass})

Variable	d.f.	Parameter estimate	SE	<i>t</i> -value	Probability > <i>t</i>
(a) Mass-based relationship ($r^2 = 0.79$, $P < 0.0001$)					
Intercept	1	0.9847	0.1941	5.07	< 0.0001
R_{mass}	1	0.3408	0.0416	8.20	< 0.0001
(b) Area-based relationship ($r^2 = 0.62$, $P < 0.0001$)					
Intercept	1	0.3846	0.3581	1.07	0.2960
R_{area}	1	3.2856	0.5798	5.67	< 0.0001

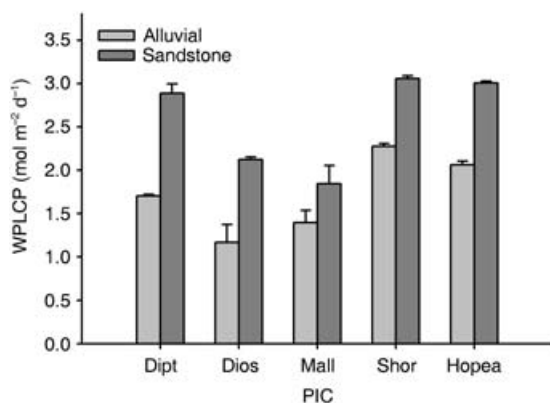


Fig. 5. Phylogenetically independent contrasts (PIC) of mean whole-plant light compensation point (WPLCP, \pm SE) for congeneric or confamilial species pairs from the sandstone and alluvial soil types. Genus abbreviations are as follows: *Dipterocarpus* (Dipt); *Diospyros* (Dios); *Mallotus* (Mall); *ShoreaParashorea* (Shor); *Hopea* (Hopea). Species names and habitat preferences for each pair can be found in Table 1 in addition to a brief description of the two soil habitats. Paired *t*-test results indicate that sandstone specialists have higher WPLCP than alluvial specialists, regardless of phylogeny ($t = -7.10$, $P = 0.0021$).

determinants of shade tolerance; (ii) shade-tolerance-related differences in species rankings across light environments; (iii) the contribution of physiological and morphological traits to whole-plant light compensation point (WPLCP); and (iv) the role of below-ground resource availability in determining WPLCP. Some previous studies have suggested that light-demanding species will maintain higher growth rates regardless of light environment and that low survivorship is the primary

determinant of shade tolerance (e.g. Kitajima 1994; Kobe 1999). We demonstrate that the modelled threshold light levels for positive growth and survivorship show essentially a 1 : 1 relationship across species ranging widely in shade tolerance, suggesting that more shade-tolerant species in this system are not capable of continued survival at light levels substantially lower than those required for net growth. We also provide evidence of growth rate crossovers between light-demanding and shade-tolerant species as a result of systematically steeper slopes in the relationships between RGR and light availability in more light-demanding species. Both findings are in keeping with similar work by Sack & Grubb (2001) and contradict the hypothesis that the trade-off between high-light growth and low-light survival solely determines shade tolerance with little or no contribution of differential growth rates under low light. Our results also highlight the importance of physiological parameters, in particular foliar respiration rates, in determining shade tolerance. Although WPLCP correlated strongly with a number of traits (both physiological and morphological), dark respiration alone was the best predictor of WPLCP in multiple regression models. Finally, we demonstrate that evolved responses to below-ground resources have a major impact on shade tolerance. At our study site alluvial soil specialists had consistently lower WPLCP than sandstone specialists, potentially as a consequence of physiological adaptations in sandstone soil specialists necessary for tolerating periodic drought (Baltzer *et al.* 2005).

SURVIVAL VS. GROWTH IN THE DETERMINATION OF SHADE TOLERANCE

It has been suggested that more light-demanding species have consistently higher growth rates than shade-tolerant species regardless of light environment, and that low-light survival is in fact the basis of shade tolerance (e.g. Kitajima 1994; Kobe 1999). Two corollaries of this 'survival hypothesis' of shade tolerance are that growth rate crossovers do not occur across the light gradient, and that more shade-tolerant species require higher light environments for growth than survival. Our data do not support either corollary. First, there was a positive relationship between species light requirements and the slope of the relationship between RGR and light, suggestive of species growth rate crossovers across the light availability gradient. The generality of this result is suggested by similar patterns documented in previous studies (Moad 1992; Valladares *et al.* 2000; Sack & Grubb 2001; Montgomery & Chazdon 2002). Growth rate crossovers were also directly detected between low- and high-light environments in the present study (Table 3). In higher light, more light-demanding species certainly had greater growth potential, adding to the wide support for a trade-off between high-light growth and low-light survival; however, the existence of growth rate crossovers refutes the notion that high survival under low light will correspond with lower growth rates

under all light environments. Second, our data do not support the corollary that shade-tolerant species have lower light thresholds for survivorship than for growth as a result of allocation of resources to storage rather than growth in low light. Rather, there is a remarkably close correspondence between the threshold light levels for survivorship and growth in the species for which this could be tested, consistent with the hypothesis that some low level of new growth is mandatory for survival in the understorey. Our data are suggestive of a slightly higher light requirement for growth than survivorship, although this difference was not statistically significant (Fig. 3). This could be viewed as support for the hypothesis that saplings may persist without net growth in the understorey through conservative resource allocation and use of carbohydrate stores (Kitajima 1994; Kobe 1997). Whether this small apparent difference is real and is maintained over a longer time period is not clear. What is evident from our data is that any shift of the relationship from that of unity is not biased toward shade-tolerant species, as would be predicted by the notion of differential low-light survival as the primary basis for shade tolerance.

PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS AS PREDICTORS OF WPLCP

Foliar dark respiration was the strongest predictor of WPLCP in multiple regression analyses, while neither of the other gas-exchange parameters was retained in the minimum AIC-selected model (Table 4). This result supports the long-held assertion that shade tolerance is closely and inversely related to tissue respiratory costs (e.g. Grime & Jeffery 1965). Dark respiration rates are temporally fairly stable and are incurred both day and night; thus, instantaneous foliar measures of respiration may be good correlates of carbon loss and, consequently, carbon balance. In contrast, rain forest understorey light environments fluctuate greatly throughout the course of the day; therefore finding a single predictor of carbon gain may be more difficult, despite the importance of carbon gain to carbon balance. Although we examined only foliar respiration, previous studies have commonly found a strong positive relationship between foliar, root and whole-plant respiration rates (Reich *et al.* 1998b; Walters & Reich 1999). There is also evidence that shade-intolerant species have higher whole-plant respiration rates (Walters *et al.* 1993; Reich *et al.* 1998b; Baltzer & Thomas 2007). This would have important consequences in a light-limited environment as a given respiration rate consumes a greater proportion of the energy available for growth or storage when light availability (and consequently carbon gain) is low (Reich *et al.* 2003). A whole-plant shade tolerance strategy should focus on the maintenance of captured resources as opposed to high levels of carbon gain (Reich *et al.* 2003); low respiration rates will maintain fixed carbon through reductions in metabolic carbon costs while potentially indirectly increasing survival

probability through reduced attractiveness to herbivores as a result of reduced leaf protein content (Givnish 1988; Reich *et al.* 1998a). Other traits, including leaf life span, A_{\max} , LMA and LLCP, showed significant direct correlations with WPLCP; however, all of these traits correlated strongly with R_d (Table S2) and did not contribute significantly to the model. Our results apparently diverge with those of a recent survey of saplings of 53 Bolivian tree species, for which leaf life span and mass-based photosynthetic rates were the strongest correlates of a shade tolerance index based on mean crown exposure (Poorter & Bongers 2006). However, the mean crown exposure of saplings should depend on the relative recruitment and growth of a given taxon across light environments, in addition to actual minimum light requirements for growth and survivorship. Moreover, the placement of successful reproductive trees has an important stochastic component and consequently relative recruitment in a given area will in part be dictated by chance rather than actual resource requirements. For these reasons a close relationship between mean crown exposure and WPLCP might not be expected.

Biomass allocation and leaf display efficiency are frequently cited as important functional determinants of shade tolerance (Givnish 1988; Kohyama & Hotta 1990; King 1991; DeLucia *et al.* 1998). Our data do not support this hypothesis: neither leaf overlap nor the leaf allocation measure showed any relationship with WPLCP or with any of the physiological traits. There is a mounting body of evidence to suggest that differences in morphology, chemistry, metabolism and tissue turnover rates among species are more relevant to species shade tolerance than biomass allocation patterns (Reich 2002). In a corresponding study of temperate deciduous tree seedlings where whole-plant allocation patterns were quantified with harvests, we similarly found no contribution of biomass allocation to WPLCP, but rather a strong physiological signal (Baltzer & Thomas 2007). Nevertheless, some prior comparative studies have found LAR to be significantly correlated with growth patterns and measures of shade tolerance (Paz 2003; Lusk 2004), and direct allocation measures and more detailed measures of display efficiency (Percy, Muraoka & Valladares 2005) might reveal a stronger role of morphology than suggested by our results.

One caveat of the above conclusions is that physiological traits contributing to species shade tolerance, such as R_d , A_{\max} , and LMA, are known to vary with plant size and age (Thomas & Winner 2002; Niinemets 2006). Likewise, allocation patterns may differ: for example, more shade-tolerant species increased their leaf area ratio and decreased root mass fraction with age/size when compared with less shade-tolerant species, resulting in rank reversals in biomass allocation (Lusk 2004). Studies that directly examine variation in WPLCP and its physiological correlates with tree size and age are required to clarify this issue.

HABITAT ASSOCIATIONS AND WHOLE-PLANT
LIGHT COMPENSATION POINT

Species naturally occurring on the sandstone soil type consistently had a higher WPLCP than alluvial specialists. This was not simply an artefact of the differences in growth environment of the sandstone and alluvial specialists: there was no evidence of phenotypic shifts in WPLCP in response to soil type. At least three important differences exist between the two habitats in terms of resource availability that could contribute to increased WPLCP in the sandstone specialists: saplings occurring in the sandstone understorey experience greater light availability in combination with lower soil water and nitrogen, compared with those in the alluvial understorey (Baltzer *et al.* 2005). Differences in tissue nitrogen are unlikely to be driving WPLCP differences as lower tissue nitrogen concentrations should correspond with reduced metabolic costs (e.g. Ryan 1995) and consequently lower WPLCP (given the strong positive relationships between tissue nitrogen and both foliar respiration rates and WPLCP; Table S2).

A second mechanism by which differential resource availability could be contributing to WPLCP differences is that sandstone specialists tend to have proportionally greater dark respiration rates than alluvial specialists as a result of their more conservative water-use strategy (Baltzer *et al.* 2005). Support for the role of differential patterns of water use is mixed, with both stomatal conductance and integrated WUE showing moderate correlations with WPLCP and R_d but no relationship of instantaneous WUE with either trait (Table S2). Finally, the habitat-based differences in WPLCP may be due to differences in light environments between the two habitats. Understorey light levels are significantly higher on the sandstone soils due to differences in forest structure (Baltzer *et al.* 2005); consequently, measured differences in WPLCP may have little to do with differential soil resources but rather be a function of species adaptation to the light environments in which they most frequently occur.

Understorey survivorship of sandstone specialists was lower when saplings were grown on the alluvial soil type than the sandstone soil type (Nilus 2004). This is likely to be due, in part, to the higher WPLCP of the sandstone specialists. Thus, differences in shade tolerance between sandstone and alluvial specialists may contribute to the exclusion of sandstone specialists from the alluvial forest type. However, this is not likely to represent a complete explanation for observed patterns of habitat specialization: generalist species did not differ from the alluvial specialists in WPLCP, which should be the case if light requirements were driving the maintenance of alluvial specialization. Additionally, this explanation does not clarify why sandstone specialists do not establish in gaps on the alluvial soil type. Although alluvial specialists have a competitive advantage in terms of growth and photosynthetic rates over the sandstone specialists, random

chance and dispersal limitation should occasionally place competitively inferior sandstone specialists in canopy openings. These factors in combination suggest that some additional mechanism is contributing to alluvial specialization; further investigation would be warranted.

Our results suggest a potentially important influence of evolved responses to below-ground resources to interspecific variation in shade tolerance. There was no support, however, for plastic responses of WPLCP to variable soil conditions. An important issue raised by this result is the origin of evolved differences in shade tolerance, and the extent to which adaptations to soil resources might be involved. In the present study, the sapling 'populations' on sandstone and alluvial soil types almost certainly were the product of genetic exchange between adult trees on both soil types. However, ecotypic divergence within a species at broader spatial scales is expected to be due to differences in soil parent material and climate (e.g. Oleksyn *et al.* 1998; Bauerle *et al.* 2003) and is likely to result in shifts in species' WPLCP (Wright *et al.* 1998). The large interspecific differences documented in the present study almost certainly originated at this broader scale. Ultimately it would be desirable to have a picture of the evolutionary processes that give rise to the remarkable range of shade tolerance observed in tropical rain forests. We conjecture that adaptations to below-ground resources may be a key part of this picture.

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Supplementary material

The following supplementary material is available for this article.

Table S1. High and low light sampling locations for all study species

Table S2. Type II coefficients of determination for all measured traits

Figure S1. Locations of all experimental gap sites at the Sepilok Forest Reserve, Sabah, Malaysia.

Figure S2. Species-specific relationships between total light availability (Total PPFD) and above-ground relative growth rate from which whole plant light compensation point (WPLCP) values were estimated

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