# Leaf traits of dipterocarp species with contrasting distributions across a gradient of nutrient and light availability

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## Abstract

***Background***: Tree species composition at the landscape scale is often tightly associated with underlying soil type in tropical forests. Changes in soil type may have effects on forest structure that drive changes in both light and soil resource availability, since light availability in the understorey tends to be lower in more fertile sites. Plant functional traits may determine species distributions across gradients of light and soil resource availability.

***Aims***: To test whether tree species with contrasting distributions exhibit leaf traits that reflect adaptation to the resources most limiting in their native environment.

***Methods***: We measured foliar nutrient concentrations, stomatal density, leaf $\delta^{13}C$ values, leaf mass per area, and leaf lifespan for saplings of nine common dipterocarp species at Sepilok Forest Reserve, Malaysian Borneo, possessing varying associations to soil resource habitats.

***Results***: Species specialised in their adult distribution to nutrient-poor sandstone soils had traits indicative of a nutrient conservation strategy. Species specialised to more fertile alluvial soils had a wider spectrum of leaf N and P concentrations and leaf lifespan, reflecting greater variance in strategies for resource acquisition and use among species in this habitat.

***Conclusions***: Understorey light regimes co-vary with soil type, and both light and soil resource availability influence leaf trait adaptations that may contribute to species-habitat associations.

Key words: Foliar nutrient concentrations; Leaf lifespan; Leaf mass per area; Shade-tolerance; South-east Asia

## Introduction

Species habitat associations play an important role in maintaining the tree species richness of tropical forests (Gentry 1988; Clark et al. 1998; Webb and Peart 2000; Harms et al. 2001; Condit et al. 2013). The high diversity of tree species in Borneo is in part due to high beta-diversity driven by the specialisation of tree species to distinct underlying soil types (Ashton 1964; Ashton and Hall 1992; Potts et al. 2002). As a result, community level studies of primary forest in South-east Asia show that floristic composition is tightly associated with edaphic variation (Ashton 1964, 1973; Newbery and Proctor 1984; Ashton and Hall, 1992; Potts et al. 2002; Palmiotto et al. 2004). To determine the mechanisms that maintain tropical tree distributions and diversity both the availability of essential resources on different soil types, and the response of tree species to differential availability of light, nutrients and water need to be investigated (Whitmore and Brown 1996; Burslem et al. 1995, 1996; Baltzer et al. 2005; Russo et al. 2008).

The availability of light and below-ground resources may co-vary with soil type in Bornean lowland forests (Baltzer et al. 2005; Baltzer and Thomas 2007; Russo et al. 2012). The shade generated by a forest canopy is determined by tree crown structure, leaf biomass and leaf areas, inclinations and lifespans (Coomes and Grubb 2000). Light availability at ground level tends to be lower in more productive sites because fertile soils support forests with tall, multi-layered canopies that intercept more light than forests overlying less fertile soils (Ashton 1964; Ashton and Hall 1992; Coomes and Grubb 1996). For example, in Lambir Hills National Park, Borneo, the understorey of the most productive forests, found on clay soils, receives a lower daily photosynthetic photon flux density than the understorey of forests on more nutrient-depleted and better-drained loam soils (Russo et al. 2012). Therefore, the length of the gradient in light availability, and the range of shade-tolerance niches, may vary with underlying changes in soil nutrient availability (Coomes et al. 2009).

Although the trade-offs associated with light and nutrient limitation are well studied in tropical forests (Kitajima 1994; Baraloto et al. 2005; Russo et al. 2008; Dent and Burslem 2009; Wright et al. 2010; Grubb 2016), there is more limited understanding of how shade-tolerance varies along gradients of soil fertility (Thompson et al. 1992 a,b; Raaimakers et al. 1995; Baltzer and Thomas 2007, 2010). It is predicted that shade-tolerance will be more developed in fertile, high productivity ecosystems with infrequent disturbance (Coomes and Grubb 2000; Valladares and Niinemets 2008). In support of this prediction, a study from north Borneo found that tree species associated with fertile alluvial soils were consistently more shade-tolerant than congeneric species restricted to less fertile sandstone ridges (Baltzer and Thomas 2007). However, a study from temperate forests in New Zealand found nutrient-rich alluvial soils supported forests with a wider range of growth rates and shade tolerances, rather than consistently higher shade tolerance, as compared to adjacent sites on nutrient-poor soils (Coomes et al. 2009). The authors have suggested that this is because nutrient-rich soils can support both fast-growing species, with low leaf mass per area (LMA) and high nutrient concentrations, and slow-growing shade-tolerant species that persist in the shade under the dense canopy of these forests (*sensu* Givnish 1988). In contrast, nutrient-poor soils constrain the growth rates of all species, which limits the variation in response to light availability (Coomes et al. 2009).

Variation in resource availability is related to the evolution of a group of interrelated plant traits reflecting differentiation in strategies for resource use and conservation (Coley 1988; Reich et al. 1992, 2003; Wright et al. 2004; Freschet et al. 2011). Species native to resource-limited environments exhibit a conservative strategy that includes slow growth rates, low rates of photosynthesis, low nutrient concentrations, high LMA, slow turnover of plant parts and increased allocation to plant defenses to reduce herbivory (Reich et al. 1999; Fortunel et al. 2014), while species indigenous to resource-rich areas show the converse set of traits (Reich et al. 1999, 2003). However, natural habitats may display simultaneous variation in multiple resources and plant species may be expected to express traits that result from trade-offs in response to co-occurring gradients in light, nutrients and water (Craine and Dybzinski 2013).

Species that are able to establish and persist in the understorey of tropical forests exhibit traits that enable them to maintain a positive carbon balance in very low light conditions (Kitajima and Myers 2008), such as low respiration rates (Machado et al. 2003; Valladares et al. 2000; Baltzer and Thomas 2007), long leaf lifespans (Coley 1988; Reich et al. 2003; Poorter and Bongers 2006; Kitajima et al. 2013) and thick and/ or tough leaves that resist herbivory (Veneklaas and Poorter 1998; Walters and Reich 1999; Poorter et al. 2009). Plants adapted to nutrient-poor soils have traits that enable them to maintain net growth at low nutrient supply, including low nutrient to carbon ratios and long leaf lifespans (Aerts and Chapin 2000; Ordonez et al. 2011). Low nutrient to carbon ratios maximise the amount of plant tissue produced per unit nutrient, while tissue longevity allows plants with slow growth rates to accumulate tissue (Aerts 1990; Reich et al. 1992; Falster et al. 2012). Stomatal conductance and LMA may contribute to photosynthetic water use efficiency and differentiate plants along gradients of water availability (Reich et al. 2003). Plants of drier habitats reduce transpiration by maintaining small leaf areas and thick leaf cuticles, and have higher carbon fixation at a given stomatal conductance than plants of more mesic habitats (Wright et al. 2001; Wright and Westoby 2002). Some traits, such as tough leaves with high LMA, are common to plants adapted to low resource availability, regardless of the resource that is most limiting. Conversely, extended leaf lifespans are associated with shade-tolerance and adaptation to nutrient limitation but not water shortage, while low nutrient concentrations reflect adaptation to low nutrient availability, and low stomatal densities and reduced stomatal conductance illustrate adaptation to drought (Diefendorf et al. 2010; Craine et al. 2012). Therefore, trait values may enable us to infer the relative availability of different resources within a given habitat as well as identify the variation in resource availability across that habitat.

The Sepilok Forest Reserve in Sabah, Malaysian Borneo, contains distinct floristic associations of lowland dipterocarp forest that occur in association with different soils and geological substrates. Broadly defined, these associations distinguish forest growing on flat alluvial land interspersed with low mudstone hills (hereon referred to as 'alluvial forest') from that on steep hills and ridges derived from sandstone interspersed with mudstone ('sandstone forest'). Nutrient and water availability are higher in the alluvial soils than in those derived from sandstone, whereas mean daily irradiance at 1 m above ground level is lower in the alluvial forest than the sandstone forest (Baltzer et al. 2005; Dent et al. 2006). However, canopy gaps in the alluvial forest tend to be larger and receive higher irradiance than gaps in the sandstone forest and so there is greater spatial variance in light environments in the alluvial than the sandstone forest (Baltzer et al. 2005; Dent and Burslem, 2009, Appendix 1). Therefore, the relative importance of limitation by light, nutrients and water varies between forest habitats and competition for these resources among saplings of common tree species may determine species distributions and community structure. Thus, our first prediction was that saplings of common tree species would exhibit traits that reflected differential adaptation to the resources most limiting in their native environment; sandstone specialists would exhibit leaf traits typical of nutrient and water limitation, and alluvial specialists would exhibit traits typical of a shade-tolerant strategy. Second, we expected traits would be inter-correlated and so would co-vary along gradients of resource availability. Third, since below-ground resources are consistently limiting in the sandstone forest, while light availability varies considerably in the alluvial forest allowing for a wider range of shade-tolerance niches, we predicted that both inter- and intra-specific variation in trait values would be lower for sandstone than alluvial species. Finally, we predicted that generalist species, which are found on both soil types, would have the highest intra-specific variation in trait values and would express greater plasticity in trait values that specialist species.

## Materials and methods

### *Study site*

The study was conducted in the Sepilok Forest Reserve (5º 10' N, 117º 56' E; SFR) located on the east coast of Sabah, Malaysian Borneo. The reserve is a 4475-ha patch of lowland dipterocarp and heath forest ranging between 0 and 170 m a.s.l. (Fox 1973, DeWalt et al. 2006). Mean annual rainfall for the period 1976-1995 was 2975 mm, with no month receiving less than 100 mm on average (Malaysian Meteorological Department, unpublished data). However, throughout the year there is distinct variation in rainfall distribution; April is generally the driest month and December and January the wettest with 45% of annual precipitation falling from early November to mid-February (Fox 1973).

Sepilok Forest Reserve supports two lowland dipterocarp forest communities (alluvial forest and sandstone forest defined above) that differ significantly in their species composition and occur in association with changes in the underlying soil and geological substrate (Fox 1973; Nilus 2004). Alluvial forest occurs on ultisols overlying alluvial flats and gently sloping, low mudstone hills (Fox 1973), while the sandstone forest occurs on well-drained ultisols on steeply sloping sandstone ridges and valleys interbedded with mudstone (for further details see Fox 1973; Baltzer et al. 2005; Dent et al. 2006; DeWalt et al. 2006; Margrove et al. 2015). Tree species diversity and basal area are lower in the sandstone forest than in the alluvial forest, and stem density is greater (Nilus 2004).

Alluvial forest soils have significantly greater concentrations of total N and P than the sandstone forest soils (Dent et al. 2006; Dent and Burslem 2009; Appendix 1). Concentrations of nitrate and base cations are also significantly greater in alluvial than sandstone soils, while pH and concentrations of available P, ammonium and Al do not differ. Gravimetric soil water content was significantly lower in the well-drained sandstone soils than in alluvial soils (Appendix 1). The alluvial forest understorey receives less irradiance than the sandstone forest understory (2.81 $\pm$ 0.15 vs 3.21 $\pm$ 0.19 mol $m^{-2}$ $d^{-1}$ respectively) and the frequency distributions of photosynthetically active radiation (PAR) received in the understorey differ significantly with forest type (Kolmogorov-Smirnov Z = 2.19, $P < 0.001$; C.D. Philipson et al., unpublished data). Over a sampling window of 24 days, the alluvial forest understorey had a greater proportion of intervals receiving less than 0.25 μmol PAR $m^2$ 10 $min^{-1}$ than the sandstone forest understory (52% vs 47%), but also more intervals receiving 8-10 μmol PAR $m^2$ 10 $min^{-1}$. The sandstone forest understorey experiences a more temporally constant light environment than the alluvial forest, suggesting that canopy structure and light environments differ between the two forest types (Baltzer et al. 2005).

### *Study species and sampling strategy*

The Forest Research Centre, Sabah, maintains nine 4-ha plots within SFR, including three plots on sandstone scarps and ridges and three plots in the alluvial forest (Nilus 2004; DeWalt et al. 2006; Dent et al. 2006). Species of Dipterocarpaceae dominate tropical lowland forests in South-east Asia, and the species selected for this study were the most abundant dipterocarps among individuals > 50 mm diameter at breast height (DBH) in the alluvial plots and sandstone plots respectively at SFR (Nilus 2004). Nine species of Dipterocarpaceae were selected for the study based on analyses of tree distribution, abundance and habitat association in these plots: four species associated with alluvial and mudstone forests (*Dipterocarpus caudiferus, Dryobalanops lanceolata*, *Parashorea tomentella* and *Shorea xanthophylla*), four sandstone specialists (*Dipterocarpus acutangulus, D. grandiflorus, Hopea beccariana* and *Shorea multiflora*) and one generalist species (*Shorea smithiana*). The distribution of six of these species on a single 68 ha plot confirms these soil type classifications (Margrove et al. 2015) and updates the status of *D. caudiferus*, which was classified as a habitat generalist by Baltzer et al. (2005). See Table 1 for species descriptions, and the total numbers of individuals sampled per species.

Between three and seven individual saplings for each alluvial species and *S. smithiana* were identified within a single randomly selected 1-ha plot from each of the three 4-ha plots in the alluvial forest (total of 9-21 individuals per species, see below). The same protocol was followed for the sandstone plots (total of 16-21 individuals per species). Study saplings were growing in the shaded understory and thus all the sampled leaves had developed in shade. All saplings were monitored for leaf demography, and a subsample of five individuals was used for measurement of other leaf traits. Individuals were 205 - 580 cm in height and had 10.0 – 31.2

mm DBH. Sampled saplings were uniformly distributed within this height range to take account of ontogenetic shifts in traits. Damaged or unhealthy individuals, or those growing in or near a canopy gap, were excluded.

### *Measurement of leaf traits*

We measured six traits: foliar N and P concentrations, stomatal density (SD), leaf $\delta^{13}C$ values ($\delta^{13}C$), LMA and leaf lifespan (LL). These traits are associated with nutrient conservation (N, P, LMA and LL; Aerts and Chapin 2000), shade-tolerance (N, LMA and LL; Kitajima et al. 2013), and drought tolerance (SD, $\delta^{13}C$ and LMA; Reich et al. 2003). Leaf $\delta^{13}C$ isotope values ($\delta^{13}C$) represent the isotopic ratio of $^{13}C$ to $^{12}C$ in plant tissue and, since plants discriminate against $^{13}C$ during photosynthesis, $\delta^{13}C$ can be used as an indicator of stomatal opening and water use efficiency (Farquhar et al. 1989).

Three fully expanded mature leaves were selected from the upper crown of five randomly selected saplings for the determination of leaf nutrient concentrations, $\delta^{13}C$ and LMA. Immediately after collection, leaves (with petiole removed) were photocopied, and the area of each leaf was calculated by weighing the photocopies and calibrating with a known area of paper. The leaves were then dried to constant mass at 60 ºC for 48 h and weighed. Leaf mass per area (LMA; total leaf dry-mass excluding petiole divided by leaf area) was calculated per leaf. The dried leaf samples were then finely ground and digested using a sulphuric acid-hydrogen peroxide digest procedure (Allen 1989). Concentrations of N were analysed using a continuous-flow analyser and P concentrations were assessed using a flow-injection auto-analyser (Dent 2004; Dent et al. 2006). Values of $\delta^{13}C$ were assessed using continuous-flow isotope ratio mass spectrometry (Europa Scientific Ltd., Crewe, UK; see Robinson et al. 2000). Two additional leaves were collected from these same five randomly selected saplings to assess SD; two 20 mm x 30 mm sections were cut from the lamina of each leaf, one section on each side of the mid-rib. The sections were stored in 70% ethanol, and stomatal densities were made on clear nail polish impressions from preserved leaves (Sampson 1961).

### *Measurement of leaf demography*

To estimate leaf lifespan, production and loss, two branches within the upper crown were marked and all leaves were labelled with a unique code using a permanent marker pen. The plants were then resurveyed on four further occasions at 5-, 11-, 16- and 24-months after the original survey. At each survey, all new leaves on previously marked branches were labelled and a record was made of all new leaves and leaves lost. Over the course of the study > 5900 leaves were monitored with a mean of 32.1 leaves (± 2.18 SE) per sapling for 178 individual saplings. Leaf lifespan was estimated using a demographic approach that accounts for censored data (Williams et al. 1989):

$$L = \left(\frac{N_{t\alpha}}{d} + \frac{N_{t1} - N_{t\alpha}}{b}\right) \times (t_2 - t_1)$$

Where $L$ is leaf lifespan, $b$ is leaf production between censuses, $d$ is leaves abscissed between censuses, $N_{t1}$ represents initial number of leaves and $N_{t\alpha}$ represents number of leaves at $t_1$ plus number of leaves produced between $t_1$ and $t_2$. This calculation provides an estimate of average leaf longevity based on cumulative leaf production and deaths.

### *Data analysis*

Analysis of variance was used to determine significant differences in mean trait values among species and between soil types. Multiple comparisons among means were made using Tukey's honest significant difference tests with the error rate corrected to 0.05. We used Student's t-tests to assess whether trait values of *S. smithiana* on alluvial soils differed significantly from those of *S. smithiana* on sandstone soils.

Mean values of N, P, SD, $\delta^{13}C$, LMA and LL were calculated per species per soil type, and all possible bivariate trait relationships were plotted. Standardised major axis slopes with 95% confidence intervals were fitted to these bivariate trait relationships using logged trait values to describe the trends of association between variables and to test the statistical significance of those relationships (R package 'smatr'; Warton et al. 2012). Values of $\delta^{13}C$ were converted to positive values prior to log transformation. Principal components analysis (PCA; function 'prcomp' in R package 'stats') was used to determine patterns of covariance in leaf traits; we used species means for this analysis, except for *S. smithiana* where population-level means were used (segregated by soil type). Positive values of $\delta^{13}C$ were also used in the PCA to allow comparison of trends with bivariate trait relationships.

Coefficients of variation (CV) were calculated for each trait both within species to characterize intraspecific variation, and among mean species values for each soil type to calculate interspecific variation by soil type. We used Kruskal-Wallis tests to determine if intraspecific CV differed significantly with soil type. It was not possible to test for statistical differences in interspecific variation between soil types as we were limited to one CV value per trait per soil type. All statistical analyses were conducted using R 3.1.1 (The R Foundation for Statistical Computing, 2014)

## Results

### *Comparisons of traits between soil types and among species*

Sandstone specialists had significantly lower foliar concentrations of N and P, less negative $\delta^{13}C$ values, and lower SD than alluvial forest specialists (Table 2; Figure1). However, LL and LMA did not differ significantly between sandstone and alluvial specialists, and instead exhibited greater variation among species than between soil types (Table 2; Figure 1). Leaf N and P concentrations and SD were all significantly correlated with the first axis of the PCA (variance explained = 52.6%; Table 3). This first axis clearly splits species into alluvial and sandstone specialists, with the two populations of *S. smithiana* nested within the cluster appropriate to the habitats where the individuals were sampled (Figure 2). The second axis of the PCA accounted for 23.5% of the variance and was correlated significantly with leaf lifespan (Table 3). This axis did not segregate the alluvial and sandstone specialists, but ordered species according to leaf lifespan, with species possessing the longest and shortest-lived leaves at the extremes (Figure 2).

Sandstone specialists had more constrained leaf lifespans (35 – 56 months) than alluvial specialists that had leaf lifespans ranging from ca. 25 months (*P. tomentella* and *D. caudiferus*) to > 80 months (*S. xanthophylla*). Leaf lifespans differed significantly among species (Table 4 Figure 1), and post-hoc tests indicated that leaf lifespans of *D. caudiferus*, *P. tomentella* and *S. smithiana* (growing on alluvial soil) were significantly shorter than those of the other alluvial specialists *D. lanceolata* and *S. xanthophylla* (Figure 1). Leaf lifespans of the sandstone specialists occupied the centre of the range and were not significantly different from one another or from the alluvial specialists (Figure 1). A similar pattern was seen in LMA values, which differed significantly among species but not between soil types (Table 2). The alluvial specialists with long-lived leaves also had significantly greater LMA than the three alluvial species with short-lived leaves (Figures 1 and 2). Therefore, the alluvial specialists occupied the extremes, and sandstone specialists the centre of the range of LMA and leaf lifespan values.

### *Correlations among traits*

Corroborating the results from the PCA, bivariate plots indicated that N, P and SD were positively correlated with each other across all species (Figure 3; Table 5; sandstone specialists occupied one extreme and alluvial specialists the other extreme of this continuum. However, foliar N and P concentrations were not well correlated with $\delta^{13}$C, LMA or leaf lifespan across species; rather, the groups of alluvial and sandstone specialists each exhibited different relationships among these traits. In contrast, across all species there was a positive, but non-significant, trend between LMA and leaf lifespan (Figure 3; Table 5). Thus species occupy a continuum from short-lived leaves with low investment per unit leaf area to more robust and long-lived leaves, but without species segregated by soil association.

### *Differentiation in trait values across soil types for a generalist species*

The generalist species *S. smithiana* had significantly lower foliar N and P concentrations, greater LMA and longer leaf lifespans when growing on sandstone than on alluvial soils (Table 1). However, SD and $\delta^{13}$C values did not differ with soil type. For N, P and LL, *S. smithiana* exhibited higher intra-specific variation than other species, but variation in other traits (LMA, SD and $\delta^{13}$C) was in the same range as that seen in non-generalist species (Table 4).

### *Inter- and intra-specific variation in trait values*

Alluvial species did not exhibit consistently greater interspecific variation in trait values than sandstone species (Table 4). Among alluvial species there was greater variation in leaf N and P concentrations and LL than for sandstone species, but for other traits, variation among species either did not differ considerably with soil type (LMA and SD) or variation was greater among sandstone than alluvial species ($\delta^{13}C$). Intraspecific variation also showed few consistent patterns (Table 4). Species-specific coefficients of variation indicated that intraspecific variation in LL, P concentration, SD and $\delta^{13}C$ did not differ with soil type. In contrast, intraspecific variation in LMA was higher in alluvial than sandstone species, whereas intraspecific variation in foliar N concentration was higher in sandstone species.

## Discussion

### *Trait differentiation across resource gradients*

Comparisons between sandstone and alluvial specialists illustrate differences in traits that underlie nutrient conservation and drought tolerance; sandstone specialists had consistently lower foliar N and P concentrations and stomatal density, and less negative $\delta^{13}C$ values, than alluvial specialists. These are all traits that show adaptation to limited availability of soil-borne resources (Aerts and Chapin 2000; Ordonez et al. 2009). The generalist species (*S. smithiana*) also shifted trait values to adopt a strategy of increased nutrient conservation when growing on sandstone compared to alluvial soils, with significantly lower N and P concentrations, greater LMA and extended leaf lifespans. In contrast, SD and $\delta^{13}C$ values did not differ with soil type for *S. smithiana*, suggesting that traits associated with drought tolerance may not be as plastic as those associated with nutrient availability and response to light environment, or that there was no drought episode during the lifetime of this cohort of leaves to trigger the associated shifts in $\delta^{13}C$

and SD (Nagy and Proctor 2000; Robinson et al. 2000; Diefendorf et al. 2010). This finding supports a number of studies from South-east Asia, showing that species restricted to less fertile sandstone-derived soils tend to have constrained growth rates and traits associated with a strategy of resource conservation compared to species specialised to more fertile soils (Palmiotto et al. 2004; Baltzer et al. 2005; Russo et al. 2008; Dent and Burslem 2009). However, it remains unclear how soil type interacts with light availability to drive the relative availability of multiple resources within a given habitat, and the implications of these patterns for trait expression.

In contrast to other traits, LMA and leaf longevity exhibited greater variation in trait values among species than between the two soil types, which may be explained by differences in the spatial and temporal distribution of nutrients, water and light across the two forest types. Evidence suggests that below-ground resources are consistently limiting in the sandstone forest and less limiting in the more fertile alluvial forest (Dent et al. 2006). In contrast, light availability varies spatially and temporally in both forest types, but there is greater variance in light environments in the alluvial than the sandstone forest (Baltzer et al. 2005; Dent and Burslem 2009; C.D. Philipson et al. unpublished data). This contrast in the balance of different limiting resources between sandstone and alluvial specialists may result in the differential expression of traits that are uniquely associated with either nutrient conservation (e.g. foliar N and P concentrations), or drought tolerance (e.g. $\delta^{13}C$ or SD), but not for traits that may be associated with shade-tolerance (e.g. LMA and leaf lifespan). Instead, variation in LMA and leaf lifespan among species is indicative of specialisation to distinct light environments in the forest understory (Baltzer and Thomas 2007; Philipson et al. 2012, 2014).

### *Inter- and intra-specific trait variation in relation to resource availability*

We predicted that both inter- and intra-specific variation in shade-tolerance trait values would be less for sandstone than alluvial species. This pattern was not clear, although interspecific trait variation either tended to be greater among alluvial than sandstone species (e.g. N, P and LL) or similar across the two soils (e.g. LMA and SD), potentially lending some support to this hypothesis. We only present data from four species per soil type in this study and a larger number of species would be required to quantify patterns of interspecific variation across these two soil types. The only trait that had higher variation among sandstone than alluvial species was $\delta^{13}C$; sandstone forest occurs on sandstone soils overlying ridges and gullies, and it is likely that water availability varies with topography within this habitat (Daws et al. 2002). Differentiation among in $\delta^{13}C$ may be associated with these topographic gradients in water availability and specialisation of species to distinct microhabitats within the sandstone forest habitat (Gibbons and Newbery 2003; Diefendorf et al. 2010). Intraspecific variation also showed few consistent patterns, although intraspecific variation in LMA was greater in alluvial than sandstone species, potentially due to the greater extremes in light availability in alluvial forest driving plastic responses in leaf morphology in the understory (Poorter 1999, Valladares et al. 2000).

Traits of plants growing in natural environments have evolved in response to the spatio-temporal variation in multiple limiting resources. Therefore trait values may enable us to infer the relative availability of different resources within a given habitat, and also identify the variation in resource availability across that habitat. There was greater variation among alluvial species than among sandstone species in LL, which is strongly associated with shade-tolerance (Kitajima et al. 2013). This mirrors the greater variability in the understory light regime in the alluvial than the sandstone forest (Baltzer et al. 2005; Dent and Burslem, 2009; C.D. Philipson et al. unpublished data). Differences in understorey light environment for forests growing on different soil types may lead to soil-related differences in the range of light-mediated regeneration niches available, resulting in diversification of key functional traits and demographic rates (Poorter and Arets 2003, Coomes et al. 2009, Heineman et al. 2011). The wide range of leaf lifespans and large intra-specific variation in LMA among alluvial forest species suggests that alluvial soils may support species spanning a wide range of shade-tolerance strategies, including fast-growing species with low LMA and short leaf lifespans (e.g. *P. tomentella*) and slow-growing shade-tolerant species with high LMA and long-lived leaves (e.g. *S. xanthophylla*). In contrast, these traits were constrained among species native to sandstone soils likely due to primary limitation by edaphic resources.

### *Implications for diversification in ecological strategies and species coexistence*

The different shade-tolerance and below-ground resource conservation strategies that we report here are based on interpretation of trait data, thus our inference is limited since we do not have data to describe how traits affect demographic rates for these species. However, other studies from SFR report growth and mortality rates of alluvial and sandstone specialists (Baltzer and Thomas 2007; Dent and Burslem 2009; Eichhorn et al. 2010; Born et al. 2014). These studies indicate that sandstone species have relatively constrained growth rates and are unable to up-regulate growth rates when resources are abundant, which is typical of species adapted to conserve nutrients (Baltzer and Thomas 2007; Dent and Burslem 2009). In contrast, growth rates vary widely among alluvial species (Baltzer and Thomas 2007; Dent and Burslem 2009; Born et al. 2014). These studies suggest that availability of edaphic resources constrains growth rates on sandstone soils, while light availability drives differentiation of ecological strategies among alluvial species. Although the studies at SFR have been based on small subsets of the species pool, demographic data from all individuals >1 cm DBH within the 52-ha forest plot at Lambir Hills National Park in Sarawak exhibit a similar pattern; growth rates were constrained on soils with the lowest fertility, and exhibited the greatest variation on higher fertility soils where fast-growing pioneer species coexist with slow-growing non-pioneers (Russo et al. 2005). A more recent study from the same field site also indicates that forests on the high fertility soils had significantly darker understorey environments than forests on less fertile soils (Russo et al. 2012), suggesting that there is greater variation in light availability between understorey and gap sites in forests growing on high than low fertility soils. Thus at high-fertility sites there is both greater variation in light availability and a greater diversity of growth rates, while at low-fertility sites edaphic resources limit growth rates of all species (Ashton 1964; Coomes and Grubb 2000; Coomes et al. 2009).

Diversification of shade-tolerance strategies on fertile soils may drive increased species diversity in more productive forest ecosystems (Coomes et al. 2009). Within SFR, species composition differs significantly with underlying soil type, and alluvial forests have fewer individuals but greater species richness per hectare than forests on less fertile soils (Nilus 2004; DeWalt et al. 2006). Alluvial forests support a greater number of species, genera and families than the less fertile sandstone forests. It has long been accepted that the high diversity of tree species in Borneo is partly due to high beta-diversity driven by tree species associations with distinct soil types and soil nutrient availability gradients (Ashton 1964; Potts et al. 2002; Sukri et al. 2012). Our results suggest that understorey light regimes also co-vary with soil type, and thus multiple resource gradients interact to determine both species richness and composition in these forests (Pearson et al. 2003; Dent and Burslem 2009; Russo et al. 2008). Resource gradients may vary in opposite directions, thus generating contrasting environmental selection pressures: for example sites with greater nutrient and water availability may also have lower light availability in the understorey (Baltzer and Thomas 2007; Coomes et al. 2009; Russo et al. 2012). Tropical tree species respond differentially to nutrient and light availability, and experimental studies with relatively small sub-sets of species have shown that these resources interact to determine niche separation (Metcalfe et al. 2002; Palmiotto et al. 2004; Baraloto et al. 2005, 2006; Dent and Burslem 2009). Further studies at the community level are now needed to understand how soil resources can determine differences in light availability, and how the co-variation of multiple resources within and across habitats structures plant community composition and diversity.

## Conclusions

Understorey light regimes co-varied with soil type in the lowland dipterocarp forests of SFR. Leaf trait values were constrained among species native to sandstone soils, likely due to primary limitation by edaphic resources; while light availability drove the differentiation of ecological strategies among alluvial species. Our data indicate that both light and soil resource availability influence leaf trait adaptations and may contribute to species-habitat associations in tropical forests. Our data indicate that both light and soil resource availability influence leaf trait adaptations and may contribute to species-habitat associations in tropical forests.

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Table 1. Dipterocarp study species soil type association, distribution, shade tolerance and the number of individuals sampled per species to examine leaf traits on two contrasting soil types at Sepilok Forest Reserve (SFR), Malaysian Borneo. Ecological data are summarized from Meijer and Wood (1964), Nicholson (1965), Burgess (1966), Turner (1990), Newman et al. (1996, 1998), Whitmore and Brown (1996), Zipperlen and Press (1996), and Bungard et al. (2002).

| **Species** | **Soil type association** | **Description and shade tolerance (if known)** | **Abbreviation** | **Number of individuals sampled** |
|---|---|---|---|---|
| *Dipterocarpus caudiferus* | Alluvial | Relatively light-demanding species. Large stature tree, typically found on undulating land below 800 m across most of Borneo. | DC | 18 |
| *Dryobalanops lanceolata* | Alluvial | Shade-tolerant species. Widespread on fertile soils in North Borneo. | DL | 17 |
| *Parashorea tomentella* | Alluvial | Relatively light demanding species. The most abundant canopy dipterocarp species on alluvial soils in SFR. | PT | 20 |
| *Shorea xanthophylla* | Alluvial | Shade-tolerant species. Small- to medium-sized tree that seldom forms part of the upper canopy. Widespread in the lowland forests of Borneo. | SX | 21 |

| | | | | |
|---|---|---|---|---|
| *Shorea smithiana* | Generalist | One of only two dipterocarp species found on both alluvial and sandstone soils in SFR. Large stature tree that is one of the most common *Shorea* species in Borneo. | SS | Alluvial forest: 9<br>Sandstone forest: 16 |
| *Dipterocarpus acutangulus* | Sandstone | Restricted to sandy soils on coastal hills and inland ridges up to 1000 m. | DA | 21 |
| *Dipterocarpus grandiflorus* | Sandstone | A very large tree restricted mainly to hills and ridges in Borneo. Also found in hill dipterocarp forest in Peninsular Malaysia. | DG | 16 |
| *Hopea beccariana* | Sandstone | Common on the sandstone hills and ridges of SFR. | HB | 20 |
| *Shorea multiflora* | Sandstone | Shade-tolerant species. A very common species on the sandstone hills and ridges of SFR. | SM | 20 |

**Table 2.** Comparisons between soil types and among saplings of nine dipterocarp species for six leaf traits on two contrasting soil types at Sepilok Forest Reserve, Malaysian Borneo. Mean trait values (± SE) per soil type are presented for the eight specialist species sampled on only one soil type (top panel) and for individuals of the generalist *Shorea smithiana* growing on alluvial and sandstone soils (bottom panel). Statistical comparisons between soil types and among species were conducted using ANOVA. Statistical comparisons between soil types within the generalist species (*S. smithiana*) were conducted using t-tests. Bold text indicates significant effects: *, *P* <0.05; **, *P* <0.01; ***, *P* <0.001.

| **Soil type** | **N (mg $g^{-1}$)** | **P (mg $g^{-1}$)** | **Stomatal density ($mm^{-2}$)** | **$\delta^{13}C$ (‰)** | **LMA (g $m^{-2}$)** | **Leaf lifespan (months)** |
|---|---|---|---|---|---|---|
| **Comparisons between soil types and among species** | | | | | | |
| **Alluvial** | 16.3 ± 0.41 | 1.02 ± 0.05 | 272.8 ± 21.3 | -35.9 ± 0.26 | 8.89 ± 0.38 | 48.7 ± 6.24 |
| **Sandstone** | 11.7 ± 0.35 | 0.50 ± 0.02 | 124.6 ± 9.81 | -34.3 ± 0.30 | 9.32 ± 0.63 | 46.6 ± 3.92 |
| **Soil (*F*)** | **169.1 ***** | **147.0 ***** | **36.8 ***** | **11.9 **** | 1.05 (NS) | 0.14 (NS) |
| **Species (*F*)** | **6.01 ***** | 0.88 (NS) | **6.00 ***** | 2.87 (NS) | **7.07 ***** | **4.10 ***** |
| **Comparisons between generalist species (*S. smithiana*) growing on alluvial and sandstone soils** | | | | | | |
| **Alluvial** | 19.1 ± 0.49 | 1.19 ± 0.09 | 174.8 ± 23.4 | -34.6 ± 0.46 | 7.45 ± 0.35 | 16.7 ± 2.90 |
| **Sandstone** | 12.7 ± 0.48 | 0.53 ± 0.01 | 190.0 ± 41.8 | -34.9 ± 0.74 | 8.91 ± 0.09 | 61.9 ± 18.5 |
| **Soil (*t*)** | **9.34 ***** | **6.98 **** | -0.98 (0.344) | 0.25 (0.081) | **-3.89 *** | **-2.47 *** |

**Table 3.** Results of the principal components analysis on six leaf traits of saplings of nine dipterocarp species on two contrasting soil types at Sepilok Forest Reserve, Malaysian Borneo; results indicate the loading of variables on the principal three axes, and the correlation coefficients between each trait and the PCA axes scores. Bold text indicates significant correlations: *, *P* <0.05; **, *P* <0.01; ***, *P* <0.001.

| | **PC1** | | **PC2** | | **PC3** | |
|---|---|---|---|---|---|---|
| **Eigenvalue** | 3.156 | | 1.407 | | 0.923 | |
| **Variance (%)** | 52.6 | | 23.5 | | 15.4 | |
| | **Weighting** | **Correlation** | **Weighting** | **Correlation** | **Weighting** | **Correlation** |
| **N** | -0.519 | **-0.921***** | -0.091 | -0.108 | 0.343 | 0.330 |
| **P** | -0.516 | **-0.916***** | 0.051 | 0.061 | 0.196 | 0.188 |
| **SD** | -0.446 | **-0.793**** | 0.289 | 0.342 | 0.182 | 0.175 |
| **$\delta^{13}$C** | -0.362 | -0.643 | 0.471 | -0.558 | -0.484 | 0.465 |
| **LMA** | 0.284 | 0.504 | 0.379 | 0.449 | 0.750 | **0.720*** |
| **LL** | 0.233 | 0.413 | 0.736 | **0.873***** | -0.119 | -0.114 |

**Table 4.** Coefficients of variation that illustrate inter- and intra-specific variation of six leaf traits of saplings of nine dipterocarp species on two contrasting soil types at Sepilok Forest Reserve, Malaysian Borneo. Values represent coefficients of variation of trait values within species (upper section of table) and within soil type (lower section of table). Statistical comparisons of intraspecific variation between alluvial and sandstone species were conducted using Kruskal-Wallis tests. Bold text indicates significant effects: *, *P* <0.05; **, *P* <0.01; *** *P* <0.001.

| **Species** | **Soil-type specialisation** | **N** | **P** | **Stomatal density** | **$\delta^{13}C$** | **LMA** | **Leaf lifespan** |
|---|---|---|---|---|---|---|---|
| Interspecific variation: Coefficient of variation among species per soil type | | | | | | | |
| | Alluvial | 10.37 | 15.64 | 1.10 | 25.75 | 12.55 | 58.35 |
| | Sandstone | 5.85 | 7.17 | 2.73 | 34.76 | 17.39 | 17.99 |
| Intraspecific variation: Coefficient of variation within species | | | | | | | |
| *Shorea smithiana* | Generalist | 22.14 | 43.82 | 18.98 | 3.78 | 11.92 | 122.43 |
| *Dipterocarpus caudiferus* | Alluvial | 5.51 | 6.55 | 13.69 | 1.39 | 15.26 | 62.18 |
| *Dryobalanops lanceolata* | Alluvial | 5.83 | 24.07 | 37.93 | 4.73 | 12.10 | 60.42 |
| *Parashorea tomentella* | Alluvial | 6.67 | 28.15 | 32.04 | 3.72 | 13.99 | 91.39 |
| *Shorea xanthophylla* | Alluvial | 9.96 | 16.94 | 52.07 | 2.56 | 10.50 | 41.00 |
| *Diptercarpus acutangulus* | Sandstone | 8.38 | 18.51 | 55.59 | 2.00 | 6.81 | 35.63 |
| *Dipterocarpus grandiflorus* | Sandstone | 16.16 | 12.83 | 28.78 | 2.74 | 9.03 | 80.07 |
| *Hopea beccariana* | Sandstone | 15.95 | 19.36 | 32.53 | 2.02 | 6.97 | 46.19 |
| *Shorea multiflora* | Sandstone | 11.53 | 5.14 | 41.87 | 5.56 | 5.84 | 44.28 |
| *Difference in intraspecific variation between* | | | | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *alluvial and sandstone species (Kruskal-Wallis)* | **4.08 *** | 0.76 (NS) | 0.33 (NS) | 0.02 (NS) | **5.33 *** | 0.75 (NS) |

**Table 5.**
Type II regression parameters for log-log bivariate trait relationships for six leaf traits from saplings of nine dipterocarp species on two contrasting soil types at Sepilok Forest Reserve, Malaysian Borneo. Bold text indicates significant relationships: no asterisk, *P* < 0.1, *, *P* <0.05; **, *P* <0.01; ***, *P* <0.001.

| | **N** | **P** | **SD** | **$\delta^{13}C$** | **LMA** | **LL** |
|---|---|---|---|---|---|---|
| **N** | ------- | **0.856***** | **0.412*** | 0.171 | 0.050 | **0.331** |
| **P** | | ------- | **0.436*** | **0.331** | 0.077 | 0.181 |
| **SD** | | | ------- | **0.393*** | 0.035 | 0.028 |
| **$\delta^{13}C$** | | | | ------- | 0.129 | 0.015 |
| **LMA** | | | | | ------- | **0.369** |
| **LL** | | | | | | ------- |

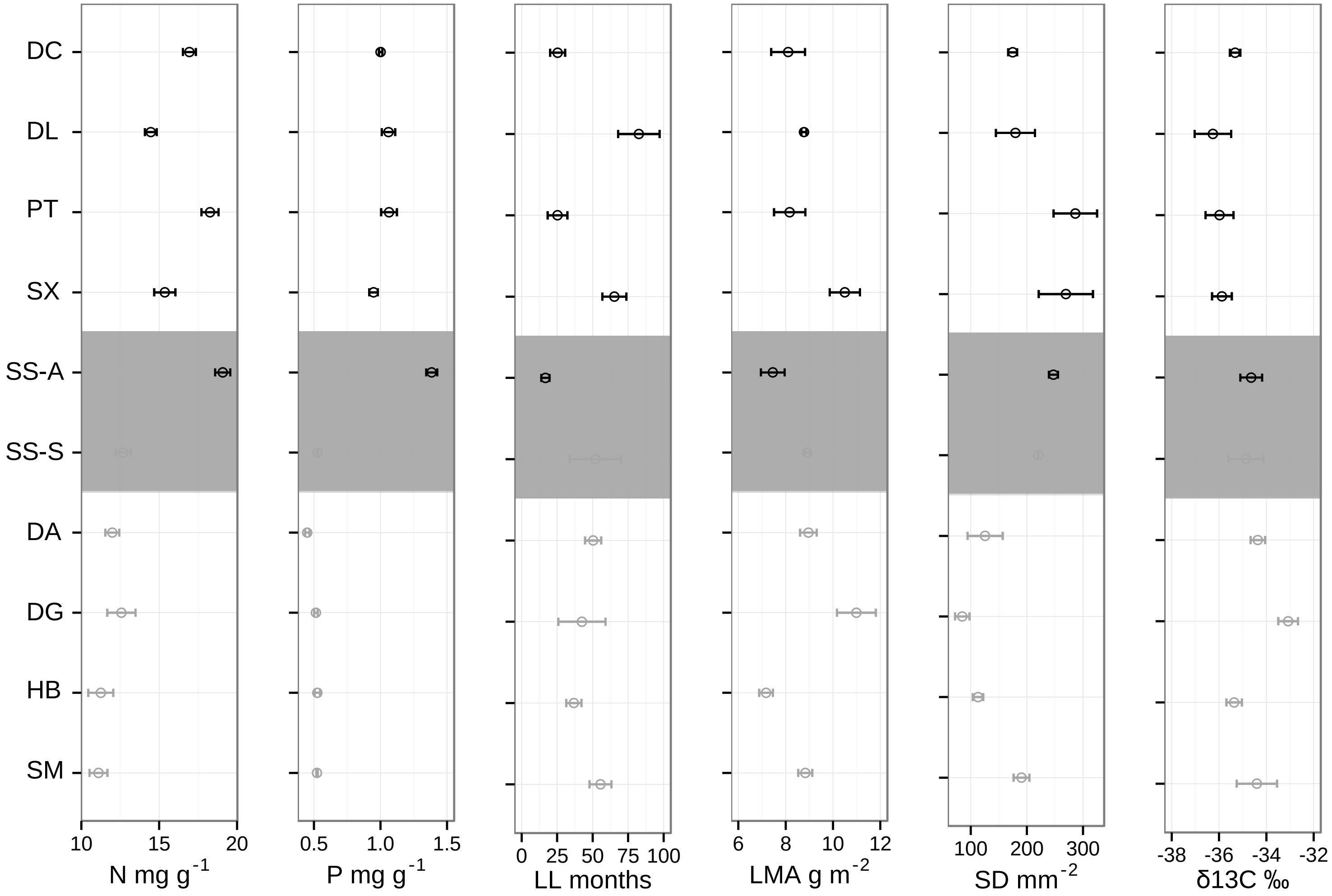

**Figure 1.** Mean trait values for saplings of nine dipterocarp species growing in alluvial (black) and sandstone soils (grey) at Sepilok Forest Reserve, Malaysian Borneo. Species abbreviations are provided in Table 1. *Shorea smithiana* is a generalist species; the shaded panel includes mean trait values from *S. smithiana* saplings growing on alluvial soil (SS-A), and sandstone soil (SS-S). Traits include foliar N concentration (N mg g$^{-1}$), foliar P concentration (P mg g$^{-1}$), stomatal density (SD mm$^{-2}$), leaf $\delta^{13}$C values (delta 13C $^{0}/_{00}$), leaf mass per area (LMA g m$^{-2}$) and leaf lifespan (LL months).

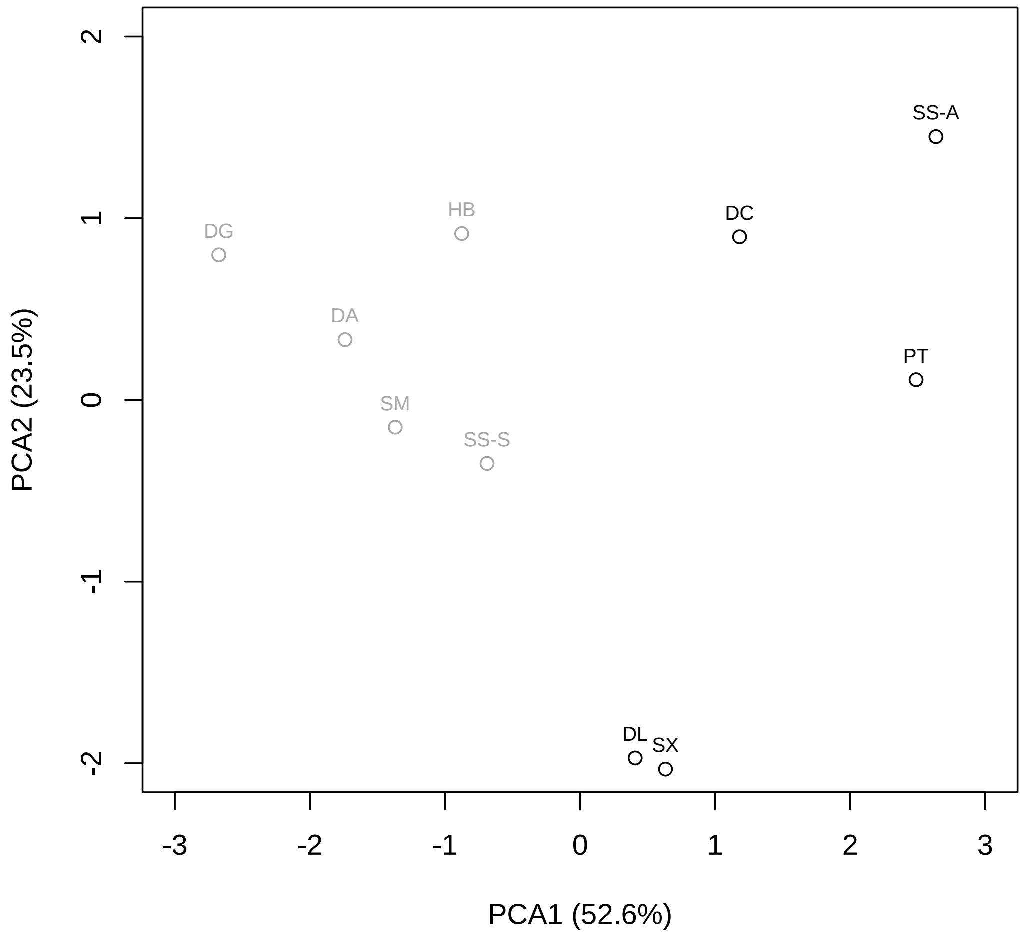

**Figure 2.** Plot of the first two components from PCA of leaf traits from saplings of nine dipterocarp species growing in alluvial (black) and sandstone soils (grey) at Sepilok Forest Reserve, Malaysian Borneo. Traits included in the analysis as in Table 2 and species abbreviations as in Table 1.

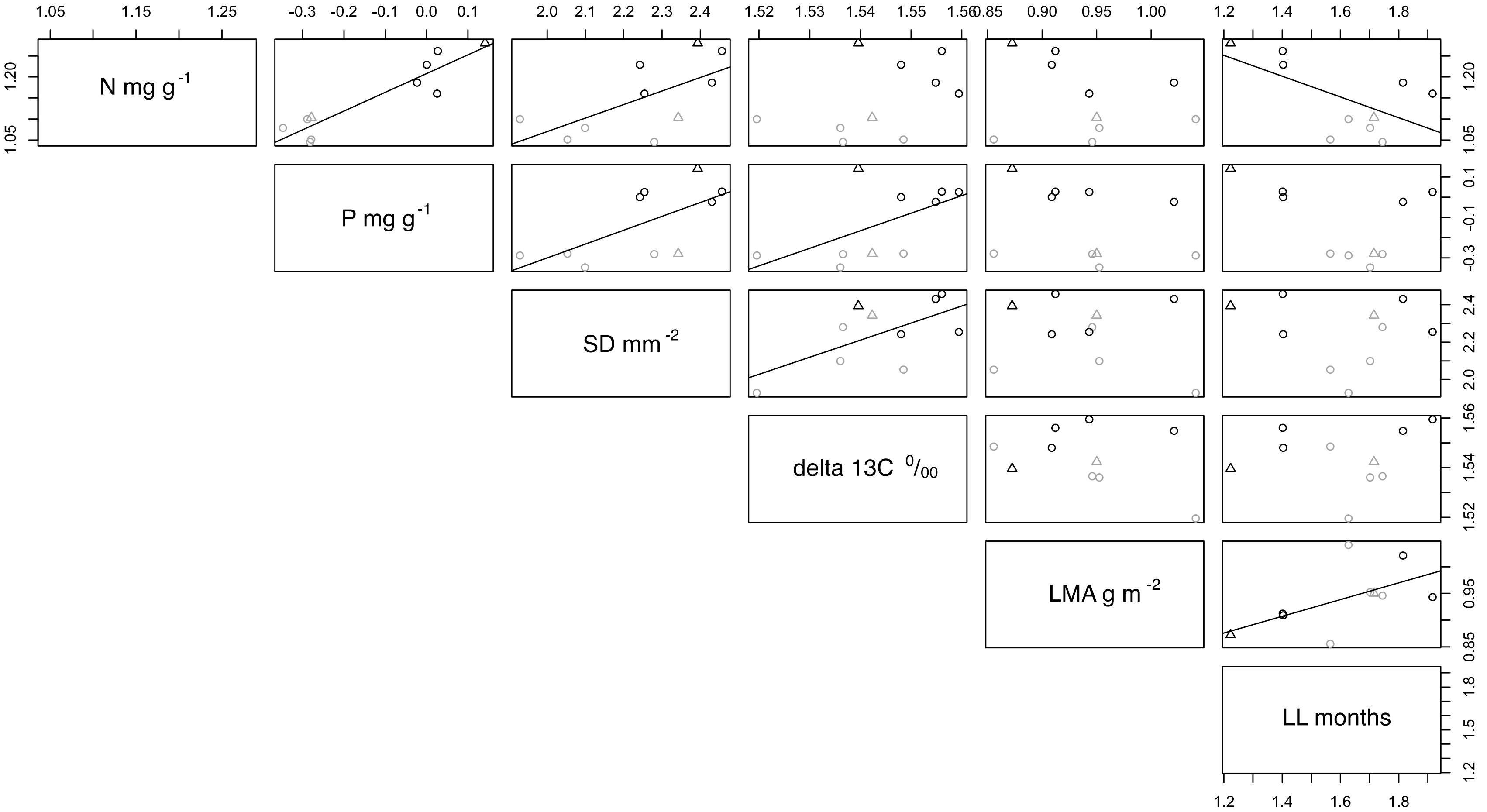

**Figure 3.** The relationships between log mean values of foliar N concentration (N mg $g^{-1}$) and mean foliar P concentration (P mg $g^{-1}$), stomatal density (SD $mm^{-2}$), leaf $\delta^{13}C$ values (delta 13C $^{0}/_{00}$), leaf mass per area (LMA g $m^{-2}$) and leaf lifespan (LL months) for saplings of nine dipterocarp species growing in alluvial (black) and sandstone soils (grey) at Sepilok Forest Reserve, Malaysian Borneo. The generalist species, *Shorea smithiana*, is represented by triangular symbols. Lines represent bivariate trait relationships for significant ($P < 0.05$), and marginally significant ($P < 0.1$) relationships (see Table 5). Values represent means per species per soil type.

Appendix 1. Environmental characteristics of experimental gap and understory sites in alluvial and sandstone forests at Sepilok Forest Reserve, Malaysian Borneo, including total daily PPFD (mol $m^{-2}\cdot d^{-1}$; Baltzer et al. 2005), yearly mean soil gravimetric water content (g $g^{-1}$) at 12–17 cm below the litter layer, and pH and concentrations of major nutrients (mg $kg^{-1}$) at 0–5 cm below the litter layer. All values represent means (± 1 SE) based on N = 5 (PPFD measurements), N = 12 (soil water content) and N = 10 (soil chemical analyses). Means with the same superscript are not significantly different ($P > 0.05$) using Tukey's HSD range test. For details of sampling and analytical techniques see Dent (2004).

| | Alluvial | | Sandstone | |
|---|---|---|---|---|
| | Gap | Understorey | Gap | Understorey |
| Direct PPFD (mol $m^{-2}\cdot d^{-1}$) | 13.3 ± 0.14 | 2.49 ± 0.14 | 10.9 ± 0.14 | 2.90 ± 0.18 |
| Diffuse PPFD (mol $m^{-2}\cdot d^{-1}$) | 1.60 ± 0.01 | 0.31 ± 0.01 | 1.02 ± 0.01 | 0.31 ± 0.01 |
| Gravimetric water content soil (g $g^{-1}$) | 0.38 ± 0.03 $^{a}$ | 0.28 ± 0.02 $^{b}$ | 0.32 ± 0.03 $^{b}$ | 0.21 ± 0.02 $^{c}$ |
| pH | 4.65 ± 0.05 $^{a}$ | 4.67 ± 0.17 $^{a}$ | 4.54 ± 0.03 $^{a}$ | 4.45 ± 0.14 $^{a}$ |
| Total P | 281.1 ± 22.39 $^{a}$ | 343.7 ± 70.50 $^{a}$ | 53.01 ± 12.11 $^{b}$ | 74.82 ± 14.11 $^{b}$ |
| Total N | 2882 ± 247 $^{a}$ | 3306 ± 276 $^{a}$ | 1046 ± 218 $^{b}$ | 1517 ± 161 $^{b}$ |
| Available P | 0.83 ± 0.17 $^{a}$ | 0.96 ± 0.22 $^{a}$ | 0.88 ± 0.35 $^{a}$ | 2.12 ± 0.87 $^{a}$ |
| $NO_{3-}$ | 17.3 ± 3.13 $^{a}$ | 13.1 ± 3.82 $^{a}$ | 5.51 ± 0.73 $^{b}$ | 5.15 ± 1.44 $^{b}$ |
| $NH_{4+}$ | 31.4 ± 5.28 $^{a}$ | 22.7 ± 2.67 $^{a}$ | 20.1 ± 4.77 $^{a}$ | 23.2 ± 3.12 $^{a}$ |
| Exchangeable K | 0.135 ± 0.023 $^{a}$ | 0.125 ± 0.022 $^{a}$ | 0.060 ± 0.012 $^{b}$ | 0.056 ± 0.007 $^{b}$ |

| | | | | |
|---|---|---|---|---|
| Exchangeable Ca | 0.446 ± 0.059 $^{a}$ | 0.354 ± 0.040 $^{a}$ | 0.137 ± 0.021 $^{b}$ | 0.111 ± 0.012 $^{b}$ |
| Exchangeable Mg | 0.148 ± 0.050 $^{a}$ | 0.134 ± 0.045 $^{a}$ | 0.038 ± 0.011 $^{b}$ | 0.039 ± 0.006 $^{b}$ |