Summary

1. Plant adaptation to gradients of light availability involves a well-studied functional trade-off, as does adaptation to gradients of nutrient availability. However, little is known about how these two major trade-offs interact and thus it remains unclear whether and how the nature of the growth-shade tolerance trade-off differs on soils of contrasting fertility.
2. We asked if juvenile growth-shade tolerance trade-offs differed in slope and elevation between tree assemblages on nutrient-rich basalt and nutrient-poor rhyolite soils in an Australian subtropical rainforest.

3. We measured the growth of, and range of light environments occupied by, juveniles (40-120 cm tall) of eight basalt specialists, six rhyolite specialists, and one generalist that was common on both substrates. In situ minimum light requirements were estimated from the 5th percentile of the distribution of naturally regenerated juveniles in relation to daily light transmittance. Stem growth was measured for 12 to 16 months across a wide range of light environments to estimate the light compensation point of growth of each species.

4. Light compensation points of growth showed nearly a 1:1 correspondence with in situ minimum light requirements of species, indicating that whole-plant carbon balance is a key driver of ecological success in low light. Minimum light requirements were negatively correlated with relative growth rate in low light, but correlated positively with growth in high light. Soil type had no effect on either the slope or the elevation of this trade-off, all species aligning around a common growth-shade tolerance trade-off, but our results do show a wider range of growth rates and shade tolerance on the nutrient-rich basalt soil than on the nutrient-poor rhyolite.

5. Our results suggest that adaptation to light availability involves fundamentally similar trade-offs on these two substrates of differing fertility. However, a wider range of growth rates and shade tolerance on the nutrient-rich basalt soil than on the nutrient-poor rhyolite may help to explain the higher species richness and greater structural complexity of forest stands on the former substrate.
Key words: basalt, dark respiration, habitat specialization, light compensation point of growth, relative growth rate, rhyolite

Introduction

The tolerance of a species to a given stress often declines when other abiotic or biotic limitations or pressures co-occur (Niinemets & Valladares 2006; Craine et al. 2012). For example, shade tolerance of woody seedlings may be reduced by drought or soil infertility (Kobe et al. 1995; Walters & Reich 1997; Sanchez-Gomez, Valladares & Zavala 2006), while drought tolerance may be reduced by herbivory due to suppressed root development following defoliation (Howe 1990). However, despite the common coexistence of multiple stresses in nature (Hall & Harcombe 1998; Niinemets & Valladares 2004; Laanisto & Niinemets 2015), variation in tolerance to simultaneous stresses is not well-understood.

Plant adaptation to gradients of nutrient and light availability involve fairly well-understood trade-offs. Adaptive trade-offs associated with light availability have been widely documented (e.g. Kobe et al. 1995; Lin et al. 2002; Baltzer & Thomas 2007; Lusk & Jorgensen 2013)--species that survive well in deep shade have physiological and morphological traits associated with low light compensation points (i.e. the light level at which net growth equals zero) (Givnish 1988; Baltzer & Thomas 2007), but these traits cause them to be out-competed by faster-growing species in high light conditions (Kobe et al. 1995; Walters & Reich 1996). This trade-off between survival in low light and growth in high light contributes to habitat specialization along light gradients within forest communities (Kobe et al. 1995; Kobe 1999; Montgomery & Chazdon 2002; Poorter & Bongers 2006). Adaptations to soils of contrasting fertility
have also been studied extensively and result in a trade-off between performance on nutrient-rich soils and persistence on nutrient-poor soils (Grime 1977; Berendse & Aerts 1987; Russo et al. 2005; Reich 2014). Plants which are capable of surviving on nutrient-poor soils, and competing well for limited nutrients, often retain nutrients efficiently by having long-lived, sclerophyllous leaves and perhaps long-lived roots (Monk 1966; Reich, Ellsworth & Walters 1991; Escudero et al. 1992; Aerts 1995). These species have low mass-based assimilation rates and their growth is often relatively unresponsive to added nutrients, preventing them from growing quickly on fertile soils (Lambers & Poorter 1992; Valladares et al. 2000). Having ‘slow’ traits (including low growth rate, low tissue nutrient concentrations and long-lived tissues) is generally adaptive for both low nutrient availability and low light availability (Reich 2014), with rapid resource acquisition adaptive at high supply rates of both. However, the same ‘slow’ traits are not necessarily the most important for each resource (Baltzer & Thomas 2007). It is thus timely to ask whether the growth-shade tolerance trade-off varies in assemblages associated with contrasting soil conditions, as this might contribute to the maintenance of species richness in forested landscapes (Svenning et al. 2004; Coomes et al. 2009; Lusk, Sendall & Clarke 2014).

It is unclear whether differences in soil nutrient availability will influence the light requirements of plants. Nutrient-poor soils might raise plants’ light compensation points of growth due to greater root mass fraction and/or greater allocation to microbial symbionts (Ibrahim, Proe & Cameron 1997; Baltzer & Thomas 2007). Both of these changes in carbon allocation would result in an increased respiratory cost due to a shift in the proportion of photosynthetic:respiratory tissues, and as a result, we may find that species are less tolerant of shade on nutrient-poor
soils relative to soils with more abundant resources, as observed experimentally for several species (Walters & Reich 2000). Alternatively, individuals or species found on nutrient-poor soils may have lower average tissue nitrogen concentrations and associated lower rates of tissue respiration (Ryan 1995; Reich et al. 2006; Reich et al. 2008), which could lower the overall respiratory cost of growth and maintenance of structural support tissues for individuals and lead to lower compensation points. It may also be asked whether nutrient availability influences the range of functional diversity in tree assemblages: is a wider range of growth rates and shade tolerance present on more fertile sites? (Coomes et al. 2009; Mason et al. 2012).

Here, we examine the effect of soil fertility on the growth-shade tolerance trade-off by comparing juvenile performance of 15 tree species differing in reputed shade tolerance on two distinct soil types in subtropical rainforest. One of the species measured was a generalist that was common on both soil types, while the remaining 14 species were specialists occurring largely on a single soil type. We quantified sapling relative growth rate (RGR) of each species as a function of light environment, and used these relationships to estimate light compensation points of growth. We also quantified the natural distribution of juveniles in relation to light availability, to estimate the minimum light levels tolerated by each species. We addressed the following questions: 1) Do light compensation points of growth accurately predict the \textit{in situ} minimum light levels occupied by species? Multiple factors such as soil microtopography or herbivory can influence the distribution of light habitats where a species occurs, and it is therefore unclear how well a single measure of physiological tolerance to shade will correspond to the darkest environments where a species is found. 2) Is there a trade-off in growth under high versus low light availability and

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does the slope and/or elevation of the trade-off differ between assemblages associated with basalt (more fertile) versus rhyolite (less fertile) soils? 3) Does low nutrient availability truncate the range of RGR and light compensation points of growth in assemblages associated with rhyolite soil compared to basalt soil? 4) Do species associated with rhyolite soil have “slow” traits such as low tissue nutrient content and low assimilation rates compared to species associated with basalt soil? 5) Can morphological or physiological leaf traits predict compensation points of growth and *in situ* minimum light requirements?

### Materials and Methods

#### Study area

The study was carried out in Nightcap National Park (NSW, Australia), which has a subtropical climate with high rainfall in the summer and autumn, and a short dry season in winter. Mean annual rainfall at the nearest meteorological station (Whian Whian) is estimated at 2,300 mm and mean annual temperature at 17.6 °C (Bureau of Meteorology, http://www.bom.gov.au/climate/). Our measurements were made in two forest stands of ca. 10 ha in area located at 28° 63’S, 153° 36’E and 28° 64’S, 153° 34’E at elevations of 200-300 meters above sea level. The first stand at Nightcap Range Road is associated with rhyolite soil, while the second stand at Rocky Creek Dam grows on basalt soil. The basalt soils are deeper and more fertile, containing much higher levels of phosphorus than rhyolite soils, as well as a significantly lower C:N ratio (Table 1). As a result of this difference in resource availability, the forest communities are quite different. Stands on basalt are much more species-rich, while stands on rhyolite are relatively low in complexity and often dominated by just a few
species (Royer et al. 2009). We chose sites on each substrate with little relief to ensure that drainage and water availability did not vary much between comparisons.

Study species

We aimed to sample subsets of species that represented the range of shade tolerance and growth rates present in old-growth assemblages on the two substrates (Table 2). To this end, we selected the most abundant of those tree species that were well-represented by juveniles in shaded understories (e.g. *Argyrodendron trifoliolatum* and *Castanospermum australe* on basalt, *Elaeocarpus sedentarius* on rhyolite), as well as the most common of those regenerating mainly on recently-disturbed open sites (e.g. *Polyscias murrayi* on basalt, *Callicoma serratifolia* on rhyolite), and some that were common in intermediate light environments (e.g. *Diploglottis australis* on basalt, *Austrostilbus swainii* on rhyolite). Previous work has confirmed the existence of a wide range of shade tolerance in assemblages on basalt (Lusk et al. 2010), but less is known about the light requirements of species associated with rhyolite. Our selection included one generalist species that was fairly common on both substrates (*Sarcopteryx stipata*).

Growth measurements

Naturally occurring saplings with an initial height of 40-120 cm were selected across as wide a range of light environments as possible, sampling along forest margins as well as within the forest stands. We selected the first plants we encountered that met our prerequisite of height. Stratified random sampling may have yielded measurements from saplings growing in a more normal distribution of light environments, but this would have been far more time-consuming and less efficient at
determining light responses (as there would have been excessive sampling at intermediate light levels). We tagged at least 30 trees per species initially, though the final sample size is less than 30 in some cases due to either mortality or the inability to relocate saplings. For the species occurring on both soil types, we tagged 30 trees per species on each substrate. Two growth parameters were measured: height (measured as the vertical distance between the stem base and the base of the highest live meristem) and basal diameter (measured as the average of the diameter on two orthogonal axes 5 cm above the soil surface). Plants were remeasured at the end of the study period, which ranged from 12 to 16 months.

Growth measurements were obtained to estimate light compensation points of growth for each species (Baltzer & Thomas 2007), following the specific methods of Lusk & Jorgensen (2013). This measure utilizes the positive relationship often seen between the light environment of individual plants and their relative growth rates (King 1991; Makana & Thomas 2005; Baltzer & Thomas 2007). The light level at which a plant experiences zero net growth (the compensation point) represents the point at which long-term gross carbon gain equals losses due to respiration, tissue turnover and herbivory. We used a non-destructive estimate of stem volume as a proxy for whole-plant biomass, which was calculated as:

\[
\text{Whole-plant biomass} = \text{stem length} \times \pi \times \text{basal radius}^2
\]

Relative growth rate (RGR) was calculated as:

\[
\text{RGR} = \frac{\ln(h_2 \times \pi (d_2/2)^2) - \ln(h_1 \times \pi (d_1/2)^2)}{(t_2 - t_1)}
\]
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. Using both diameter and height parameters in calculating growth provides a more robust growth rate measure than height alone, as height growth alone can be highly variable due to leader loss. This measure of growth is for aboveground tissues only, but because $h \times \pi(d/2)^2$ is linearly related to total biomass, RGR of aboveground tissues will correlate with RGR of total biomass.

**Hemispherical photography and minimum light requirements**

A Nikon Coolpix digital camera with a 182° fisheye adapter was used to take hemispherical photographs above each individual. Photos were taken when trees were tagged initially as well as when final growth measurements were made, and the average photosynthetic photon flux (PPFD) value was used in analyses to account for any changes in light regime over the course of the study. Photos were analyzed using the Gap Light Analyzer software package (Frazer, Canham & Lertzman 1999) to obtain the mean daily PPFD transmittance above each sapling. Cloudiness, spectral fraction, and beam fraction were estimated using MODIS satellite photos to quantify the frequency of cloud cover above our main worksites on basalt and rhyolite, during the 16-month study period. The Gap Light Analyzer software inputs include these factors, as well as site latitude and date range of the study. Thus, our estimates of mean daily PPFD transmittance account for seasonal variation in sun angle and cloudiness.
The 5\textsuperscript{th} percentile of the range of PPFD (mean daily photon flux; mol m\textsuperscript{-2}) measured for each species was used as an estimate of the minimum light level each species can tolerate (PPFD\textsubscript{5}; Table 2). Shade-tolerant species such as *A. trifoliolatum* have low PPFD\textsubscript{5} values, while light-demanding species such as *P. murrayi* have high PPFD\textsubscript{5} values.

*Leaf-level gas-exchange*

Area-based light-saturated photosynthetic capacity (*A\textsubscript{area}*) and dark respiration rates (*Rd\textsubscript{area}*) were measured on fully-expanded leaves from the outer crown of five individuals of each species using an LI-6400 (LI-COR, Lincoln, NE), with the exception of *E. sedentarius* and *C. serratifolia*. *E. sedentarius* is a protected species, so any potentially destructive measurements were not permitted. *C. serratifolia* was added to the study to improve the representativeness of our sampling of the rhyolite assemblage after gas-exchange measurements had been completed. Trees growing in microsites with 3-5 mol m\textsuperscript{-2}day\textsuperscript{-1} daily PPFD were chosen so that comparisons could be made across individuals of all species acclimated to similar levels of light availability. Environmental conditions were controlled within the leaf cuvette as follows: CO\textsubscript{2} concentration of 380 μmol mol\textsuperscript{-1}, 50-70% relative humidity and block temperature of 25°C. Irradiance was held at 1000 μmol m\textsuperscript{-2}s\textsuperscript{-1} using the LI-6400 LED light source and at 0 μmol m\textsuperscript{-2}s\textsuperscript{-1} for respiration measurements.

Specific leaf area (SLA) was calculated using one fully-expanded leaf or leaflet harvested from the outer portion of the crown of each individual tagged for growth measurements. For individuals used for gas-exchange measurements, the leaf or leaflet measured was marked to ensure that it was collected for SLA. Leaves were
scanned and the projected area was determined using the image-processing software ImageJ (Abramoff, Magelhaes & Ram 2004). All samples were oven-dried at 70°C for at least 72 hours to determine dry leaf mass. A subset of samples were ground and analyzed for nitrogen and phosphorus concentrations (ECS 4010 CHNSO Analyzer, Costech Analytical Technologies Inc., Valencia, CA).

**Statistical analysis**

Prior to analyses, mean daily photon flux was log$_{10}$ transformed, which linearized the response of growth to light and roughly normalized the distribution (Lusk & Jorgensen 2013). To model sapling relative growth rates (RGR), we utilized linear regressions with log(PPFD) as the predictor. Although other modelling of sapling growth has used nonlinear Michaelis-Menten functions (Pacala et al. 1994; Kobe 1996; Wright et al. 1998), 90% of saplings in this study were growing in <20% full sunlight. Of the individuals growing in >20% full sunlight, the majority were of the two most light-demanding species, *Callicoma serratifolia* and *Polyscias murrayi*. Approximately 95% of saplings of these species were found in <30% full sunlight. Thus, asymptotic growth rates (i.e. growth where light was not limiting) were rarely achieved and biplots indicated reasonably linear relationships between response and explanatory variables (see Appendices S1 and S2 in Supporting Information). The light level corresponding with zero net growth in regressions of RGR against log(PPFD) was assumed to characterize the light compensation point of growth for each species (Makana & Thomas 2005). The light compensation points of 10 of the 15 species fell within the data cloud, but were based on extrapolation of the RGR vs PPFD relationships for the other five (e.g. *P. murrayi* and *A. swainii*).
To determine whether compensation points differed among species, we used a likelihood ratio test to compare two models: one in which compensation points were constrained to be equal for all species, and another in which they varied. The test statistic (twice the difference in log-likelihood between the two models) is Chi-square with degrees of freedom equal to the difference in the number of parameters in the two models (Pawitan 2006). Minimum light requirements (PPFD$_5$) were regressed against light compensation points of growth to test whether compensation points accurately predicted the minimum light levels occupied by species. We ran a general linear model (GLM) using compensation points, soil type and their interaction as independent variables to determine whether this relationship differed among soil substrates.

To test for a trade-off between growth in high and low light, we compared linear regression fits of species’ minimum light requirements (PPFD$_5$) and RGR estimated at 2, 4, 8, and 12 mol m$^{-2}$ day$^{-1}$. Using the species RGR estimates from each of these four light levels, we ran general linear models to determine whether the trade-off in RGR differed among soil substrates. These models included PPFD$_5$, soil type and their interaction as independent variables. Because some of the above relationships utilize extrapolated RGR of species at light levels where they do not often occur (e.g. *Polyscias murrayi* is rarely found in light levels less than 5 mol m$^{-2}$ day$^{-1}$), we also examined the relationship between species’ minimum light requirements and the slopes of the RGR-mean daily photon flux fits (this slope indicates responsiveness of growth of each species to light) from Appendices S1 and S2. Here, we compared fits of both linear and non-linear regression analyses, and present results using an
exponential fit as it seemed most appropriate based on the $R^2$-value and pattern of residuals.

Linear regression analyses were used to examine the relationships of minimum light requirements with the following physiological and morphological traits: specific leaf area (SLA), percent leaf nitrogen and phosphorus, area-based maximum photosynthetic rates ($A_{area}$) and area-based dark respiration rates ($R_{darea}$). We pooled data from both soil types for these analyses because of the low number of species measured on rhyolite (see leaf-level gas-exchange section above for details).

We used two-sample $t$-tests to examine average species differences in compensation points and physiological and morphological traits across soil substrates. Two-sample $t$-tests were also used to compare these traits across soil types for our generalist species, *Sarcopteryx stipata*. All statistical analyses were conducted in JMP statistical analysis software (JMP 11, SAS Institute, Cary, NC).

**Results**

Relative growth rate (RGR) of all species was positively related to daily PPFD transmittance ($p<0.05$), with light availability explaining between 16 and 70% of variation in growth among individuals within each species (Fig. 1; Appendices S1 and S2). Light compensation points of growth estimated from these relationships were significantly correlated with *in situ* minimum light requirements (PPFD$_5$) of species based on their microhabitat distributions (Fig. 2), these two variables scaling close to 1:1 on a log-log basis (slope=$1.02 \pm 0.13$ SE). This relationship was similar on both soil substrates (rhyolite slope=$1.37 \pm 0.17$ SE, basalt slope=$1.03 \pm 0.25$ SE), as evidenced by the lack of significant effect of soil in the GLM analysis, or of the

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interaction of soil x compensation point. Compensation point estimates varied significantly among species based on the likelihood ratio test described above ($\chi^2=14.22$, $p=0.012$), and a wider range of compensation points was observed on nutrient-rich basalt soils. Estimates of compensation points ranged from 1.03 to 1.92 mol m$^{-2}$ day$^{-1}$ for rhyolite species and 0.85 to 3.35 mol m$^{-2}$ day$^{-1}$ for basalt species (Figs 1 and 2). These values reflect a range from $\approx 2$ to 7% of full light.

Those species with the lowest in situ light requirements were also the fastest growing species in low light. Predicted RGR under low light availability (2 and 4 mol m$^{-2}$ day$^{-1}$) was strongly negatively related to PPFD$_5$ (slope=-0.23, $p<0.01$; slope=-0.13, $p<0.01$, respectively)---i.e., under low light availability, species with lower in situ light requirements had higher RGR than those with higher light requirements---but when light was less limiting, this relationship was neutral (slope=0.05, $p=0.381$) or marginally positive (slope=0.11, $p=0.073$; Fig. 3). These relationships were similar on both soil types under all light levels, as evidenced by the lack of significant soil main effect or soil x PPFD$_5$ interactions in the GLM analyses ($p>0.05$ in all cases), indicating that the growth-shade tolerance trade-off was similar on both soil types. Responsiveness of growth to light as indicated by the RGR-mean daily photon flux slopes, was also significantly related to PPFD$_5$ using an exponential fit ($p<0.001$), with more light-demanding species having steeper slopes than shade tolerant species (Fig. 4).

Leaf traits differed substantially among species and across soil types, but were not always significant predictors of minimum light requirements (PPFD$_5$) or light compensation points of growth (Table 3). Only dark respiration rates ($R_{d,area}$) and

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light-saturated photosynthetic rates \( (A_{\text{area}}) \) were significantly related to minimum light requirements \( (p=0.008 \) and \( p=0.011 \), respectively; Fig 5). Specific leaf area (SLA) and percent nitrogen \((N)\) and phosphorus \((P)\) were not significantly related to minimum light requirements \( (p=0.352, p=0.415 \) and \( p=0.551 \), respectively; data not shown). \( R_{\text{darkarea}} \) was the only significant predictor of light compensation points, though \( A_{\text{area}} \) was marginally significant in this respect \( (p=0.004 \) and \( p=0.064 \), respectively). Leaf gas exchange rates and nutrient content were higher on average in species growing on basalt soil, though mean minimum light requirements \( (\text{PPFD}_5) \) and compensation points did not differ significantly among soil types (Table 4). Leaf nitrogen \((N)\) and phosphorus \((P)\) levels were nearly twice as high for basalt species, specific leaf area \((\text{SLA})\) and dark respiration rates \( (R_{\text{darkarea}}) \) were approximately 50% higher, and maximum photosynthetic rates \( (A_{\text{area}}) \) were 25% higher on average (Table 4).

* SARCOPTERYX STIPATA * individuals growing on basalt had lower minimum light requirements \( (\text{PPFD}_5) \) compared to those growing on rhyolite (Table 5). * S. stipata * on basalt also achieved a higher relative growth rate in high light \( (10 \text{ mol m}^{-2} \text{ day}^{-1}) \). Gas-exchange rates did not vary by substrate, though SLA and percent \( N \) and \( P \) were significantly higher for individuals growing on basalt (Table 5).

**Discussion**

Our study showed a strong growth-shade tolerance trade-off for 40-120 cm-tall juvenile evergreen trees (Fig. 3). The species with the lowest minimum light requirements \( \) (based on microhabitat distributions) outgrew all others in deep shade and had the lowest plant-scale light compensation points, but were outgrown at higher light levels and had a lower responsiveness to increasing light availability. We asked
whether this growth-shade tolerance trade-off would differ for species associated with two soil types; nutrient-rich basalt soils and nutrient-poor rhyolite soils. Because species on rhyolite had lower levels of tissue nutrients and assimilation rates (Table 4), they were expected to be less responsive to changes in light availability than species growing on fertile soils (Kobe et al. 1995; Walters & Reich 1996, Walters & Reich 2000). This hypothesis was not supported, and instead our results indicate that this trade-off is similar on both soil types; as evidenced by similar slopes of growth vs. PPFD across the range of light requirements (Figures 1 and 3).

Our results contrast with studies reporting similar growth rate rankings of species under high and low light availability (Kitajima 1994; Poorter 1999). Rather, our results add to a large body of evidence for rank changes or reversals in growth rates, with shade-tolerant species showing (often subtle) growth rate advantages in very low light (e.g. Moad 1992; Sack & Grubb 2001; Montgomery & Chazdon 2002; Baltzer & Thomas 2007; Lusk & Jorgensen 2013). We observed substantial rank changes in relative growth rates (RGR) across light environments on both substrates (Fig. 3): for example, the two slowest-growing species on both substrates at a light level of 2 mol m\(^{-2}\)day\(^{-1}\) (*Callicoma serratifolia* and *Polyscias murrayi*) became the two fastest growers at 12 mol m\(^{-2}\)day\(^{-1}\), while other species that were among the fastest growers at a light level of 2 mol m\(^{-2}\)day\(^{-1}\) (e.g. *Mallotus philippensis* and *Argyrogendron trifoliolatum*) fell to middle or lower growth rankings at 12 mol m\(^{-2}\)day\(^{-1}\).

Minimum light requirements of naturally regenerated individuals correlated with the ability to maintain a positive carbon balance. Light compensation points of growth (mol m\(^{-2}\)day\(^{-1}\)) showed nearly a 1:1 correspondence with distribution-based minimum
light requirements (mol m$^{-2}$day$^{-1}$) of species (Fig. 2), suggesting that although each metric has limitations, in this instance they appear to capture essential aspects of performance and distribution. Light compensation points differed significantly among species, and for the most part, corresponded well with previous reports of the relative shade tolerance of our measured species (Kariuki et al. 2006; Lusk et al. 2010), though little was previously known about the light requirements of species associated with rhyolite. We observed that the range of compensation points was wider on basalt soils than on rhyolite (Fig. 1), with some species on basalt (Sarcopteryx stipata and Argyrodendron trifoliolatum) able to survive under light conditions that were approximately 15% lower than any on rhyolite. Moreover, assemblages on basalt included species with higher light requirements than those associated with rhyolite soils. The lack of species found in extremely low light on rhyolite suggests that the cost of adaptation to low nutrient availability may truncate the lower end of the range of compensation points on poor soils.

The relatively weak relationships of light availability with growth of some species may be due to factors such as measurement error, variation in soil conditions, or herbivory. Understory saplings sometimes have crooked stems that are difficult to measure accurately, so measurement error is likely responsible for some of this scatter. Though we took care to sample in areas with similar relief to minimize spatial variation in soil parameters, saplings growing only a few meters apart could experience different conditions due to variability in microtopography. For example, Royer et al. (2009) found that soil depth varied from 30 to 80 cm on rhyolite, while variation in topography and soil depth was minimal on basalt. Spatial variation in belowground resource availability thus also likely contributed to the weak
relationships between light availability and growth of some species on the rhyolite. However, in closed-canopy mesic forests, light availability has been shown to explain most of the variation in sapling growth, with fine-scale variation in water and soil nutrients explaining far less (Pacala et al. 1994; Finzi & Canham 2000). Only two species, Diploglottis australis and Flindersia schottiana showed signs of intense damage by natural enemies during our study. D. australis was damaged by stem borers, while leaf galls were present on most F. schottiana individuals. Herbivore damage and parasitism negatively affects plant growth (Schaffer & Mason 1990), again possibly weakening the overall growth vs. light availability relationships. However, our fits (average $R^2 = 0.40$) are similar (very slightly weaker) than those presented by Baltzer & Thomas (2007) and Lusk, Jorgensen & Bellingham (2015) (average $R^2 = 0.45$ and 0.42, respectively), and are stronger than those presented by Lusk & Jorgensen (2013) (average $R^2 = 0.21$). This suggests that the measurement approach we used worked as well as in these other studies.

As expected, species growing on nutrient-poor rhyolite soils had lower leaf nitrogen and dark respiration rates on average (Table 4), which should act to lower light requirements relative to basalt species. However, plants adapted to and growing on nutrient-poor soils have been shown to produce larger root fractions compared to those on fertile soils (Reich 2002; Paz 2003); all else being equal, this should reduce the ratio of whole-plant carbon gain to respiratory losses (Baltzer & Thomas 2007). Species associated with phosphorus-poor soils also tend to have smaller leaves (McDonald et al. 2003), which results in a higher degree of self-shading and lower light interception efficiency (Falster & Westoby 2003). These factors would lead to increased light requirements on average for species adapted to nutrient-poor soils.
Thus, it is possible that the effects of tissue-specific respiration rates and biomass allocation may cancel each other out, resulting in similar growth-shade tolerance trade-offs on the two different substrates. Light-demanding species on basalt had the highest observed light requirements and compensation points, most likely due to traits such as short leaf lifespan and high dark respiration rates (Poorter & Bongers 2006).

Like Baltzer and Thomas (2007), we found the leaf-level trait most closely related to the compensation point was dark respiration rate. Photosynthesis and respiration rates had similar predictive power for minimum light requirements, but as net photosynthetic capacity was lower in species that had higher carbon gain in low light, it is unlikely that this contributes directly to their shade tolerance. The relationship of respiration rate to light compensation point and minimum light requirements provides further support (cf. Reich et al. 1998; Lusk & Reich 2000) for the long-standing hypothesis that shade tolerant species have inherently lower tissue respiratory costs (Grime 1965). Although this study only focused on leaf-level traits, it has also been shown that shade tolerant species have lower whole-plant respiratory costs (Reich et al. 1998; Walters & Reich 1999), which is of greatest consequence in deeply shaded conditions when dark respiration is likely to be a greater fraction of whole-plant carbon balance than in high-light environments (Givnish 1988; Walters, Kruger & Reich 1993). Therefore, adaptation to low light availability is achieved through low dark respiration rates and associated carbon losses, as well as low rates of tissue turnover (Reich et al. 2003).
There are two mechanisms by which differential resource availability on the two soil types could contribute to differences in compensation points observed for the generalist species, *Sarcopteryx stipata*. Saplings growing on rhyolite had lower tissue nutrient concentrations but higher compensation points, indicating that differences in compensation points are likely not driven by differences in leaf nutrients. Instead, it is more likely that traits such as increased root fractions are driving the increase on rhyolite (Reich 2002; Paz 2003; Poorter et al. 2012). Alternatively, differences in compensation points across soil types could be due to differences in light availability between the two habitats. Understory light levels were higher on average on rhyolite soil, and therefore differences in compensation points could be a function of species acclimation to light and have little to do with nutrient availability.

Despite the clear evidence that differences in growth-light relationships among species correspond with habitat light affinity, it is important to note that shade tolerance is known to vary with ontogeny (Lusk 2004). We measured a relatively narrow range of sapling size, but traits associated with shade tolerance, such as leaf gas-exchange and specific leaf area, may still have varied among our sampled trees due to size differences (Thomas 2010; Sendall & Reich 2013). Likewise, ontogenetic patterns of RGR and allocation may differ for species with different shade tolerance rankings. For example, Lusk (2004) observed significant size-related declines in root mass fraction for shade tolerant species, while light-demanders experienced no change. Research specifically examining ontogenetic variation in shade tolerance, RGR, and related traits are necessary to clarify this point. Additionally, due to our method of sampling trees, a few of our estimates of compensation points are largely influenced by the growth of relatively few plants at the tails of the PPFD distribution.
We conclude that species growing on basaltic and rhyolitic soils aligned around a common growth versus shade tolerance trade-off. However, the range of shade tolerance and growth rates observed on nutrient-rich basalt was wider than on nutrient-poor rhyolite. We are confident that we measured the fastest-growing common species on both soils: *Polyscias murrayi* on basalt and *Callicoma serratifolia* on rhyolite. Our data also include the species that are most common as juveniles in forest understories on both substrates: *Argyroderon trifoliolatum* on basalt *Sarcopteryx stipata* on rhyolite. However, there may be rare species that are more shade-tolerant than any of those measured here. The differences we documented between populations of *Sarcopteryx stipata* growing on the two soil types also indicate some degree of divergence due to soil type, potentially from adaptations to belowground resources or differences in understory light availability, but not to the degree that the growth trade-off was affected.

**Acknowledgements**

We thank Rob Kooymans for assistance locating suitable forest stands and the New South Wales National Parks and Wildlife Service for permission to work at Nightcap National Park. This work was supported by ARC Discovery Project 1094606 and the Wilderness Research Foundation.

**Data Accessibility**

Data deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.j09v3 (Sendall et al. 2015)

**Literature cited**


Table 1. Nutrient concentrations (Mean ± SE) in topsoil on basalt and rhyolite substrates in Nightcap National Park.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Total N (%)</th>
<th>Total C (%)</th>
<th>C:N</th>
<th>Total P (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basalt</td>
<td>0.49 ± 0.13</td>
<td>5.6 ± 1.4</td>
<td>11.3 ± 0.4</td>
<td>1709 ± 313</td>
</tr>
<tr>
<td>Rhyolite</td>
<td>0.45 ± 0.07</td>
<td>11.6 ± 2.3</td>
<td>26.0 ± 1.4</td>
<td>172 ± 5</td>
</tr>
</tbody>
</table>

Table 2. Study species with light compensation points of growth (LCP; mol m\(^{-2}\)day\(^{-1}\)) and the 5\(^{th}\) percentile of the distribution of juveniles (40-120 cm tall) in relation to photosynthetic photon flux transmittance (PPFD\(_{5}\); mol m\(^{-2}\)day\(^{-1}\)) as indicators of minimum light requirements for each species growing in a subtropical rainforest. Species growing on two soil types were measured: nutrient-rich basalt and nutrient-poor rhyolite. *Sarcopteryx stipata* was present on both soil types and is therefore classified as a generalist.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Species</th>
<th>Family</th>
<th>LCP</th>
<th>PPFD(_{5})</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basalt</td>
<td><em>Sarcopteryx stipata</em> (F.Muell) Radlk.</td>
<td>Sapindaceae</td>
<td>0.84</td>
<td>0.69</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td><em>Argyrodon trifoliolatum</em> F.Muell</td>
<td>Malvaceae</td>
<td>0.98</td>
<td>0.80</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td><em>Mallotus philippensis</em> (Lam.) Muell.Arg.</td>
<td>Euphorbiaceae</td>
<td>0.86</td>
<td>1.04</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td><em>Castanospermum australe</em> A.Cunn &amp; C.Fraser ex Hook.</td>
<td>Fabaceae</td>
<td>1.15</td>
<td>1.22</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td><em>Diploglottis australis</em> (G.Don) Radlk.</td>
<td>Sapindaceae</td>
<td>1.98</td>
<td>1.47</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td><em>Toona australis</em> (Kuntze) Harms</td>
<td>Meliaceae</td>
<td>2.57</td>
<td>2.31</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td><em>Flindersia schottiana</em> F.Muell</td>
<td>Rutaceae</td>
<td>2.38</td>
<td>2.41</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td><em>Polyscias elegans</em> (C.Moore &amp; F.Muell) Harms</td>
<td>Araliaceae</td>
<td>3.34</td>
<td>2.50</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td><em>Polyscias murrayi</em> (F.Muell) Harms</td>
<td>Araliaceae</td>
<td>2.87</td>
<td>3.64</td>
<td>32</td>
</tr>
<tr>
<td>Rhyolite</td>
<td><em>Elaeocarpus sedentarius</em> (G.Read AQ 562114)</td>
<td>Elaeocarpaceae</td>
<td>1.03</td>
<td>0.79</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td><em>Sarcopteryx stipata</em> (F.Muell) Radlk.</td>
<td>Sapindaceae</td>
<td>1.22</td>
<td>0.90</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td><em>Austrobuxus swanii</em> (Beuzev. &amp; C.T.White) Airy Shaw</td>
<td>Picrodendraceae</td>
<td>1.28</td>
<td>1.45</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td><em>Cryptocarya rigida</em> Meisn.</td>
<td>Lauraceae</td>
<td>1.34</td>
<td>1.52</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td><em>Schizomeria ovata</em> D.Don</td>
<td>Cunoniaceae</td>
<td>1.41</td>
<td>1.59</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td><em>Elaeocarpus reticulatus</em> Sm.</td>
<td>Elaeocarpaceae</td>
<td>1.46</td>
<td>1.73</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td><em>Callicoma serratifolia</em> Andrews</td>
<td>Cunoniaceae</td>
<td>1.92</td>
<td>2.38</td>
<td>27</td>
</tr>
</tbody>
</table>
Table 3. Summary of regression analyses including leaf dark respiration (Rdarea) and photosynthesis (Aarea), specific leaf area (SLA), and percent nitrogen (N) and phosphorus (P) as predictors, and *in situ* minimum light requirements (PPFD5) and light compensation points of growth (LCP) as dependent variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PPFD5 (mol m⁻²day⁻¹)</th>
<th>LCP (mol m⁻²day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R²</td>
<td>Slope</td>
</tr>
<tr>
<td>Rdarea (μmol m⁻²s⁻¹)</td>
<td>0.46</td>
<td>3.24</td>
</tr>
<tr>
<td>Aarea (μmol m⁻²s⁻¹)</td>
<td>0.43</td>
<td>0.42</td>
</tr>
<tr>
<td>SLA (cm²g⁻¹)</td>
<td>0.07</td>
<td>0.01</td>
</tr>
<tr>
<td>Percent N</td>
<td>0.06</td>
<td>0.32</td>
</tr>
<tr>
<td>Percent P</td>
<td>0.03</td>
<td>2.71</td>
</tr>
</tbody>
</table>

Table 4. Comparison of sapling traits (Mean ± SE) including minimum light requirements (PPFD5), light compensation points of growth (LCP), specific leaf area (SLA), percent nitrogen (N) and phosphorus (P), and area-based rates of leaf photosynthesis (Aarea) and respiration (Rdarea). Traits were averaged for 15 species growing on two soil substrates in a subtropical rainforest. Eight species were measured on nutrient-rich basalt, six species were measured on nutrient-poor rhyolite, and one generalist species was measured on both substrates. Letters designate means that differ significantly (p < 0.05) from a two-sample t-test.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>PPFD₅ (mol m⁻²day⁻¹)</th>
<th>LCP (mol m⁻²day⁻¹)</th>
<th>SLA (cm² g⁻¹)</th>
<th>Percent N</th>
<th>Percent P</th>
<th>Aarea (μmol m⁻²s⁻¹)</th>
<th>Rdarea (μmol m⁻²s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basalt</td>
<td>1.79 ± 0.38 (a)</td>
<td>1.88 ± 0.32 (a)</td>
<td>247 ± 27 (a)</td>
<td>2.37 ± 0.12 (a)</td>
<td>0.15 ± 0.012 (a)</td>
<td>5.5 ± 0.41 (a)</td>
<td>0.66 ± 0.04 (a)</td>
</tr>
<tr>
<td>Rhyolite</td>
<td>1.48 ± 0.24 (a)</td>
<td>1.38 ± 0.10 (a)</td>
<td>168 ± 9.4 (b)</td>
<td>1.33 ± 0.10 (b)</td>
<td>0.07 ± 0.007 (b)</td>
<td>4.4 ± 0.52 (b)</td>
<td>0.41 ± 0.04 (b)</td>
</tr>
</tbody>
</table>

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Table 5. Comparison of sapling traits (Mean ± SE) for *Sarcopteryx stipata* juveniles growing in a subtropical rainforest (*n* = sample size per measurement type). Traits included minimum light requirements (PPFD$_5$), relative growth rate (RGR) at high light availability, specific leaf area (SLA), percent nitrogen (N) and phosphorus (P), and area-based rates of leaf photosynthesis (A$_{area}$) and respiration (Rd$_{area}$). Individuals were measured on two soil substrates: nutrient-rich basalt and nutrient-poor rhyolite. Letters designate means that differ significantly (*p* < 0.05) from a two-sample t-test.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>PPFD$_5$ (mol m$^{-2}$day$^{-1}$)</th>
<th>RGR at 10 mol m$^{-2}$ day$^{-1}$</th>
<th>SLA (cm$^2$ g$^{-1}$)</th>
<th>n</th>
<th>Percent N</th>
<th>n</th>
<th>Percent P</th>
<th>n</th>
<th>A$_{area}$ (μmol m$^{-2}$s$^{-1}$)</th>
<th>Rd$_{area}$ (μmol m$^{-2}$s$^{-1}$)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basalt</td>
<td>0.69</td>
<td>0.91</td>
<td>204 ± 6.4 (a)</td>
<td>30</td>
<td>1.94 ± 0.05 (a)</td>
<td>15</td>
<td>0.10 ± 0.005 (a)</td>
<td>9</td>
<td>5.1 ± 0.38 (a)</td>
<td>0.63 ± 0.03 (a)</td>
<td>5</td>
</tr>
<tr>
<td>Rhyolite</td>
<td>0.90</td>
<td>0.77</td>
<td>184 ± 6.2 (b)</td>
<td>33</td>
<td>1.66 ± 0.05 (b)</td>
<td>15</td>
<td>0.09 ± 0.006 (b)</td>
<td>9</td>
<td>5.9 ± 0.50 (a)</td>
<td>0.54 ± 0.16 (a)</td>
<td>5</td>
</tr>
</tbody>
</table>
Figure Legends

Figure 1. Fits of the relationship between relative growth rate and mean daily photon flux for juveniles of nine tree species growing on nutrient-rich basalt soils and seven tree species growing on nutrient-poor rhyolite soils. The dashed horizontal line represents zero growth. The light level corresponding with the point at which each species’ fit crosses the dashed line is its light compensation point of growth. Individual species fits and significance levels can be found Appendices S1 and S2.

Figure 2. Relationship between minimum light requirements (PPFD₅) and light compensation points of growth for saplings of 14 tree species growing on one of two soil substrates in a subtropical rainforest, and 1 species growing on both soils. The line shown is the pooled linear regression fit for all species; fits for both soil types are not shown as they did not differ significantly (i.e. neither the soil main effect nor the soil x compensation point interaction term was <0.05 in an analysis including both terms and their interaction). Regression equation: \( \log(\text{PPFD}_5) = -0.014 + 1.015 \times \log(\text{compensation point}) \).

Figure 3. Relationship between relative growth rate (RGR) and minimum light requirements (PPFD₅) for saplings of 14 tree species growing on one of two soil substrates in a subtropical rainforest, and 1 species growing on both soils. Each data point corresponds to a single species; RGR in each light level was estimated from the regression fits shown in Appendices S1 and S2. The lines shown are the pooled linear regression fits for all species; fits for both soil types are not shown as they did not differ significantly (i.e. neither the soil main effect nor the soil x PPFD₅ interaction terms were <0.05 in GLM analyses including both terms and their interaction). No line is shown for the fit at 8 mol m⁻²day⁻¹ because this fit was not significant, while a dashed line is shown at 12 mol m⁻²day⁻¹ because the fit was marginally significant (p<0.10).

Figure 4. Relationship of responsiveness of growth to light and minimum light requirements (PPFD₅) for saplings of 14 tree species growing on one of two soil substrates in a subtropical rainforest, and 1 species growing on both soils. Responsiveness of growth to light is assessed by the slope of the relationship of RGR to light availability. Each data point corresponds to a single species. The line shown is the pooled fit for all species. Nonlinear regression equation: slope = 0.367 x \exp(0.545 \times \text{PPFD}_5).

Figure 5. Relationships between minimum light requirements (PPFD₅) and area-based rates of leaf respiration (Rdarea) and photosynthesis (Aarea) for 14 tree species growing on one of two soil substrates in a subtropical rainforest, and 1 species growing on both soils. Each data point corresponds to the average value for a single species. Filled circles represent species growing on basalt and open circles represent species growing on rhyolite.