



Light availability drives tree seedling success in a subtropical coastal dune forest in South Africa



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ABSTRACT

In subtropical coastal dune forests of South Africa, the microenvironment of tree seedlings is largely influenced by a pervasive understorey woody herb, *Isoglossa woodii*. We examined whether the additional shading by *I. woodii* explains the competitive response of tree seedlings from these forests. Seedlings of four common mid- to late-successional tree species (*Diospyros natalensis*, *Euclea racemosa*, *Sideroxylon inerme* and *Apodytes dimidiata*) were grown at three densities of *I. woodii* in a common garden experiment under greenhouse conditions. The seedlings were grown at 1.6% and 13.5% of full sunlight and supplied with 1% and 10% nitrogen in half-strength Hoagland's nutrient solution. Total biomass and biomass allocation parameters were used to measure the competitive response of the seedlings. Seedlings attained maximum biomass at high light and high nutrient levels and showed species- and light-specific responses to biomass of *I. woodii* neighbours. Seedlings' allocation to roots increased with increasing light levels but decreased at higher nutrient levels. The leaf mass fraction (LMF) response to light and nutrient levels was opposite to that shown by root allocation. Specific leaf area (SLA) and leaf area ratio (LAR) decreased with increasing light conditions but were not responsive to manipulation of nutrients. The presence of *I. woodii* neighbours reduced LMF whilst the responses of SLA to neighbours depended on the light level and species. Leaf trait responses to manipulation of light conditions, *I. woodii* neighbour density and soil nutrient concentration are complex but overall demonstrate an overwhelming role of light in influencing seedling establishment in coastal dune forests. The competitive response of these seedlings to low irradiance reiterates the notion of phenotypic clustering at the seedling stage amongst shade tolerant tree species, which promotes seedling persistence and gradual transition into the tree layer. Our results highlight the role of additional understorey shading by the herb stratum in influencing tree recruitment dynamics and ultimately tree community structure in many of Africa's tropical lowland forests.

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1. Introduction

The physical environment for tree recruitment in closed canopy forests may be modified by ubiquitous understorey plants (George and Bazzaz, 1999). In tropical and temperate forest communities, understorey plants have a profound effect on tree recruitment (Nilsen et al., 2001; George and Bazzaz, 2003; Griffiths et al., 2007; Tsvuura et al., 2010). Their influence is often negative, and may include transfer of herbivorous insects and pathogens from overstorey plants to seedlings, and size asymmetric competition for resources between tree seedlings and the understorey (Denslow et al., 1991; Horsley, 1993; Abe et al., 2001; Nilsen et al., 2001). However, understorey plants may

also have positive effects on tree regeneration, for example, through promoting hydraulic lift (Dawson, 1996; Brooks et al., 2002). These influences may determine the density, species composition and size structure of tree seedlings.

Tree seedling recruitment in subtropical coastal dune forests of South Africa is influenced by the pervasive understorey herb, *Isoglossa woodii* C.B. Clarke (Acanthaceae). The species reproduces and regenerates synchronously within dense (4–10 stems m⁻²) and relatively tall (± 2 m) monospecific stands in the understorey that can extend for thousands of hectares (Griffiths et al., 2010; Tsvuura et al., 2011). During its vegetative stages, the herb filters and reduces the light reaching the forest floor to < 1% of photosynthetically active radiation (PAR). In general, low levels of PAR reach the seedling stratum in forest ecosystems (Chazdon et al., 1996; George and Bazzaz, 2003). The low levels of PAR in these dune forests may be limiting for tree seedling establishment (Griffiths et al., 2007; Tsvuura et al., 2007, 2010, 2012). Moreover, herbaceous understorey vegetation can compete with or modify nutrients and moisture for woody seedlings whose roots are initially in the superficial layers of the soil alongside those of the herb layer. Hence,

Abbreviations: SLA, Specific leaf area; LAR, Leaf area ratio; LMF, Leaf mass fraction; RMF, Root mass fraction; SMF, Stem mass fraction.

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understorey vegetation may suppress seedling establishment in closed canopy forests (Denslow et al., 1991).

A suppressive understorey comprising species that are different to the overstorey is common in African and some Asian forests (Richards, 1963; Chapman et al., 1999; Carine and Scotland, 2000; Fashing and Gathua, 2004; Meyer and Laverigne, 2004). In particular, *I. woodii* and other Acanthaceae herbs are abundant in the understorey of African forests (Struhsaker, 1997; Fashing and Gathua, 2004; Paul et al., 2004; Griffiths et al., 2007). Understanding the effects of a dominant herbaceous understorey on tree seedling establishment and on the composition of the tree species community and its dynamics is essential for understanding ecological succession in African forests (Struhsaker, 1997; Paul et al., 2004; Lawes and Chapman, 2006; Griffiths et al., 2007; Tsvuura et al., 2010, 2011).

The *I. woodii* understorey may be a selective ecological filter that shapes the abundance, structure, species composition, and species interactions of trees that constitute the overcanopy layer (Chapman et al., 1999; Griffiths et al., 2007; Tsvuura et al., 2010, 2012). In particular, *I. woodii* may create a light regime on the forest floor that favours species whose seedlings are tolerant of deep shade. An extension of this view predicts phenotypic clustering, whereby the dominance of *I. woodii* and its relatively long maturation time has selected against light demanding tree species, which have therefore been progressively lost from the community (Tsvuura et al., 2010). Here, we investigate whether morphological traits of selected representative tree species from coastal dune forests are consistent with predictions of ecological filtering and phenotypic clustering of shade tolerance in the tree community (Griffiths et al., 2007; Tsvuura et al., 2010).

This paper experimentally examines patterns of phenotypic plasticity in morphological traits of representative dune forest tree species under different light and nutrient conditions that reflect the range found in these forests. We emphasise the potential species-sorting role of the suppressive herb *I. woodii* particularly at the seedling stage. A previous paper (Tsvuura et al., 2012) compared relative growth rate and biomass-based performance of tree seedlings grown with *I. woodii*, using the competition index of Armas et al. (2004). We complement that earlier study by presenting analyses of interaction terms (viz. competition \times resource) for each biomass allocation parameter and morphological traits of seedlings of the same tree species, and relate these parameters to survival and persistence in the understorey. This approach allows us to expand on the findings of our earlier (Tsvuura et al., 2012) paper. We examine the following questions: (1) to what extent is the competitive response of coastal dune forest tree seedlings explained by their biomass allocation patterns and morphological traits; and (2) what is the influence of *I. woodii* neighbours on tree seedling responses to light and nutrient manipulation?

We hypothesise that *I. woodii* competes with tree seedlings by pre-empting nutrient and light resources, which results in species-sorting patterns that reflect adaptation (shade tolerance) and plasticity of response to resource availability. We predict that: (1) at low light levels, tree seedlings allocate more biomass to capturing light (Aerts, 1999; Poorter, 1999; Poorter and Nagel, 2000), represented by high leaf mass fraction and high SLA; (2) at high light levels and low nutrients, leaf mass fraction and SLA will decrease as biomass is allocated belowground; (3) leaf mass fraction will decrease with density of neighbouring *I. woodii* plants i.e. increasing competition for belowground resources; and (4) SLA will increase with neighbour density in response to lower light levels.

2. Methods

2.1. Study site and species

The study plants were sourced from coastal dune forest at Cape Vidal (28°16'S, 32°29'E) in the iSimangaliso Wetland Park in KwaZulu-Natal (KZN) Province, South Africa. Cape Vidal has a subtropical climate

with mean annual precipitation of approximately 1200 mm and mean annual temperature of 21 °C (Schulze, 1997). The soils are deep sands of low fertility (Boyes et al., 2010). The forest is part of the Indian Ocean Coastal Belt forest, which has a subtropical component in eastern South Africa and southern Mozambique, and a tropical component that extends into southern Somalia (Tinley, 1985; Mucina and Rutherford, 2006).

I. woodii (Acanthaceae) is a broad-leaved, semi-woody herb that dominates the understorey of coastal dune forests of eastern southern Africa. The species is a clonal synchronous monocarp (Griffiths et al., 2010) that produces flowers and fruits at 4–10 year intervals and regenerates from seed within a year of reproduction (Van Steenis, 1978; Tsvuura, 2010). Four tree species from Cape Vidal were selected for growing trials with *I. woodii*, to investigate the effects of the herb on forest regeneration, using contrasting light and nutrient treatments in a common garden experiment under greenhouse conditions. The four tree species are relatively abundant with >20 ind. ha⁻¹ (Nzunda et al., 2007). *Diospyros natalensis* (Harv.) Brenan and *Sideroxylon inerme* L. are late-succession species, the former mainly a reseed and the latter mainly a resprouter, with contrasting seedling densities in the forest (Appendix 1; Nzunda et al., 2007). *Euclea racemosa* Murray is a mid-to late-succession mature phase subcanopy resprouter whilst *Apodytes dimidiata* E. Mey ex Arn. is a non-resprouting mid-successional species (Appendix 1; Tsvuura et al., 2012). All four tree species are evergreen. As these species belong to different genera, they will be referred to using their genus names.

2.2. Experimental design

To determine the density effects of *I. woodii* on tree seedling leaf traits and growth, seedlings of *Diospyros*, *Euclea*, *Sideroxylon* and *Apodytes* were grown with seedlings of *I. woodii* in 4 L pots (185 \times 244 \times 206 mm; bottom diameter \times top diameter \times height) in a greenhouse (mean daytime temperature of 24 °C from May to August, and 27 °C from October to April) at the University of KwaZulu-Natal, Pietermaritzburg. The pots had perforated bases and contained sterilised sand collected from the field site. Sand was sterilised to prevent the germination of any seeds collected with the soil, which would confound our experiment.

We used a factorial design with nutrients, light and *I. woodii* density as main factors. Half-strength Hoagland's nutrient solution (Hewitt, 1966) containing either 1% or 10% nitrogen was used as the nutrient source and 100 ml (increased to 200 ml after 10 months) were applied every third day. The lower level of N was based on soil samples from the field. We used half-strength nutrient solution because of the low native fertility of the soil (Boyes et al., 2010). The plants were provided with additional water at weekly intervals. The light treatment was imposed by manipulating sunlight transmission in the greenhouse to achieve specified levels of photosynthetically-active radiation (PAR). The "shade" treatment (1.6% PAR, $15.4 \pm 4.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 1200 h on a sunny day) was located inside a shade structure made from commercially available 80% shade cloth, whilst the "sun" treatment (13.5% PAR, $160.3 \pm 13.0 \mu\text{mol m}^{-2} \text{s}^{-1}$) was positioned outside, but adjacent to, the shade structure in the greenhouse. These light levels are consistent with the conditions beneath the understorey (ca. 1%) and above it (8%), respectively (Griffiths et al., 2007). The lower light level ($15.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) is one order of magnitude greater than the light compensation point of many species from these forests (Tsvuura et al., 2010), and may drive positive photosynthesis as expected of tree seedlings growing beneath *I. woodii* thickets and gaps (Griffiths et al., 2007). Both *I. woodii* habitats occur beneath the tree canopy. For each tree species, a single seedling was grown with zero, one or three *I. woodii* seedlings as neighbours in the same pot in an additive design (Goldberg and Scheiner, 2001). The densities of *I. woodii* used were inferred from those observed in the field at early (1–2 years old) and late (4–7 years) vegetative stages, which range from ca. 30 stems to 10 stems per m², respectively (Tsvuura et al., 2010). Our replicated factorial design required 192

pots (four seedling species \times two nutrient levels \times two light levels \times three neighbour densities \times four replicates).

Prior to starting the experiment, seeds of *Apodytes* and *Sideroxylon* were germinated on soil in seedling trays in the greenhouse. *Euclea* and *Diospyros* seedlings were collected from the forest at Cape Vidal where a few trees of these species had been monitored from seed dispersal to seedling emergence. Seedlings of *I. woodii* were derived from shoot cuttings that were collected from adult plants at Cape Vidal and allowed to root in sand in a mist house. We used similar-sized seedlings of each species at planting (Appendix 1).

At 6-week intervals during the course of the experiment, pots were shifted within the shade or sun structures to reduce position effects whilst keeping the split-plot design of the experiment unchanged. After 16 months seedlings were harvested. For each seedling the stem, leaves and roots were separated and the combined leaf area of 6 to 10 leaves measured using a LI-3100 area metre (Li-Cor Inc., Lincoln, Nebraska, USA). All these components were oven dried separately at 70 °C for 48 h before being weighed.

2.3. Data analysis

We used split-plot analysis of covariance (ANCOVA) to compare the performance of each species amongst the light and nutrient treatments. Specific leaf area, LAR, total biomass, and stem, root and leaf mass fractions (proportions of plant mass in stem, root and leaf, i.e. SMF, RMF, and LMF) were the dependent variables, with light as the main plot factor and nutrients as a sub-plot factor nested within the light treatment, species as a block factor and biomass of *I. woodii* neighbours as a covariate. We used total biomass because it is a good surrogate for fitness (Keddy et al., 2000; Aarssen and Keogh, 2002), whilst SLA indicates a plant's response to competitive interactions with neighbours for light (Violle et al., 2009). The total biomass data were $\log(x + 1)$ -transformed before analysis to normalise residuals (Quinn and Keogh, 2002), which also controls for big differences in growth that the large plants may exert on the mean values when comparing amongst the levels of competition. When the covariate term was significant, we carried out one-way analysis of variance (ANOVA) for each light and nutrient combination with neighbour density as the independent variable to identify combinations of the light and nutrient treatments that contributed to overall significance of the ANCOVA model (Goldberg and Scheiner, 2001). Competition was demonstrated by a density effect in the ANCOVA. Light and nutrient resources may influence seedlings even when there is no competition. In cases where both density and resources had significant effects on seedling traits, we assumed that tree seedlings and *I. woodii* were competing for those resources. These analyses were carried out in GenStat v. 14.1 (VSN International, 2011).

3. Results

The leaf mass fraction (LMF) differed amongst species and decreased significantly with increasing neighbour density and light levels (Table 1, Fig. 1) but increased with increasing nutrient levels ($P < 0.001$, Table 1). A significant relationship amongst species and light conditions (significant species \times light interaction; Table 1) indicates that the effect of high light levels on LMF (Fig. 1(a)) was not consistent amongst species. Lack of consistency amongst species may result from the high LMF values of *Apodytes* growing at high neighbour density compared with the three other species whose highest LMF values were realised in the absence of *I. woodii* neighbours (data not shown). *Diospyros*, *Euclea* and *Sideroxylon* also showed larger decreases in LMF in response to increasing light compared with *Apodytes*. The LMF was low at low light levels in the presence of *I. woodii* neighbours, a trend consistent amongst species at the low light level (Fig. 1(b)). The influence of neighbour density on LMF appears to be a presence-absence effect of *I. woodii*, rather than an effect of neighbour density per se (Fig. 1(b)).

The proportion of biomass allocated to stems differed significantly amongst species and between the light and nutrient treatments ($P < 0.05$ in all cases; Table 1). Under different light conditions, stem mass fraction (SMF) varied inconsistently amongst species and amongst densities of *I. woodii* neighbours (Fig. 1(c); Table 1). Unlike the other species, the SMF of *Diospyros* was greater at high rather than low light (significant light \times species interaction; Fig. 1(c); Table 1). The seedlings grown at high light without *I. woodii* neighbours allocated more biomass to stems than seedlings grown at a low light level, and the trend was reversed in the presence of *I. woodii* (significant light \times density interaction; Fig. 1(d)).

Seedling root mass fraction (RMF) was consistently lower at low light levels amongst all species (Fig. 1(e); Table 1), complementing the response of leaf mass fraction to light, and consistent with our first prediction. Amongst the four species, *Euclea* showed the largest decrease ($>82\%$) in RMF in response to light (Fig. 1(e)). Consistent with the response by LMF, there was a strong effect of light on RMF but there was no density effect by *I. woodii* neighbours (Fig. 1(f); Table 1). Total seedling biomass increased with both the light and nutrient treatments (Fig. 2(a), (b); Table 1). At each light condition, seedling biomass decreased in the presence of *I. woodii* neighbours, more so under low than high light conditions (i.e. significant light \times neighbour density interactions; Fig. 2(b); Table 1).

Leaf area ratio (LAR) decreased significantly with increasing light levels whilst nutrients and neighbour density had no effect (Fig. 2(c), (d); Table 1). Similarly, SLA decreased significantly in all species by 57% to 189% with an increase in light levels but did not change in response to nutrients. The response of SLA to neighbour density treatments was inconsistent between the light levels (i.e. significant light \times neighbour density interactions; Fig. 2; Table 1).

Table 1

F-ratios and associated probabilities for split-plot analysis of covariance (ANCOVA) for the effect of light, nutrients, species and the covariate biomass of *Isoglossa woodii* neighbours on total biomass, leaf area ratio (LAR), specific leaf area (SLA), root-, leaf- and stem mass fractions (RMF, LMF, SMF) of tree seedlings. Total biomass data were $\log(x + 1)$ -transformed before analysis.

Source of variation	d.f.	LMF	SMF	RMF	SLA	LAR	Total biomass
Species (S)	3	8.89***	121.89***	50.73***	22.59***	116.79***	295.03***
Light (L)	1	135.49***	5.29*	232.64***	825.23***	151.18***	88.29***
Nutrients (N)	1	12.73***	16.78***	60.64***	1.09	0.06	128.14***
S \times L	3	6.76***	15.68***	16.90***	27.18***	121.86***	1.02
S \times N	3	1.17	2.80*	0.19	1.55	3.08*	5.83***
L \times N	1	0.36	0.97	0.06	0.56	0.01	6.5*
S \times L \times N	3	0.93	0.54	0.96	0.50	3.15*	0.16
Neighbour density	1	30.55***	8.21**	78.52***	9.05**	0.02	157.37***
Residual	173						

*** Indicates 0.001 significance level.

** Indicates 0.01 significance level.

* Indicates 0.05 significance level.

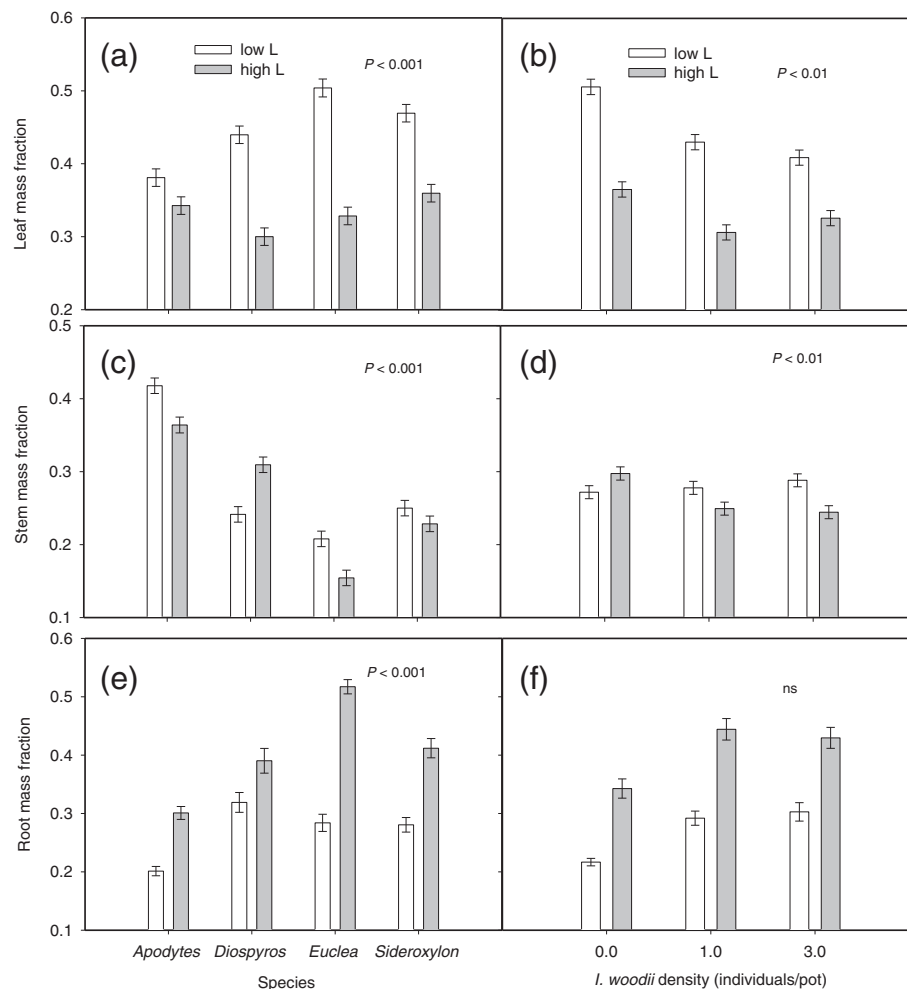


Fig. 1. Leaf, stem and root mass fractions (mean ± 1 SE) of tree seedlings grown with *Isoglossa woodii* in the greenhouse. The P -value for the interaction term is given in each panel. Densities of one and three neighbours correspond to mean *I. woodii* biomass values of 18.7 ± 1.4 and 20.1 ± 1.5 g, respectively.

4. Discussion

We demonstrate the significant effects of light conditions imposed by a suppressive herb on biomass, biomass allocation (LMF, SMF, RMF) and leaf traits (LMF, LAR and SLA) of tree seedlings from representative species in subtropical coastal dune forest. These responses from species differing widely in functional traits may be generally representative of broader dune forest tree assemblage (Tsvuura et al., 2010). However, we note that leaf level competitive responses of forest tree species may be convergent at the seedling stage and irrelevant at adult stages (Poorter et al., 2005, 2008; Lusk et al., 2008). Our findings indicate that light limitation plays a far greater role than soil nutrients and competition from understorey plants in influencing seedling establishment. Our results suggest that *I. woodii* does not compete for soil nutrients with tree seedlings, but effectively excludes seedlings through shading (Griffiths et al., 2007; Tsvuura et al., 2012). The exclusion of seedlings through shading leads to convergence in shade tolerance amongst the remaining species (Tsvuura et al., 2010), achieved through leaf trait plasticity, a necessary response in forests where there is a pervasive herb stratum.

Our results are consistent with the expectation that seedling competition with *I. woodii* will increase biomass allocation to leaves and increase LAR under low light conditions to enhance light capture by seedlings. Understorey vegetation influences tree seedling growth through belowground interactions, which reduce biomass allocation to leaves and decreases seedling LAR, or through aboveground competition for light, which increases LAR. Higher leaf areas can also be a

response to self-shading or to the longer leaf life-spans amongst evergreen species (Lusk, 2002), which are both important traits for maintaining a positive carbon gain amongst shade tolerant plants. Our finding that LMF decreases with an increase in *I. woodii* density is consistent with belowground competition. Overall, there was a 31% decrease in the total leaf area when seedlings were grown with *I. woodii* and this decrease was more pronounced at low light conditions indicating greater plasticity in light-driven allocation patterns. Our third prediction, that seedling LMF will decrease in response to an increase in *I. woodii* density was upheld, and is consistent with increasing competition for belowground resources. As *I. woodii* density increases, belowground competition with seedlings is expected to increase, causing further shifts in allocation patterns to meet the increased transpiration or nutrient demands of tree seedlings (Aerts, 1999; Paz, 2003; Dybzinski and Tilman, 2007).

The leaf traits of tree seedlings (SLA, and LAR) were not influenced by the nutrient treatment, which is consistent with some studies (Walters and Reich, 1996; Dent and Burslem, 2009; Gunton et al., 2010), but contrary to others (Witkowski and Lamont, 1991; Poorter and Nagel, 2000; Niinemets and Kull, 2003; Dent and Burslem, 2009). For example, Niinemets and Kull (2003) measured leaf morphological and chemical traits of woody plant species from three sites of contrasting soil fertility and vegetation and found that SLA was positively correlated with foliar phosphorus (P) concentrations on P-limited acidic or calcareous soils, and with both phosphorus and nitrogen on floodplain soils. Wright et al. (2005) reported a strong relationship between SLA and soil nutrients, although the relationship between SLA and

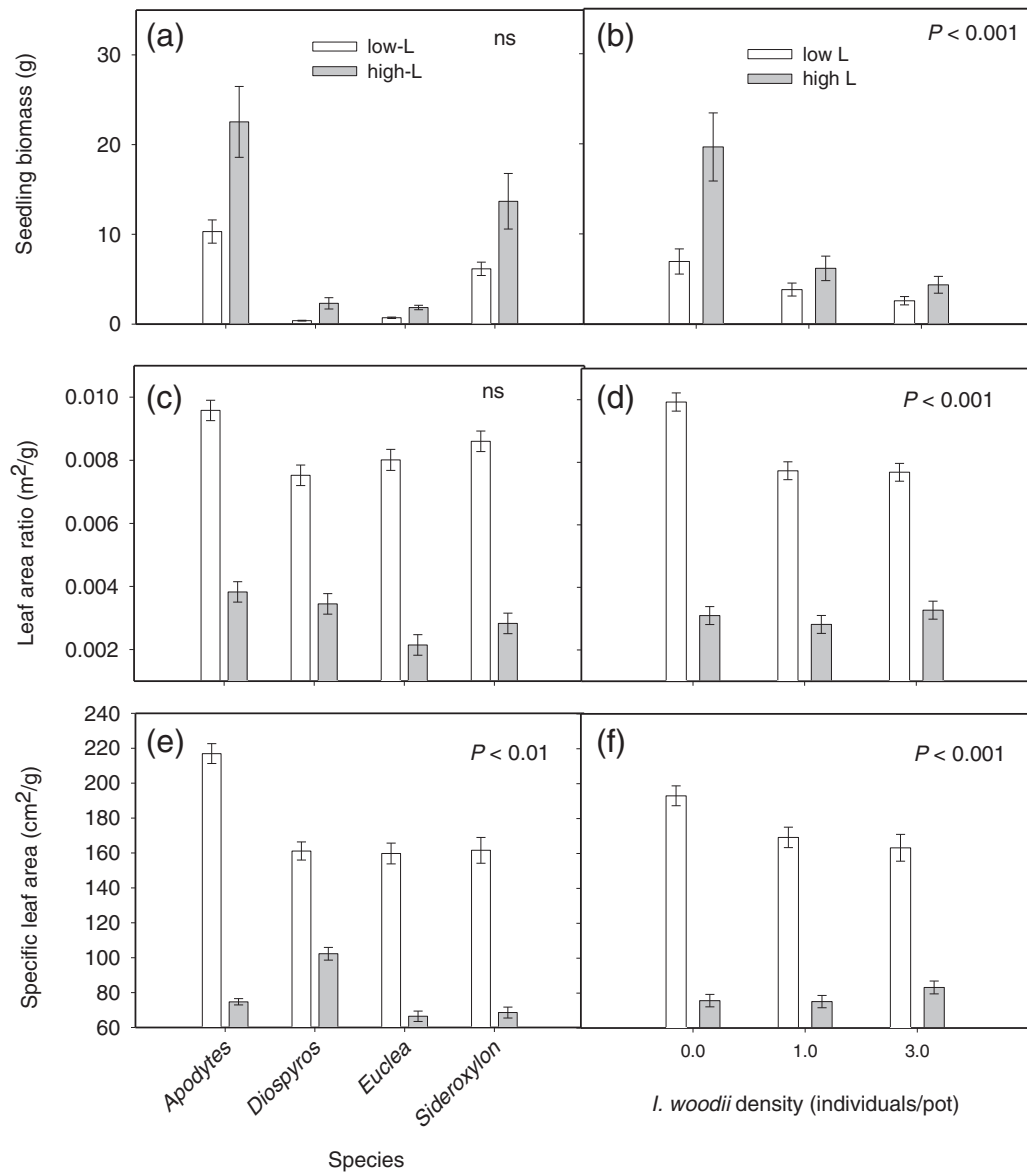


Fig. 2. Biomass, leaf area ratio and specific leaf area (mean \pm 1SE) of tree seedlings grown with *Isoglossa woodii* in the greenhouse. The P -value for the interaction term is given in each panel. Densities of one and three neighbours correspond to mean *I. woodii* biomass values of 18.7 ± 1.4 and 20.1 ± 1.5 g, respectively.

irradiance was stronger, as reported here. In our study, the levels of nutrients used (1% and 10% nitrogen in Hoagland's nutrient solution) were based on ranges known to occur at the site (Boyes et al., 2010), and may therefore not provide sufficient contrast to affect differences in leaf traits. Nonetheless, our results show a nutrient response by total seedling biomass as well as by root, stem and leaf allocations.

The performance and productivity of most woody plants in tropical forest ecosystems may be enhanced by mycorrhizal symbionts (Alexander, 1989). Root symbionts buffer nutrient depletion by enhancing nutrient uptake across the soil–root interface (Smith and Read, 2008). The effect of root symbionts was excluded in this study because we used sterilised soil. Although we are not aware of the extent to which tree species used in this study are mycorrhizal, their nutrient demands for growth at low light conditions are likely to be low (Burslem et al., 1995). The implication is that light conditions imposed by understorey vegetation may be more important in influencing seedling establishment. At our study site, soil fertility in *I. woodii* gaps and *I. woodii* thickets was similar in spite of the latter's lower density and

species richness of tree seedlings (Griffiths et al., 2007), supporting our contention that limiting light and not soil fertility influences recruitment dynamics and community structure of tree seedlings in subtropical dune forests.

The strong influence of the light gradient on leaf traits supports and extends the findings of an earlier study. Tsvuura et al. (2010) reported that photosynthetic traits of tree seedlings in these forests were commensurate with shade tolerance imposed by *I. woodii*, which also acts as an ecological filter of light demanding species. We found that tree seedlings growing in the deep shade created by a dense herbaceous understorey employ several strategies to enhance performance. Our results indicate that leaf traits (high SLA, LAR and LMF at low light) are likely to increase seedling survival and persistence in the forest understorey. Leaf traits and patterns of biomass allocation of these species extend the tight coupling of photosynthetic traits and shade tolerance reported earlier, and reinforce the view that light is the most limiting and critical constraint of seedling establishment in coastal dune forests.

5. Conclusion

The response of tree seedling to low irradiance in the understorey of coastal dune forest is reflected in changes to leaf traits in a way that confirms earlier predictions of phenotypic convergence in shade tolerance and associated leaf traits. A combination of high density *I. woodii* neighbours and diminished light conditions has selected for tolerance to deep shade by many tree species in dune forest (Tsvuura et al., 2010). The leaf traits of the species examined suggest that soil fertility may not be as important as light in determining seedling survival. In the context of Africa's tropical lowland forests characterised by widespread understorey herb cover, our findings highlight the suppressive role of herb stratum in influencing tree recruitment dynamics and forest tree community structure.

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Appendix 1. Successional position of the tree species, their abundance at the field site, and sizes of tree seedlings at the start of the experiment.

Species	Successional position	Abundance (% of total stem basal area)	Mean (\pm SE) height (mm)	Mean (\pm SE) stem diameter (mm)
<i>Apodytes dimidiata</i>	Mid-succession	1.3	128.7 \pm 3.2	2.1 \pm 0.03
<i>Diospyros natalensis</i>	Late-succession	12.6	73.1 \pm 1.5	1.1 \pm 0.02
<i>Euclea racemosa</i>	Mid- to late-succession	4.7	64.9 \pm 1.5	1.2 \pm 0.01
<i>Sideroxylon inerme</i>	Late-succession	8.5	105.8 \pm 2.5	3.1 \pm 0.06
<i>Isoglossa woodii</i>	–	–	98.5 \pm 1.3	–

References

Aarssen, L., Keogh, T., 2002. Conundrums of competitive ability in plants: what to measure? *Oikos* 96, 531–542.

Abe, M., Miguchi, H., Nakashizuka, T., 2001. An interactive effect of simultaneous death of dwarf bamboo, canopy gap, and predatory rodents on beech regeneration. *Oecologia* 127, 281–286.

Aerts, R., 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant–soil feedbacks. *Journal of Experimental Botany* 50, 29–37.

Alexander, I., 1989. Mycorrhizas in tropical forests. In: Proctor, J. (Ed.), *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*. Blackwell Scientific Publications, Oxford, pp. 169–188.

Armas, C., Ordiales, R., Pugnaire, F.I., 2004. Measuring plant interactions: a new comparative index. *Ecology* 85, 2682–2686.

Boyes, L.J., Griffiths, M.E., Manson, A.D., Lawes, M.J., 2010. Soil nutrients are not responsible for arrested succession in disturbed coastal dune forest. *Plant Ecology* 208, 293–305.

Brooks, J.R., Meinzer, F.C., Coulombe, R., Gregg, J., 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology* 22, 1107–1117.

Burslem, D.F.R.P., Grubb, P.J., Turner, I.M., 1995. Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rainforest in Singapore. *Journal of Ecology* 83, 113–122.

Carine, M.A., Scotland, R.W., 2000. The taxonomy and biology of *Stenosiphonium* Nees (Acanthaceae). *Botanical Journal of the Linnean Society* 133, 101–128.

Chapman, C.A., Chapman, L.J., Kaufman, L., Zanne, A.E., 1999. Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. *African Journal of Ecology* 37, 81–92.

Chazdon, R.L., Pearcy, R.W., Lee, D.W., Fetcher, N., 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), *Tropical Forest Plant Ecophysiology*. Chapman and Hall, New York, NY, pp. 5–55.

Dawson, T.E., 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* 16, 263–272.

Dent, D.H., Burslem, D.F.R.P., 2009. Performance trade-offs driven by morphological plasticity contribute to habitat specialization of Bornean tree species. *Biotropica* 41, 424–434.

Denslow, J.S., Newell, E., Ellison, A.M., 1991. The effects of understory palms and cycloanthus on the growth and survival of *Inga* seedlings. *Biotropica* 23, 225–234.

Dybowski, R., Tilman, D., 2007. Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *The American Naturalist* 170, 305–318.

Fashing, P.J., Gathua, J.M., 2004. Spatial variability in the vegetation structure and composition of an East African rain forest. *African Journal of Ecology* 42, 189–197.

George, I.O.G., Bazzaz, F.A., 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80, 833–845.

George, I.O.G., Bazzaz, F.A., 2003. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. In: Gillian, F.S., Roberts, M.R. (Eds.), *The Herbaceous Layer in Forests of Eastern North America*. Oxford University Press, Oxford, pp. 265–282.

Goldberg, D.E., Scheiner, S.M., 2001. ANOVA and ANCOVA: field competition experiments. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments*. Oxford University Press, Oxford, pp. 77–98.

Griffiths, M.E., Lawes, M.J., Tsvuura, Z., 2007. Understorey gaps influence regeneration dynamics in subtropical coastal dune forest. *Plant Ecology* 18, 227–236.

Griffiths, M.E., Tsvuura, Z., Franklin, D.C., Lawes, M.J., 2010. Pollination ecology of *Isoglossa woodii*, a long-lived synchronously monocarpic herb from coastal forests in South Africa. *Plant Biology* 12, 495–502.

Hewitt, E., 1966. *Sand and Water Culture Methods Used in the Study of Plant Nutrition*. Commonwealth Agricultural Bureaux, second ed. Farnham Royal.

Horsley, S.B., 1993. Mechanisms of interference between hay-scented fern and black cherry. *Canadian Journal of Forest Research* 23, 2059–2069.

Keddy, P., Gaudet, C., Fraser, L.H., 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *Journal of Ecology* 88, 413–423.

Lawes, M.J., Chapman, C.A., 2006. Does the herb *Acanthus pubescens* and/or elephants suppress tree regeneration in disturbed Afrotropical forest? *Forest Ecology and Management* 221, 278–284.

Lusk, C.H., 2002. Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. *Oecologia* 132, 188–196.

Lusk, C.H., Reich, P.B., Montgomery, R.A., Ackerly, D.D., Cavender-Bares, J., 2008. Why are evergreen leaves so contrary about shade? *Trends in Ecology & Evolution* 23, 299–303.

Meyer, J.Y., Laverne, C., 2004. *Beautes fatales: Acanthaceae species as invasive alien plants on tropical Indo-Pacific Islands*. Diversity and Distributions 10, 333–U334.

Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* Vol 19. South African National Biodiversity Institute, Pretoria.

Niinemets, U., Kull, K., 2003. Leaf structure vs. nutrient relationships vary with soil conditions in temperate shrubs and trees. *Acta Oecologica* 24, 209–219.

Nilsen, E.T., Clinton, B.D., Lei, T.T., Miller, O.K., Semones, S.W., Walker, J.F., 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? *The American Midland Naturalist* 145, 325–343.

Nzunda, E.F., Griffiths, M.E., Lawes, M.J., 2007. Resprouting enhances seedling persistence in a subtropical coastal dune forest. *African Journal of Ecology* 46, 32–38.

Paul, J.R., Randle, A.M., Chapman, C.A., Chapman, L.J., 2004. Arrested succession in logging gaps: is tree seedling growth and survival limiting? *African Journal of Ecology* 42, 245–251.

Paz, H., 2003. Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. *Biotropica* 35, 318–332.

Poorter, L., 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* 13, 396–410.

Poorter, H., Nagel, O., 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* 27, 595–607.

Poorter, L., Bongers, F., Sterck, F.J., Wöll, H., 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology* 93, 256–267.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., Wright, I.J., 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology* 89, 1908–1920.

Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.

Richards, P.W., 1963. Ecological notes on West African vegetation III. The upland forests of Cameroons mountain. *Journal of Ecology* 51, 529–554.

- Schulze, R.E., 1997. South African Atlas of Agrohydrology and Climatology. Water Research Commission, Pretoria (report no. TT82/96).
- Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis. third ed. Academic Press, London.
- Struhsaker, T.T., 1997. Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation. University of Florida Press, Gainesville, FL.
- Tinley, K.L., 1985. Coastal Dunes of South Africa. Foundation for Research Development, Pretoria (report no. 109).
- Tsvuura, Z., 2010. The Influence of the Monocarpic Herb *Isoglossa Woodii* (Acanthaceae) on Subtropical Forest Tree Dynamics and Diversity (Ph.D. thesis) University of KwaZulu-Natal, Pietermaritzburg, South Africa.
- Tsvuura, Z., Griffiths, M.E., Lawes, M.J., 2007. The effect of herbaceous understory cover on fruit removal and seedling survival in coastal dune forest trees in South Africa. *Biotropica* 39, 428–432.
- Tsvuura, Z., Griffiths, M.E., Gunton, R.M., Franks, P.J., Lawes, M.J., 2010. Ecological filtering by a dominant herb selects for shade tolerance in the tree seedling community of coastal dune forest. *Oecologia* 164, 861–870.
- Tsvuura, Z., Griffiths, M.E., Gunton, R.M., Lawes, M.J., 2011. Predator satiation and recruitment in a mast fruiting monocarpic forest herb. *Annals of Botany* 107, 379–387.
- Tsvuura, Z., Griffiths, M.E., Lawes, M.J., 2012. Density effects of a dominant understorey herb *Isoglossa woodii* (Acanthaceae) on tree seedlings in a subtropical dune forest in South Africa. *Biotropica* 44, 163–170.
- Van Steenis, C.G.G.J., 1978. Gregarious flowering in the monocarpic genus *Isoglossa* (Acanthaceae). *Bothalia* 12, 553.
- Violle, C., Garnier, E., Lecoœur, J., Roumet, C., Pothier, C., Blanchard, A., Navas, M.-L., 2009. Competition, traits and resource depletion in plant communities. *Oecologia* 160, 747–755.
- VSN-International, 2011. GenStat for Windows. VSN International, Hemel Hempstead.
- Walters, M.B., Reich, P.B., 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77, 841–853.
- Witkowski, E.T.F., Lamont, B.B., 1991. Leaf specific mass confounds leaf density and thickness. *Oecologia* 88, 486–493.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I., Westoby, M., 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14, 411–421.