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Growth and biomass allocation in seedlings of rain-forest trees in New Caledonia: monodominants vs. subordinates and episodic vs. continuous regenerators

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Abstract: Some species-rich secondary forests in New Caledonia have a monodominant canopy. Here we investigate growth and biomass allocation traits that might explain single-species' dominance of these post-disturbance stands, and their later decline in the absence of large-scale disturbance. Seedlings of 20 rain-forest trees were grown in two light treatments in a nursery house. In the sun treatment, monodominants grew faster (56.7 ± 1.4 mg g^{-1} wk^{-1}) than subordinates (40.2 ± 2.6 mg g^{-1} wk^{-1}). However, some episodically regenerating (ER) subordinates had high growth rates similar to those of monodominants. In the shade treatment, monodominants and subordinates had similar growth rates (33.7 ± 2.6 and 34.0 ± 1.9 mg g^{-1} wk^{-1} respectively). Notably, monodominants in both sun and shade treatments had lower root mass fraction (0.29 ± 0.02 and 0.27 ± 0.02 g g^{-1} respectively) than subordinates (0.39 ± 0.02 and 0.37 ± 0.02 g g^{-1}). Fast growth in sunny conditions is probably imperative for these relatively shade-intolerant ER monodominants. In field conditions, high shoot mass fraction combined with efficient root performance may facilitate faster growth in monodominants competing with other ER species in sunlit sites. Slower growth in shade may contribute to loss of dominance over time in undisturbed forests.

Key Words: biomass allocation, forest dynamics, growth rates, monodominance, New Caledonia, *Nothofagus*, regeneration, shade tolerance, tropical rain forest, ultramafic soil

INTRODUCTION

Rain forests in New Caledonia, in the south-west Pacific, commonly have a high diversity of flowering plants, including in forests on ultramafic substrates (Isnard *et al.* 2016, Morat 1993). Despite this diversity, some secondary forests are dominated by a single tree species. For example, *Nothofagus* spp. (Nothofagaceae) and *Arillastrum gummiferum* (Myrtaceae) commonly dominate the upper canopies of forests on ultramafic soils on the southern massif (Jaffré 1980), with *Cerberiopsis candelabra* (Apocynaceae) dominating smaller stands (Read *et al.* 2008). Population size structures and tree-ring analysis suggest that these monodominant forests established after large-scale disturbances such as fires or cyclones, and that long-term persistence of dominance is unlikely in the hypothetical absence of severe disturbance, at least at low to mid-elevations (Demenois *et al.* in press, McCoy *et al.* 1999, Read & Jaffré 2013, Read *et al.* 2008). This scenario contrasts with many monodominant forests elsewhere in the world that are dominated by shade-tolerant species, where dominance can persist without catastrophic disturbances (Connell & Lowman 1989, Hart 1990, Nascimento *et al.* 2007, Peh *et al.* 2011, Torti *et al.* 2001).

Here we ask what traits allow these species to achieve dominance in floristically diverse secondary forests. Traits promoting persistent monodominance have been discussed across a number of species (Henkel *et al.* 2005, McGuire 2007a, b; Peh *et al.* 2011, Torti *et al.* 2001). There has been less discussion of traits promoting non-persistent monodominance by long-lived trees, especially in species-rich rain forests (Ibanez & Birnbaum 2014, Newbery *et al.* 2010, 2013), and little investigation of seedling traits of either type of monodominant (but see

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Hart 1995, Newbery *et al.* 2006, 2010), even though community dynamics is strongly influenced by processes acting on seedlings (Green *et al.* 2014).

Non-persistent monodominants are likely to be fast-growing and shade-intolerant, in contrast to the slow-growing, shade-tolerant strategy predicted in persistent monodominants (Connell & Lowman 1989, Hart 1990). Measurements of leaf-level photosynthesis confirmed that seedlings of these New Caledonian monodominants are relatively shade-intolerant (Read *et al.* 2015). However, maximum rates of net photosynthesis (A_{max}) of monodominants were not higher than in some subordinate shade-intolerant species that also regenerate episodically (Read *et al.* 2015). Instead, plant-level traits may be key to understanding how these species achieve dominance. In particular, interspecific differences in growth responses to irradiance may explain differences in dominance and regeneration, with indirect effects via carbon partitioning (Veneklaas & Poorter 1998). For example, high growth rates to pre-empt resources in sunny post-disturbance environments may be facilitated by some aspect of efficient biomass allocation. Notably, the soils that develop over ultramafic substrates, supporting both monodominant and mixed-canopy forests, are very infertile, with low P, K and Ca:Mg, and high levels of metals that are potentially toxic, including Ni (Jaffré & Veillon 1990, Read *et al.* 2006). Therefore, there are likely to be strong trade-offs for resources – for root development to access soil nutrients versus stem and leaf development to optimize carbon gain relative to competitors.

In this study we investigate growth rates and biomass allocation traits that might allow species to dominate post-disturbance stands but decline in the absence of subsequent large-scale disturbance. We test the following predictions: (1) Seedlings of monodominant species grow rapidly in sunny conditions that follow a large disturbance; (2) This rapid growth is due in part to efficient biomass allocation to (a) leaves for carbon gain and (b) roots for nutrient uptake; (3) In shade, growth of monodominants is slower, similar to or lower than that of subordinate species. We also test these predictions more generally in shade-intolerant species showing episodic regeneration versus shade-tolerant species showing continuous regeneration. Growth traits were studied in seedlings of 20 tree species grown in contrasting light regimes in a nursery house.

METHODS

Species selection and growth conditions

Twenty canopy species were selected from *Nothofagus*-dominated and adjacent mixed-canopy rain forests, including three *Nothofagus* spp., *A. gummiferum* and *C. candelabra* (Table 1). Species were categorized as monodominant vs subordinate species and as episodically regenerating (ER) vs continuously regenerating (CR) species (Table 1). Monodominants were categorized based on canopy cover: they commonly dominate the upper canopy of forests in terms of foliar cover, but not necessarily in terms of stand basal area (>80%: Hart 1990) (Demenois *et al.* in press, Read *et al.* 2000, 2008). Regeneration was categorized from the fit of population size structures (based on diameters at breast height) to the Weibull probability density function across monodominant *Nothofagus* forests and mixed rain forests (Read & Jaffré 2013). Weibull analysis gives a measure of curve shape, c, that can provide an index of regeneration mode: values ≤ 1 indicate reverse-J and negative exponential curves which suggest continuous regeneration; values >1 suggest increasingly synchronous establishment up to $c \cong 3.6$ where the curve approximates the normal distribution, and $c > 3.6$ indicates negative skewing (Bailey & Dell 1973). We used $c \leq 1.2$ to indicate actual or potential continuous regeneration, following Read *et al.* (2015). Regeneration patterns of two species (*Gastrolepis austrocaledonica* and *Planchonella wakere*) could not easily be categorized and were not included in that analysis. Forest seedlings were collected, where possible, to increase the likelihood of mycorrhizal inoculation, but some species were grown from seed (Table 1). Both seedlings and seeds were collected in the south-east of the main island, with localities given in Read *et al.* (2015). Seedlings were collected over an area of 0.3–1 ha, from multiple parents where possible. Plant ages were estimated as *c.* 6–18-mo-old (10–30 cm high) at the start of the experiment.

Seedlings were acclimated in nursery houses for at least 10 wk at the Vale-NC nursery facility in the Plaine des Lacs (22.27°S, 166.91°E, 260 m asl) in the south of the main island. The houses had shade-cloth walls (*c.* 30% shade) and a translucent plastic roof (*c.* 50% shade). The seedlings were planted in 3-L planter bags in soil collected from *Nothofagus*-dominated rain forest near the Pic du Pin Reserve in the Plaine des Lacs (collected at *c.* 20–25 cm depth across *c.* eight locations). The soil was sieved, then mixed with perlite and coconut fibre in the ratio of 75:15:10 to reduce compaction and assist drainage. Forest litter and humus were added to all pots to increase the likelihood of mycorrhizal inoculation.

For the experiment, four replicate blocks each of sun and shade treatments (eight blocks) were created in a nursery house using shade cloth. Shade cloth covered the ceiling and sides of each block to 30 cm above the benches, allowing air circulation across the blocks. The shade cloth created *c.* 50% and 20% incident irradiance in the sun and shade blocks respectively, with another layer added after 10 wk to provide *c.* 30% and 10% incident irradiance. Midday photosynthetic photon flux density (PPFD) was measured in the centre of each block once per week with a Li-Cor (Li-190R) quantum sensor, averaging

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Table 1. Rain-forest canopy species from New Caledonia used in this study, with their dominance and regeneration categories. 's' after the species name indicates the species was collected as seed rather than seedlings. Species codes are those used in figures. For each species it is indicated whether they are typically monodominant (M) or subordinate (S), and episodic (ER) or continuous regenerators (CR) (Read *et al.* 2015). Average Weibull *c* is taken from Read *et al.* (2015) based on values from 1–5 sites, not including values from disjunct population size structures. Nomenclature follows Florical vers. 22.IV.2016 (http://www.botanique.nc/herbier/florical), including retaining *Nothofagus* rather than *Trisyngyne* Baillon as reinstated by Heenan & Smissen (2013). *Agathis lanceolata* has been reported to sometimes dominate small stands (Grignon *et al.* 2010, Manauté *et al.* 2009).

	Species code	Dominance	Regeneration	Weibull *c*
Agathis lanceolata (Araucariaceae) (s)	al	S	CR	0.88
Alphitonia neocaledonica (Rhamnaceae) (s)	an	S	ER	1.42
Archidendropsis granulosa (Mimosaceae)	agr	S	CR	0.85
Arillastrum gummiferum (Myrtaceae) (s)	ag	M	ER	1.29
Calophyllum caledonicum (Calophyllaceae)	cc	S	CR	0.90
Cerberiopsis candelabra var. *candelabra* (Apocynaceae)	cec	M	ER	2.44
Codia discolor (Cunoniaceae)	cd	S	ER	1.57
Cryptocarya transversa (Lauraceae)	ct	S	CR	1.20
Diospyros parviflora (Ebenaceae)	dp	S	CR	1.18
Elaeocarpus yateensis (Elaeocarpaceae)	ey	S	CR	1.18
Flindersia fournieri (Rutaceae) (s)	ff	S	CR	0.83
Gastrolepis austrocaledonica (Stemonuraceae)	ga	S	?	1.22
Gongrodiscus bilocularis (Sapindaceae)	gb	S	CR	1.16
Hibbertia lucens (Dilleniaceae) (s)	hl	S	ER	5.00
Myodocarpus fraxinifolius (Myodocarpaceae) (s)	mf	S	CR	1.20
Nothofagus aequilateralis (Nothofagaceae)	na	M	ER	2.04
N. balansae	nb	M	ER	1.96
N. discoidea	nd	M	ER	1.68
Planchonella wakere (Sapotaceae) (s)	pw	S	?	-
Stenocarpus trinervis (Proteaceae)	st	S	CR	1.15

473 (94–1361) μmol m^{-2} s^{-1} in the sun treatment and 175 (31–441) μmol m^{-2} s^{-1} in the shade treatment. In comparison, PPFD was 20–600 μmol m^{-2} s^{-1} at 20 cm above ground level in a canopy gap (c. 8 m diam.) in a nearby *Nothofagus* forest, 6–12 μmol m^{-2} s^{-1} and 24–30 μmol m^{-2} s^{-1} at two locations below an undisturbed *Nothofagus* canopy and 6–12 μmol m^{-2} s^{-1} below an undisturbed canopy at two locations in adjacent mixed rain forest (5–10 measurements at each location, in sunlight, at midday). Hence the shade treatment was mild compared with forest conditions, but was chosen so that sufficient leaf growth occurred across all species to allow photosynthesis measurements on new leaves (Read *et al.* 2015). The eight light-treatment blocks were positioned randomly (drawn blind) in a row. Up to four seedlings per species were positioned randomly (drawn blind) in a grid in each block, i.e. up to 16 seedlings per species per light treatment.

At the start of the experiment, a low dosage of slow-release fertilizer (2 g 270-d Nutricote® Hot Aussie Blend (Yates Australia): N, 18.1%; P, 2.6%; K, 6.7%) was added to each pot to simulate ongoing nutrient input in rain-forest soils from leaf litter. The watering regime varied with seasonal weather change, but most commonly consisted of light watering for 10 min three times daily, with 5 min h^{-1} of misting between 09h30 and 15h30. During the experimental growth period the maximum daily temperature averaged 25.3°C (18.1–31.6°C) in the sun treatment and 23.9°C (18.1–31.1°C) in the shade treatment, and the minimum daily relative humidity averaged 70% and 75% in the sun and shade treatments respectively (Thermocron® iButtons: Maxim Integrated, San Jose, CA, USA).

Growth rates and biomass allocation

A harvest of 7–15 seedlings per species was undertaken at the start of the experiment (July 2011) to provide initial mass and leaf area for calculation of relative growth rate (RGR) and net assimilation rate (NAR) over the full growth period. RGR was calculated per block as $(\ln W_1 - \ln W_0)$/time, where W_0 is the initial seedling dry mass and W_1 is the dry mass at the final harvest, following Hunt *et al.* (2002). NAR, providing an estimate of the carbon assimilation capacity of the leaves, was calculated per block as $[(W_1 - W_0)(\ln A_1 - \ln A_0)]/[(A_1 - A_0) \times \text{time}]$, where A_0 and A_1 are the total seedling leaf area at the initial and final harvests respectively (Hunt *et al.* 2002). These traditional methods were used rather than fitting allometric models due to the large numbers of seedlings required for multiple harvests. Plants were removed from their pots and washed, then partitioned into roots, stems and leaves. Leaves were scanned at 300 dpi, with total area measured by image analysis (Mix Image: R. Stolk & G. Sanson, Monash University). All parts were then dried to constant mass at 60°C and weighed. There were insufficient seedlings of *N. discoidea* for an initial harvest, and RGR and NAR were not measured.

The final harvest was undertaken after 21–23 wk (December 2011). Stem height was measured, then

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Table 2. Tests of sun and shade treatment effects and differences among species in growth and biomass allocation traits in seedlings of 19–20 New Caledonian rain-forest tree species. The results from the linear mixed effects model are presented. Additive models, where appropriate ($P > 0.25$ for the interaction term), did not alter the conclusions of tests of main effects, so results of initial multiplicative models are shown. L, data log-transformed for analysis. RMF, root mass fraction; SMF, stem mass fraction; LMF, leaf mass fraction; SRL, specific root length; RLR, root length ratio; $\%TRL_{0.25}$, % terminal rootlet length <0.25 mm diameter; LAR, leaf area ratio; SLA, specific leaf area; RGR, relative growth rate; NAR, net assimilation rate.

	Light treatment		Species		Treatment × species	
Plant traits	F	P	F	P	F	P
RMF	10.7	0.016	26.7	<0.001	0.4	0.992
SMF	4.6	0.075	34.2	<0.001	0.7	0.828
LMF	0.3	0.614	31.7	<0.001	0.4	0.979
SRL_L	0.9	0.389	88.3	<0.001	2.1	0.008
RLR_L	3.9	0.097	72.6	<0.001	2.3	0.004
$\%TRL_{0.25}$	1.3	0.296	31.5	<0.001	0.8	0.758
LAR_L	29.9	0.002	11.6	<0.001	0.7	0.844
SLA_L	73.3	<0.001	36.4	<0.001	0.9	0.626
Leaf area: total root $length_L$	7.3	0.036	30.7	<0.001	1.7	0.065
Stem height : total mass	12.4	0.012	42.6	<0.001	0.8	0.657
RGR	48.8	<0.001	9.0	<0.001	3.4	<0.001
NAR	44.2	<0.001	3.9	<0.001	1.5	0.109

seedlings were harvested and measured as described above. In addition, roots of five replicate seedlings per species per treatment were scanned at 600 dpi, and a terminal 5-cm section of root (and branches) (predominantly first-order roots, whose primary role is resource acquisition: Comas *et al.* 2002) was scanned separately. Proteoid root clusters were counted in *Stenocarpus trinervis* seedlings and one cluster per plant was scanned at 1200 dpi. Image analysis was used to estimate total root length and root diameter profile (both including root clusters) following Read *et al.* (2010). Plant parts were then dried at 60°C and weighed. The following allocation variables were calculated: root mass fraction (RMF, root dry mass as a proportion of total plant dry mass), stem mass fraction (SMF), leaf mass fraction (LMF), leaf area ratio (LAR, total plant leaf area per unit total plant dry mass), specific leaf area (SLA, leaf area per unit leaf dry mass), specific root length (SRL, root length per unit root dry mass), root length ratio (RLR, root length per plant dry mass), percentage of roots and terminal rootlets <1 mm, <0.5 mm, <0.25 mm and <0.15 mm, leaf mass per unit total root length, and plant height per total dry mass. *D-X*, a point-based estimate of plasticity, was calculated, modified from Portsmuth & Niinemets (2007): $(X_{sun} - X_{shade})/X_{sun}$, where X is any growth variable.

Data analysis

The effects of treatment and species on plant traits were examined via a linear mixed-effects model (LMM) (Pinheiro & Bates 2000) that incorporated block as a random effect in order to account for the spatial dependency structure. Models included the additive effects of light regime (sun and shade) and species (ordinate with 19–20 species per light regime) if initial multiplicative models found no evidence of interactions ($P > 0.25$). Subsequent contrasts (with Holm P-value adjustments) were used to further explore specific comparisons (monodominants vs subordinates, and ER vs CR species) within each light regime. The LMM and contrasts were fitted using the nlme (http://CRAN.R-project.org/package=nlme) and multcomp (Hothorn *et al.* 2008) packages respectively in R 3.2.2 (R Core Team, https://www.R-project.org/). Data assumptions were first checked and log-transformations were used for some variables. Trait associations across species were tested by Pearson correlation using species' means (means of the four block averages), including associations of RGR and NAR with A_{max}, on both leaf-area and dry-mass basis, measured in the same plants in November–December 2011 (Read *et al.* 2015). Patterns across species were explored with principal components analysis (PCA). Since traits from sun and shade plants were very highly correlated except for RGR and NAR, only values for sun plants were included for biomass allocation traits. RGR and NAR of both sun and shade plants were included, and also *D*-RGR and *D*-NAR (plasticity). Since species' regeneration responses to light occur along a continuum, associations of growth traits with Weibull c were also tested by Pearson correlation. Correlation analysis and PCA were undertaken with SYSTAT v. 13.

RESULTS

Variation in biomass allocation traits and growth rates across species and light treatments

Significant differences were recorded among species for all traits (Table 2). Root, stem and leaf mass fractions varied 2–3-fold across species and light treatments (Figure 1).

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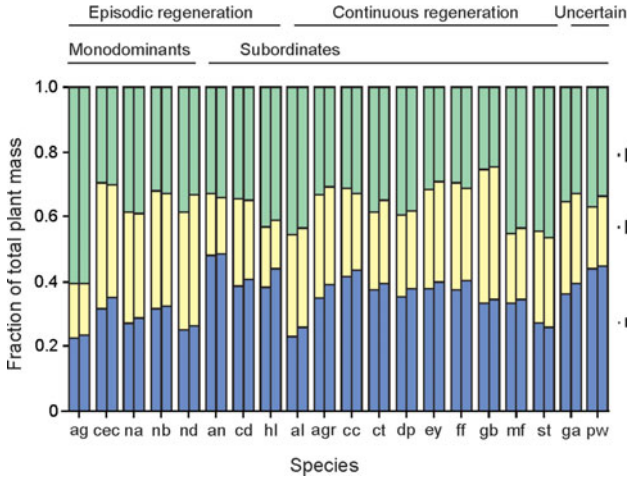

Figure 1. Fractional biomass allocation to roots, stems and leaves in 20 rain-forest tree species from New Caledonia. The data presented are the means of block averages of RMF, SMF and LMF (g g^{-1}), with the minimum and maximum SE shown on the right of the graph for each organ. The left hand column is the shade treatment for each species, and the right hand column is the sun treatment. Roots, blue; stems, yellow; leaves, green. Species codes are given in Table 1. The status of each species with respect to monodominant vs subordinate, and continuous vs episodic regeneration, is shown.

RMF was slightly but significantly higher in sun plants (0.363 ± 0.016 g g^{-1}) than shade plants (0.342 ± 0.015 g g^{-1}), but SMF and LMF were not affected by light treatment (Table 2, Figure 1).

There were substantial differences among species in root profiles. SRL varied 50-fold and RLR varied 32-fold across species and light treatments (Table 2, Figure 2a & b). No difference was recorded between light treatments pooled across species, but effects of light differed among species for both root traits (Table 2). For the root profile, we present only the percentage of terminal rootlet length <0.25 mm diameter (%$TRL_{0.25}$): there was *c.* 20-fold variation across species and light treatments, but with no significant effect of light treatments (Table 2, Figure 2c). High SRL values in *Codia discolor* (Figure 2a) may be due to small seedling size, with little woody root. SRL and RLR were the only traits that correlated significantly with plant size (stem height) across species (in both sun and shade treatments, all log-transformed: $R_P = 0.46, 0.56$; $P = 0.04, 0.01$ respectively), but not when *C. discolor* was excluded ($P > 0.08$). SRL, RLR and %$TRL_{0.25}$ may have been underestimated in *Agathis lanceolata* as the finest rootlets appeared brittle and some may have been lost during washing.

LAR and SLA varied 2–3-fold across species and light treatments (Table 2, Figure 3a & b). Although there was no effect of light treatment on LMF, both LAR and SLA were higher in shade plants (5.8 ± 0.3 m^2 kg^{-1} and 160 ± 10 cm^2 g^{-1} respectively) than sun plants (4.9 ± 0.2 m^2 kg^{-1} and 137 ± 8 cm^2 g^{-1}) (Table 2, Figures 3a & b).

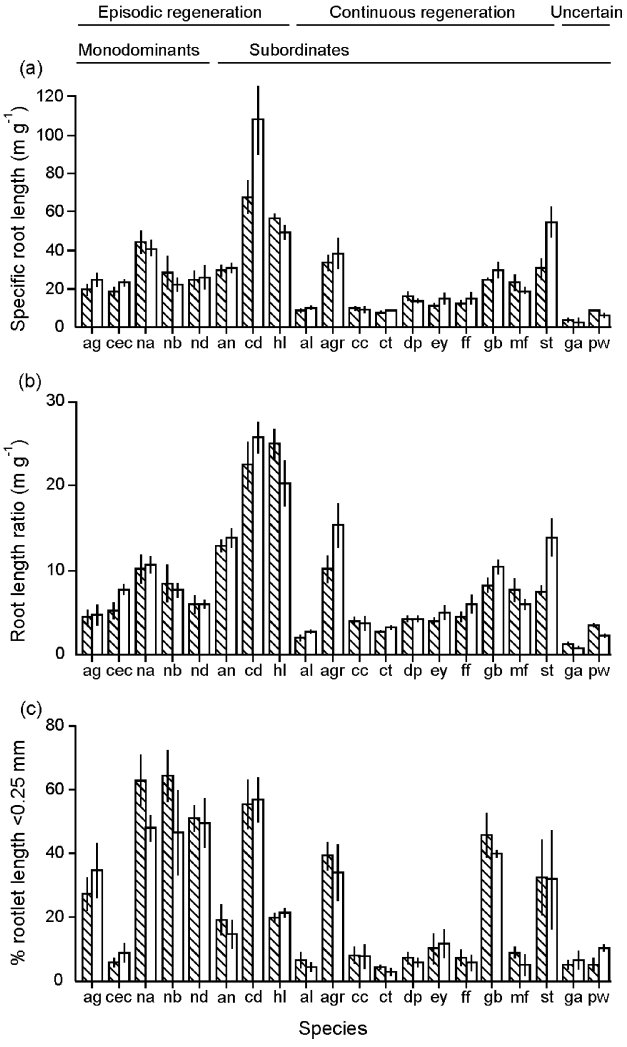

Figure 2. Root allocation in 20 rain-forest tree species from New Caledonia. The data presented are the means of block averages with SE of specific root length (a), root length ratio (b), and %$TRL_{0.25}$, the percentage of terminal rootlet length <0.25 mm diameter (c). The left hand hatched column is the shade treatment for each species, and the right hand open column is the sun treatment. Species codes are given in Table 1. The status of each species with respect to monodominant vs subordinate, and continuous vs episodic regeneration, is shown.

Leaf area:total root length varied 15-fold across species and treatments, higher in shade plants (13.9 ± 2.1 cm^2 m^{-1}) than sun plants (12.4 ± 2.5 cm^2 m^{-1}) (Table 2, Figure 3c), i.e. shade plants enhanced potential light interception relative to soil exploration. Stem height:total plant mass was higher in shade plants (26.3 ± 3.7 cm g^{-1}) than sun plants (22.8 ± 3.2 cm g^{-1}) (Table 2, Figure 4).

RGR and NAR varied 3-fold across species and treatments, higher in sun plants (43.7 ± 2.6 mg g^{-1} wk^{-1} and 7.93 ± 0.39 g m^{-2} wk^{-1} respectively) than shade plants (33.9 ± 1.6 mg g^{-1} wk^{-1} and 6.03 ± 0.26 g m^{-2} wk^{-1}), with the magnitude of effect of light treatment varying among species for RGR (Table 2,

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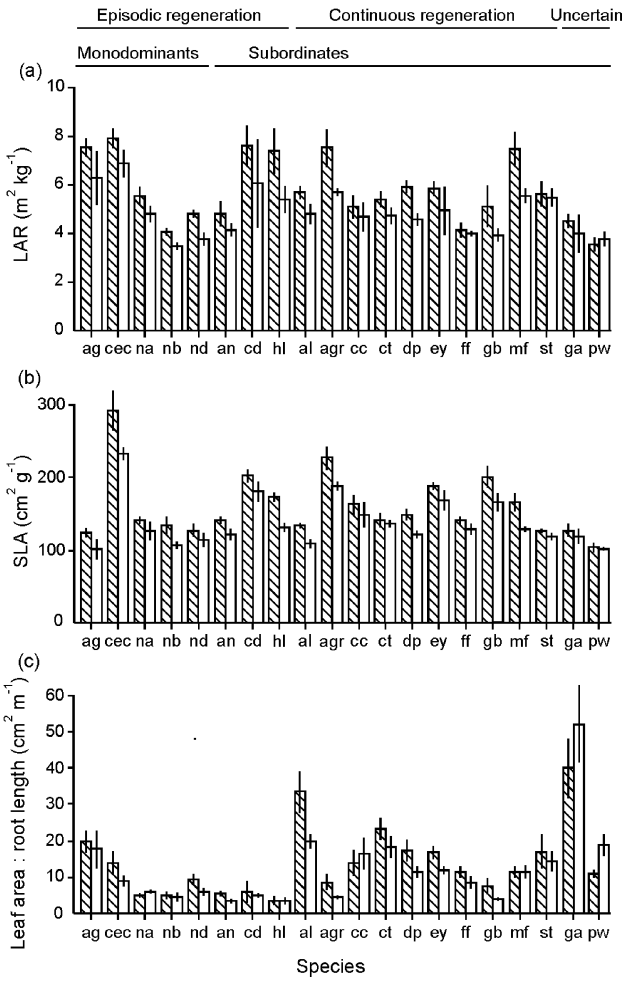

Figure 3. Leaf allocation in 20 rain-forest tree species from New Caledonia. The data presented are the means of block averages with SE of LAR (a), SLA (b) and leaf area relative to total root length (c). The left-hand hatched column is the shade treatment for each species, and the right hand open column is the sun treatment. Species codes are given in Table 1. The status of each species with respect to monodominant vs subordinate, and continuous vs episodic regeneration, is shown.

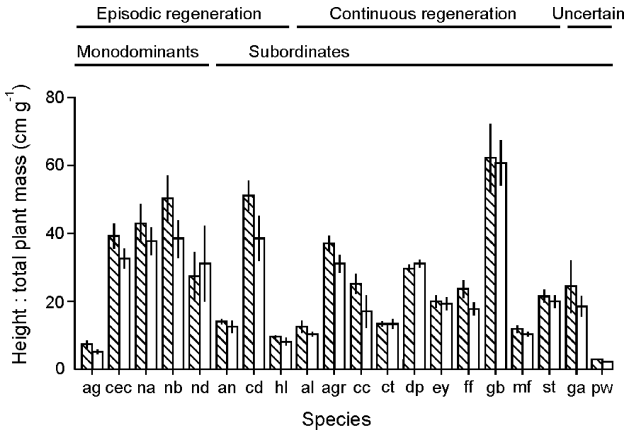

Figure 4. Stem height per total plant mass in 20 rain-forest tree species from New Caledonia. The data presented are the means of block averages with SE. The left-hand hatched column is the shade treatment for each species, and the right hand open column is the sun treatment. Species codes are given in Table 1. The status of each species with respect to monodominant vs subordinate, and continuous vs episodic regeneration, is shown.

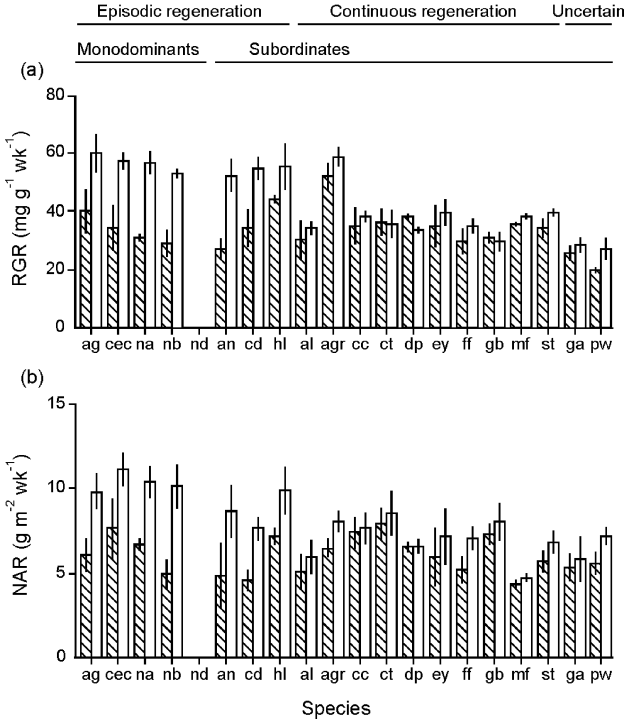

Figure 5. Relative growth rate (a) and net assimilation rate (b) in 19 rain-forest tree species from New Caledonia. The data presented are the means of block values with SE (no data available for *Nothofagus discoidea*). The left-hand hatched column is the shade treatment for each species, and the right hand open column is the sun treatment. Species codes are given in Table 1. The status of each species with respect to monodominant vs subordinate, and continuous vs episodic regeneration, is shown.

Figure 5). Plasticity with respect to light treatment, *D*, varied considerably among traits, ranging from relatively low values in mass fractions to high plasticity in RGR and NAR in monodominant and ER species, and in leaf area:total root length in CR species (Table 3).

For all biomass allocation traits, values in sun versus shade plants were very highly correlated across all species ($P < 10^{-6}$), but for RGR and NAR were only weakly correlated ($P = 0.027$ and 0.033 respectively). Trait correlations within light treatments are given in Appendix 1. LMF was negatively correlated with RMF and SMF in both sun and shade plants ($P = 0.006$–0.028), but RMF was not correlated with SMF. Root length traits were strongly positively intercorrelated in both sun and shade plants ($P = <0.001$–0.003), and negatively correlated with leaf area : total root length ($P = <0.001$–0.005).

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Table 3. Plasticity (*D*) of growth and biomass allocation traits in seedlings of 17–20 New Caledonian rain-forest tree species grown in sun and shade. *D* is calculated as $(X_{sun} - X_{shade})/X_{sun}$, where *X* is any of the measured variables, with the data presented as means ± SE. Significant P-values from ANOVA of monodominants vs subordinates and ER vs CR species are shown: **, P < 0.01; ***, P < 0.001. Acronyms are explained in the caption of Table 2.

Plant traits	Monodominants	Subordinates	ER	CR
RMF	0.06 ± 0.02	0.05 ± 0.01	0.06 ± 0.02	0.06 ± 0.01
SMF	−0.04 ± 0.04	−0.06 ± 0.02	−0.08 ± 0.03	−0.04 ± 0.02
LMF	−0.03 ± 0.03	−0.02 ± 0.01	−0.02 ± 0.02	−0.03 ± 0.02
SRL	0.02 ± 0.09	0.00 ± 0.07	0.04 ± 0.08	0.07 ± 0.07
RLR	0.07 ± 0.07	0.03 ± 0.08	0.04 ± 0.06	0.15 ± 0.07
$\%TRL_{0.25}$	−0.03 ± 0.15	−0.13 ± 0.08	−0.05 ± 0.10	−0.24 ± 0.09
LAR	−0.19 ± 0.03	−0.18 ± 0.03	−0.22 ± 0.03	−0.19 ± 0.04
SLA	−0.19 ± 0.03	−0.15 ± 0.02	−0.19 ± 0.03	−0.16 ± 0.03
Leaf area:total root length	−0.24 ± 0.14	−0.27 ± 0.10	−0.23 ± 0.09	−0.40 ± 0.12
Stem height:total mass	−0.19 ± 0.08	−0.18 ± 0.04	−0.19 ± 0.06	−0.15 ± 0.05
RGR	0.41 ± 0.03	0.14 ± 0.04**	0.39 ± 0.04	0.18 ± 0.03***
NAR	0.39 ± 0.05	0.18 ± 0.03**	0.38 ± 0.03	0.12 ± 0.02***

Stem height:total plant mass was positively correlated with SMF (P <0.001) and $\%TRL_{0.25}$ (P = 0.009–0.017), and negatively with LMF (P = 0.007–0.010) in sun and shade plants. NAR and RGR were positively correlated in sun plants (P = 0.001), but not in shade plants (P = 0.122). RGR of sun plants correlated positively with all root length traits (P = 0.002–0.006), and LAR (P = 0.011), and negatively with leaf area : total root length (P = 0.014). RGR of shade plants correlated strongly and positively with LAR (P < 0.001) and weakly with SLA (P = 0.022). NAR in sun plants correlated weakly with $\%TRL_{0.25}$ (positively) and leaf area:total root length (negatively) (P = 0.031–0.032), but was not correlated with any trait in shade plants.

Trait differences between monodominants vs subordinates and CR vs ER species

Monodominants had lower RMF than subordinates and low RMF compared with subordinate ER species (*Alphitonia neocaledonica*, *C. discolor* and *Hibbertia lucens*) (Table 4, Figure 1, with mean values given for all traits in Appendix 2). Notably, of the two subordinate species showing a similarly low RMF (Figure 1), *A. lanceolata* has root nodules and *S. trinervis* has root clusters. RMF did not differ between ER and CR species (Table 4, Figure 1). SMF was higher in monodominants than subordinates (Table 4), although low in *A. gummiferum*, and very weakly lower in ER than CR species, notably low in the three ER subordinates (Table 4, Figure 1). LMF was higher in monodominants than subordinates due to high LMF in *A. gummiferum*; there was no clear difference between LMF of other monodominants and subordinates (Table 4, Figure 1). LMF was higher in ER than CR species (Table 4, Figure 1).

The low RMF in monodominants may be explained by efficient mass distribution: SRL was higher in monodominant species, in both sun and shade (log-transformed), with a high $\%TRL_{0.25}$ (Table 4, Figure 2a & c). However, SRL and $\%TRL_{0.25}$ were also high in some subordinate species, such as *C. discolor*, *H. lucens* and *S. trinervis* (Figure 2). *Nothofagus* spp. had particularly high $\%TRL_{0.25}$, as did the subordinate ER species *C. discolor* (Figure 2c). *Cerberiopsis candelabra* was notable among monodominants by its low $\%TRL_{0.25}$ (Figure 2c). RLR did not differ significantly between monodominant and subordinate species, but was higher in ER than CR species, as were SRL and $\%TRL_{0.25}$ (Table 4, Figure 2).

There was no difference in LAR or SLA between monodominants and subordinates, or ER and CR species (Table 4, Figure 3a & b). For the monodominants, LAR was notably high in *A. gummiferum* and *C. candelabra*, but not in *Nothofagus* spp., and SLA was particularly high in *C. candelabra* (Figure 3a & b). However, leaf area:total root length was lower (Figure 3c), and stem height:total plant mass was higher (Figure 4), in monodominants than subordinates and in ER than CR species (Table 4). In addition, NAR and RGR were higher in sun plants (but not shade plants) of monodominants than subordinates (Table 4), although similarly high values were recorded in some subordinate species (Figure 5). Similarly, NAR and RGR were higher in sun plants of ER than CR species (Table 4). *D*-RGR and *D*-NAR were higher in monodominants than subordinates, and in ER than CR species (Table 3). No other significant differences in *D* were recorded for either contrast.

Weibull *c* correlated positively with SRL and RLR and negatively with leaf area:total root length in shade plants (Table 5). Similar but non-significant trends were recorded in sun plants, but RGR and NAR of sun plants correlated positively with Weibull *c* (Table 5), as did *D*-RGR ($R_P = 0.48$, P = 0.042) and *D*-NAR ($R_P = 0.47$, P = 0.048).

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Table 4. Planned contrasts of growth and biomass allocation traits in seedlings of 17–20 New Caledonian rain-forest tree species: monodominants (M) vs subordinates (S) and episodically (ER) vs continuously regenerating (CR) species. Additive models of light regime and species were used if initial multiplicative models found no evidence of interactions ($P > 0.25$), with Holm P-value adjustments. L, data log-transformed for analysis. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant. Acronyms are explained in Table 2. Means with SE are given in Appendix 2.

	Monodominants vs subordinates			ER vs CR		
Plant traits	shade	sun	additive	shade	sun	additive
RMF			M < S***			ns
SMF			M > S***			ER < CR*
LMF			M > S***			ER > CR***
SRL_L	M > S***	M > S***		ER > CR***	ER > CR***	
RLR_L	ns	ns		ER > CR***	ER > CR***	
$\%TRL_{0.25L}$			M > S***			ER > CR***
LAR_L			ns			ns
SLA_L			ns			ns
Leaf area: total root $length_L$	M < S**	M < S***		ER < CR***	ER < CR***	
Stem height : total mass			M > S***			ER > CR***
RGR	ns	M > S***		ns	ER > CR***	
NAR	ns	M > S***		ns	ER > CR***	

Table 5. Correlations of seedling biomass allocation and growth rate with Weibull *c* in 18–19 New Caledonian rain-forest tree species. The data presented are Pearson correlation coefficients (R_P) using species' means (means of block averages), with asterisks indicating the level of significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Acronyms are explained in the caption of Table 2. Weibull *c* was log-transformed for analysis, as were some other traits (L).

Plant traits	Shade	Sun
RMF	−0.02	0.06
SMF	−0.08	−0.14
LMF_L	0.11	0.10
SRL_L	0.51*	0.39
RLR_L	0.53*	0.40
$\%TRL_{0.25L}$	0.27	0.35
LAR_L	0.27	0.17
SLA_L	0.18	0.06
Leaf area:total root $length_L$	−0.56*	−0.44
Stem height:total mass	0.06	0.06
RGR	0.10	0.55*
NAR	0.22	0.64**

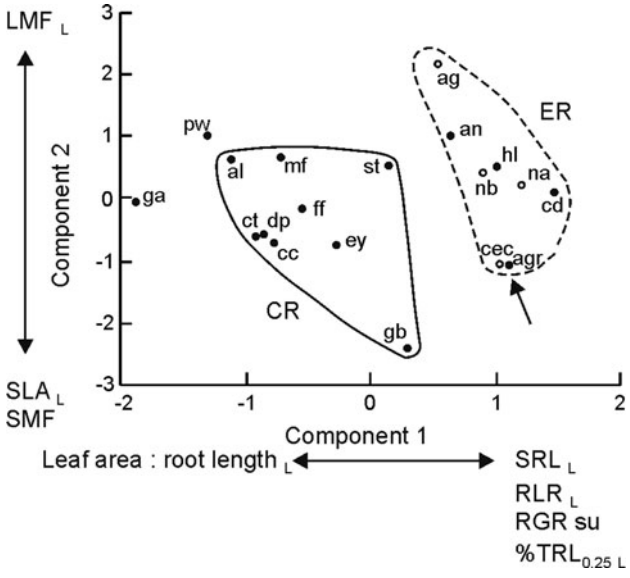

Figure 6. PCA configuration plot of biomass allocation and growth rate traits in 19 rain-forest tree species from New Caledonia. Component loadings are shown where ≥ 0.80 on Component 1 and ≥ 0.70 on Component 2. Monodominant species, open circles; subordinate species, filled circles. Groupings are shown for ER and CR species, with an outlier of the latter group (*Archidendropsis granulosa*) shown by an arrow. The biomass allocation traits used were from sun plants (values were highly correlated with those from shade plants), plus RGR and NAR from both sun and shade plants and *D*-RGR and *D*-NAR. L, log-transformed for analysis.

Trait syndromes

The first two components of PCA explained 56% of the total variance among species, with root diameter ($\%TRL_{0.25}$) and length traits, plus RGR of sun plants, contributing most to the first component (36% of variance explained). LMF, and to a lesser extent SLA, SMF and height:total mass, contributed most to the second component (20% of variance explained) (Figure 6). Three main features were evident in the configuration plot (Figure 6). Overall, monodominant species were not more similar to each other than to other ER species. Second, ER species were generally distinct from CR species, based largely on variation in root length and RGR of sun plants. The exception was *Archidendropsis granulosa*, a CR species with more trait similarity to ER species. Third, *P. wakere* and *G. austrocaledonica*, whose regeneration patterns were uncertain based on field data, were aligned with CR species. Component 1 of the PCA was positively correlated with Weibull *c* ($R_P = 0.54$, $P = 0.020$).

In addition to the trends among growth traits, RGR and NAR correlated strongly with A_{max} in sun plants on the basis of leaf area ($R_P = 0.83, 0.68$; $P = <0.001$,

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0.001 respectively) and leaf dry mass ($R_P = 0.69, 0.51$; $P = 0.001, 0.027$ respectively); RGR and NAR did not correlate with A_{max} in shade plants ($P \geq 0.07$).

DISCUSSION

Growth rates of monodominants vs subordinates, ER vs CR species

These monodominants are secondary (ER) species, dominating after large-scale disturbances. Hence, they were predicted to have high growth rates in sunny environments, such as are likely after a large-scale disturbance. This was confirmed, with higher RGR and NAR than subordinate species in the sun treatment. However, ER species in general had high RGR and NAR compared with CR species in the sun treatment, with similarly high RGR and NAR in monodominants as in other ER species. Hence, high RGR and NAR may be necessary traits for these monodominants, but do not explain their dominance compared with other ER species, at least under these experimental growth conditions, and at this ontogenetic stage. The predicted slower growth of monodominants in shaded than sunny conditions was also demonstrated, with no significant difference in RGR or NAR between monodominant and subordinate species in the shade treatment. The same trend was seen in ER vs CR species, and consistent with species' regeneration responses to light occurring along a continuum, RGR and NAR in sun plants correlated positively with Weibull *c*. Plasticity in RGR and NAR also correlated positively with regeneration/shade-tolerance (Weibull *c*), a similar trend to that reported elsewhere (Agyeman *et al.* 1999, Osunkoya *et al.* 1994).

The components of RGR (NAR and LAR) that best explain interspecific variation in RGR across all species varied according to light treatment, as found in studies elsewhere (Bloor & Grubb 2003, Osunkoya *et al.* 1994, Poorter 1999). Consistent with some previous reports of rain-forest seedlings (Poorter 1999, Veneklaas & Poorter 1998), NAR best explained interspecific variation in RGR in the sun treatment (Poorter: >10–15% daylight), whereas LAR contributed most strongly to RGR in the shade treatment. As found elsewhere (Kitajima 1994), RGR correlated positively with A_{max}, but only in the sun treatment.

Biomass allocation traits of monodominants vs subordinates, ER vs CR species

There were a few notable differences between monodominants and subordinates, but traits generally varied considerably within both groups. For example, *Nothofagus* spp. had relatively similar traits, but the other monodominants, *C. candelabra* and *A. gummiferum*, often differed, as summarized in the PCA. This suggests that dominance can be achieved by differing suites of traits, probably in concert with different combinations of biochemistry, physiology and mycorrhizal associations.

Nevertheless, there were also some clear patterns. In particular, monodominants had a low RMF, on average combined with high SRL and percentage of very fine rootlets. However, while *Nothofagus* spp. had a very high percentage of very fine rootlets, *C. candelabra* did not, and some subordinate species also had high values, especially *C. discolor.* Since organs may have multiple functions, and allocation patterns show some plasticity, interpreting relationships between biomass allocation patterns and function is not necessarily straightforward (Weiner 2004). However, in the context of the low fertility of ultramafic soils, these species were potentially allocating root biomass very efficiently for uptake of soil nutrients and water. SRL and fine roots have been linked to rapid resource acquisition (Comas *et al.* 2002), suggested to form part of a single root trait spectrum representing the trade-off between nutrient conservation (high RMF and thicker or denser roots) and acquisition (high uptake rates and SRL) (Larson & Funk 2016, Roumet *et al.* 2006). Recent work, however, suggests a multidimensional root trait spectrum, with root tissue density, but not SRL, aligning with the plant economic spectrum (Kramer-Walter *et al.* 2016). Nevertheless, SRL and fine root length have been shown to decline across successional phases in some tropical systems (Zangaro *et al.* 2012). High SRL may allow rapid uptake of water, and enhance exploitation of pulses of soil nutrients and water (Eissenstat 1991) and is commonly, but not always, associated with rapid growth, its effect possibly being context-dependent (Larson & Funk 2016). For example, in our study, root length traits, including SRL, correlated positively with RGR in sun-grown plants but not shade-grown plants. In addition, the lower RMF and consequently high shoot mass fraction must contribute to high growth rates in monodominants by maximizing foliar access to light through height growth and/or leaf display. A potential cost of fine roots is shorter lifespans and higher turnover-rates (Eissenstat 1991), and thicker or denser roots may provide valuable protection against desiccation and pests as part of a conservative strategy in resource-limited environments (Comas *et al.* 2002, Roumet *et al.* 2006).

Monodominants, except *A. gummiferum*, had relatively high SMF and stem height:total plant mass, potentially enhancing height growth for light interception. There was little or no significant difference between monodominants and subordinates in leaf allocation traits, and considerable variation among monodominant species. *Cerberiopsis*

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candelabra had particularly high SLA, and both *A. gummiferum* and *C. candelabra* had a high LAR, the former due to high LMF, and the latter to its high SLA. However, SLA and LAR (and RGR) was not higher on average in shade-intolerant (ER) species than shade-tolerant (CR) species in shade conditions, in contrast to the study of tropical seedlings by Kitajima (1994). The lower leaf area:root length in monodominant than subordinate species, and in ER than CR species, may reflect greater limitations of soil water and nutrients relative to light in the regeneration environments of shade-intolerant vs shade-tolerant species.

Notably, the subordinate species that commonly differed most from the monodominant species across all traits were known shade-tolerant (CR) species (Read *et al.* 2015), such as *C. caledonicum*, *C. transversa* and *D. parviflora*. Known shade-intolerant species, such as *A. neocaledonica*, *C. discolor* and *H. lucens* (Read *et al.* 2015) often had similar trait values to those of the monodominant species. However, these are generalist species that also occur in maquis (shrub-dominated vegetation), so may be less comparable to the monodominants that are predominantly forest species. For example, their higher RMF (contributing to high RLR) and low SMF and height:total plant mass may be better suited to a shrubland environment on sites where nutrient deficits may be more severe, and water more limiting during the dry season than in relatively closed forest (Jaffré 1980). However, the monodominant *A. gummiferum* shared some of these traits. Excluding the ER generalists, the monodominants tend to have higher SRL and fine rootlet fraction than subordinates, except *C. candelabra* for the latter. Notably, *S. trinervis* had high root mass efficiency via its root clusters (Lamont 2003), and *A. lanceolata* from mycorrhizal (presumed) root nodules (cf. Morrison & English 1967).

What seedling traits are associated with forest dominance and regeneration patterns?

We previously showed for the same plants (Read *et al.* 2015) that ER species, including monodominants, had leaf-level photosynthesis traits typical of shade intolerance, with higher A_{max} (on a leaf area basis) in sun plants than CR species, and high plasticity. However, these traits did not differ between monodominants and other ER species. CR species had leaf-level photosynthesis traits consistent with shade tolerance, including lower dark respiration rates than ER species in shade plants (Read *et al.* 2015). The trends in RGR and NAR in the current study are consistent with the leaf-level photosynthesis traits of the same plants. Hence, while assimilation and growth rate traits are largely consistent with regeneration patterns across species, they do not explain why some shade-intolerant species achieve monodominance and others do not.

The lack of evidence for superior growth rates in monodominants compared with other ER species in the sun treatment may be due in part to an insufficiently high light regime (*c.* 30% incident irradiance), such that, at least on some cloudy days, photosynthetic rates (and so potentially growth) were light-limited. However, it is not certain that seedlings of monodominants have higher light demands than those of other ER species (Read *et al.* 2015). Ontogenetic changes in biomass partitioning influence whole-plant responses to understorey light conditions (Givnish 1988, Lusk *et al.* 2008, Veneklaas & Poorter 1998), with the possibility that differences in growth rates among ER species become apparent in older juveniles. It is also possible that other aspects of the growth regime, including soil nutrient levels, mycorrhizal inoculation and humidity, affected biomass allocation patterns and growth differentially in monodominants relative to other ER species (Béreau *et al.* 2005, Weiner 2004). This might occur if the experimental growth environment was suboptimal for the monodominants, or alternatively, if the growth environment did not display suboptimal features that might confer an advantage to the monodominants, either abiotic or biotic, including herbivory (Sack & Grubb 2001, 2003). In particular, Corrales *et al.* (2016) suggested that the ectomycorrhizal (EM) symbiosis may provide a competitive advantage to seedlings of EM monodominants (e.g. *Nothofagus* spp., *A. gummiferum*) by competition of EM fungi with soil microbes for nitrogen, thereby slowing litter decomposition and reducing availability of inorganic nitrogen. Multiple co-occurring stresses may influence field performance (Sack & Grubb 2003, Valladares & Niinemets 2008). Indeed, monodominance may be achieved through superior survival of stresses associated with exposed post-disturbance conditions, such as drought, either directly (drought resistance) or indirectly via effects on growth rate. It is also possible that reproductive traits such as mast seeding (common to these monodominant species) play a key role in achieving monodominance, especially if linked to climate events that promote canopy disturbances (Read *et al.* 2008). Hence, field studies should provide important complementary insights to those gained from nursery-house studies (Sack & Grubb 2003).

The slower growth of monodominants (and other ER species) in the shade treatment may explain, at least in part, the predicted or actual temporal decline in dominance shown by monodominants in undisturbed stands: if growth rates of monodominants in shade do not differ from those of subordinate species they are less likely to achieve a competitive advantage, particularly taking into account effects of stochastic factors such as time of establishment. RGR and NAR of ER species

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were substantially lower in the shade treatment than the sun treatment, but this was not the case in CR species. Therefore, it is possible that in more severe shade, RGR and NAR of monodominant (and other ER) species would decline below values recorded in CR species. Our shade treatment (*c.* 10% incident irradiance) was not as severe as found in the undisturbed understorey (and was less heterogeneous, e.g. sunflecks, and probably differed spectrally) (Bloor 2003, Sack & Grubb 2001, Watling *et al.* 1997). Such rank reversals in RGR frequently occur between 2% and 10% daylight irradiance in seedlings and saplings (Agyeman *et al.* 1999, Sack & Grubb 2001, 2003). In addition, superior growth rates in CR species may develop in older seedlings due to ontogenetic changes (Lusk *et al.* 2008, Niinemets 2006, Sack & Grubb 2001).

However, although there is evidence that growth rates contribute to shade-tolerance (Baltzer & Thomas 2007, Sack & Grubb 2001), the predicted higher RGR of tolerant than intolerant species has not always been recorded in shade-grown seedlings (Kitajima 1994, Valladares & Niinemets 2008, Walters & Reich 1999). Seedling tolerance of shade may be strongly influenced by other traits that influence mortality directly or via effects on net growth (where net growth include losses to all causes: Walters & Reich 1999) and thereby competitiveness. These traits include large seeds with reserves that may buffer against a range of stresses in the forest understorey (Grubb & Metcalfe 1996, Osunkoya *et al.* 1994, Walters & Reich 2000), tolerance or resistance to pathogens and herbivores (Augspurger 1984, Kitajima 1994, Kitajima *et al.* 2013, McCarthy-Neumann & Kobe 2008), carbon storage (Canham *et al.* 1999, Kobe 1997, Myers & Kitajima 2007) and longer leaf lifespans that reduce costs of canopy maintenance (Lusk *et al.* 2011).

Perhaps most important in drawing conclusions from our results is that seedlings in this study were grown independently, without interactions among species. If grown in limited space where species competed for light, nutrients and water, stronger patterns might emerge. In particular, in sunny conditions, monodominant species might preempt soil nutrients by effective root architecture and/or nutrient uptake physiology (including mycorrhizal benefits), leading to enhanced above-ground productivity and competitive success. This scenario may be important in any forest system, but probably more so on these ultramafic soils where levels of P, K and Ca are particularly low (Jaffré & Veillon 1990, Perrier *et al.* 2006, Read *et al.* 2006). For example, higher P uptake rates have been associated with finer roots (Comas *et al.* 2002), and furthermore, species with high densities of fine roots can impede establishment by seedlings of some competing species (Zangaro *et al.* 2016). In addition, *Nothofagus* spp. and *A. gummiferum* have ectomycorrhizal relationships (Demenois *et al.* in press, Perrier *et al.* 2006), with hyphal networks potentially enhancing sharing of mineral nutrients and carbon among plants (Finlay & Read 1986a, b; McGuire 2007b). Such networks might allow crucial transfer of carbon from adults to juveniles, extending the duration of a seedling bank in the forest understorey until disturbance facilitates recruitment (Demenois *et al.* in press, Newbery *et al.* 2010). A similar mechanism may enhance seedling establishment following a major disturbance if networks survive, e.g. after a cyclone. It is likely that below-ground interactions contribute significantly to the structure and diversity of these forest communities (Steidinger *et al.* 2015, Valverde-Barrantes *et al.* 2013).

CONCLUSIONS

High growth rates in sunlit conditions, such as occur after a large disturbance, are likely to contribute substantially to the capacity for monodominance in *Nothofagus* spp., *A. gummiferum* and *C. candelabra* in these species-rich forests, and efficient root allocation probably plays an important role in achieving high RGR. However, RGR in monodominant species was not higher than in other ER species under these experimental conditions, so may not alone explain dominance. It is not clear whether the growth conditions used were not sufficient to allow superior growth rates in monodominants, or whether superiority would be apparent at a later ontogenetic stage, or when grown in competition. But it is also possible that some aspect of tolerance of exposed conditions other than irradiance may play a key role in achieving post-disturbance dominance by monodominant species, either by promoting higher rates of survival directly, or indirectly by effects on growth rates. It is also possible that other traits, such as mast seeding, play a key role in facilitating dominance. Field studies of establishment, growth and survival should provide further insights into these issues.

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Appendix 1. Associations across biomass allocation and growth rate traits, separately for sun and shade plants, in seedlings of 19–20 New Caledonian rain-forest tree species. Data presented are Pearson correlation coefficients (R_P) based on species' means (means of block averages), $n = 20$ for all traits except RGR and NAR ($n = 19$). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. RMF, root mass fraction; SMF, stem mass fraction; LMF, leaf mass fraction; SRL, specific root length; RLR, root length ratio; $\%TRL_{0.25}$, % terminal rootlet length <0.25 mm diameter; LAR, leaf area ratio; SLA, specific leaf area; LA: Rt, leaf area:total root length; Ht:TM, plant height:total plant mass; RGR, relative growth rate; NAR, net assimilation rate. L, log-transformed for analysis.

Trait	RMF	SMF	LMF_L	SRL_L	RLR_L	$\%TRL_{0.25\,L}$	LAR_L	SLA_L	$LA:Rt_L$	Ht:TM	RGR
Shade plants											
SMF	−0.35										
LMF_L	−0.54*	−0.59**									
SRL_L	−0.14	0.03	0.09								
RLR_L	0.15	−0.08	−0.06	0.95***							
$\%TRL_{0.25L}$	−0.35	0.28	0.04	0.79***	0.69**						
LAR_L	−0.28	−0.17	0.39	0.46*	0.39	0.14					
SLA_L	0.09	0.38	−0.44	0.33	0.37	0.07	0.65**				
$LA:Rt_L$	−0.25	−0.06	0.27	−0.81***	−0.90***	−0.66**	−0.04	−0.22			
Ht:TM	−0.15	0.76***	−0.56*	0.39	0.33	0.57**	0.05	0.50*	−0.38		
RGR	−0.23	−0.10	0.27	0.37	0.32	0.22	0.77***	0.52*	−0.07	0.05	
NAR	−0.05	0.21	−0.16	−0.07	−0.06	−0.14	0.19	0.38	0.05	0.14	0.37
Sun plants											
RMF											
SMF	−0.41										
LMF_L	−0.49*	−0.58**									
SRL_L	−0.19	0.05	0.12								
RLR_L	0.04	0.00	−0.04	0.96***							
$\%TRL_{0.25L}$	−0.32	0.26	0.01	0.71***	0.64**						
LAR_L	−0.14	−0.29	0.38	0.43	0.37	0.04					
SLA_L	0.30	0.30	−0.58**	0.31	0.39	0.05	0.53*				
$LA:Rt_L$	−0.14	−0.17	0.30	−0.78***	−0.86***	−0.60**	0.00	−0.30			
Ht:TM	−0.16	0.75***	−0.59**	0.39	0.38	0.53*	−0.12	0.46*	−0.50*		
RGR	−0.14	−0.15	0.23	0.67**	0.64**	0.61**	0.57*	0.27	−0.55*	0.12	
NAR	−0.06	0.08	−0.05	0.41	0.42	0.50*	0.20	0.23	−0.49*	0.27	0.71**

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Appendix 2. Means ± SE of growth and biomass allocation traits in seedlings of 17–20 New Caledonian rain-forest tree species: monodominants vs subordinates and episodically (ER) vs continuously regenerating (CR) species. Acronyms are explained in the caption of Appendix 1.

	Monodominants		Subordinates		ER		CR	
Plant traits	shade	sun	shade	sun	shade	sun	shade	sun
RMF ($g\ g^{-1}$)	0.274 ± 0.018	0.293 ± 0.022	0.365 ± 0.016	0.386 ± 0.016	0.328 ± 0.030	0.345 ± 0.031	0.342 ± 0.017	0.363 ± 0.020
SMF ($g\ g^{-1}$)	0.324 ± 0.040	0.314 ± 0.041	0.271 ± 0.015	0.257 ± 0.016	0.283 ± 0.032	0.267 ± 0.035	0.293 ± 0.018	0.283 ± 0.017
LMF ($g\ g^{-1}$)	0.401 ± 0.054	0.393 ± 0.056	0.364 ± 0.016	0.357 ± 0.016	0.389 ± 0.035	0.383 ± 0.034	0.365 ± 0.023	0.355 ± 0.023
SRL ($m\ g^{-1}$)	27.1 ± 4.8	27.3 ± 3.5	22.9 ± 4.8	27.1 ± 7.1	36.3 ± 6.5	40.5 ± 10.2	17.8 ± 3.0	21.1 ± 4.8
RLR ($m\ g^{-1}$)	6.8 ± 1.1	7.4 ± 1.0	8.0 ± 1.8	8.9 ± 1.9	11.8 ± 2.8	12.1 ± 2.6	5.5 ± 0.9	7.0 ± 1.4
$\%TRL_{0.25}$	42.3 ± 11.3	37.7 ± 7.6	18.3 ± 4.3	17.2 ± 4.2	38.3 ± 8.1	35.1 ± 6.4	17.0 ± 4.9	14.9 ± 4.5
LAR ($m^2\ kg^{-1}$)	5.97 ± 0.75	5.05 ± 0.68	5.72 ± 0.33	4.79 ± 0.19	6.21 ± 0.55	5.11 ± 0.44	5.79 ± 0.33	4.85 ± 0.19
SLA ($cm^2\ g^{-1}$)	162 ± 32	135 ± 24	158 ± 9	137 ± 7	166 ± 20	139 ± 16	163 ± 10	141 ± 8
Leaf area:total root length ($cm^2\ m^{-1}$)	10.7 ± 2.8	8.6 ± 2.4	15.0 ± 2.7	13.6 ± 3.1	8.5 ± 2.0	6.9 ± 1.7	15.9 ± 2.4	12.1 ± 1.7
Stem height:total mass ($cm\ g^{-1}$)	33.6 ± 7.6	28.9 ± 6.1	23.9 ± 4.2	20.7 ± 3.8	30.3 ± 6.5	25.5 ± 5.1	25.7 ± 4.8	23.0 ± 4.8
RGR ($mg\ g^{-1}\ wk^{-1}$)	33.7 ± 2.6	56.7 ± 1.4	34.0 ± 1.9	40.2 ± 2.6	34.3 ± 2.3	55.6 ± 1.0	35.6 ± 2.0	38.1 ± 2.5
NAR ($g\ m^{-2}\ wk^{-1}$)	6.34 ± 0.59	10.34 ± 0.29	5.94 ± 0.29	7.28 ± 0.33	5.97 ± 0.47	9.64 ± 0.43	6.19 ± 0.36	7.02 ± 0.36

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