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Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Managing successional trajectories in alien-dominated, novel ecosystems by facilitating seedling regeneration: A case study

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ARTICLE INFO

Article history:

Received 25 August 2009
Received in revised form 12 April 2010
Accepted 19 April 2010
Available online xxxx

Keywords:

Adaptive management
Cinnamomum verum
Forest gap
Oceanic island
Root competition
Seychelles

ABSTRACT

Managing novel ecosystems that emerge after strong anthropogenic disturbance and the spread of alien species poses complex problems. As a case example, we discuss efforts on the tropical oceanic island Mahé (Seychelles) to promote the regeneration of native trees in tropical secondary forest dominated by the invasive tree *Cinnamomum verum* (true cinnamon).

We monitored the growth of transplanted and self-sown native and alien tree seedlings in both artificially created forest gaps and in the understorey of closed forest. In the understorey, native species survived but grew very slowly, indicating that any recovery of native tree populations would also be very slow. In larger gaps, seedlings of certain invasive species grew particularly fast, suggesting that these species would rapidly dominate. Nutrient addition had only a minor positive effect on seedling growth, especially in the understorey.

Although neither closed canopy conditions nor large gaps are conducive to the recovery of native seedlings, our data indicate that intermediate levels of canopy disturbance, i.e. those attained by felling one or a few trees, provide a combination of below- and aboveground resource limitation of seedling growth that may favour native species over invasive species. Based on these findings, we propose a strategy for restoring native vegetation that entails making small gaps in cinnamon-dominated forest and planting them with native tree species.

This study illustrates how management strategies can be improved by combining insights gained from past interventions with the results of field and greenhouse experiments.

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1. Introduction

The spread of alien species is one of the main reasons for the loss of biodiversity (Millennium Ecosystem Assessment, 2005), and the urgent need to prevent further invasions is now internationally recognized (cf. McNeely et al., 2001). The ideal strategy for achieving this would be to identify potentially invasive species before they spread into natural areas, for example by preventing the import of species at national borders (Wittenberg and Cock, 2001). However, many invasive plant species are already abundant in areas of high conservation value (e.g. Stohlgren et al., 2001), in particular on oceanic islands (Denslow, 2003; Kueffer and Daehler, 2009; Kueffer et al., 2010, 2004), and control measures must therefore be integrated into strategies for habitat management (e.g. D'Antonio and Meyerson, 2002; Zavaleta et al., 2001).

Developing an appropriate management strategy for uninvaded and undisturbed forest is straightforward – prevent anthropogenic disturbance and the introduction of potentially invasive alien species to the area. However, where the vegetation already consists of

a mixture of native and alien species, the situation may be more complex (e.g. Kueffer et al., 2007; Lugo, 2004; Wisser et al., 2002). Such ecosystems, which have been termed 'novel ecosystems' (Hobbs et al., 2006), are characterized by new combinations of species resulting from habitat disturbance, the introduction of alien species, and other anthropogenic interferences. Under these circumstances, restoring the natural vegetation can be difficult because of drastic changes that have occurred in species composition and habitat conditions (Hobbs et al., 2006, 2009; Jackson and Hobbs, 2009; Kueffer and Daehler, 2009; Lugo, 2004; Seastedt et al., 2008). Context-specific management measures must therefore be designed and tested in an adaptive management framework, i.e. through iterative, experimental testing and adapting of management interventions (Kueffer and Daehler, 2009; Seastedt et al., 2008). In particular, a balance must be struck between removing alien species to facilitate regeneration of native species and avoiding disturbance of the forest canopy, which may allow other alien plants to invade (compare Adler et al., 1998; Firn et al., 2010; Hata et al., 2006; Zavaleta et al., 2001).

The mid-altitude forests of the mountainous oceanic island of Mahé (Republic of Seychelles, Indian Ocean) represent such novel ecosystems, with alien species, mainly *Cinnamomum verum* (true

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cinnamon), accounting for 70–90% of canopy trees. Native trees, however, still occur in scattered patches, and small number of juveniles can be found in the understorey (Fleischmann, 1997; Kueffer, 2006; Kueffer et al., 2007). The present dominance of alien trees in these forests is a consequence of the exploitation of native trees for timber during the 19th century, which was followed by the spread of cinnamon from spice plantations.

The novel characteristics of the resulting ecosystem are particularly evident in the case of the regeneration niche. In the former native forest the ground was probably covered with a thick layer of slowly decomposing leaf litter of endemic species such as the tree *Northea hornei* (Sapotaceae) and several palms and pandans. Most seedlings probably established in microhabitats such as decaying wood and accumulations of organic matter on rocks, with seedling densities of some 10 individuals per square meter; these are conditions that now occur only in pockets of relatively undisturbed palm-dominated and cloud forest. In contrast, cinnamon litter decomposes quickly, producing a thin litter layer and a more nutrient-rich soil (Kueffer, 2010; Kueffer et al., 2008), and densities of 100 seedlings per square meter are usual (Kueffer, 2006). A second novel factor that strongly shapes regeneration is root competition by adult cinnamon trees, which produce a dense root mat just below the soil surface (Kueffer et al., 2007). Indeed, there is good evidence that on these very nutrient-poor soils (Kueffer, 2010; Kueffer et al., 2008), cinnamon shapes the ecosystem through strong belowground competition. This is in contrast to more nutrient-rich habitats, where alien woody species often form dense thickets, suppressing native plants mainly through competition for light. Thirdly, regeneration dynamics have fundamentally changed due to the dominance of alien species on a landscape scale, which results in a seed rain that is composed almost exclusively of alien species and seed limitation of native trees (Kueffer, 2006; Kueffer et al., 2007).

Although the mid-altitude forests of the Seychelles are now dominated by alien trees, they support many threatened native plant and animal species (Carlstrom, 1996; Fleischmann, 1997; Gerlach, 2008; Huber and Ismail, 2006; Stoddart, 1984) and for this reason much of the forest is now protected. Indeed, they are the only habitat where some endemic plants can be conserved in the wild, though many species are now represented only by a few old adults. In an enumeration of some 60,000 seedlings only 1.5% were from native species and about half of these were of the common endemic palm, *Phoenixophorium borsigianum* (Kueffer, 2006). Seed limitation is certainly one reason for the poor regeneration of many native species (Kueffer, 2006), and unless action is taken their populations will decline further.

The aim of this study was to explore methods to increase native tree regeneration in this novel ecosystem. One option that has been considered is to remove cinnamon from large areas of forest, as has been attempted for invasive trees in Mauritius (cf. Cheke and Hume, 2008) and Hawaii (Loh and Tunison, 2009; Tunison and Stone, 1992). However, in Seychelles this drastic measure has proved unsatisfactory (Dogley, 2004; Kueffer, 2003), because removing cinnamon can lead to an increase in other alien species (Kueffer et al., 2007), which form dense thickets that hinder native re-growth more (Kueffer and Vos, 2004). Cinnamon has also become an important food source for endemic birds (Kueffer et al., 2009). Furthermore, it appears that the large-scale removal of alien species in these forests increases erosion without significantly promoting native tree growth (Dogley, 2004; Simara et al., 2009; Valentin et al., 2008).

A second option, which appears more promising, is to create many small, scattered gaps in the forest. In this study, we investigate how this approach would affect the balance of seedling regeneration between native and invasive species. We monitored the growth of tree seedlings transplanted into artificially created gaps

and into the undisturbed understorey. In addition, we also included a nutrient treatment to test whether nutrient availabilities modulated the effect of gap formation, because low nutrient levels are known to restrict seedling growth in these forests (Kueffer, 2010; Schumacher et al., 2009). In addition, we monitored the growth of self-sown cinnamon seedlings along transects from the forest understorey to the interior of gaps. We used these seedlings, which we call phytometers, to evaluate how seedling growth responded to variation in environmental conditions from the edge to the centre of gaps.

2. Methods

2.1. Study area

The study was carried out in a mid-altitude forest at Mare aux Cochons (MC) within the Morne Seychellois National Park on the island of Mahé (4° S, 55° E, 154 km², Republic of Seychelles). The MC site is in a forested upland valley (c. 450 m.a.s.l.) situated in the rugged North-West of Mahé (see map in Appendix A), where altitude increases rapidly from sea level to Morne Seychellois, at 900 m.a.s.l. the highest peak of the Seychelles.

By the beginning of the 20th century the native vegetation at MC was almost completely destroyed and the area heavily invaded by cinnamon. From the early 20th century until the 1970s leaves and bark from feral cinnamon were collected commercially. In our study area, about 85% of the forest canopy is made up of cinnamon trees, including a very dense layer of tree seedlings (>100 per m²), mainly comprised of cinnamon (Kueffer, 2006).

The soils at MC are ferrasols with a pH of c. 4.5 that have developed on granitic bedrock. Nutrient availabilities are generally low, and plant growth appears to be limited mainly by the availability of phosphorus and nitrogen, though possibly also by other nutrients including potassium (Kueffer, 2010; Kueffer et al., 2008). Mean total N, P and C contents of mineralic topsoil were measured as 2.1 mg g⁻¹, 0.3 mg g⁻¹, and 47 mg g⁻¹, respectively (Kueffer et al., 2008). Mean leaf nutrient concentrations (and ranges) in seedlings of two native and two invasive species in the forest understorey at MC were 12.5 (10.9–15.2) mg g⁻¹ N and 1.1 (0.9–1.2) mg g⁻¹ P (Schumacher et al., this study).

During the study period, the annual rainfall was c. 3400 mm. Although there is no pronounced seasonality on Mahé, the period between June and September is generally drier than that between November and February. At low to mid-altitudes (<600 m.a.s.l.), monthly mean rainfall typically ranges from 80 to 150 mm in the 'dry' period, and 300–450 mm in the 'wet' period (Cazes-Duvat and Robert, 2001). At MC, the mean annual air temperature measured at 1 m above ground was 23 °C under closed canopy and 24 °C in a forest gap, while the corresponding values for mean annual air humidity were 98.5% and 96.5%, respectively (data obtained by an Onset HOBO Pro RH/Temp sensor).

2.2. Species

We selected four native and five invasive alien tree species that are abundant in the forests on Mahé and for which either seeds or seedlings were available at the time of the experiment (Table 1). Both groups (native vs. invasive) encompassed a broad ecological range from early-successional to shade-tolerant species, and we avoided having closely related species within the same group (cf. Schumacher et al., 2009). The native species included two indigenous and two endemic species. All species have small to medium sized seeds (2–10 mm in diameter) except *Syzygium jambos*, which has seeds of 15–20 mm diameter.

Table 1

Characterization of the tree species used in the transplant experiment. Data sources: nomenclature and maximal stem height from Friedmann (1994); ecological group from Kueffer et al. (2008), except for *Tabebuia pallida*; seed size, defined as the longest diameter, from Kronauer (2005), except for *Alstonia macrophylla* and *Tabebuia pallida* from Friedmann (1994). Abbreviations: P = pioneer, U = understorey, C = canopy. In the two last columns the biomass of seedlings at the onset of the experiment and the number of replicates per species at the end of the experiment are indicated.

Species	Family	Stem height (m)	Seed size (mm)	Ecological group	Initial biomass (g)	Replicates
<i>Invasives</i>						
<i>Alstonia macrophylla</i> (Am)	Apocynaceae	15	5 ^c	P	0.04	7
<i>Cinnamomum verum</i> (Cv)	Lauraceae	15	11.5	C	0.53	20
<i>Psidium cattleianum</i> (Pc)	Myrtaceae	7	4.9	U	0.13	20
<i>Syzygium jambos</i> (Sj)	Myrtaceae	10	16.7	U	0.86	19
<i>Tabebuia pallida</i> (Tp)	Bignoniaceae	10	20 ^c	P	0.13	15
<i>Natives</i>						
<i>Aphloia theiformis</i> ^a (At)	Flacourtiaceae	12	2.4	P	0.04	19
<i>Canthium bibracteatum</i> (Cb)	Rubiaceae	8	4.9	P	0.15	20
<i>Erythroxylum sechellarum</i> ^b (Es)	Erythroxylaceae	7	10.6	?	0.11	19
<i>Memecylon eleagni</i> ^b (Me)	Melastomataceae	10	6.2	U	0.05	16

^a Subsp. *madascariensis* var. *seychellensis*.

^b Species endemic to the Seychelles.

^c Including wings.

For the phytometer experiment, we used self-sown *C. verum* seedlings in the experimental gaps and surrounding forest.

Nomenclature follows Friedmann (1994).

2.3. Experiment 1: transplant experiment

2.3.1. Experimental setup

Five clearings of approximately 15 by 15 m² (area c. 225 m²) were made by felling all adult trees (mainly cinnamon); fallen trees were then removed and piled up at the edge of the gap. Near to each gap, an understorey plot was chosen in closed forest (see map in Appendix A).

Four of the species – the aliens cinnamon and *Tabebuia pallida*, and the natives *Canthium bibracteatum* and *Memecylon eleagni* – were grown from seed collected in the forest. Ripe fruits were collected directly from 5 to 15 parent trees per species, and the mixed seed sown into seedling trays immediately after collection. When the seedlings had developed the first true leaves (three to six months after sowing), the plants were transplanted into 1-l pots filled with forest soils. For the other species – the invasives *Alstonia macrophylla*, *Psidium cattleianum* and *S. jambos*, and the natives *Aphloia theiformis* and *Erythroxylum sechellarum* – no seed was available and we therefore collected young plants in the field, similar in size to those grown from seed. All plants were allowed to adapt to the pot environment for two weeks before being transplanted into the forest at the onset of the experiment.

A split-plot design was used, with light availability as the main-plot factor and nutrient treatment as the split-plot factor. Mean light levels were 10% (range 8.2–12.6%) of ambient light in the understorey plots and 63% (56–69%) in the gap plots. The mean total N concentration in the soil at the plots (understorey and gap sites combined) was 1.4 mg g⁻¹ (range 0.1–2.8 mg g⁻¹), while that of P was 0.34 mg g⁻¹ (range 0.14–0.58 mg g⁻¹) (data from one pooled sample of topsoil per subplot, i.e. 2 pooled samples per gap viz. understorey plot, 20 samples in total). Two subplots (2 × 2 m²) spaced 2 m apart were placed in the centre of each gap and understorey plot. All herbs and seedlings were removed from the subplots, but the sparse leaf litter layer was left. Two seedlings of each species (i.e. 18 seedlings in all) were planted at randomly selected points on a regular grid with a distance of 35 cm between neighbouring seedlings. One of each pair of subplots was randomly assigned to the ambient nutrient (LN, no nutrients added) and the other to the high nutrient treatment (HN, addition of fertilizer) (see map in Appendix A). For the HN treatment, 1 g of slow release N–P–K-fertilizer (Osmocote 16:11:11,

Osmocote, Scotland) was added around each seedling every two months.

The experiment was started in early March 2004 and ran until January 2005. During this period, seedlings were watered as necessary and any unwanted plants were removed.

2.3.2. Data collection

At the beginning of the experiment, six seedlings per species were selected at random from the surplus plants and harvested to determine the initial dry weight. For the remaining plants, stem height, number of leaves and total leaf area were recorded at the beginning and end of the experiment. To estimate leaf area, linear regressions of leaf area against the product of leaf length and breadth were calculated for a sample of leaves (50–100 per species). These were placed beneath a glass plate and photographed with a digital camera (Nikon Coolpix 995, resolution at 2048 × 1536 pixels); the images were then used to determine leaf length and breadth using Adobe Illustrator™ 10, and area using Adobe Photoshop™ 7.0 (cf. Dietz and Steinlein, 1996). The plants were harvested and divided into leaves, stems plus petioles, and roots. All material was then oven-dried at 80 °C for 48 h.

The raw data were used to calculate the following growth parameters: relative growth rates of dry plant biomass (RGR), leaf area (RGR_{LA}) and height (RGR_H); specific leaf area (SLA, leaf area per dry leaf biomass); leaf area ratio (LAR, leaf area per dry plant biomass); and root shoot ratio (RSR, dry root to shoot biomass ratio). For two native species (*A. theiformis*, *C. bibracteatum*) and two invasive species (cinnamon, *P. cattleianum*) foliar nitrogen and phosphorus contents were measured at the end of the experiment. The data for RGR_H and RGR_{LA} showed very similar patterns and were highly correlated with RGR ($r > 0.6$, $P < 0.01$), therefore the data is not shown.

2.4. Experiment 2: cinnamon phytometer experiment

In three of the five gaps, we monitored the growth of established cinnamon seedlings between July 2004 and February 2005 (Gaps 1, 2 and 3; Appendix A). The seedlings studied lay along two perpendicular transects (orientation S–N and E–W) passing through the centre of each gap and extending 7 m into the forest on both sides; for the analysis the transects in each gap were treated as four sub-transects running from the gap into the forest. Established seedlings c. 20–30 cm tall were chosen at the following distances along each subtransect: –7, –5, 0, 2, 4 and 6 m (where 0 represents the edge of the gap and negative values are in the

forest; Appendix A). At each sampling point three randomly chosen seedlings were marked. Additionally, at two spots >30 m from any gap we monitored growth of eight seedlings (control plants). At the end of the study, number of leaves, stem height, and dry above-

ground leaf and stem biomass were recorded. We then calculated the change in leaf number and stem height during the study period and aboveground RGR.

2.5. Statistical analysis

All statistical analyses were performed with JMP V 6.0 (SAS Institute Inc., 2005).

2.5.1. Experiment 1: transplant experiment

In each gap and understorey plot, the average of the two replicate plants was used for the analysis. We used general linear models with light level, nutrient level, species status (native vs. invasive) and their interactions as fixed factors, and species identity (nested in species status) as well as plot type (gap vs. understorey, nested in light treatments) as random factors. To analyse differences among species we ran a separate model with light level, nutrient level, species identity and their interactions as fixed factors as well as plot type (gap vs. understorey, nested in light treatments) as a random factor. *A. macrophylla* was excluded from this analysis because all individuals died in the understorey treatments. The leaf area of each plant at the start of the experiment was included as a covariable to account for differences in initial plant size. The dependent variables were relative growth rates of biomass, and the allocation parameters SLA, LAR, RSR. To remove heteroscedascity, SLA, LAR and RSR were log-transformed.

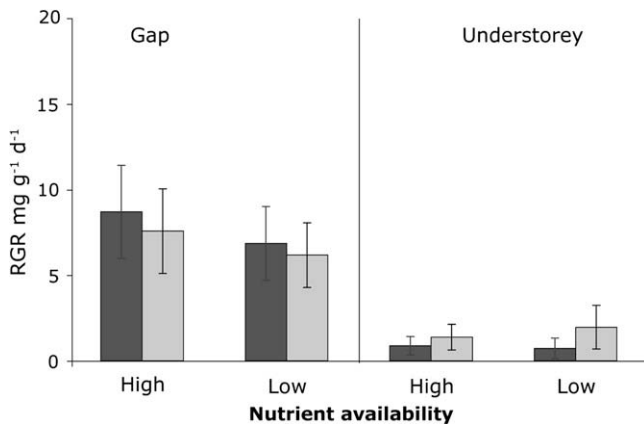


Fig. 1. Relative growth rate of total dry biomass (RGR) of invasive (black bars) and native (grey bars) seedlings (mean \pm SE). Data are shown for plants growing under two light levels (forest understorey and gap) and two levels of nutrients (low and fertilized). Growth rates differed significantly between gap and understorey but not between invasive and native species. See text for further information.

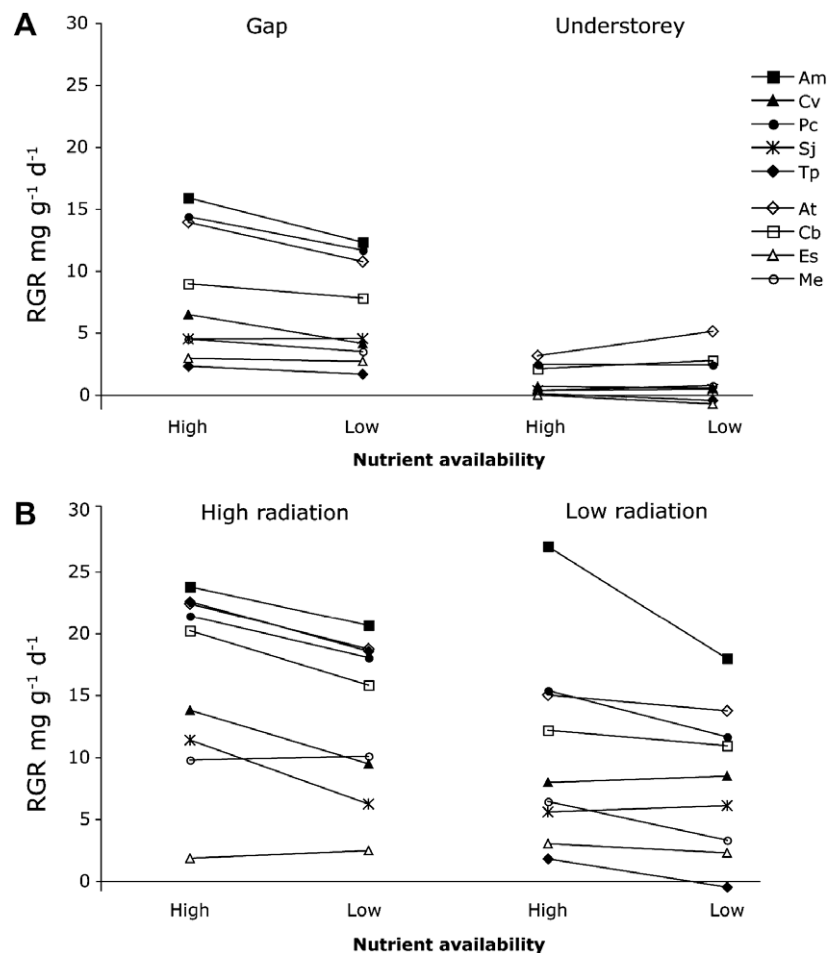


Fig. 2. RGR of the species grown in the transplant experiment (A) compared with that of the same species set in a common garden experiment (B). Filled symbols, invasives species; open symbols, native species. In the understorey plots all individuals of *Alstonia macrophylla* died. In both experiments growth rates differed significantly between the two light treatments but not between invasive and native species (see main text and Schumacher et al. (2009)). For acronyms of species names see Table 1.

2.5.2. Experiment 2: phytometer experiment

The analyses used the mean values of the three replicate cinnamon seedlings at each sampling position. To avoid pseudo-replication, we pooled the data for the four sub-transects in each gap, resulting in one value per transect position. We used general linear models with plot (i.e. three replicate gaps) and distance from gap edge as fixed factors. Various models were made using total dry biomass, number of leaves and stem height produced over the experimental period as the dependent variables.

3. Results

3.1. Experiment 1: transplant experiment

3.1.1. Mortality and relative growth rates

Overall 26% of the individuals died, but because we planted two individuals per subplot few replicates were lost (Table 1). For three

invasive and one native species (cinnamon, *P. cattleianum*, *S. jambos*, *C. bibracteatum*) <10% of the individuals died (i.e. 0–4 individuals per species). One native species (*E. sechellarum*, 40%) and two invasive species (*A. macrophylla*, 100%; *T. pallida*, 50%) suffered relatively high mortality in the understorey.

Both groups of species grew faster (relative growth rate of total dry biomass, RGR) in the gap plots than in the understorey plots ($P < 0.001$, Fig. 1, and Appendix B), and plants in gaps also profited more from added nutrients (significant interaction between light and nutrient, $P = 0.003$, Fig. 1, and Appendix B). The range of RGR values among species was greater in the gaps (2–16 $\text{mg g}^{-1} \text{d}^{-1}$) than in the understorey (–0.5 to 5 $\text{mg g}^{-1} \text{d}^{-1}$; Fig. 2A). Species showed significantly different responses to light (species \times light, $P < 0.001$) but not to nutrients (species \times nutrient, $P > 0.1$). However, RGR did not differ significantly between the invasive and native groups in any treatment ($P \geq 0.3$), and the variation among species was independent of species status (species effect in

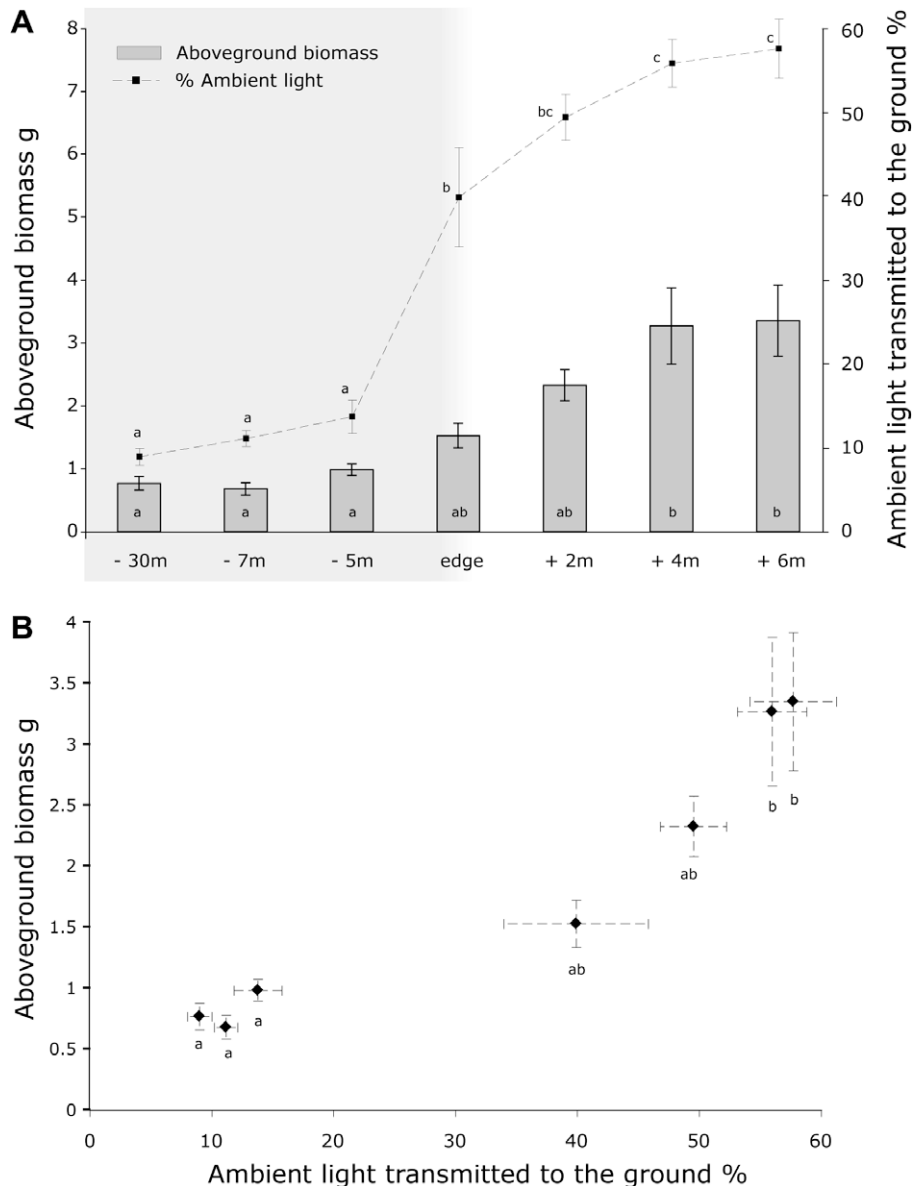


Fig. 3. Growth of naturally established *Cinnamomum verum* (cinnamon) juveniles along transects from the understorey to the centre of the gap plot. Dry aboveground biomass at the final measurement (mean \pm SE) is plotted against (A) position along transect (distances from the gap edge into the forest understorey are indicated by negative numbers and those into the gap interior by positive numbers) and (B) % ambient light transmitted to the ground (mean \pm SE). Different letters indicate significant differences (Tukey test).

separate ANOVA, $P < 0.001$). There was a tendency for invasive species to respond more positively to nutrient addition than native species (Fig. 2A), but the results were not fully consistent.

3.1.2. Biomass allocation and foliar nutrient contents

The specific leaf area (SLA) of all species was significantly lower in gaps than in understorey plots ($100\text{--}130\text{ cm}^2\text{ g}^{-1}$ vs. $170\text{--}200\text{ cm}^2\text{ g}^{-1}$; respectively; $P = 0.003$), and leaf area ratio (LAR) also tended to be lower in gaps than in the understorey ($50\text{ cm}^2\text{ g}^{-1}$ vs. $60\text{ cm}^2\text{ g}^{-1}$; $P = 0.1$). However, nutrient addition had no effect on either SLA or LAR ($P \geq 0.2$), and these parameters did not differ significantly between native and invasive species for any treatment ($P \geq 0.4$, Appendix B).

Plants in the understorey plots developed a slightly higher mean root:shoot ratio (RSR) than those in gap plots ($P = 0.04$, Appendix B), but this parameter was not affected by the nutrient treatment ($P = 0.5$). However, native and invasive species did not differ significantly in RSR ($P = 0.9$).

There were no significant effects of light ($P = 0.1$), nutrient addition ($P = 0.6$) or species identity ($P = 0.2$) on foliar nutrient content for the two native and two invasive species in which this trait was measured.

3.2. Experiment 2: phytometer experiment

On the phytometer transects, light intensity at ground level in the gaps ranged from 40% to 55% of ambient light ($P < 0.001$) (Fig. 3). At the gap edge, light levels decreased abruptly and soon levelled off in the interior of the forest, where they ranged from c. 8–14% of full daylight (Fig. 3).

Growth of cinnamon seedlings was low in the understorey part of the transect, but increased from the edge of the gap towards the centre (Fig. 3). Final seedling biomass ($P = 0.002$), number of new leaves ($P = 0.05$) and absolute stem height growth ($P < 0.001$) all increased by a factor of 5–10 from the understorey to the gap centre. Only differences in growth parameters between points in the forest interior (i.e. $\geq 5\text{ m}$ from the gap edge) and the gap centre (i.e. $\geq 4\text{ m}$ from the gap edge) were significant (Fig. 3).

4. Discussion

4.1. The effect of understorey and gap conditions on seedling growth

The gaps had a strong positive effect on the growth of seedlings in both the transplant experiment and the transect study with cinnamon seedlings (Figs. 1–3). In addition, there was a weak positive response of the seedlings in the gaps to nutrient addition (Figs. 1 and 2). These are well known patterns of response in tropical forests (e.g. Coomes and Grubb, 2000; Turner, 2001; and references therein). The relative growth rates of transplanted and self-sown cinnamon phytometer seedlings were very similar (data not shown), indicating that the process of transplanting had little effect on the results.

The mean relative growth rate for all species varied rather little among the five gaps, with the highest value being 1.5-times greater than the lowest ($P = 0.5$). In contrast, mean values among understorey plots varied by a factor of more than 30 ($P = 0.002$), probably because of differences in light availability. Linear regressions of RGR against light calculated separately for the understorey and plots revealed that most species increased their RGR by a factor of two or three as light levels increased in the understorey from c. 8% to 12.5% ($r > 0.6$, $P < 0.1$), while there was no strong tendency for seedling growth to increase in the range of light conditions represented in the gaps (55–70% ambient light; $r < 0.2$, $P > 0.5$). Other studies also show that the response of tropical tree seedlings to

increased light is strongest below 5–20% of ambient light, and levels off quickly at higher levels (Coomes and Grubb, 2000; Turner, 2001).

Both native and invasive species profited strongly from the gaps (Figs. 1 and 2), confirming results from pot experiments that the response to gap conditions is related more to the growth strategies of individual species than to their status as natives or invasives (Schumacher et al., 2009, 2008). However, the fastest growing species in gaps were two invasive species (*A. macrophylla* and *P. cattleanum*). And contrary to what might be expected on oceanic islands (Schumacher et al., 2003), the data show no general advantage of native over invasive species in the understorey plots. This may be because we did not include any late-successional native species in our study, these being either very rare or having very large seeds (e.g. *N. hornei*, seed diameter: c. 6 cm). Furthermore, research increasingly indicates that some invasive plant species, e.g. *P. cattleanum* in this study, are also very shade-tolerant and able to regenerate under an undisturbed forest canopy (Kueffer et al., 2010; Martin et al., 2009; Schumacher et al., 2009; Webb et al., 2000).

4.2. Comparison of seedling growth responses under field and greenhouse conditions

To evaluate the interacting factors shaping juvenile tree growth under field conditions, we compare the results presented here with those obtained in a previous study using potted plants grown under comparable light and nutrient levels in a greenhouse experiment (Schumacher et al., 2009). Under high light, the growth rates of all species were slightly lower in the field (i.e. in gaps) than in pots (Fig. 2), which could be due to differences in the substrate or to the presence of additional stressors in the field, such as occasional exposure to direct sunlight. However, the rank order of RGR values was similar in both experiments, and the means for biomass allocation parameters (SLA, LAR and RSR) in native and the invasive species differed by less than 15% in the two experiments. This indicates a good transferability of the results obtained in the pot experiment to field conditions.

In contrast, relative growth rates in the forest understorey were much lower than for plants grown under low light in pots, particularly among invasive species (Fig. 2). The most extreme difference was for *A. macrophylla*; in the forest understorey all plants of this invasive species died, whereas those in the pot experiment grew well (Fig. 2). The difference in the growth of shaded plants in the two experiments was probably due to strong root competition in the forest from mature cinnamon, which produces a dense web of fine roots just below the soil surface. Indeed, in a field experiment Kueffer et al. (2007) found that the growth of young plants, especially of invasive species, increased greatly when these adult roots were severed. The difference between the two groups may reflect the greater phenotypic plasticity of invasive species, which tend to respond to low resource availability by adjusting the relative allocation of biomass to above- and belowground structures, according to whether light or belowground resources (nutrients, water) are limiting (Schumacher et al., 2009, 2008). Native species, in contrast, tend to cope with low resource availabilities through a resource-conserving growth strategy. Invasive species that exhibit high plasticity in response to resource levels may thus suffer from conflicting allocation priorities if there are multiple stresses; while high allocation belowground is the appropriate response to strong root competition, high allocation aboveground is needed under low light conditions (compare Cahill, 1999). In support of this argument, allocation to roots was far higher in the understorey than in the pot-grown seedlings (Fig. 4A), particularly for the invasive species. Indeed, in the field the invasive species also reduced biomass allocation to the leaves (i.e. a lower leaf area ratio, Fig. 4B),

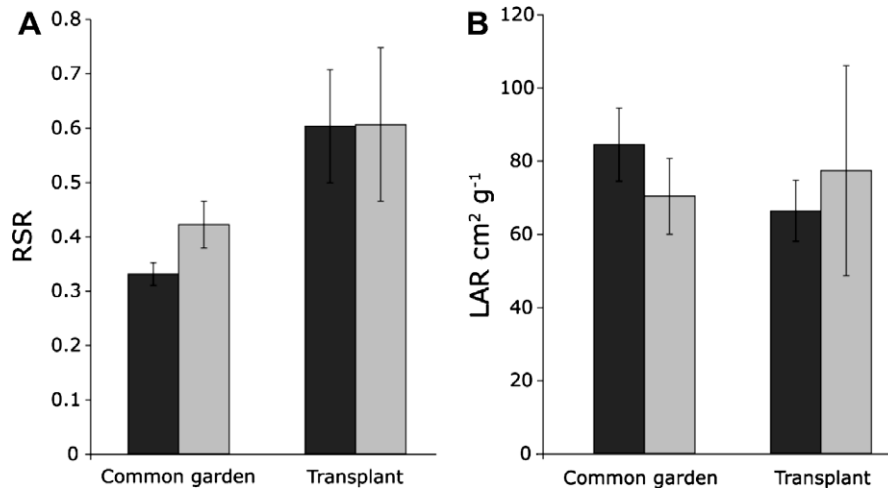


Fig. 4. Biomass allocation patterns (A: root to shoot ratio, RSR, B: leaf area ratio, LAR) under low light of plants in the common garden experiment and in the transplant experiment (mean \pm SE). Invasive species, black bars; native species, and grey bars.

despite the fact that these fast-growing species appear to need a high leaf area to survive under low light. In line with this idea – that resource limitation belowground prevents fast-growing species from producing sufficient aboveground biomass to compete with slower growing species – Hautier et al. (2009) have recently shown that in grasslands nutrient addition enables more competitive species to suppress less competitive species through increased aboveground competition for light.

4.3. Variation of seedling growth from the understorey to the gap centre

The phytometer experiment also provides evidence that root competition is an important factor limiting seedling growth in sec-

ondary cinnamon forests. The changes in growth rate from the understorey to the gap centre were rather gradual, with the increase from the understorey to the gap edge being of a similar magnitude to that from the edge of the gap to the centre (Fig. 3). These changes in growth along the transect are not consistent with the known responses of seedlings to light intensities, which are usually strongest below 5–20% of ambient light and level off quickly at higher light levels (Coomes and Grubb, 2000; Turner, 2001), a pattern for which we found also indirect evidence in the transplant experiment (see Section 4.1). In a pot experiment with cinnamon seedlings using soil from the same forest and simulating light levels in the understorey and gaps (i.e. 11% and 65% of ambient light) (Schumacher et al., 2009), aboveground biomass after 6 months was only 1.5-times larger in the high than the low light

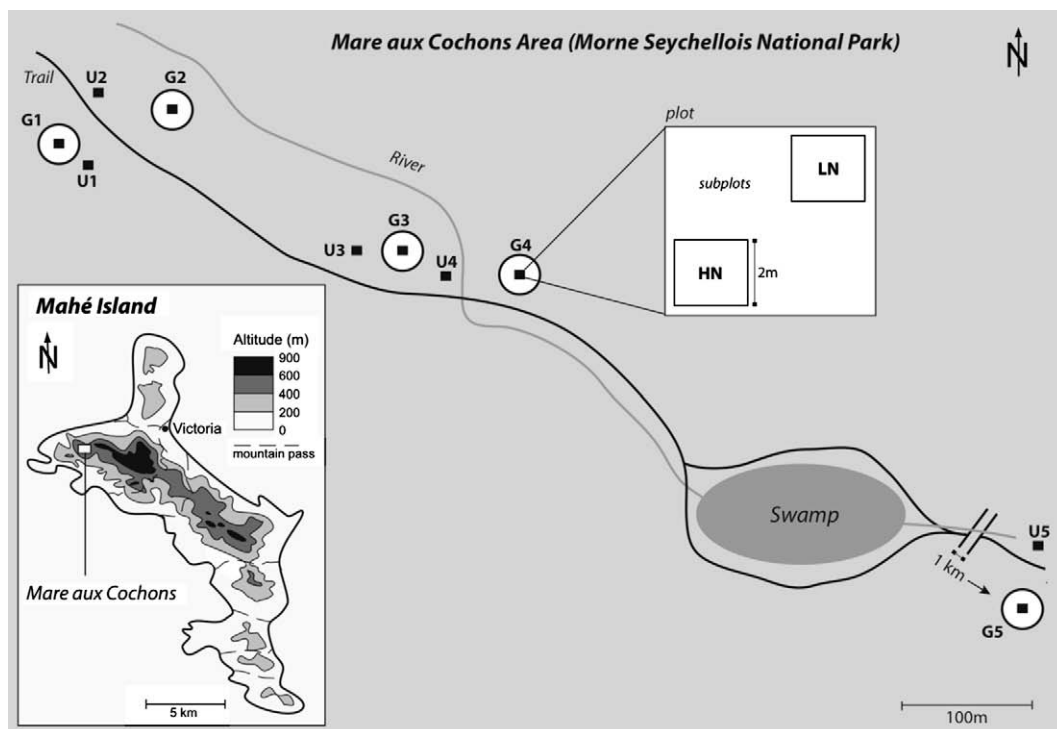


Fig. A1. Locations of gap (G) and understorey (U) plots used in the transplant experiment. Each plot was subdivided into two subplots with a high nutrient (HN) and low nutrient (LN) treatment.

treatment, while after a similar period in the phytometer experiment the seedlings in the gaps were over 3-times as large as those in the understorey. This further indicates that some factor in addition to light was restricting growth in the understorey. A possible reason for these discrepancies is that root competition from cinnamon trees also limits seedling growth in the gaps, with the importance of this factor declining with increasing distance from the gap edge. This finding suggests that root competition from adult cinnamon trees may reach some 2–3 m into a gap (Fig. 3).

4.4. Promoting native seedling regeneration in cinnamon dominated secondary forests

The aim of this study was to obtain a better ecological understanding of the factors promoting initial native seedling recovery in secondary forests dominated by cinnamon in Seychelles. Long-term studies will be needed to understand juvenile growth and mortality patterns at later life stages. However, to judge from the

size distributions of juvenile plants in the field, the common native species survive better than alien species (Kueffer et al., 2007), although some rarer native species seem vulnerable to herbivory and damping-off disease and suffer high mortality (Kueffer, 2006). More research will also be needed to test the cost-effectiveness of different techniques for promoting seedling establishment, such as sowing of seed vs. outplanting of seedlings germinated in the greenhouse. In any case, seeding is not an option for the many native species that are now so rare that little or no seed can be obtained.

4.4.1. Slow regeneration of native seedlings under understorey conditions

Our results and those of previous studies (Fleischmann, 1999; Schumacher et al., 2009) show that juveniles of several native species survive well in the shade but grow very slowly. Thus, while combined strong below- and aboveground competition by adult cinnamon trees in the understorey hinders alien species regenera-

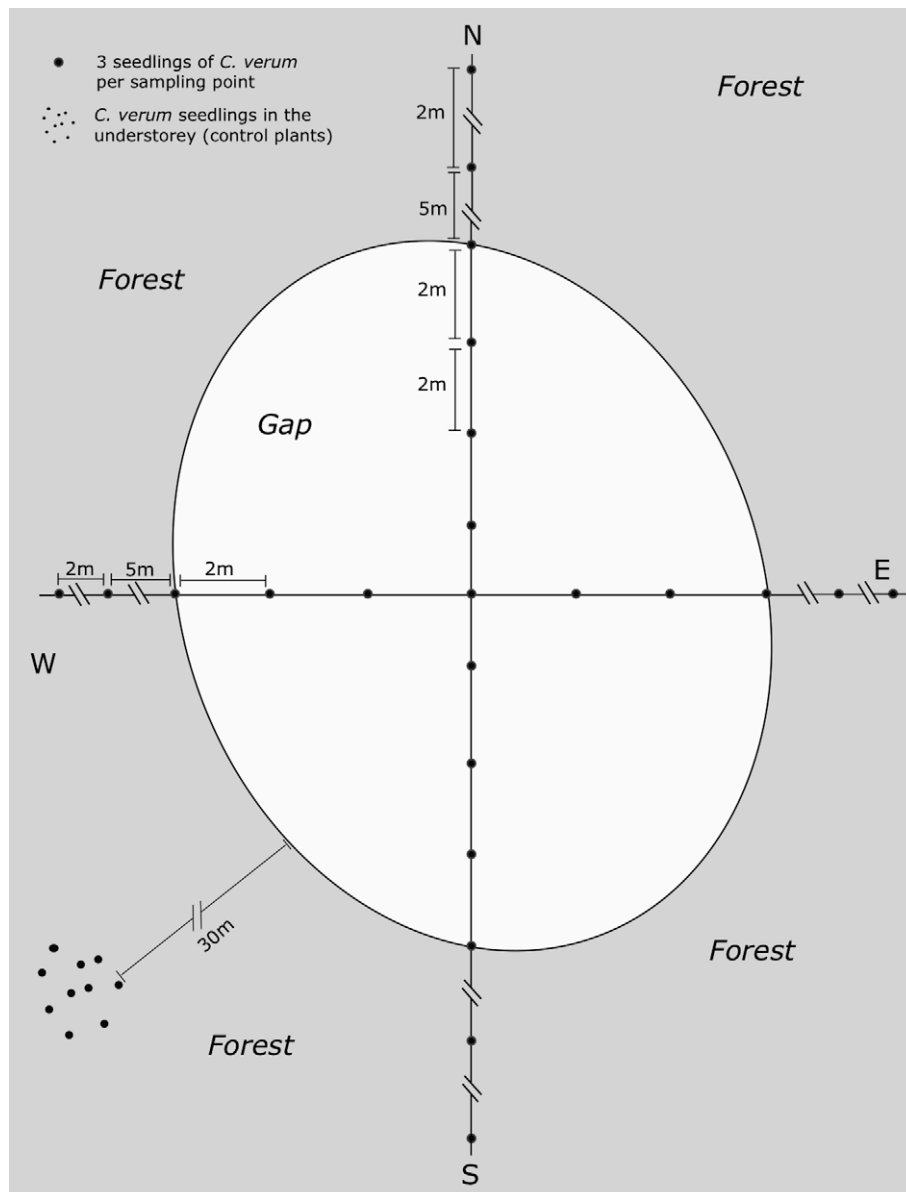


Fig. A2. Lay-out of the transects and the positions of the sampling points used in the phytometer experiment with *Cinnamomum verum* (cinnamon) seedlings. Cinnamon seedlings were also monitored at positions more than 30 m distance from a gap.

tion it also negatively affects native seedlings; thus, left to itself the recovery of native populations is likely to be at best a very slow process.

4.4.2. Large gaps promote alien seedling regeneration

Our results confirm that making large forest openings is not an effective management strategy. Although both native and invasive early-successional species grow well in open conditions, some invasive species are particularly fast growing, and may then fill gaps. Further, qualitative observations indicate that some early-successional invasive species, such as *Falcataria moluccana*, regenerate vigorously from the seed bank in gaps, producing densities of several 100 seedlings per square meter within weeks after gap formation (Schumacher, 2007). Thus, even relatively small gaps of a diameter of some 10–15 m tend to strongly favour some invasive species.

4.4.3. Scattered small gaps as a promising strategy for managing native seedling regeneration

We conclude that the most effective means of promoting native regeneration is to make small gaps of only a few meters in diameter. In these gaps, comparable to the edges of our artificial gaps, intermediate levels of shade and root competition from surrounding adult cinnamon trees tend to favour the seedlings of native species over invasive species. These conditions, which may be achieved by felling individual trees, will neither promote maximal growth of native species nor provide complete resistance against invasive species (especially against shade-tolerant invaders such as *P. cattleianum*, Schumacher et al., 2009), but they may ensure a cost-efficient promotion of the recovery of native tree species.

4.4.4. Long-term adaptive management of seedling regeneration

Our proposed adapted management strategy needs to be tested and adapted through long-term learning cycles, partly because forest conditions will change over time and with management. If root competition by cinnamon is an important factor, then tree regeneration dynamics is likely to be very different in cinnamon forests compared with vegetation dominated by native trees, where root competition is probably less important. As the proportion of native trees increases, the suppression of invasive species by cinnamon may diminish, and management procedures would need to be adapted accordingly.

Given the effects of the past anthropogenic disturbances a fully self-sustaining native vegetation can probably never be restored in the mid-altitude forests of the Seychelles and some management intervention will always be needed. Rather than attempting to eliminate all alien species, therefore, the long-term goal should be to maximise the proportion of native trees in ways that do not require unsustainable levels of management.

Acknowledgements

We thank the Seychelles Ministry of Environment and Natural Resources for their support with the conducting of the experiment, and particularly the staff of the Morne Seychellois National Park unit for permission for the creation of the forest gaps, the creation of the gaps, and assistance with data collection. Especially, we would like to acknowledge the assistance with the fieldwork by Unels Bristol and Terence Valentin, and the provision of statistical advice by Sabine Gusewell. We would also like to thank several anonymous reviewers for very helpful comments on a previous version of the manuscript.

Funding was provided by a research grant from the Swiss Federal Institute of Technology (ETH Zurich).

Appendix A

Location and lay-out of experiments (Figs. A1 and A2).

Appendix B

Statistics and results of experiment 1: transplant experiment (Tables B1–B3).

Appendix C

Tree flora of mid-elevation secondary forest on Mahé, Seychelles (Table C1).

Table B1

Results of ANOVA across two light (gap and understorey) and two nutrient levels (ambient and high nutrients). Indicated are the *F*-ratios and significance levels (***: $P < 0.001$, **: $P < 0.01$; *: $P < 0.05$, significant ones in bold) of main or interaction effects on relative growth rate of plant biomass (RGR), specific leaf area (SLA), leaf area ratio (LAR) and root shoot ratio (RSR). See text for further information.

	RGR	SLA	LAR	RSR
Species groups ^a (S)	0.1	0.6	0.2	0.0
Light (L)	55.5***	18.8**	2.9	5.6*
S × L	0.1	0.1	0.3	0.5
Nutrient (N)	11.2*	2.3	0.3	0.4
S × N	0.3	0.7	0.0	6.6
L × N	9.1**	0.0	0.0	2.5
Initial leaf area	1.1	0.9	1.0	0.0

^a Native vs. invasive.

Table B2

Mean values per species group (native vs. invasive) of different growth parameters. HN: N–P–K fertilizer treatment, LN: no fertilizer added. For explanation of other acronyms see Table B1.

		High radiation (gap)		Low radiation	
		HN	LN	HN	LN
RGR (mg g ⁻¹ d ⁻¹)	Invasive	8.7 (0.27)	6.9 (0.22)	0.9 (0.05)	0.7 (0.06)
	Native	7.6 (0.25)	6.2 (0.19)	1.4 (0.07)	2.0 (0.13)
SLA (cm ² g ⁻¹)	Invasive	132 (26)	130 (22)	202 (54)	206 (59)
	Native	108 (11)	110 (11)	179 (46)	184 (38)
LAR (cm ² g ⁻¹)	Invasive	53 (12)	55 (16)	60 (10)	66 (8)
	Native	47 (5)	51 (9)	74 (26)	77 (29)
RSR	Invasive	0.49 (0.10)	0.53 (0.09)	0.66 (0.10)	0.60 (0.10)
	Native	0.49 (0.11)	0.54 (0.11)	0.66 (0.11)	0.61 (0.14)

Table B3

Results of ANOVA across two light (gap and understorey), two nutrient levels (ambient and high nutrients) and eight species. Indicated are the *F*-ratios and significance levels (***: $P < 0.001$, **: $P < 0.01$; *: $P < 0.05$, significant ones in bold) for relative growth rate of plant biomass (RGR), specific leaf area (SLA), leaf area ratio (LAR) and root shoot ratio (RSR). See text for further information.

	RGR	SLA	LAR	RSR
Species (S)	54.9***	69.8***	27.6***	11.4***
Light (L)	86.1***	231.2***	55.7***	2.7
S × L	13.4***	18.2***	7.2***	1.2
Nutrient	5.8*	0.9	0.3	0.1
S × N	0.5	0.4	1.0	0.4
L × N	10.1**	0.0	0.2	4.9*
Initial leaf area	2.9	0.3	1.0	0.4

Table C1

Common native and alien tree species that occur in mid-elevation secondary forest on Mahé, Seychelles. Shrubs, palms and pandans are not included. Data is taken from Kueffer (2006) and Kueffer and Vos (2004). Very common species that are either major invasive species or priority native species for habitat restoration are indicated with an asterisk.

Species	Family	Status
<i>Adenantha pavonina</i>	Leguminosae	Alien
<i>Alstonia macrophylla</i> *	Apocynaceae	Alien
<i>Artocarpus heterophyllus</i>	Moraceae	Alien
<i>Chrysobalanus icaco</i>	Chrysobalanaceae	Alien
<i>Cinnamomum verum</i> *	Lauraceae	Alien
<i>Dillenia suffruticosa</i>	Dilleniaceae	Alien
<i>Falcataria moluccana</i> ^a *	Leguminosae	Alien
<i>Pentadesma butyracea</i> *	Clusiaceae	Alien
<i>Psidium cattleianum</i> *	Myrtaceae	Alien
<i>Syzygium jambos</i> *	Myrtaceae	Alien
<i>Tabebuia pallida</i>	Bignoniaceae	Alien
<i>Aphloia theiformis</i> *	Flacourtiaceae	Native
<i>Canthium bibracteatum</i> *	Rubiaceae	Native
<i>Dillenia ferruginea</i> *	Dilleniaceae	Native
<i>Erythroxylum sechellarum</i> *	Erythroxylaceae	Native
<i>Gastonia crassa</i>	Araliaceae	Native
<i>Memecylon eleagni</i> *	Melastomataceae	Native
<i>Northea hornei</i> *	Sapotaceae	Native
<i>Paragenipa wrightii</i>	Rubiaceae	Native
<i>Pittosporum senacia</i>	Pittosporaceae	Native
<i>Pouteria obovata</i>	Sapotaceae	Native
<i>Psychotria pervillei</i>	Rubiaceae	Native
<i>Timonius sechellensis</i>	Rubiaceae	Native

^a *Paraserianthes falcataria* in Friedmann (1994).

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