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RESEARCH PROJECT

Invasion of woody plants into the Seychelles tropical forests: species traits in the establishment phase

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Summary

1 The problem of plant invasions is particularly serious in island ecosystems. It is generally assumed that endemic species on small oceanic islands are less competitive due to evolutionary isolation and are less responsive to elevated resource levels than introduced species.

2 The objective of this study is to assess variations in growth responses and ecophysiological traits of tropical tree species as possible determinants of the widespread invasions of exotic woody plants into the tropical forests of the Seychelles. We hypothesize that in contrast to native plants invasive species possess opportunistic traits that allow them to take special advantage of elevated resource levels (light and nutrient availability), especially in the establishment phase.

3 To test our hypotheses we conduct controlled pot experiments comparing the growth characteristics and photosynthetic capacity of 14 species (7 invasives, 7 natives) in a factorial design including 3 light and 2 nutrient levels. We also perform water stress experiments to investigate resistance to drought.

4 To evaluate the relevance of the results of the controlled pot experiments under field conditions we conduct transplant experiments comparing the growth characteristics of invasive and native species in forest plots using two different light levels (gap and understorey) at three different altitudes (150, 450 and 720 m a.s.l.).

5 The results of the project will help to assess whether certain plant traits are characteristic for species that are invasive in the Seychelles (plant invasiveness). The study also helps to identify environmental conditions conducive for woody plant invasions. In the end, these results should facilitate control measures to prevent new introductions of potential invasive plants to or restrict existing invasions in tropical islands.

Keywords: common garden experiment, invasiveness, light availability, nutrient limitation, seedling establishment, water stress

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Introduction

Small oceanic islands are particularly prone to invasions by exotic species. Different hypotheses have been proposed to explain this phenomenon through particularities of island ecosystems, such as a high level of human disturbance, a high impact of propagule pressure from invading species due to the small population size of native species, or the development of particular plant traits in native species due to a long evolutionary isolation (see Küffer *et al.* 2003; Fleischmann *et al.* 2003). In this study we investigate whether ecophysiological differences exist between native and invasive species on the granitic islands of the Seychelles. The Seychelles are particularly interesting for our research questions. Due to their continental origin some plant species have had the longest evolutionary isolation of any island flora (65 million years).

So far, the search for general characteristics shared by successful plant invaders has not revealed any simple 'formula' for success. Nevertheless, some ecological attributes seem to be more often associated with invading species than others. These include: large plant size, high seed output, early maturity, high phenotypic plasticity, rapid growth, climatic matching between native and invaded areas and (pre-)adaptation to anthropogenic site conditions and disturbances (see Baker 1974; Grubb 1985; Crawley 1987; Drake *et al.* 1989; Williamson 1996; Dietz & Ullmann 1997; Rouget *et al.* 2000).

Many invasive species are opportunists, i.e. they rapidly take advantage of increased resource availability, furthering their invasion success by strongly increased population growth. Hence, invasive species are frequently found in disturbed habitats with high levels of unused resources (Davis *et al.* 2000).

High light, nutrient and water availability may be particularly beneficial for the popula-

tion growth of invasives relative to that of co-occurring natives, especially in disturbed tropical forest ecosystems (Fine 2002). For example, ecophysiological experiments with invasive plant species in Hawaii showed that many invasive plants use light more efficiently than native species, particularly in high-light environments (Pattison *et al.* 1998; Baruch *et al.* 2000). In general, light is the most limiting resource for a plant in a tropical forest. For many tree species regeneration is only possible in forest gaps, though small, shade tolerant seedlings may persist in the form of a "seedling bank". Recent work supports the idea that there is a trade-off between potential growth rates in gaps and the ability to survive in deep shade (e.g. Welden *et al.* 1991; Kitajima 1994). If the invasive plants benefit more from increased light availability in the forest whereas the native plants are competitively superior under shady conditions (cf. Fleischmann 1999), then the light conditions in the forest and their changes should have an important bearing on woody plant invasions into the forests.

Invasive plants may be also more efficient in sequestering nutrients for subsequent growth. For example, Baruch & Goldstein (1999) demonstrated that invasive plants in Hawaii made more efficient use of increased nutrient resources, and could achieve higher growth rates than the native Hawaiian flora. Vitousek & Walker (1989) found that the invasive species *Psidium cattleianum* showed stronger growth responses to elevated nutrient availability (shoot height increment and dry mass accumulation) than did the native species *Metrosideros polymorpha*. Generally, it seems that fast-growing species make more efficient use of increased nutrient availability, whereas shade-tolerant species often do not respond (Burslem *et al.* 1995; Raaimakers & Lambers 1996; Turner 2001).

Nutrient availability and light in tropical forest may interact in their effects on plant growth (Grubb 1996). For example, Thompson *et al.* (1992) showed that with decreasing light availability photosynthetic adjustments resulted in a lower light compensation point; these adjustments were accentuated by low nutrient supply. Fetcher *et al.* (1996) showed that light-saturated photosynthetic rate (A_{\max}) of *Cecropia schreberiana* (a pioneer tree species) increased in response to N fertilization in the open plots in Puerto Rico. In contrast, photosynthesis of *Palicourea riparia* (a shrub of tree-fall gaps and understorey) and *Manilkara bidentata* (a non-pioneer canopy tree) in the open plots was unaffected by fertilization. Interactions between nutrients and light may also influence invasion success. For example, Duggin & Gentle (1998) showed that the invasive weed *Lantana camara* significantly increased growth under high light conditions, especially in combination with high nutrient levels. In West Africa the pioneer tree *Nauclea diderrichii* showed a greater increase in initial slope of photosynthesis in relation to both light and nutrient supply than the climax species *Entandophragma angolense* (Riddoch *et al.* 1991).

Drought resistance is probably more relevant than previously thought in structuring tropical forests (Newbery *et al.* 1996; Condit 1998; Newbery *et al.* 1999; Walsh & Newbery 1999). Seedling mortality during dry periods, in particular, has been widely reported for tropical forests (Turner 1990; Condit *et al.* 1995; Coomes & Grubb 2000; Gilbert *et al.* 2001). There is some evidence that invasive species are less tolerant of water stress than natives (Alpert *et al.* 2000).

Based on this reasoning, the main objective of our study is to scrutinize whether key eco-physiological responses to resource availability are shared among invasive tropical trees. To this end we will compare functional spe-

cies traits in controlled pot experiments in which seedlings of invasive and native species are grown under varying light and nutrient conditions. In addition, a water stress experiment will be performed with the same species. We will also conduct a transplant experiment in which seedlings of the two ecological groups will be grown over a range of environmental conditions under gap and non-gap conditions in forest plots (compare Bloor 2003).

Opportunistic growth hypotheses

We hypothesize that invasive species, in contrast to native ones, possess opportunistic traits that allow them to take special advantage of elevated resource levels (light, nutrient availability), particularly in the establishment (seedling/sapling) phase (similar to the ruderal strategy *sensu* Grime 1979). We further suggest that native species are comparatively better able to survive water, nutrient, and light stress (similar to the stress tolerator strategy *sensu* Grime 1979). The maintenance of a high relative growth rate may come at the cost of lower survival probability, particularly under conditions of stress (e.g. low light, see Sack & Grubb 2001).

In the Seychelles, this assumed dichotomy in growth strategies between native and invasive species, although simplified, matches observations of relative growth rates in the field that show a dramatic difference between many invasive and native species (K. Fleischmann, personal observation). We therefore put forward the following hypotheses for woody plant species in the Seychelles forests:

Hypothesis 1. The invasive species are better able to enhance growth under elevated light levels. In contrast, the native species are better able to sustain growth under low light.

In the understorey of the Seychelles forest, growth of both invasive and natives species is severely reduced only under very low light (3–5% of total diffuse sunlight). However, even small gaps in the canopy may be sufficient to promote invasive species relative to natives (Küffer *et al.* 2003). This can be seen in a series of habitats on Mahé and Silhouette where the endemic palm *Phoenixophorium borsigianum* and the invasive alien *Cinnamomum verum* are competitors. Unlike *P. borsigianum*, *C. verum* can re-establish and regenerate only in light levels of > 7.5% diffuse site factor (Fleischmann 1999). Probably invasive species (such as *C. verum*) have a higher maximal assimilation rate and relative growth rate than native species (such as *P. borsigianum*) under high-light conditions but suffer from a higher respiration rate under low-light conditions (cf. Fig. 1).

Hypothesis 2. The invasive species are better able to enhance growth under elevated nutrient levels. In contrast, the native species are better able to sustain growth under low nutrient levels.

In the Seychelles natural soil nutrient contents are expected to be low (Piggott 1968). However, a wide range of soil nutrient content can be found presently (total N 0.05–3.4%; total P 0.03–1.2 mg/100g soil) (Wiederkehr & Anderegg 2001; Meuwly 2002; R. Mylonas & I. Sedivy, unpublished data). It has been suggested that exotic N_2 -fixing trees such as *Paraserianthes falcata* (Wiederkehr & Anderegg 2001) and fire (Meuwly 2002) lead to increased soil fertility. It can be expected that these wide variations in soil nutrient conditions have an influence on the competitive interactions between invasive and native tree seedlings because invasives are more responsive to nutrients (cf. Fig. 2).

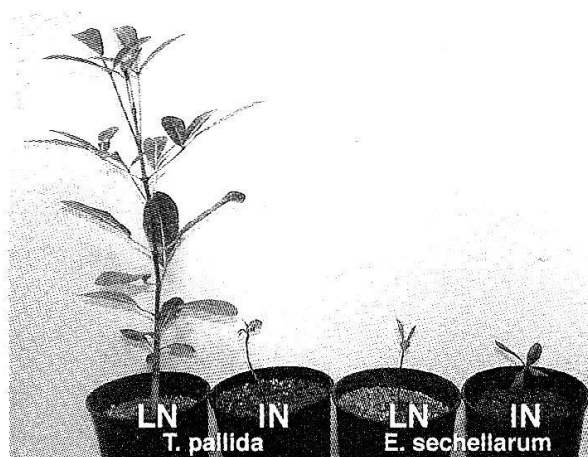


Fig. 1. Different effects of the light treatment on *Tabebuia pallida* (invasive) and *Erythroxylum sechellarum* (native). Plants are shown after six months of growth under high nutrient availability (N, 4 g of N-P-K fertilizer per pot) and either high light (L, 65% of ambient light) or low light (l, 3.5% of ambient light). The growth response of *T. pallida* to increased light was much stronger than that of *E. sechellarum*.

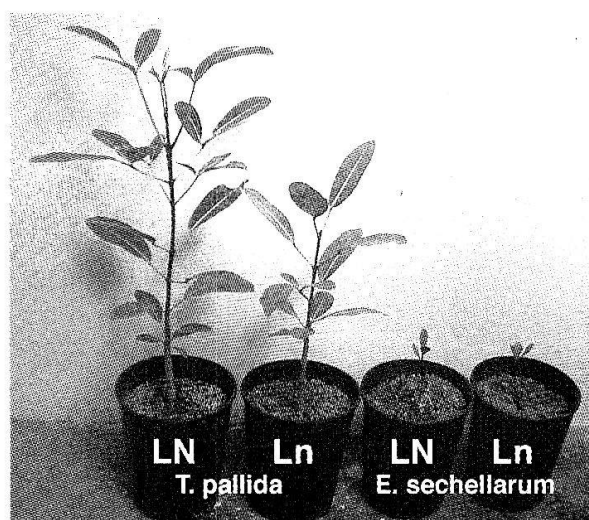


Fig. 2. Different effects of the nutrient treatment on *Tabebuia pallida* (invasive) and *Erythroxylum sechellarum* (native). Plants are shown after six months of growth under 65% of ambient light (L) and either high nutrient supply (N, 4 g N-P-K fertilizer per pot) or low nutrient supply (n, no fertilizer). The growth response of *T. pallida* to increased nutrient availability was much stronger than that of *E. sechellarum*.

Hypothesis 3. Under high light conditions the invasive species make particularly efficient use of increased nutrient levels, resulting in increased growth rates relative to the native species.

Disturbances to forest ecosystems on the Seychelles, e.g. due to fire, modify both light and nutrient availability (Meuwly 2002). The photosynthetic responses of plants to light availability often depends on nutrient supply (Thompson *et al.* 1992; Fetcher *et al.* 1996). If invasives profit more than natives from both high light and high nutrient supply (see hypotheses 1 and 2), they may profit most (relative to natives) from a combination of high-light and high-nutrient conditions (Duggin & Gentle 1998).

Hypothesis 4. Native species are better adapted to water stress than invasives.

Many of the invasive species on the Seychelles are timber, spice, fruit and ornamental trees that grow on fertile soils and are regularly watered. The seedlings and saplings of the invasive species may therefore suffer more strongly from severe drought periods than the native species, which are assumed to have experienced periods of drier conditions in their evolutionary history (see Willis & McElwain 2002).

Hypothesis 5. The negative impact of water stress on the growth and survival of invasive seedlings is more pronounced under shady conditions.

During dry spells, tropical forest seedling mortality is high, particularly for seedlings growing in the understorey (Veenendaal *et al.* 1996; Poorter & Hayashida-Oliver 2000). The root systems of seedlings in gaps are more extensive and allow better access to water (Fisher *et al.* 1991) whereas under deep shade seedlings are not able to produce enough roots (Coomes & Grubb 2000; Poorter & Hayashida-Oliver 2000). Seedlings adapted to

both shade and drought often have long-lived, thick leaves, relatively inflexible low SLA, and low LAR that allow them to persist in deep shade (Coomes & Grubb 2000). According to hypothesis 1 these traits, which are associated with a low relative growth rate, should be found in native species, rather than invasive ones, on the Seychelles.

Methods

STUDY SPECIES

The study species are shrubs or small understorey trees which occur in the intermediate forest of Mahé (Table 1). All of them are abundant or fairly abundant in the Seychelles, have small to medium sized seeds (2-10 mm in diameter), and have a relatively wide ecological amplitude. Amongst the invasive candidate species, those posing the most serious problem to conservation and those which might cause future problems were preferred. If possible, we sampled from different families.

For the first set of seedlings, 200-400 seeds of each species were collected from forest vegetation on Mahé. Seeds were taken from several parent plants to obtain a representative sample of the populations in the forest.

STUDY AREA

The pot experiment is conducted at the Sans Souci forestry station (380 m a.s.l.), on a flat area (facing East) belonging to the Ministry of Environment.

The three field sites will be located on Mahé: Barbarons (150 m a.s.l.), Mare aux Cochons (450 m a.s.l.) and Congo Rouge (720 m a.s.l.). The lowest site (Barbarons) is a disturbed lowland secondary forest, the intermediate site (Mare aux Cochons) is a secondary forest in the Morne Seychellois National Park and the highest site (Congo Rouge) is a

Table 1. Invasive and native woody species that are used in the pot and transplant experiments. The maximum height is given for all tree species. Species with an asterisk are highly invasive also in other tropical countries.

Species	Family	Max. height	Experiment
<u>Invasives</u>			
<i>Cinnamomum verum</i> *	Lauraceae	15 m	Pot/Transplant
<i>Syzygium jambos</i> *	Myrtaceae	15 m	Pot/Transplant
<i>Psidium cattleianum</i> *	Myrtaceae	7 m	Pot/Transplant
<i>Tabebuia pallida</i> *	Bigoniaceae	10 m	Pot/Transplant
<i>Ardisia crenata</i> *	Myrsinaceae	(shrub)	Pot
<i>Alstonia macrophylla</i>	Apocynaceae	15 m	Pot/Transplant
<i>Memecylon caeruleum</i>	Melastomataceae	4 m	Pot
<i>Ochna ciliata</i>	Ochnaceae	7 m	Pot
<i>Psidium guajava</i> *	Myrtaceae	< 15 m	Pot
<i>Artocarpus heterophyllus</i>	Moraceae	15 m	Pot
<u>Natives</u>			
<i>Memecylon eleagni</i>	Melastomataceae	10 m	Pot/Transplant
<i>Canthium bibracteatum</i>	Rubiaceae	< 15 m	Pot/Transplant
<i>Dillenia ferruginea</i>	Dilleniaceae	15 m	Pot
<i>Paragenipa wrightii</i>	Rubiaceae	6 m	Pot/Transplant
<i>Erythroxylum sechellarum</i>	Erythroxylaceae	7 m	Pot/Transplant
<i>Soulamea terminalioides</i>	Simaroubaceae	5–10 m	Pot
<i>Syzygium wrightii</i>	Myrtaceae	10 m	Pot
<i>Aphloia theiformis</i>	Flacourtiaceae	< 15 m	Pot/Transplant
<i>Gastonia crassa</i>	Araliaceae	10 m	Pot
<i>Mimusops sechellarum</i>	Sapotaceae	15 m	Pot

rather undisturbed mountain cloud forest. The areas include at least 15 ha of fairly homogeneous forest with gaps of different sizes (see Küffer *et al.* 2003).

GROWTH EXPERIMENTS IN POTS

The experiment was started in October 2002 with a first set of four native and three invasive species. In the end we plan to use 14 species (seven natives and seven invasives out of those in Table 1). Seedlings were germinated and transplanted into small pots filled with intermediate forest soil (65 % laterite “red” soil: 35 % brown soil vol/vol). The plants are randomly assigned to six different treatments which combine three light levels simulating

distinct gap conditions with two nutrient levels simulating intermediate and high nutrient availability in the forest. A split-plot design is used, with light as main-plot factor and nutrients as split-plot factor; main plots are arranged in a block design with six replicates (Fig. 3). Shading tents are used to produce three different light climates (3.5 %, 11 % and 65 % of ambient light), and the two nutrient levels are created by adding or not adding 4 g of slow release N-P-K-fertilizer (Osmocote 16:11:11) to each pot.

The experiments run for at least 6 months. During this time, non-destructive measurements of stem height and number of leaves are made every second week, and leaf area

and basal stem diameter are recorded monthly. Net assimilation rate and stomatal conductance are measured using a portable infrared gas analyzer (IGRA) and a porometer. Measurements are taken for one to three of the youngest expanded leaves of each plant. After harvest, further parameters (dry mass, shoot-root ratio, chemical properties of the leaf) are determined (initial biomass was determined for four seedlings per species). In

addition, we will determine leaf N and P content as an indicator of nutrient limitation during plant growth.

In addition, a water stress experiment is carried out in a similar setup, with seedlings grown under low and high light and under two different water levels (near drought conditions and ample water availability). Measurements are as mentioned above.

These data will enable us to determine biomass allocation patterns between leaves, stem and roots. The leaf measurements will provide the basis for a simple carbon balance model and for the calculation of respiration rates.

TRANSPLANT EXPERIMENTS – SAPLING ESTABLISHMENT IN GAPS

The transplant experiment will be conducted in six plots (three gap and three non-gap sites) in each of the three study areas. In this case we want to investigate the responses of the different species to variations in light availability under forest conditions (and exposed to the natural range of co-varying factors such as water and nutrient availability, herbivore pressure and competition). The spatial variation of canopy openness will be sampled in the study areas through analysis of hemispherical photographs. Each plot will be categorized as 'gap', 'intermediate' or 'understorey'. Three quadrats will be assigned to gap plots and three quadrats will be assigned to understorey plots.

Six seedlings each of at least five native and five invasive species that are also used in the pot experiment (Table 1) will be transplanted into the plots. The transplants will be watered on demand for a limited period of time after which the plots will receive no further maintenance.

In these experiments plant growth (stem height, leaf number and basal stem diameter) will be monitored monthly and net assimila-

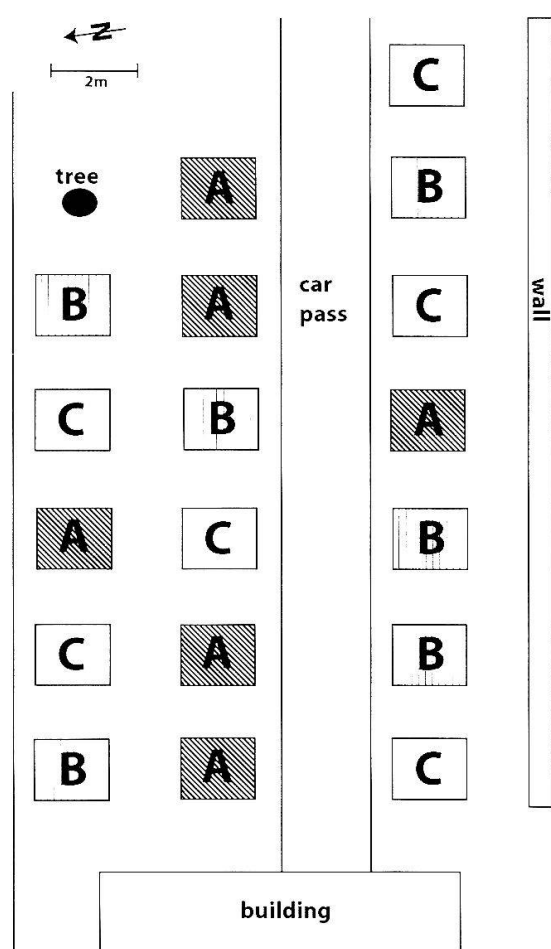


Fig. 3. Design of the pot experiment. The shading tents of the pot experiment are set up according to a randomised block design. Each row forms a block of the three light treatments (A, 3.5% ambient light; B, 11% ambient light; C, 65% ambient light), except for the top row, arranged at a rectangular angle. The nutrient treatment is nested in the light treatment. Pots are arranged randomly on a regular grid with a distance of 30 cm between pots; they are regularly re-arranged.

tion rate and stomatal conductance will be measured.

Relevance of the research project

In this study we focus on characteristics in the establishment phase, i.e. on the seedling stage. This is because (i) seedling mortality is high; (ii) seedlings react sensitively to environmental factors, and (iii) seedlings were often used in the past to define growth strategies and evolutionary adaptations in tropical trees (Lieberman 1996; Whitmore 1998; Turner 2001).

This is the first comparative study on the ecophysiological characteristics of native and invasive tree species in the Seychelles. The results of the experiments will be complementary to investigations on habitat invasibility and propagule pressure (see Küffer *et al.* 2003). The results of this study will provide a basis for assessing the growth potential and ecophysiological characteristics of problematic invasive trees in the Seychelles. They will help to assess the species' invasiveness under different habitat conditions and, therefore, contribute to better management practices to contain spread of these species.

A generalization of the results will contribute to a better understanding of woody plant invasions in tropical forests in general and, more particularly, on small tropical oceanic islands. The results can be used to adapt existing risk assessment systems (screening system) to the region of the Indian Ocean for the prevention of the import of potentially new invasive woody plant species.

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References

- Alpert, P., Bone, E. & Holzapfel, C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 52–66.
- Baker, H.G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics*, **5**, 1–24.
- Baruch, Z. & Goldstein, G. (1999) Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia*, **121**, 183–192.
- Baruch, Z., Pattison, R.R. & Goldstein, G. (2000) Responses to light and water availability of four invasive Melastomataceae in the Hawaiian islands. *International Journal of Plant Sciences*, **161**, 107–118.
- Bloor J. M. G. (2003). Light responses of shade-tolerant tropical tree species in north-east Queensland: a comparison of forest- and shade-house-grown seedlings. *Journal of Tropical Ecology*, **19**, 163–170.
- Burslem, D.F.R.P., Grubb, P.J. & Turner, I.M. (1995) Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Journal of Ecology*, **83**, 113–122.
- Condit, R. (1998) Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. *Climatic Change*, **39**, 413–427.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs*, **65**, 419–439.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1996) Changes in tree species abundance in a Neotropical forest: Impact of climate change. *Journal of Tropical Ecology*, **12**, 231–256.

- Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecological Monographs*, **70**, 171–207.
- Crawley, M.J. (1987) What makes a community invisable? *Colonization, Succession and Stability* (eds. A.J. Gray, M.J. Crawley & P.J. Edwards) pp. 429–453. Blackwell, Oxford.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
- Dietz, H. & Ullmann, I. (1997) Phenological shifts of the alien colonizer *Bunias orientalis*; Image-based analysis of temporal niche separation. *Journal of Vegetation Science*, **8**, 839–846.
- Drake, J., Mooney, H., Castri, F.d., Groves, R., Kruger, F., Rejmanek, M. & Williamson, M. (1989) *Biological Invasions: a global Perspective*. Wiley, Chichester.
- Duggin, J.A. & Gentle, C.B. (1998) Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW; Australia. *Forest Ecology and Management*, **109**, 279–292.
- Fetcher, N., Haines, B.L., Cordero, R.A., Lodge, D.J., Walker, L.R., Fernandez, D.S. & Lawrence, W.T. (1996) Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology*, **84**, 331–341.
- Fine, P.V.A. (2002) The invasibility of tropical forests by exotic plants. *Journal of Tropical Ecology*, **18**, 687–705.
- Fisher, B.L., Howe, H.F. & Wright, S.J. (1991) Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understorey. *Oecologia*, **86**, 292–297.
- Fleischmann, K. (1999) Relations between invasive *Cinnamomum verum* and the endemic *Phoenicophorium borsigianum* on Mahé island, Seychelles. *Applied Vegetation Science*, **2**, 37–46.
- Fleischmann, K., Héritier, P., Meuwly, C., Küffer, C. & Edwards, P.J. (2003) Virtual gallery of the vegetation and flora of the Seychelles. *Bulletin of the Geobotanical Institute ETH*, **69**, 57–64.
- Gilbert, G.S., Harms, K.E., Harnill, D.N. & Hubbell, S.P. (2001) Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panamá. *Oecologia*, **127**, 509–516.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester.
- Grubb, P.J. (1985) *Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization*. Handbook of Vegetation Science Vol. 3, Dordrecht.
- Grubb, P.J. (1996) *Rainforest dynamics: the need for new paradigms*. Tropical Rainforest Research - Current Issues. Kluwer, Dordrecht.
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**, 419–428.
- Küffer, C., Edwards, P.J., Fleischmann, K., Schumacher, E. & Dietz, H. (2003) Invasion of woody plants into the Seychelles tropical forests: habitat invasibility and propagule pressure. *Bulletin of the Geobotanical Institute ETH*, **69**, 65–75.
- Lieberman, D. (1996) Demography of tropical tree seedlings: a review. *The Ecology of Tropical Tree Seedlings* (ed. M.D. Swaine), pp. 131–138. UNESCO-MAB Series, Parthenon, Carnforth, England.
- Meuwly, C. (2002) *Fire and vegetation on Praslin and in the Fond Ferdinand*. Master's thesis, Geobotanical Institute ETH, Zürich.
- Newbery, D.M., Campbell, E.J.F., Proctor, J. & Still, M.J. (1996) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. *Vegetatio*, **122**, 193–220.
- Newbery, D.M., Kennedy, D.N., Petol, G.H., Madani, L. & Ridsdale, C.E. (1999) Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **354**, 1763–1782.
- Pattison, R.R., Goldstein, G. & Ares, A. (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia*, **117**, 449–459.
- Piggott, C.J. (1968) *A soil survey of Seychelles*. Government Printer, Seychelles.
- Poorter, L. & Hayashida-Oliver, Y. (2000) Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology*, **16**, 481–498.
- Raaimakers, D. & Lambers, H. (1996) Response to phosphorus supply of tropical tree seedlings: A comparison between a pioneer species *Tapirira*

- obtusata* and a climax species *Lecythis corrugata*. *New Phytologist*, **132**, 97–102.
- Riddoch, I., Lehto, T. & Grace, J. (1991) Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. *New Phytologist*, **119**, 137–147.
- Rouget, M., Richardson, D.M., Milton, S.J. & Polakow, D. (2000) Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. *Plant Ecology*, **152**, 79–92.
- Sack, L. & Grubb, P.J. (2001) Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Functional Ecology*, **15**, 145–154.
- Thompson, W.A., Kriedemann, P.E. & Craig, I.E. (1992) Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rain forest trees. 2. leaf gas exchange and component processes of photosynthesis. *Australian Journal of Plant Physiology*, **19**, 19–42.
- Turner, I.M. (1990) The seedling survivorship and growth of three *Shorea* species in a Malaysian tropical rain forest. *Journal of Tropical Ecology*, **6**, 469–78.
- Turner, I.M. (2001) *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press, Cambridge.
- Veenendaal, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebrese, I.K. & Mullins, C.E. (1996) Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology*, **84**, 83–90.
- Vitousek, P.M. & Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs*, **59**, 247–265.
- Walsh, R.P.D. & Newbery, D.M. (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society London, Series B*, **354**, 1869–1883.
- Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, **72**, 35–50.
- Whitmore, T.C. (1998) *An Introduction to Tropical Rain Forests*. Oxford University Press, Oxford.
- Wiederkehr, F. & Anderegg, M. (2001) *Problems with Paraserianthes falcata on Mahé, Seychelles*. Master's thesis, Geobotanical Institute ETH, Zürich.
- Williamson, M. (1996) *Biological Invasions*. Chapman & Hall, London.
- Willis, K.J. & McElwain, J.C. (2002) *The Evolution of Plants*. Oxford University Press, Oxford.

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