Functional Ecology 2008, **22**, 359–366 doi: 10.1111/j.1365-2435.2007.01373.x

Invasive trees show only weak potential to impact nutrient dynamics in phosphorus-poor tropical forests in the Seychelles

C. Kueffer*, G. Klingler, K. Zirfass, E. Schumacher, P. J. Edwards and S. Güsewell

Institute of Integrative Biology, ETH Zurich, 8092 Zurich, Switzerland

Summary

1. Some invasive alien plants accelerate nutrient turnover in the ecosystem because the litter they produce has a high specific leaf area (SLA), high concentrations of nutrients and low concentrations of lignin and polyphenolics, and therefore decomposes rapidly. These litter properties are typical of plants from nutrient-rich but not nutrient-poor ecosystems, and we therefore hypothesize that species that successfully invade nutrient-poor ecosystems might not exhibit them. We tested our hypothesis in a nutrient-poor tropical forest on a granitic island in the Seychelles.

2. Leaf litter properties and annual decomposition rates of six native and six invasive woody species were compared in a field experiment. Each species group included two pioneer, two understorey and two canopy species. We also compared soil fertility under trees of *Cinnamomum verum* (dominant alien canopy tree), *Falcataria moluccana* (alien pioneer N-fixing tree) and *Northea hornei* (dominant native canopy tree), measuring total nutrient concentrations and nutrient absorption by ion exchange resins.

3. Within the ecological groups of pioneer and canopy species, litter of invasive species had higher mean values of SLA (120% higher) and leaf N concentration (80% higher), and litter decomposition was 40%–80% faster (rate *k*) than for native species; however, there were no such differences in the group of understorey species. Soils sampled under the three tree species differed little in nutrient concentrations.

4. The results indicate that even on the very nutrient-poor soils of the granitic Seychelles, some pioneer invasive species produce more decomposable litter and therefore have the potential to alter rates of nutrient cycling. However, the small differences in soil fertility beneath native and invasive trees suggest that impacts of invasive species on nutrient cycling are more complex and less predictable in nutrient-poor ecosystems, where several nutrients may be co-limiting, and native and alien species coexist.

Key-words: ecosystem impact, litter decomposition, litter traits, nutrient cycling, oceanic island

Introduction

Plant invasions can dramatically alter the availability and turnover of nutrients in ecosystems (e.g. Ehrenfeld 2003; Dukes & Mooney 2004). These effects are generally ascribed to functional differences between the invading and resident plant species. In particular, many invasive species grow faster and accumulate more biomass than the species originally present in the invaded ecosystems, and their leaves often have a higher specific leaf area (SLA) (Daehler 2003), lower concentrations of lignin and polyphenolics, and higher concentrations of nutrients (Ehrenfeld 2003). As a result, litter of these invasive plants tends to decompose faster and to release nutrients more rapidly, thereby accelerating nutrient cycles and increasing nutrient availability for plant growth (e.g. Allison & Vitousek 2004; Rothstein, Vitousek & Simmons 2004). However, some invasive species produce less nutrient-rich or more recalcitrant litter than the resident vegetation (e.g. Windham 2001; Ehrenfeld 2003), and the effects of invasive species on nutrient availability are not always in the same direction (Hughes & Uowolo 2006).

The potential for invading plants to accelerate nutrient cycling by producing nutrient-rich and rapidly decomposing litter might depend on the availability of nutrients in the

---

*Correspondence author. E-mail: kueffer@env.ethz.ch

invaded ecosystem. Only a small subset of all alien species introduced to a region becomes invasive (Williamson 1996), and these are presumably those whose traits allow them to grow and compete successfully under local site conditions. Thus, we might expect that nutrient-rich ecosystems are invaded by fast-growing species with nutrient-rich biomass and rapidly decomposing litter, whereas nutrient-poor ecosystems are invaded by plant species with long-lived, nutrient-poor biomass and recalcitrant litter (Aerts & Chapin 2000). The consequences of these traits for nutrient cycling are likely to depend on the extent to which they differ from those of the dominant native species (Vitousek 1990). Pertinent questions, therefore, are whether species invading very nutrient-poor ecosystems have higher or lower nutrient concentrations than the dominant native species, and whether their litter decomposes more or less rapidly.

These questions have rarely been investigated because plant invasions mainly occur in ecosystems that are at least moderately nutrient-rich, either naturally or due to human activities (Dietz & Edwards 2006). Furthermore, many invasive plants of nutrient-poor ecosystems are N-fixing species that can rapidly increase N availability in the soil once they have invaded (Vitousek & Walker 1989); such species often possess typical properties of fast-growing plants, such as a high SLA and high nutrient concentrations (Ehrenfeld 2003). To compare native and invasive plant species under very nutrient-poor conditions, therefore, requires a system that is deficient not only in nitrogen but also in phosphorus or other mineral nutrients. Such a system is provided by the tropical forest on old, highly weathered granitic soils of the Seychelles. Analytical data and models of long-term soil development suggest that these soils are mainly very infertile, with very low levels of plant-available phosphorus (Varley 1971; Dobrovol'skiy 1986; Vitousek 2004), and that only the coastal and lowland areas are relatively nutrient-rich. About 230 alien tree species are listed in the flora of the Seychelles (Friedmann 1994), but only 10 species are invasive in the nutrient-poor upland forests (Kueffer & Vos 2004).

The questions addressed in this study are: (i) Do invasive species produce litter that is more nutrient-rich and labile than that of native species? (ii) Does the litter of invasive species decompose faster than that of native species? and (iii) Is the soil beneath stands of invasive trees more fertile than beneath native species? To answer the first two questions, we measured various properties of the litter of six native and six invasive tree species, and studied the litter decomposition. To answer the third question, we compared the properties of soils sampled in stands of two invasive and one native species.

Methods

STUDY SITES

The study was carried out at two sites in the Morne Seychellois National Park on the island of Mahé (Seychelles) in the Indian Ocean that were characterized by a tropical climate (mean annual rainfall and temperature *c.* 3500 mm and 23 °C, respectively). One site was at mid-altitude (430 m a.s.l.) in an upland valley at Mare aux Cochons (MC). The site was deforested in the early 20th century and used until the 1970s to produce oil from the bark and foliage of invasive stands of *Cinnamomum verum* (Cinnamon). Since then, secondary forest vegetation has developed containing six invasive and nine native woody dicotyledonous species that together account for > 95% of the trees. About 90% of the dicotyledonous trees were of invasive species, mostly *C. verum*, while about half the native trees were *Northea hornei*.

The second site was situated at a higher altitude (730 m a.s.l.) on a small plateau above MC known as Congo Rouge (CR). Although the vegetation is now a dense montane cloud forest, most of the area was probably heavily cut at the end of the 19th century. About 70% of the woody plants are invasive species, of which two-thirds are *C. verum* and one-third *Psidium cattleianum*. The site has 11 native woody species, of which *N. hornei* makes up around two-thirds of all individuals.

Mahé is formed of ancient granite that has never been covered by the ocean, so that soils have been continuously weathered for over 500 My (Braithwaite 1984). Concentrations of N, P, K, Ca and Mg in the soil are very low (Varley 1971; Dobrovol'skiy 1986). The soils at the two sites are ferrasols (FAO/ISRIC/ISSS 1998), tending towards pseudo-podzols in the case of CR. According to a bioassay experiment performed at the two sites using seedlings of *C. verum*, plant growth was limited by the availability of P and possibly also by other nutrients including K (Kueffer 2006).

For the decomposition studies and soil sampling we selected monospecific clumps (at least 10×10 m^2 and 100 m apart) of three tree species – *Cinnamomum verum* (CIN), *Northea hornei* (NOR) or *Falcataria moluccana* (FAL). The invasive tree *Cinnamomum verum* Presl, a native of lowland evergreen forests of India and Sri Lanka, is the most abundant tree species on the Seychelles. It grows in all habitats from sea level to the highest summits and has been the dominant canopy species in many upland forests since the invasion of large areas of deforested land in the early 19th century. The invasive *Falcataria moluccana* (Miquel) Barneby and Grimes is a native of the Moluccas, New Guinea, New Britain and the Solomon Islands, and is common in the Seychelles from sea level to mid-altitudes. It is a fast-growing, nitrogen-fixing tree. The endemic *N. hornei* grows from sea level to the highest summits and is the most common native tree in upland forests, especially in montane cloud forests. All three species occurred at MC but *F. moluccana* was absent at CR. The five combinations of tree species and site (MC CIN, MC NOR, MC FAL, CR CIN and CR NOR) are hereafter called 'stand types'. Each stand type was replicated three times at each site.

LITTER QUALITY

Six native and six invasive woody species were included in this study (Table 1). Because leaf and litter properties are known to depend on the ecological group of species, we selected for each status group two pioneer species (light-demanding and regenerating only in forest gaps), two canopy species (large trees of > 10 m stem height, able to regenerate under a closed canopy and dominant in the canopy layer) and two understorey species (shrubs or small trees of < 10 m stem height and able to regenerate under a closed canopy; see Turner 2001). All the species selected are very common in the Seychelles and together account for > 90% of mature trees in most mid-altitude and montane forests (Fleischmann 1997, and C. Kueffer unpublished data). The six invasive species belong to the group of 10 most problematic invasive plants of mid-altitude and montane forests in Seychelles (Kueffer & Vos 2004).

Table 1. The six native (N) and invasive (I) tree species included in this study. The species were selected according to three ecological groups: pioneer, understorey and canopy species. Nomenclature and maximal stem height was taken from Friedmann (1994). Date of introduction is adapted from Kueffer & Vos (2004)

Species name	Family	Status group	Stem height (m)	Date of introduction
Pioneer				
Alstonia macrophylla	Apocynaceae	I	15	*c.* 1950s
*Falcataria moluccana**	Leguminosae	I	10–40	*c.* 1910
Aphloia theiformis	Flacourtiaceae	N	12	–
Canthium bibracteatum	Rubiaceae	N	7–8	–
Understorey				
Psidium cattleianum	Myrtaceae	I	5–7	*c.* 1850
Syzygium jambos	Myrtaceae	I	7–10	1787
Memecylon eleagni	Melastomataceae	N	7–8	Endemic
Timonius sechellensis	Rubiaceae	N	7–8	Endemic
Canopy				
Cinnamomum verum	Lauraceae	I	10–15	1772
Pentadesma butyracea	Guttiferae	I	15	*c.* 1910
Dillenia ferruginea	Dilleniaceae	N	15–20	Endemic
Northea hornei	Sapotaceae	N	20	Endemic

**Paraserianthes falcataria* in Friedmann (1994).

Freshly fallen leaf litter was collected each week from mid-February to mid-March 2004 using nets placed under 3–5 trees of each species at MC. The litter was air-dried, and 6–15 subsamples per species (from different trees and sampling dates) were oven-dried at 55 °C for 96 h to determine the dry matter content. These samples were ground and analyzed in the laboratory of the Institute of Integrative Biology, ETH Zurich. Total C and N concentrations were determined using a CNS-2000 analyzer (LECO, St Joseph, MI). Kjeldahl N and P concentrations were determined after digestion with 98% H_2SO_4 and Merck Kjeltabs in a flow injection analyzer (FIA, TECATOR, Höganäs, Sweden). P concentrations were below detection level (0·05 mg g^{-1}) in some litter samples of *N. hornei*. These values were set to the lowest measured value for data analysis.

Soluble phenolics were extracted with 50% ethanol. The concentration of soluble phenolics in the supernatant was determined with the Folin Ciocalteau method, using tannic acid as a standard. Photometric analysis (absorbance at 760 nm) was performed on an Uvi Light XT2 spectrophotometer (Secoman, Ales, France).

The biochemical activity of tannins in the same litter extracts was determined through assays based on the inhibition of the enzyme α-amylase by tannic acids (adapted from Wint 1983). We used this assay because the main mechanism through which tannins may affect litter decomposition is the inhibition of catabolic enzyme activities (Joanisse *et al.* 2007). We mixed 200 μL leaf extract or standard solution (tannic acid, Bender & Hobein, Zurich, Switzerland, in 50% ethanol) with 200 μL enzyme solution (50 mg L^{-1} α-amylase from *Bacillus subtilis*, FLUKA (Buchs, Switzerland)10069, in H_2O) and waited 10 min (tannin-enzyme reaction) before adding 8 mL of starch solution (1·7 g L^{-1} soluble starch and 2·2 g L^{-1} NaCl in phosphate buffer with pH 6). After a further 20 min (hydrolysis of starch by the amylase), 1 mL of the mixture was added to 4 mL iodine indicator (16 mg I_2 and 0·4 g KI in 400 mL H_2O). Photometric analysis was performed based on the absorbance at 580 nm.

To determine SLA, leaf area was measured on air-dried leaves using a digital camera (Nikon Coolpix 995, 3·34 Megapixels). Leaf dry mass was determined after oven-drying at 55 °C for 96 h.

LITTER DECOMPOSITION

Equal amounts of air-dried litter from the different collecting nets were mixed to yield one pooled sample per species. The material was cut into pieces of roughly 200–300 mg and subsamples of 1–1·5 g were packed into 9 × 9 cm^2 net bags made from a polyamide fabric with a 0·4 × 0·6 mm^2 mesh. Additional samples (the same 12 species) were incubated in litter-bags with a coarser mesh size (2 × 2·5 mm^2) to verify that the exclusion of the soil fauna did not affect interspecific or inter-site comparisons (no difference was found, data not shown). Furthermore, cellulose (cotton) was incubated during the first 3 months as reference material.

Field incubations started in April 2004. The litter bags were placed horizontally on the soil under the natural litter layer in the nine plots at site MC. Litter of *C. verum*, *N. hornei* was also exposed in the six plots of site CR. There were four replicate litter bags per species and plot, of which two were collected after 3 months (95 days) and two after 10 months (320 days). The decaying litter was carefully removed from the bags, cleaned of extraneous material, oven-dried (55 °C for 96 h) and then weighed. For three species – *C. verum*, *N. hornei* and *F. moluccana* – N and P concentrations of litter were determined after 3 and 10 months of decomposition using the methods already described.

SOIL FERTILITY

To investigate soil chemistry, two soil cores (depth 10 cm, diameter 7 cm) were taken randomly within each of the 15 field plots. During sampling, it appeared that two types of topsoil occurred at our sites: an organic O-horizon was always present in plots of CR CIN, CR NOR, MC NOR and always absent in plots of MC FAL. In MC CIN plots, however, we found both types of topsoil, and we therefore sampled separately the areas with and without an organic O-horizon (hereafter coded as MC CIN-org and MC CIN-min, respectively).

Soil pH was determined in a 1 : 2 mixture of fresh soil and rainwater using a portable pH meter (Hanna Instruments HI 98127,

Table 2. Mean concentrations of nitrogen (N) and phosphorus (P), biochemical activity of soluble phenolics and tannins (given as tannic acid equivalents, TAE), and mean specific leaf litter areas (SLA) for leaf litter of six native and six invasive woody plant species. Results of one-way ANOVAS (native vs. invasive) are also shown. $^*P < 0{\cdot}05$

Species	N (mg g^{-1})	P (mg g^{-1})	N : P	C : N	C : P	Phenolics (mg TAE g^{-1})	Tannins (mg TAE g^{-1})	SLA (cm^2 g^{-1})
Invasive								
Alstonia macrophylla	14·1	0·37	38	35	1324	17	2	155
Cinnamomum verum	9·2	0·46	20	56	1070	45	3	95
Falcataria moluccana	15·1	0·39	39	32	1217	112	83	162
Pentadesma butyracea	11·6	0·40	29	43	1249	26	14	68
Psidium cattleianum	6·7	0·38	18	71	1228	39	12	51
Syzygium jambos	6·7	0·37	18	74	1356	110	17	67
Native								
Aphloia theiformis	7·7	0·36	21	64	1251	75	6	78
Canthium bibracteatum	8·7	0·39	22	55	1236	36	33	65
Dillenia ferruginea	6·4	0·34	19	78	1401	92	99	46
Memecylon eleagni	6·3	0·35	18	70	1369	46	35	70
Northea hornei	5·0	0·22	23	105	2756	129	109	27
Timonius sechellensis	6·8	0·33	20	75	1524	50	37	75
Invasive (mean)	10·6	0·40	27	52	1241	58	22	100
Native (mean)	6·8	0·33	21	75	1590	71	53	60
ANOVA (*F*, *P*)	5·7*	5·3*	2·5	5·0*	2·1	0·3	2·2	3·5

pHep). The remaining soil was passed through a 4 mm sieve, oven-dried at 80 °C for 48 h and ground in a mortar. Total C, N and P concentrations were determined using the methods already described for the litter samples.

Mineral N and P availability was estimated *in situ* using ion exchange resin bags made from a polyamide fabric (4 × 3 cm^2; mesh 60 µm; Sefar, Hausen, Switzerland) filled with 1·7 ± 0·1 g of a mixture of Dowex-1 and Dowex-50W (Fluka, Buchs, Switzerland) at a ratio of 1 : 0·7 (adapted from Güsewell, Jewell & Edwards 2005). Two bags per stand were placed in vertical slits in the soil at a depth of 5–10 cm. They were removed after 71 days and stored at air temperature in airtight bags. They were later washed for 10 s with deionized water and then extracted for 90 min under constant shaking in 50 mL 0·5 N HCl. Subsamples were neutralized with 2 N KOH and used to determine NH_4–N and NO_3–N concentrations in a flow injection analyzer (FIA, Tecator, Höganäs, SE), and PO_4–P concentrations as described by Watanabe & Olsen (1965) using a Uvi Light XT2 spectrophotometer. The amounts of NO_3–N, NH_4–N and PO_4–P captured per resin bag provided a relative measure of soil nutrient availability.

STATISTICAL ANALYSES

Mean litter characteristics of the 12 species were used in the data analyses. Differences between status (native vs. invasive) were tested with one-way ANOVA.

Litter decomposition rates and litter mass loss were analysed in two steps reflecting the two sources of variation in the experiment. Differences between native and invasive species were tested with one-way ANOVA using means per species (means of the 18 litter subsamples incubated at MC). Differences among tree species under which the litter was incubated were tested with one-way ANOVA based on means of all litter bags incubated in a field plot; this was done separately for MC and CR, as only two species were incubated at CR.

Soil properties were compared among the six stand and soil types (MC CIN-min, MC CIN-org, MC NOR, MC FAL, CR CIN, CR NOR) with one-way ANOVA, using means of the two soil cores per field plot. Data were transformed as necessary to meet the assumptions of ANOVA. Statistical analyses were performed with JMP v. 6·0·3 (SAS Institute Inc., Cary, NC).

Results

Litter of invasive species had higher concentrations of N and P, and lower C : N ratios than litter of native species ($P < 0{\cdot}05$; Table 2). Other leaf parameters, including SLA, C : P ratio and biochemical activity of soluble phenolics and tannins, did not vary significantly according to provenance. The magnitude of the differences between native and invasive species depended on the ecological niche of the species. Thus, the differences between the native and invasive canopy species were between 60% and 300% for all parameters, while differences among understorey species were much smaller and in some cases in the opposite direction. The pioneer species also differed greatly in SLA and N concentration but not in P litter concentration. The measurements of polyphenols varied very widely among species, with the second highest and lowest values for phenolics activity occurring in two invasive species, *F. moluccana* and *Alstonia macrophylla*, respectively.

Mean litter mass loss in invasive species was *c.* 30% higher than that in native species after 3 months, and *c.* 20% higher after 10 months, but these differences were not significant ($P > 0{\cdot}2$; Table 3); the low significance level was again due to the similarity of native and invasive understorey species. Litter mass loss after 3 months correlated positively with SLA ($r = 0{\cdot}79$, $P = 0{\cdot}002$) and N concentration ($r = 0{\cdot}63$, $P = 0{\cdot}03$), and negatively with C : N ratio ($r = -0{\cdot}50$, $P = 0{\cdot}02$) and tannin concentration ($r = -0{\cdot}60$, $P = 0{\cdot}04$). Correlations between initial litter properties and mass loss after 10 months were

Table 3. Litter decomposition rates (*k*-value from a fitted exponential decay function) and % litter mass loss after 3 and 10 months of decomposition in litter bags at the mid-altitude site (MC). Data are means (and SE) from the nine field plots at MC. Means by status groups are also given; these did not differ significantly (one-way ANOVA, $P > 0.05$)

Species	*k* (years^{-1})	3 months (%)	10 months (%)
Invasive			
Alstonia macrophylla	1·63	44·3 (1·5)	67·3 (2·6)
Cinnamomum verum	0·88	25·1 (6·7)	51·4 (2·9)
Falcataria moluccana	1·10	31·4 (1·7)	56·1 (3·0)
Pentadesma butyracea	0·90	24·0 (1·7)	53·2 (4·1)
Psidium cattleianum	0·73	19·7 (1·4)	46·1 (2·9)
Syzygium jambos	0·93	30·4 (1·4)	51·1 (2·1)
Native			
Aphloia theiformis	1·26	34·4 (2·2)	62·5 (2·8)
Canthium bibracteatum	0·69	21·0 (1·2)	43·2 (3·6)
Dillenia ferruginea	0·61	14·9 (1·4)	41·4 (3·7)
Memecylon eleagni	0·63	21·8 (0·6)	39·4 (2·0)
Northea hornei	0·36	10·2 (0·7)	26·8 (1·8)
Timonius sechellensis	1·27	30·3 (2·1)	65·7 (4·1)
Cellulose	–	17·1 (6·7)	–
Invasive (mean)	1·03	29·2	54·2
Native (mean)	0·80	22·1	46·5

similar but slightly weaker. At MC, litter mass loss after 3 months was significantly greater in the CIN than FAL plots (mean mass loss: CIN: 28·4%, FAL: 22·3%, NOR: 24·7%; one-way ANOVA: $P = 0.03$), but there was no significant difference between the plots after 10 months (CIN: 52·9%, FAL: 42·6%, NOR: 50·7%, $P = 0.09$). Similarly, at CR, litter mass loss was higher in the CIN than NOR plots after 3 months (18·9% and 16·0%, respectively; $P = 0.03$) but not after 10 months ($P = 0.9$).

Nutrient dynamics during decomposition depended more on litter quality than on site properties: across plots, litter of *N. hornei* consistently immobilized more P and retained more N than litter of *F. moluccana* and *C. verum* (Fig. 1). In contrast, the only difference among stand types was a higher immobilization of P after 10 months in FAL compared with NOR and CIN stands (124% vs. 96% and 99%, respectively; $P = 0.001$).

Soil chemistry varied significantly among the six stand types (Table 4). In particular, soil pH and C : N ratio were lower while NO_3–N availability was higher in FAL plots than in the mineral soil of CIN plots. NOR plots had lower P availability than CIN plots but higher C : N and C : P ratios.

Discussion

DOES LITTER FROM INVASIVE PLANT SPECIES DIFFER FROM NATIVE SPECIES IN QUALITY AND DECOMPOSITION RATE?

Our study revealed only small differences between litter quality of native and invasive species. The nitrogen and phosphorus concentrations were significantly higher in the litter of the invasive species, but differences in mean SLA and decomposition rates were non-significant. The directions of the differences in all traits, however, were the same as those reported from Hawaii (Allison & Vitousek 2004; Rothstein *et al.* 2004; Hughes & Denslow 2005) and many other regions of the world (Ehrenfeld 2003).

Comparisons made within ecological groups revealed strong differences between natives and invasives among pioneer and canopy species, but not among understorey species. Because we used the most common species in our ecosystem, which belonged to several plant families, we cannot exclude the possibility that these comparisons may have a phylogenetic bias. However, the differences for pioneer species fit well with those reported elsewhere for native and invasive species in disturbed and nutrient-rich environments (e.g. Daehler 2003). It may be expected that fast growing, invasive pioneer species would profit most from release from natural enemies, which could explain why despite their particular leaf properties they are also successful in these stressed ecosystems. However, other studies have shown that the differences of herbivore damage sustained by native and invasive pioneer species in the Seychelles were rather small (Dietz, Wirth & Buschmann 2004; Kueffer 2006).

The canopy species showed the biggest differences in litter characteristics between native and invasive trees, with the native canopy species – *N. hornei* in particular – having very

Fig. 1. Nitrogen (a) and phosphorus (b) immobilization during litter decomposition after 3 and 10 months. Immobilization was calculated as the remaining total nutrient amount in the decomposed litter as a percentage of the total nutrient amount in the initial litter mass. Average values for all stands in Mare aux Cochons are given. Open squares for *Northea hornei*, filled squares for *Cinnamomum verum* and open circles for *Falcataria moluccana* litter. Differences between species after 3 and 10 months, respectively, were tested with a Tukey test.

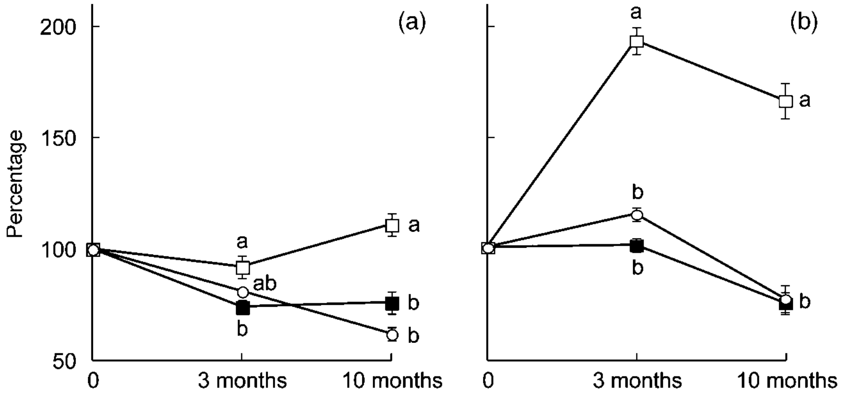

Table 4. Chemical properties of soils from three stand types (*Cinnamomum verum*, CIN; *Northea hornei*, NOR; *Falcataria moluccana*, FAL) at two altitudes (mid-altitude Mare Cochons, MC; montane Congo Rouge, CR). For MC CIN organic O-horizon (-org) and surface exposed mineral A-horizon (-min) were separately analyzed. Mean and SE are given ($N = 3$) [below detection level (b.d.l.)]. Ion exchange resin (IER) data is given as mg L^{-1} of extraction solution. The final three columns contain *F*-ratios and significance levels from one-way ANOVA for the comparison of the six stand types as well as from *a priori* contrasts for the comparison of MC FAL vs. MC CIN-min and the organic CIN vs. NOR soils (***$P < 0{\cdot}001$; **$P < 0{\cdot}01$; *$P < 0{\cdot}05$)

	MC FAL	MC CIN-min	MC CIN-org	MC NOR	CR CIN	CR NOR	Stand type	FAL–CIN	CIN–NOR
C (mg g^{-1})	64 (7)	47 (13)	399 (44)	472 (23)	435 (79)	492 (30)	26***	0	0
N (mg g^{-1})	3·8 (0·5)	2·1 (0·5)	15·0 (1·0)	14·6 (1·1)	18·1 (3·1)	16·4 (1·2)	21***	1	1
P (mg g^{-1})	0·28 (0·01)	0·29 (0·04)	0·41 (0·04)	0·38 (0·01)	0·52 (0·05)	0·39 (0·05)	6**	0	5*
C : N	17 (0)	22 (2)	26 (2)	33 (4)	24 (1)	30 (1)	10***	5*	12**
C : P	224 (27)	155 (22)	978 (86)	1261 (103)	827 (83)	1305 (161)	29***	0	17***
pH	4·4 (0·1)	4·7 (0·1)	4·2 (0·1)	4·3 (0·1)	4·3 (0·1)	4·4 (0·1)	5*	5*	2
IER–NO_3–N	4·7 (0·9)	1·6 (0·4)	1·5 (0·3)	1·7 (0·2)	1·1 (0·1)	1·1 (0·1)	10***	25***	0
IER–NH_4–N	1·6 (1·1)	4·6 (3·4)	1·7 (0·5)	2·3 (1·3)	3·2 (1·5)	1·5 (1·0)	1	1	0
IER–N total	6·3 (1·9)	6·2 (3·1)	3·2 (0·7)	3·9 (1·5)	4·3 (1·6)	2·5 (1·0)	1	0	0
IER–PO_4–P	b.d.l.	3·9 (3·6)	0·6 (0·3)	0·5 (0·5)	1·1 (0·4)	b.d.l.	–	–	–

low nutrient concentrations and SLA, and very high polyphenol concentrations. These properties have also been found for endemic canopy species on other oceanic islands (Vitousek 2004); however, it is not certain whether dominant canopy species on oceanic islands differ generally from continental species and, if so, whether such differences are due to geographic isolation or to the very nutrient-poor soils on many islands.

One important conclusion, therefore, is that the tree species invasive in the nutrient-poor soils of upland forests, although few in number, are by no means a uniform group. Some of them possess traits usually associated with rapid resource acquisition and growth, while others resemble many native species in possessing litter traits characteristic of stress tolerant plants adapted to very resource-poor conditions (compare Aerts & Chapin 2000).

In the case of the litter decomposition rates, the small differences between species may also be related to the site quality, which may explain why higher nutrient concentrations among invasive species did not generally translate into higher decomposition rates. At very infertile sites, initial rates of decomposition are often determined more by the carbon quality and polyphenol concentration of litter than by its nutrient concentrations (Hobbie 2000; Bridgham & Richardson 2003). In our study, the rate of litter decomposition was significantly correlated with several parameters, including SLA, tannin concentration, nitrogen concentration and C : N ratio, but none of these could be identified as the single most important factor. However, two other results suggest that the N concentration was of minor importance, and that C quality was the major factor limiting decomposition. First, the litter of *F. moluccana* and *C. verum* released nutrients during initial decomposition, despite having high C : N and C : P ratios compared to the values cited as the critical ratios for immobilization (cf. Bridgham & Richardson 2003). Second, we carried out an ancillary laboratory experiment where litter of *C. verum* and *N. hornei* was allowed to decompose in soils sampled at the 15 field plots, either with or without fertilisation (N, P or complete fertilizer) (Kueffer 2006). None of the fertilizer treatments influenced decomposition rates. This could not be due to high nutrient availability in soil (e.g. due to the disturbance associated with sampling, mixing and filling the pots) because cotton pieces incubated in the same way decomposed faster with complete fertilizer.

Many other studies have reported striking differences in litter traits between invasive and native tree species. However, most of these compared pioneer invasive species with late-successional (understorey or canopy) native species (e.g. Allison & Vitousek 2004; Rothstein *et al.* 2004; Hughes & Uowolo 2006), making it impossible to distinguish between effects due to provenance (i.e. whether native or invasive) and those due to ecological group (e.g. early vs. late-successional). In contrast, in another study where invasive and native species were compared within ecological groups (vine, shrub, tree) decomposition rates did not generally differ (Ashton *et al.* 2005). These results confirm the importance of controlling for ecological group as well as phylogeny when comparing native and invasive species.

IS THE SOIL UNDER INVASIVE PLANTS MORE FERTILE?

An important assumption of our study is that any differences in soil conditions under the three tree species were caused by the trees themselves. Although we cannot exclude the possibility that pre-existing site differences determined where each trees species grew, we think this is unlikely because all trees are found under a wide variety of environmental conditions (Fleischmann 1997; Kueffer & Vos 2004) and they grow closely interspersed in apparently uniform areas.

Our study revealed three main differences in soil nutrient availability. First, P concentrations (total and ion-resin extractable) were higher in CIN than in NOR stands while C : N and C : P ratios were lower. Second, N was mainly mineralized as nitrate in FAL soils but as ammonium in CIN. While nitrification increases the availability of N for some plants it can also lead to higher leaching losses (Bardgett

2005). Third, P availability was lower in FAL than in CIN stands. The lower soil pH of the FAL stands might have contributed to these differences by enhancing P fixation to Fe and Al hydroxides (Bardgett 2005).

Despite these significant effects, the general weakness of the impacts of *C. verum* and *F. moluccana* on nutrient availability was unexpected. In particular, the enhancement of soil N availability by the *F. moluccana* was negligible compared to the 17- to 121-fold increases in N availability under *F. moluccana* on young volcanic flows in Hawaii (Hughes & Denslow 2005). Similarly, the increase in P availability in CIN stands was much smaller than might have been expected from the data on litter properties. We can think of two main reasons why nutrient conditions in the three stand types were not more different.

First, N-fixation of *F. moluccana* may be restricted by phosphorus deficiency (compare e.g. Vitousek *et al*. 2002). Although we did not measure N-fixation, we observed nodules containing the characteristic pink colour of leghaemoglobin on the roots of both trees and saplings of *F. moluccana*. However, the measures of soil P availability indicate that P levels were indeed very low below *F. moluccana* stands. The generally low levels of phosphorus in upland soils may also explain why several N-fixing alien species, some of them invasive in the lowlands (e.g. *Leucaena leucocephala*) and others used in reforestation schemes (e.g. *Albizia lebbeck* or *Gliricidia sepium*), have been unable to invade established upland forest stands (Kueffer & Vos 2004).

Second, the stands we studied were small, so that ‘edge effects’ may have played a role. For example, the litter of *F. moluccana* probably also contributes significantly to nutrient input through litterfall in the other stands. We measured litterfall under the different stands over a period of several months and estimated that *c.* 20% of the litterfall was from species other than the one dominating the stand. A patchy distribution may also have allowed a regular exchange of the soil fauna between the stands with fast- and slow-decomposing litters, and this may have reduced stand-level effects on litter decomposition like those found in invasions by *F. moluccana* over large areas in Hawaii (Hughes & Uowolo 2006). The presence of patches of early-successional invasive species (and of clumps of native species such as *N. hornei*) in a matrix of secondary forests dominated by late-successional invasive species such as *C. verum* is the common invasion pattern in the Seychelles. More generally, secondary forests containing mixtures of both alien and native species may be typical of long-term secondary successions on oceanic islands, while the mono-specific alien forests often studied (e.g. Hughes & Denslow 2005) may be a transient early-sucessional stage (compare Lugo 2004).

Future research is needed to clarify other possible explanatory factors specific to very nutrient-poor forests. We suggest that the few species that do invade these forests possess particular adaptations promoting the efficient uptake or use of nutrients (reviewed in Kueffer 2006), and that these reduce nutrient cycling rates or soil nutrient availability despite nutrient-rich litter. For instance, *C. verum* forms a very dense root mat in the topsoil, making it an aggressive competitor for below-ground resources (Kueffer *et al*. 2007). Similarly, *F. moluccana* is known to be very efficient in taking up P and can therefore reduce soil P availability when grown in plantations (Binkley & Ryan 1998). And besides P limitation, co-limitation by micronutrients such as potassium could also have played a role, though little is known about the impact of invasive plants on soil nutrients other than nitrogen and phosphorus (Ehrenfeld 2003). An indication that K availability is very low in the upland forests of the Seychelles is provided by data on litter K concentrations. In the case of *N. hornei* (0·26 mg g^{-1}), this value was about half the lowest concentration measured in litter of an ecologically similar tree, *Metrosideros polymorpha,* in Hawaii (0·51 mg g^{-1}) (Hobbie 2000). Such a low level of availability could have an impact upon invasive species with a higher K requirement; indeed, litter K concentration was much higher in the invasive species we studied (*C. verum*: 2·20 mg g^{-1}; *F. moluccana*: 1·68 mg g^{-1}) than in the native species (*N. hornei*: 0·26 mg g^{-1}, *M. eleagni*: 0·68 mg g^{-1}).

In conclusion, our study indicates that in secondary forests on very nutrient-poor soils invasive plants may have only limited impact upon nutrient dynamics or impacts that are complex and difficult to predict. Many of the most problematic invasive species possess growth traits similar to those of native species, and P limitation may moderate impacts of any differences that do exist between native and invasive species. Future research is needed to clarify the role of these and possibly other factors, including co-limitation by potassium or efficient nutrient-uptake by invasive species such as *C. verum* or *F. moluccana*. We expect that the patterns observed in this study are more generally relevant for ecosystems on very nutrient-poor soils.

Acknowledgements

We thank the staff of the Seychelles Ministry of Environment and Natural Resources for assistance in the field and logistic support, and Rose Trachsler and Marilyn Gaschen (Institute of Integrative Biology, ETH Zurich), and Paul van der Ven and Jos Verhoeven (Landscape Ecology, Utrecht University) for the assistance with the chemical analyses of the litter and soil samples. The paper profited from comments by Harry Olde Venterink and three anonymous reviewers. Funding was provided by a research grant from the Swiss Federal Institute of Technology (ETH Zurich).

References

Aerts, R. & Chapin III, F.S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1–67.

Allison, S.D. & Vitousek, P. (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. *Oecologia*, **141**, 612–619.

Ashton, I.W., Hyatt, L.A., Howe, K.M., Gurevitch, J. & Lerdau, M.T. (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecological Applications*, **15**, 1263–1272.

Bardgett, R. (2005) *The Biology of Soil. A Community and Ecosystem Approach*. Oxford University Press, Oxford.

Binkley, D. & Ryan, M.G. (1998) Net primary production and nutrient cycling in replicated stands of *Eucalyptus saligna* and *Albizia facaltaria*. *Forest Ecology and Management*, **112**, 79–85.

Braithwaite, C.J.R. (1984) Geology of the Seychelles. *Biogeography and Ecology of the Seychelles Islands* (ed. D.R. Stoddart), pp. 17–38. DR W. Junk Publishers, The Hague.

Bridgham, S.D. & Richardson, C.J. (2003) Endogenous nutrient control over decomposition and mineralization in North Carolina peatlands. *Biogeochemistry*, **65**, 151–178.

Daehler, C.C. (2003) Performance comparisons of co-occuring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution and Systematics*, **34**, 183–211.

Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359–1367.

Dietz, H., Wirth, L.R. & Buschmann, H. (2004) Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahé, Seychelles. *Biological Invasions*, **6**, 511–521.

Dobrovol'skiy, V.I. (1986) Weathering crust and soils of the Seychelles Islands. *Pochvovedeniye*, **6**, 18–28.

Dukes, J.S. & Mooney, H.A. (2004) Disruption of ecosystem processes in western North America by invasive species. *Revista Chilena de Historia Natural*, **77**, 411–437.

Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503–523.

FAO/ISRIC/ISSS (1998) *World Reference Base for Soil Resource*. FAO, Rome.

Fleischmann, K. (1997) Invasion of alien woody plants on the islands of Mahé and Silhouette, Seychelles. *Journal of Vegetation Science*, **8**, 5–12.

Friedmann, F. (1994) *Flore des Seychelles*. Orstrom, Paris.

Güsewell, S., Jewell, P.L. & Edwards, P.J. (2005) Effects of heterogeneous habitat use by cattle on nutrient availability and litter decomposition in soils of an Alpine pasture. *Plant and Soil*, **268**, 135–149.

Hobbie, S.E. (2000) Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. *Ecosystems*, **3**, 484–494.

Hughes, R.F. & Denslow, J.S. (2005) Invasion by a N_2-fixing tree alters function and structure in wet lowland forests of Hawaii. *Ecological Applications*, **15**, 1615–1628.

Hughes, R.F. & Uowolo, A. (2006) Impacts of *Falcataria moluccana* invasion on decomposition in Hawaiian lowland wet forests: the importance of stand-level controls. *Ecosystems*, **9**, 977–991.

Joanisse, G.D., Bradley, R.L., Preston, C.M. & Munson, A.D. (2007) Soil enzyme inhibition by condensed litter tannins may drive ecosystem structure and processes: the case of *Kalmia angustifolia*. *New Phytologist*, **175**, 535–546.

Kueffer, C. (2006) *Impacts of Woody Invasive Species on Tropical Forests of the Seychelles*. Diss. ETH No. 16602, ETH Zurich, Zurich.

Kueffer, C. & Vos, P. (2004) *Case Studies on the Status of Invasive Woody Plant Species in the Western Indian Ocean: 5. Seychelles*. Forestry Department, FAO, Rome.

Kueffer, C., Schumacher, E., Fleischmann, K., Edwards, P.J. & Dietz, H. (2007) Strong belowground competition shapes tree regeneration in invasive *Cinnamomum verum* forests. *Journal of Ecology*, **95**, 273–282.

Lugo, A.E. (2004) The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and Environment*, **2**, 265–273.

Rothstein, D.E., Vitousek, P.M. & Simmons, B.L. (2004) An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. *Ecosystems*, **7**, 805–814.

Turner, I.M. (2001) *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press, Cambridge.

Varley, J.A. (1971) Soil analyses and agricultural research in the Seychelles. Report of a visit. Foreign and Commonwealth Office, Overseas Development Administration.

Vitousek, P.M. (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos*, **57**, 7–13.

Vitousek, P.M. (2004) *Nutrient Cycling and Limitation. Hawaii as a Model System*. Princeton University Press, Princeton.

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.

Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Field, C.B., Grimm, N.B., Howarth, R.W., Marino, R., Martinelli, L., Rastetter, E.B. & Sprent, J.I. (2002) Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry*, **57/58**, 1–45.

Watanabe, F.S. & Olsen, S.R. (1965) Test of an ascorbic acid method for determining phosphorus in water and $NaHCO_3$ extracts from soil. *Soil Science Society of America Proceedings*, **1965**, 677–678.

Williamson, M. (1996) *Biological Invasions*. Chapman & Hall, London.

Windham, L. (2001) Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay) in brackish tidal marsh of New Jersey. *Wetlands*, **21**, 179–188.

Wint, G.R.W. (1983) The effects of foliar nutrients upon the growth and feeding of a lepidopteran larva. *Nitrogen as an Ecological Factor* (eds J.A. Lee, S. McNeil & I.H. Rorison), pp. 301–320. Blackwell, Oxford.

Received 10 June 2007; accepted 21 November 2007
Handling Editor: Jim Dalling