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ORIGINAL PAPER

Reduced risk for positive soil-feedback on seedling regeneration by invasive trees on a very nutrient-poor soil in Seychelles

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Abstract Invasive plants sometimes alter habitat conditions so as to promote further invasion, either by the same or by other non-native species. Such positive feedbacks often occur because the non-native species increases soil fertility, thereby favouring recruitment of non-native seedlings. This has been demonstrated in nitrogen-poor habitats invaded by nitrogen-fixing species, but it is unclear whether similar processes operate in habitats limited by phosphorus and other nutrients. I compared the growth of seedlings of *Cinnamomum verum*, an abundant invasive tree on phosphorus-poor soils in the Seychelles, in soils taken from beneath different tree species. I expected that soil phosphorus availability would be higher beneath stands of *C. verum* than beneath stands of either the native *Northea hornei* or the non-native nitrogen-fixing species, *Falcataria moluccana*. I therefore predicted that *C. verum* seedlings would grow faster in soil taken from beneath *C. verum* trees than in soil taken from beneath either of the other two species. To test this hypothesis, I performed a bioassay experiment with seedlings of *C. verum* grown in soils from stands of *C. verum*, *F. moluccana* and *N. hornei*. Different nutrient treatments (control, plus phosphorus (P), plus nitrogen (N), plus N and P, and plus complete fertilizer) were applied to investigate how nutrient availabilities modulate the effects of the trees. In the control treatment without added nutrients, there was a weak tendency for seedlings to perform better in the soils from beneath invasive than native trees. However, seedling growth in soils from beneath invasive species was markedly higher following the addition of phosphorus in the case of the *F. moluccana* soil, and complete fertilizer in the case of the *C. verum* soil. These results indicate that on very nutrient-poor soils, a low supply of nutrients other than N may reduce the risk of a soil-feedback by invasive trees on seedling regeneration.

Keywords Oceanic island · Phosphorus · Potassium · Soil fertility · Tropical forest · Nitrogen fixation

Introduction

Invasions of non-native plant species pose major threats to biodiversity and ecosystem functioning (Millennium Ecosystem Assessment 2003), especially on oceanic islands (Denslow 2003). While many studies have focused on the introduction, establishment and spread of invasive non-native plants (Dietz and Edwards 2006; Mack et al. 2000), more research is needed to investigate whether and how these species persist and influence their habitat in the longer term (Strayer et al. 2006).

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According to one influential hypothesis, invasive species may alter the invaded habitat so as to favour further invasion by the same or other non-native species (Levine et al. 2003, 2006; Simberloff and Von Holle 1999). In particular, it has been shown that invasive species can increase the soil fertility of invaded stands (Hughes and Denslow 2005; Vitousek et al. 1987) and thereby facilitate the growth of nutrient-demanding, fast-growing invasive species (Adler et al. 1998; Hughes and Denslow 2005; Ostertag and Verville 2002). This risk may be particularly high on oceanic islands, which tend to lack fast-growing native species that can compete with invasive species under high resource conditions (Denslow 2003; Schumacher et al. 2008, 2009).

Such positive soil-feedbacks on the regeneration of invasive species have been studied mainly in nitrogen-poor habitats invaded by nitrogen-fixing invasive species (cf. Ehrenfeld 2003; Levine et al. 2003), and it is unclear whether similar processes operate where growth is limited by phosphorus or other nutrients. It has been shown that the regeneration of invasive species in phosphorus-poor tropical forest can be enhanced by adding this nutrient to the soil (Ostertag and Verville 2002). However, the potential for the plants themselves to increase soil fertility in situations other than nitrogen-limitation is not well understood (Kueffer et al. 2008).

The purpose of this study was to investigate how invasive trees influence seedling regeneration via their impacts on soil properties. The study area was a tropical forest on a very nutrient-poor soil in the Seychelles (Indian Ocean). These oceanic islands are formed of ancient granite that has never been covered by the ocean, so that soils have been continuously weathered for over 500 million years (Braithwaite 1984). Analytical data and models of long-term soil development suggest that most of these soils are poor in most nutrients, especially phosphorus (Dobrovol'skiy 1986; Kueffer et al. 2008; Varley 1971; Vitousek 2004).

I studied the influence upon seedling growth of two ecologically contrasting invasive trees, *Cinnamomum verum* (true Cinnamon) and *Falcataria moluccana*. *C. verum* is now the commonest invasive tree in Seychelles, and typically makes up more than 80% of the canopy of secondary forests (Fleischmann 1997; Kueffer and Vos 2004). It has been shown to increase soil phosphorus availability compared to native tree stands in Seychelles (Kueffer et al. 2008). *F. moluccana* is the most common nitrogen-fixing invasive tree in Seychelles, and has been shown to increase the availability of nitrogen but not phosphorus (Kueffer et al. 2008). I hypothesized that mature *C. verum* would facilitate seedling growth by increasing phosphorus availability; in contrast, I predicted that in these phosphorus-limited soils *F. moluccana* would not promote seedling growth, even though nitrogen-fixing plants have been shown to facilitate invasive species in nitrogen-limited ecosystems (Hughes and Denslow 2005).

To address these hypotheses, I performed a bioassay experiment in which I compared the growth of *C. verum* seedlings in soils from stands of the two invasive trees *C. verum* and *F. moluccana* with seedlings grown in soil from stands of the native tree, *Northea hornei*. I included five different nutrient treatments (control, plus phosphorus (P), plus nitrogen (N), plus N and P, and plus complete fertilizer) to test whether the impact of the three tree species on seedling growth differs depending on the availability of N or P. The complete fertilizer addition was included as an additional treatment to explore whether other nutrients also limit growth.

Methods

Study species

Cinnamomum verum Presl. (Lauraceae) (synonym: *C. zeylanicum*; true Cinnamon) was introduced to the Seychelles in the 1770s and is now the most abundant woody species on most of the granitic islands (Kueffer and Vos 2004). It grows in all habitats from sea level to the highest montane forests at 900 m above sea level, and since the early nineteenth century has been the dominant canopy species in many upland forests. The species is a native of lowland, evergreen climax forests of the Western Ghats of India and Sri Lanka where it occurs up to an altitude of 1,800 m above sea level. It forms a small tree 10–15 m tall.

The endemic *N. hornei* (Sapotaceae) also grows from sea level to the highest montane forests. It is the commonest native tree in upland forests, especially in montane cloud forests. It is usually 10–12 m high but can reach 20 m (Friedmann 1994).

The non-native tree *F. moluccana* (Miquel) Barneby and Grimes (Leguminosae) (synonyms: *Albizia falcataria* (L.) Fosberg and *Paraserianthes falcataria* (L.) Nielsen) is common in the Seychelles from sea level to mid-altitude forests, especially on deeper soils in valleys (Kueffer and Vos 2004). However, it can also grow in poor and degraded soils both in the Seychelles and in other areas. It is native to the Moluccas, New Guinea, New Britain, and the Solomon Islands, but has become a problematic invader in the Seychelles and on many Pacific islands including those of Micronesia, French Polynesia and Hawaii (Hughes and Denslow 2005). It is a fast-growing, nitrogen-fixing tree that can achieve an annual height increment of 6 m and reach over 30 m.

Soil collection

Soil was collected from stands dominated by *C. verum*, *F. moluccana* or *N. hornei* (soil types) from a mid-altitude forest (Mare aux Cochons, an upland valley at 430 m above sea level) situated in the Morne Seychellois National Park on the island of Mahé (4°S, 55°E, 154 km^2). The soils are ferrasols (FAO/ISRIC/ISSS 1998) with sandy A horizon (90% sand, 5% silt, 5% clay) and loamy B horizon (60% sand, 20% silt, 20% clay). Because of the long history of weathering (Braithwaite 1984), the soils in upland forests on Mahé are poor in most nutrients, especially phosphorus (Dobrovol'skiy 1986; Kueffer et al. 2008; Varley 1971). Mean annual precipitation is ca. 3,500 mm, with the highest rainfall occurring from November till March. The mean annual air temperature under a closed canopy is ca. 23°C, and the mean annual air humidity is close to 100%.

For each soil type, a soil sample was collected from three replicate stands at least 100 m apart, a stand being defined as a forest patch $>10 \times 10$ m^2 dominated by a single species. Each sample consisted of soil from the top 10 cm of the A horizon taken randomly at various points in each stand. The three replicate samples were then mixed to obtain one pooled sample per stand type and site.

Bioassay

The experiment was conducted in an open greenhouse ($12 \times 6 \times 3.20$ m, covered with green shading material of ca. 65% ambient light transmittance) at Sans Souci forestry station (380 m above sea level) on the eastern slope of Morne Seychellois. The microclimate in the greenhouse was similar to forest conditions, with a highest temperature of ca. 32°C and a minimum relative humidity of ca. 75% around noon on a sunny day.

Seed of *C. verum* was collected from ripe fruits from ca. 50 trees widely scattered in the Mare aux Cochons area, and sown immediately into trays filled with local forest soil. After 2 months seedlings were randomly selected and transplanted into 1-l pots filled with soil from the three different soil types (*C. verum* CIN, *F. moluccana* FAL, *N. hornei* NOR). The five nutrient treatments (with number of replicate pots) were: Control (6 pots), +N (6), +P (6), +NP (4) and +All nutrients (4). This yielded 26 pots per soil type, and 78 pots in total. Plants were watered every second day as necessary, and the position of the pots was randomized every week.

Based on the biomass of 6 months old *C. verum* seedlings (3.25 g dry mass, Schumacher et al. 2009) and on conversion factors of 40 mg g^{-1} for N and 8 mg g^{-1} for P, a total 140 mg N (as NH_4NO_3) and/or 30 mg P (as NaH_2PO_4) were applied. The complete fertilizer (+All) treatment consisted of 1.4 ml of an all-in-one garden fertilizer (Wuxal, Maag Agro, Dielsdorf, Switzerland) containing 140 mg N, 61 mg P, and 74 mg K per plant, and trace amounts of B, Cu, Fe, Mn, Mo, Zn and vitamin B$_1$. Pots were fertilized weekly, with the amounts of nutrients being gradually increased to allow for plant growth (final additions were five times initial additions, i.e. N: 1.9–9.4 mg per week, P: 0.4–2 mg per week, Wuxal: 0.02–0.09 ml per week).

After 6 months (June–November 2004) the height and number of leaves per plant were measured. Plants were then harvested and both the fresh and dry weights of the leaves, stem and roots were recorded (drying at 55°C for 96 h). Three plants were lost during the experiment.

Data analyses

I used a two-way ANOVA model with nutrient treatment (control, +N, +P, +NP, +All), and soil type (CIN, FAL, NOR) as fixed factors to test for effects on total biomass at the end of the experiment. The response variable was log-transformed to remove heteroscedasticity. Using different response variables to calculate relative growth rate (aboveground biomass, stem height, number of leaves, total leaf area, or root dry mass) yielded very similar results, these further analyses are therefore not shown. Statistical analyses were performed with JMP V7.0.1 (SAS Institute Inc.).

Results

The total biomass of the *C. verum* seedlings at the end of the experiment was significantly affected by nutrient treatment ($P < 0.001$, $df = 4$, $F = 23.7$), soil type ($P < 0.001$, $df = 2$, $F = 14.5$), and nutrient treatment × soil type ($P < 0.03$, $df = 8$, $F = 2.4$). Across all nutrient treatments, growth was significantly higher in FAL soils than CIN and NOR soils, which did not differ (Tukey test, $P < 0.05$). Across soil types, the following significant nutrient treatment effects were found: control^{ab}, +N^{a}, +P^{c}, +NP^{bc}, +All^{d} (treatments with different superscripts differed [Tukey test, $P < 0.05$]).

The response of seedlings to nutrient treatments varied among soil types (Fig. 1). In NOR and CIN soils, only the +All treatment increased seedling growth compared to the control, while in FAL soils growth was also increased by the +P and +NP treatments. In the control treatment, mean seedling biomass was ca. 40% higher in soil from stands of the two invasive species than in soil from the native species (CIN 2.0 g, FAL 1.9 g, NOR 1.4 g). However, there was a much greater contrast between the soils of invasive and native trees in the relevant nutrient addition treatments, +All in the case of CIN, and +P, +NP and +All in the case of FAL (Fig. 1). This effect was particularly pronounced in the +All treatment, with seedlings being 80% larger in CIN soil and 235% larger in FAL soil, in both cases compared with NOR soil (CIN 5.6 g, FAL 7.3 g, NOR 3.1 g).

Discussion

In the control nutrient treatment, biomass production of seedlings was not markedly increased on the soils from stands of the two invasive trees *C. verum* and *F. moluccana* compared to soils from stands of the dominant native tree *N. hornei*. These results contradict the first hypothesis—that *C. verum* leads to enhanced seedling growth through an impact on soil properties, but confirm the second—that the

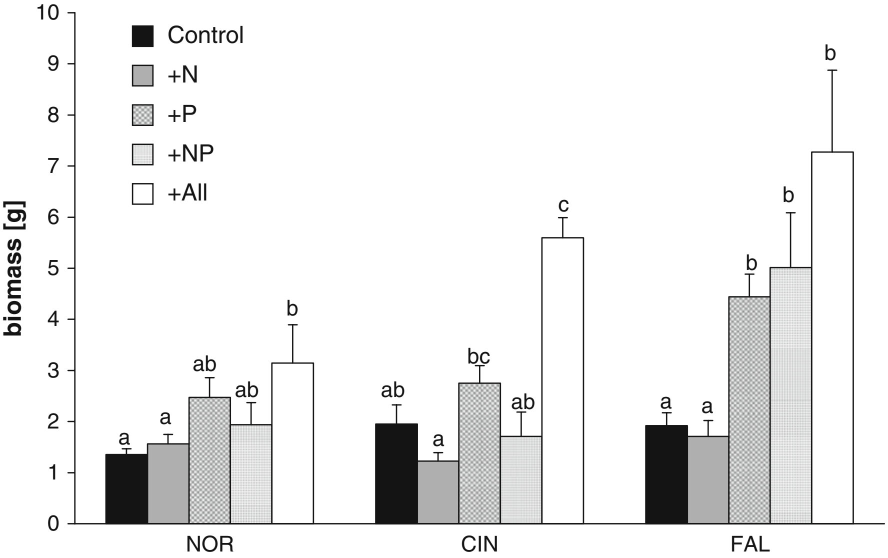

Fig. 1 Bioassay experiment with *Cinnamomum verum* seedlings grown on three different soil types (*NOR Northea hornei*, *CIN Cinnamomum verum*, *FAL Falcataria moluccana*). Mean (+SE) of total biomass at the end of the experiment is shown. Differences among nutrient treatments were tested with a Tukey test ($P < 0.05$). The same letter indicates that there is no significant difference between nutrient treatments within the respective soil type. Nutrient treatments were as follows: control, and nitrogen (+N), phosphorus (+P), N and P (+NP), and complete fertilizer (+All) addition

nitrogen-fixing tree *F. moluccana* does not facilitate growth on phosphorus-poor soils. This latter result is in contrast to what has been found in other tropical forests on nitrogen-limited sites (Adler et al. 1998; Hughes and Denslow 2005).

There are two main explanations for the lack of a soil-feedback on seedling growth. First, any increase in soil fertility under invasive compared to native trees may be smaller on the phosphorus-poor soils of the Seychelles than on nitrogen-limited sites elsewhere. Previous work indicates that phosphorus availability does increase somewhat under *C. verum*, but may actually decrease under *F. moluccana* (Kueffer et al. 2008). Indeed, I am unaware of any study from a very nutrient-poor site showing a major increase in phosphorus availability as a result of a plant invasion. This could be because the species that are able to invade such sites exhibit a resource-conserving growth strategy similar to that of the native flora (Funk and Vitousek 2007; Kueffer 2006; Schumacher et al. 2009), and therefore do not greatly accelerate nutrient cycling (Kueffer et al. 2008).

Second, invasive trees seem to increase the availability of either N (in the case of *F. moluccana*) or P (in the case of *C. verum*), but not both (Kueffer et al. 2008). However, on the highly weathered soils of the Seychelles, several nutrients including N, P and K are in very short supply, and only some of the potentially limiting nutrients may be affected by a particular invasive tree. In the bioassay experiment, therefore, increased growth compared to *N. hornei* could only be observed after P fertilization in the case of *F. moluccana*, or addition of a complete fertilizer in the case of *C. verum* (Fig. 1). Besides direct effects on soil nutrient availability, impacts on soil biota have been shown to be involved in soil-feedbacks on plant growth (Ehrenfeld et al. 2005), and differences in biotic processes may also be implicated in the faster seedling growth in soils from invasive tree compared to *N. hornei* stands after complete fertilizer addition. An indication that N, P and K availabilities are indeed very low in the upland forests of the Seychelles is also provided by data on litter nutrient concentrations (Kueffer et al. 2008): the N (5.0 mg g^{-1}) and P (0.22 mg g^{-1}) contents of leaf litter of *N. hornei* were similar to those of an ecologically similar tree, *Metrosideros polymorpha*, on the oldest, P-limited sites in Hawaii (N: 3.7 mg g^{-1}, P: 0.22 mg g^{-1}) (Vitousek 2004); and the litter K content of *N. hornei* (0.26 mg g^{-1}) was only about 50% of the lowest values found for *M. polymorpha* in Hawaii (0.51 mg g^{-1}) (Hobbie and Vitousek 2000). These well-studied soils in Hawaii are considered to represent some of the most nutrient-poor soils in the world (Vitousek 2004).

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

In conclusion, it appears that on these very nutrient-poor soils, low supplies of nutrients other than N reduce the potential of invasive trees to increase soil fertility for seedling growth. In contrast to N, invasive plants seem to have a lower potential to increase availabilities of P or K. Further, multiple nutrients may co-limit plant growth, and as long as invasive plant species cannot increase the availabilities of all limiting nutrients simultaneously, seedlings growth will not be enhanced. The situation may change if the forests were invaded by an invasive plant with the ability to increase nutrients other than N, or if this were to happen through anthropogenic disturbance. In such a case, early-successional invasive species would profit compared to the majority of the native species, as has been shown by a separate experiment with different nutrient treatments (Schumacher et al. 2009). This study indicates that very old and highly weathered soils may face a reduced risk of a soil-feedback on seedling regeneration by an invasive tree, but more research is clearly need to study the effect of invasive plants on nutrients other than nitrogen (cf. Ehrenfeld 2003).

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