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Plant–soil feedback induces shifts in biomass allocation in the invasive plant *Chromolaena odorata*

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Summary

1. Soil communities and their interactions with plants may play a major role in determining the success of invasive species. However, rigorous investigations of this idea using cross-continental comparisons, including native and invasive plant populations, are still scarce.

2. We investigated if interactions with the soil community affect the growth and biomass allocation of the (sub)tropical invasive shrub *Chromolaena odorata*. We performed a cross-continental comparison with both native and non-native-range soil and native and non-native-range plant populations in two glasshouse experiments.

3. Results are interpreted in the light of three prominent hypotheses that explain the dominance of invasive plants in the non-native range: the enemy release hypothesis, the evolution of increased competitive ability hypothesis and the accumulation of local pathogens hypothesis.

4. Our results show that *C. odorata* performed significantly better when grown in soil pre-cultured by a plant species other than *C. odorata*. Soil communities from the native and non-native ranges did not differ in their effect on *C. odorata* performance. However, soil origin had a significant effect on plant allocation responses.

5. Non-native *C. odorata* plants increased relative allocation to stem biomass and height growth when confronted with soil communities from the non-native range. This is a plastic response that may allow species to be more successful when competing for light. This response differed between native and non-native-range populations, suggesting that selection may have taken place during the process of invasion. Whether this plastic response to soil organisms will indeed select for increased competitive ability needs further study.

6. The native grass *Panicum maximum* did not perform worse when grown in soil pre-cultured by *C. odorata*. Therefore, our results did not support the accumulation of local pathogens hypothesis.

7. *Synthesis*. Non-native *C. odorata* did not show release from soil-borne enemies compared to its native range. However, non-native plants responded to soil biota from the non-native range by enhanced allocation in stem biomass and height growth. This response can affect the competitive balance between native and invasive species. The evolutionary potential of this soil biota-induced change in plant biomass allocation needs further study.

Key-words: accumulation of local pathogens, biological invasions, biomass allocation, *Chromolaena odorata*, enemy release, evolution of increased competitive ability, *Panicum maximum*, plant–soil interactions

Introduction

Invasive plants are a threat to natural and semi-natural ecosystems world-wide and invasions are taking place at an unprecedented rate (Elton 1958; Vitousek *et al.* 1997; Mack *et al.* 2000). Several hypotheses have been formulated to test mechanisms that might explain plant invasions. When invaders are assisted by humans to cross natural dispersal barriers they can become released from control by their natural enemies, a process known as enemy release (ER) (Keane & Crawley 2002). Pathogens in a new range may lead to natural selection for genotypes with less allocation to defence and increased allocation to growth and reproduction, leading to evolution of increased competitive ability (EICA) (Blossey & Nötzold

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1995). Also, invasive species may indirectly facilitate their own performance in the non-native range by accumulating soil organisms that are adverse to native plant species, a hypothesis known as accumulation of local pathogens (ALP) (Eppinga *et al.* 2006). Here, we consider an invasive plant species from these three perspectives in relation to interactions with soil biota.

Soil biota may play an important role in the regulation of plant diversity (Van der Putten 2003; Van der Heijden, Bardgett & Van Straalen 2008). They can influence succession, plant abundance, plant competition and plant community composition (Van der Putten, Van Dijk & Peters 1993; Bever 1994; Van der Putten & Peters 1997; Klironomos 2002; De Deyn, Raaijmakers & Van der Putten 2004; Kardol, Bezemer & Van der Putten 2006). The interactions between plants and their associated soil communities can, therefore, result in dynamic feedback where plants influence soil organisms and soil organisms in return influence plants (Bever, Westover & Antonovics 1997; Wardle *et al.* 2004). The outcome of these interactions can range from negative to neutral or positive. Interactions are considered negative when the net effects of all soil pathogens, root herbivores, symbiotic mutualists and decomposers reduce plant performance, whereas interactions are considered positive when the benefits brought about by symbionts and decomposers overwhelm the negative effects of soil pathogens and root herbivores and enhance plant performance (Bever, Westover & Antonovics 1997; Wardle *et al.* 2004). Negative interactions enhance plant community diversity by exerting density-dependent control (Packer & Clay 2000; Klironomos 2002; Reinhart *et al.* 2003) and speed up successional replacement (Van der Putten, Van Dijk & Peters 1993). The rate at which plants promote soil-borne pathogens differs among species (Van der Putten, Van Dijk & Peters 1993; Klironomos 2002), functional groups (Kardol *et al.* 2007) and successional position (Kardol, Bezemer & Van der Putten 2006).

In the native range of plants, specialized pathogenic soil organisms often dominate the net effects of plant–soil interactions, resulting in negative effects on plant performance (Kulmatiski *et al.* 2008; Petermann *et al.* 2008). In the non-native range where the natural soil-borne enemies are absent, interactions with non-specialized mutualistic soil biota may positively influence plant performance (Klironomos 2002; Reinhart *et al.* 2003; Callaway *et al.* 2004; Van Grunsven *et al.* 2007). The enemy release hypothesis states that when exotic plants experience a decrease in regulation by their specialist enemies, the abundance of these plant species in their novel range will increase rapidly, as they are able to profit from a reduction in enemy regulation, resulting in increased population growth (Keane & Crawley 2002). Traditionally, studies on enemy release and exotic plants have focused mostly on (specialized) insect herbivores. However, recent studies have found support for the enemy release hypothesis with respect to soil-borne enemies of plants (Beckstead & Parker 2003; Reinhart *et al.* 2003; Callaway *et al.* 2004; Knevel *et al.* 2004; Reinhart & Callaway 2004; Van der Putten *et al.* 2007; Van Grunsven *et al.* 2007).

According to the EICA hypothesis, exotic invasive plants benefit from the absence of enemies in their non-native range through less need for defence, which selects for genotypes with greater allocation of resources to growth and reproduction (Blossey & Nötzold 1995). These genotypes would then have a competitive advantage over the native vegetation. This hypothesis stems from the observation that plants often grow bigger and more vigorous in their non-native than in their native range (Leger & Rice 2003; Jakobs, Weber & Edwards 2004). Tests of the EICA hypothesis have yielded mixed results (Siemann & Rogers 2003; Van Kleunen & Schmid 2003; Bossdorf *et al.* 2005), and the majority of studies have focused only on plant size and fecundity as a proxy for competitive ability and fitness (Willis, Memmott & Forrester 2000; Siemann & Rogers 2003; Van Kleunen & Schmid 2003; Vila, Gomez & Maron 2003; Bossdorf *et al.* 2004; Jakobs, Weber & Edwards 2004). However, shifts in biomass allocation patterns may also create a competitive advantage for the introduced species. This may lead to, for example, enhanced shade tolerance by increasing specific leaf area (SLA), increased allocation to structures that promote plant height, enhanced photosynthetic capacity by increasing leaf mass per unit area or enhanced water-use capacity by increasing allocation to root tissue (Schlichting 1986; Pattison, Goldstein & Ares 1998; Grotkopp, Rejmanek & Rost 2002; DeWalt, Denslow & Hamrick 2004; Feng, Wang & Sang 2007; Morrison & Mauck 2007; Meyer & Hull-Sanders 2008). Alternative to increasing competitive ability, evolution might as well reduce competitive ability if a species experiences less competition in the non-native range and if competitive ability involves traits with a fitness cost attached to them. This is core to the evolution of reduced competitive ability hypothesis; reduced competitive ability can be beneficial for invasive species that mainly have intraspecific competitive interactions (Bossdorf *et al.* 2004). These hypotheses have not yet been tested in conjunction with release from soil-borne pathogens, although shifts in allocation patterns are known to be triggered by changes in the soil community (D'Hertefeldt & Van der Putten 1998; Bourne *et al.* 2008).

Several reports have shown that exotic plants can cultivate a soil community that is beneficial to their own growth (Klironomos 2002; Reinhart *et al.* 2003; Reinhart & Callaway 2004). This will contribute to the escape of exotic plants from density-dependent control (Bever 2003) and, consequently, may result in dense monospecific stands in the non-native range. This is certainly not the only soil-borne influence on plant invasiveness, as exotic plants may, for example, disrupt mycorrhizal communities (Stinson *et al.* 2006) and alter decomposition (Kourtev, Ehrenfeld & Haggblom 2003) in the non-native range. Alternatively, exotic invasive plants may enhance the abundance of local soil pathogen communities, thereby indirectly outcompeting native plants, a phenomenon described in the ALP hypothesis (Eppinga *et al.* 2006). ALP has been found for *Chromolaena odorata* and *Ageratina adenophora* in Asia (Niu *et al.* 2007; Mangla, Inderjit & Callaway 2008). A preferable approach to studying plant invasions is to compare the performance of the invasive plant in native and

non-native soils (Hierro, Maron & Callaway 2005). Few studies have examined plant performance in relation to native and non-native soil communities within the same experimental set-up (Reinhart *et al*. 2003; Callaway *et al*. 2004; Knevel *et al*. 2004). So far, no study has examined how interactions with the soil community may influence biomass allocation patterns in native and non-native ranges. Our new contribution is that we compared effects of soil communities on plant performance in both native and non-native-range soil using both native and non-native plant populations.

In the present study, we investigate whether dynamic interactions between plants and their soil community affect growth and biomass allocation of the (sub)tropical invasive shrub *Chromolaena odorata* (L.) King & Robinson (Asteraceae, Eupatorieae). *Chromolaena odorata* originates from South and Central America and is a major threat to the biodiversity and functioning of a wide variety of ecosystems, ranging from tropical rain forests to savannas (McFadyen & Skarratt 1996; Kriticos, Yonow & McFadyen 2005; Raimundo *et al*. 2007). *Chromolaena odorata* is a perennial semi-lignified shrub forming tangled bushes 1.5–2 m in height and reaching up to 6 m as a climber on other plants. The species can reproduce apomictically (Gautier 1992) and has a prolific seed production of light, wind-dispersed seeds. A single shrub can produce as many as 800 000 seeds (Witkowski & Wilson 2001). *Chromolaena odorata* forms dense monospecific stands along river courses and forest margins, thereby outshading most native vegetation and denying humans and animals access to invaded areas (Goodall & Erasmus 1996). The invasive success of *C. odorata* is thought to depend upon the combination of its high reproductive capacity, high relative growth rate and net assimilation rate (Ramakrishnan & Vitousek 1989) and its capacity to suppress native vegetation through light competition (Kushwaha, Ramakrishnan & Tripathi 1981; Honu & Dang 2000). In its native range *C. odorata* is controlled by a large number of insects and pathogens, both specialists and generalists (Cruttwell McFadyen 1988; Barreto & Evans 1994). In its non-native ranges, however, only a few phytophagous insects feed on *C. odorata* (Kluge & Caldwell 1992). Many specialist insect herbivores that attack leaves, stems and seeds have been tested for potential inclusion in biocontrol programmes (Kluge 1991; Barreto & Evans 1994; Zachariades, Strathie-Korrubel & Kluge 1999; Muniappan, Reddy & Po-Yung Lai 2005). Very little is known, however, about potential biocontrol by soil-borne pathogens.

We performed a cross-continental comparison with native and non-native-range soils and native and non-native-range *C. odorata* populations. In two glasshouse experiments, one with fresh field soil and one with conditioned soil, we determined biomass production and allocation responses to native and non-native-range soils in order to test the enemy release hypothesis. We also determined the allocation patterns of the native and non-native-range *C. odorata* populations in soils from the native and non-native ranges in order to test for indications of EICA. In the second experiment a native co-occurring grass, *Panicum maximum* Jacq., was added to test the ALP hypothesis.

Materials and methods

SEED AND SOIL COLLECTION

We collected *C. odorata* soil and seeds from three different sites in the plant's non-native range in Hluhluwe–iMfolozi game reserve, South Africa (28°4′18.52′ S, 32°2′23.74′ E) in November 2004 and from three different sites in its native range in northern Puerto Rico (18°24′40.95′ N, 66°34′39.74′ W) in February 2005. The closest sites were at least 10 km apart; therefore plants from the different sites were regarded as different populations. We specifically choose Puerto Rico to sample *C. odorata* populations as previous work has shown that South African *C. odorata* is likely to have originated from the Northern Caribbean (Von Senger, Barker & Zachariades 2002; Zachariades, Von Senger & Barker 2004). Within each site three replicate soil samples of 1.5–2 kg were collected from the rhizosphere of *C. odorata* shrubs by randomly selecting three shrubs of *c*. 1.5 m height. Soil was collected by digging up each shrub and carefully collecting all soil that remained connected to the root system. These soil samples from the same plant species (conspecific soils) were pooled per site. Seeds were collected from several separate plants and pooled per site as well. We used the same soil sampling procedure to collect rhizosphere soil from grass tussocks *c*. 20 m away from each *C. odorata* shrub sampled. The grass tussocks had a finer root structure, but the roots occurred in the same soil layer as *C. odorata* roots. These soil samples (called heterospecific soils as they were from a different plant species) were combined per site as well. The most abundant grass species in these tussocks in both ranges was *P. maximum*. This grass species can grow up to 2 m tall and is native to South Africa while invading large parts of South and Central America. *Panicum maximum* seeds were obtained commercially from McDonalds Seeds, Pietermaritzburg, South Africa. We included *P. maximum* in the present study, as it is an important competitor for *C. odorata* in South Africa (M. te Beest, unpublished data). Also, as *P. maximum* co-occurred with *C. odorata* in both ranges it could be used to pre-culture heterospecific soils (i.e. soils pre-cultured with a species other than *C. odorata*) of both native and non-native ranges in experiment 2. It is not known which herbivores and pathogens control this species in its native range.

EXPERIMENT 1

To test whether native and non-native-range soils have different effects on growth and biomass allocation of native and non-native *C. odorata* we performed a glasshouse experiment with an inoculum of fresh field soil. The experiment was performed at the Biological Centre in Haren, the Netherlands. In experiment 1, we grew *C. odorata* plants from both the native and non-native ranges in 1500-mL pots with 1250 g of field soil (based on dry wt.) that we obtained locally and that had been sterilized by γ-irradiation (40 kGy). Soil was then inoculated with 250 g of either sterilized or non-sterilized inoculum. We used inocula originating from the native as well as the non-native ranges, collected from conspecific (*C. odorata*) or heterospecific (grass) rhizospheres. We used *C. odorata* seeds from one site in the native range and one site in the non-native range. Seeds were germinated in plastic containers on sterile glass beads in a glasshouse (14/10 h light/dark at 22/16 °C) and then transplanted into the pots, one plant per pot.

The experiment was set-up as a randomized block design. Soils from the three sites per range were kept separate as replications within a block and each block was replicated three times, totalling 144 pots:

2 soil origins (native versus non-native) × 3 sites per range × 2 soil sources (conspecific versus heterospecific) × 2 plant origins (native versus non-native) × 2 sterilizations × 3 replicates. To account for differences in light and temperature within the glasshouse the position of each block was changed every week. Moisture levels were kept constant at 30% (w/w) by weighing and watering twice a week, and pots were covered with tin foil to reduce evaporation. In order to prevent nutrient limitation, pots were supplied with full-strength Hoagland solution once a week (Hewitt 1967), starting 2 weeks after planting to avoid salt stress (Olff *et al.* 2000). To meet increasing plant requirements, the amount of Hoagland solution was increased at 2-week intervals from 12.5 to 17.5 mL and eventually 30 mL and then remained constant until the end of the experiment.

We measured height and number of leaves per internode once per week. After 10 weeks, when the soil volume was well colonized, the plants were harvested. Leaves, stems and roots were separated. Roots were washed and all plant parts were dried at 70 °C for 48 h and weighed. Photographs of all fresh leaves of each plant were taken to determine leaf area and analysed using the program Sigmascan Pro 5.0 (SPSS Inc., Chicago, IL, USA). SLA was calculated by dividing the leaf area by the dry weight of the leaves. In order to measure differences in allocation between plants, leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR) were calculated by dividing the biomass of each plant part by the total biomass.

EXPERIMENT 2

To test for effects of native and non-native soil communities on growth and biomass allocation of native and non-native *C. odorata* we conditioned soil from experiment 1 to set-up experiment 2. For logistic reasons we combined the soils from the different sampling sites per range. Next, we cultured the native and non-native soil with either a conspecific (*C. odorata*) or a heterospecific (*P. maximum*) plant, resulting in four soil treatments: native range/conspecific, native range/heterospecific, non-native range/conspecific and non-native range/heterospecific. All treatments were replicated six times. Experiment 2 had four stages. We first cultured the soil by growing the same plant species three times in succession (stages 1–3), using one plant per pot. Plants were harvested after 10 weeks, when the soil volume was colonized by roots. Then, a new plant was planted in the same soil. Native and non-native conspecific soils were planted with native and non-native *C. odorata* respectively. Native and non-native heterospecific soils were planted with *P. maximum*. At the end of the second stage, colonization of roots by arbuscular mycorrhizal fungi was measured under a dissecting microscope using the gridline intersect method (Giovannetti & Mosse 1980). In stage 4, we sterilized half of the pre-cultured soil by autoclaving for 3 h at 120 °C. We planted each of the plant populations and species (non-native-range *C. odorata*, native-range *C. odorata* and *P. maximum*) on each of the soil treatments, while keeping the six replicates separate, totalling 144 pots (2 soil origins (native versus non-native) × 2 soil pre-culture treatments (conspecific versus heterospecific) × 3 plant populations/species × 2 sterilizations × 6 replicates). The replicates were kept separate throughout the four stages of the experiment. The experimental procedure was the same as for experiment 1, except that we filled the 1500-mL pots with 1200 g of the local sterilized field soil, which we then inoculated with 300 g of sterilized or non-sterilized pre-cultured inoculum. Also, we used much lower nutrient levels to avoid negative effects on the soil community; for example, nutrient supply might suppress root infection by arbuscular mycorrhizal fungi. During stages 1, 2 and 3 of the experiment, pots were supplied with 15 mL of 25% Hoagland solution once every 2 weeks. In stage 4, we applied 20 mL full-strength Hoagland only once, in the fifth week of the experiment, to avoid side effects of the nutrients. Furthermore, we separated above-ground biomass into primary (main stem and leaves directly attached to it) and secondary (stems branching off the main stem and leaves attached to these) biomass and did not calculate SLA.

DATA ANALYSIS

Experiment 1 was analysed for the overall effects of soil biota on growth and allocation of both *C. odorata* populations using a mixed-effects model ANOVA with a split-plot design in R (R Development Core Team 2008), as we collected the soil in a nested design on different scales, from continent to site to rhizosphere. Therefore, the factor soil origin (native versus non-native) was treated as the highest level, nested herein were consecutively site, soil source (conspecific versus heterospecific), sterilization (sterile versus non-sterile soil), and plant origin (native versus non-native). Site was treated as a random factor. As all factor levels except site were both hierarchical and informative (fixed), a split-plot design was used rather then a nested design. We tested for differences among fixed-effect levels in total biomass; leaf, stem and root biomass; LWR, SWR, RWR; height; internode length; and SLA.

Experiment 2 was analysed for the same overall effect of soil biota on growth and allocation of both *C. odorata* populations using a mixed-effects model ANOVA with soil origin (native versus non-native), soil pre-culture treatment (conspecific versus heterospecific); sterilization (sterile versus non-sterile soil) and plant origin (native versus non-native) as fixed factors. Block was added as a random factor in the ANOVA model to reduce variability due to different planting cycles and positions in the glasshouse. We did not use a split-plot design here as we did not have hierarchical levels anymore in this design. To test for plant–soil interactions, we calculated inoculation effects as the proportional reduction in total biomass production by the inoculated (non-sterilized) soil community: (total biomass non-sterilized soil − total biomass sterilized soil)/total biomass sterilized soil (Van Grunsven *et al.* 2007). We analysed the data for both *C. odorata* populations with a three-way ANOVA using soil origin (native versus non-native), pre-culture treatment (conspecific versus heterospecific) and plant origin (native versus non-native) as fixed effects. To test for ALP, we calculated inoculation effects for *P. maximum* and compared them to non-native- range *C. odorata* for non-native-range soil only using a two-way ANOVA with pre-culture treatment (conspecific versus heterospecific) and species (*C. odorata* versus *P. maximum*) as fixed effects. We excluded the data from four pots in which the plants died. Mycorrhizal colonization was tested with a two-way ANOVA with range (native versus non-native) and species (*C. odorata* versus *P. maximum*) as fixed effects. Analyses for experiment 2 were carried out using SPSS 14.0.0 (SPSS Inc.).

Results

EFFECTS OF SOIL TREATMENTS ON GROWTH AND ALLOCATION PATTERNS OF *C. ODORATA*

Experiment 1

Biomass of native and non-native *C. odorata* plants did not increase when grown in non-native-range soil, contrary to

predictions based on the enemy release hypothesis. However, we observed significant shifts in biomass allocation patterns as a response to the soil treatments. Non-native-range *C. odorata* responded to soil biota from the non-native range by investing significantly more in stem biomass, both in terms of relative and absolute stem biomass (Soil Origin × Plant Origin: SWR: $F_{1,16} = 7.94$, $P = 0.01$, Fig. 1A; stem biomass: $F_{1,16} = 11.3$, $P < 0.01$). Stem biomass of non-native *C. odorata* plants increased by two-thirds and relative allocation to the stems by a quarter when plants were grown in non-native-range soil relative to native-range soil. The investment in stem biomass of non-native *C. odorata* plants was highest in non-native-range conspecific soils, with more than a third of the total biomass allocated to stems (Soil Origin × Soil Source × Plant Origin, SWR: $F_{1,16} = 5.73$, $P = 0.03$). Interestingly, this higher investment in stem biomass did not occur in *C. odorata* plants grown from seeds originating from the native range (Fig. 1A). Stem allocation in non-native *C. odorata* showed a trade-off with root allocation (RWR), which was more than 25% lower in conspecific soils from the non-native range (Soil Origin × Soil Source, RWR: $F_{1,4} = 14.2$, $P = 0.02$, Fig. 1B). About half of the total biomass was allocated to leaves. Leaf allocation did not respond to soil range, but was 5% higher in conspecific soils relative to heterospecific soils ($F_{1,4} = 13.08$, $P = 0.02$).

The effect of soil sterilization on plant performance was consistent for both *C. odorata* populations. Total biomass increased by almost 30% in sterilized soils relative to non-sterilized soils (total biomass: $F_{1,8} = 22.8$, $P = 0.001$), suggesting a net negative effect of soil biota for both the native and non-native ranges. Again opposite to the enemy release hypothesis, the effect of sterilization was most pronounced in non-native-range soils, where biomass increased by almost 50% (Soil Origin × Sterilization, Total Biomass: $F_{1,8} = 9.94$, $P = 0.01$). In sterilized soils almost 20% more biomass was allocated to roots relative to non-sterile soils (RWR: $F_{1,8} = 5.87$, $P = 0.04$), at the expense of leaf biomass (LWR: $F_{1,8} = 6.85$, $P = 0.03$). Stem allocation (SWR) did not respond to sterilization. We did not find significant changes in SLA in response to the soil and sterilization treatments.

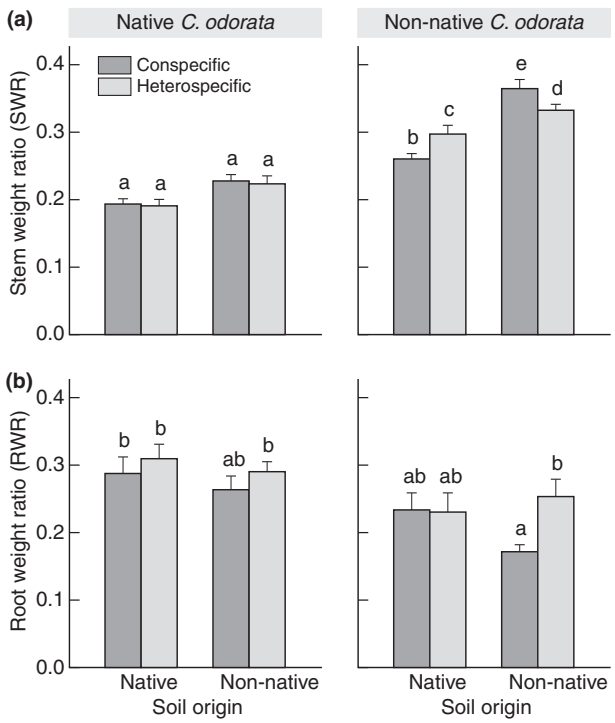

Fig. 1. Experiment 1. Relative biomass allocation to stem (a) and root (b), expressed as the ratio stem : total weight (SWR) and root; total weight (RWR). The data presented are based on populations of *Chromolaena odorata* originating from the native (left) and non-native (right) ranges. All plants were grown in soil from the native and non-native range (as indicated on the *x*-axis). The soil was collected from rhizospheres of conspecific (dark bars) or heterospecific (light bars) plant species. Mean values (± SE) are shown. Different letters denote significant differences in *post hoc* tests after one-way ANOVA.

Experiment 2

Experiment 2 showed the same growth and allocation patterns of *C. odorata* as found in experiment 1. Soil treatments did not affect total biomass, but stem allocation increased with by 10% at the expense of root allocation in non-native-range soil relative to native-range soil (SWR: $F_{1,5} = 22.1$, $P < 0.01$; RWR: $F_{1,5} = 22.6$, $P < 0.01$), while leaf allocation did not significantly respond to soil treatments. Allocation to root mass was again lowest in conspecific pre-cultured soils (soil pre-culture treatment, RWR: $F_{1,5} = 14.3$, $P < 0.01$). Interestingly, in this experiment there were no significant interactions between soil treatments and plant origin. The effects of soil sterilization were similar to experiment 1 as well. Overall, total biomass increased by almost 20% due to sterilization ($F_{1,5} = 6.05$, $P = 0.057$) and sterilization effects were most pronounced in the roots, with a 20% increase in root allocation (root biomass: $F_{1,5} = 28.3$, $P < 0.01$; RWR: $F_{1,5} = 38.6$, $P < 0.01$) at the expense of investment in leaves (LWR: $F_{1,5} = 32.6$, $P < 0.01$), while stem allocation did not respond to sterilization.

To test if interactions with the soil community affect performance of *C. odorata* we calculated inoculation effects. Figure 2 shows the effect of inoculation with pre-cultured soil on biomass of *C. odorata*. We did not find a difference in inoculation effects between native and non-native-range soils ($F_{1,36} = 0.12$, $P = 0.73$), providing no evidence for the enemy release hypothesis. However, there was a difference in response to soil inoculation between native and non-native-range populations of *C. odorata*. Non-native *C. odorata* had significantly more biomass when grown in soil that was inoculated with soil pre-cultured by *P. maximum*, irrespective of the range where the soil originated from (pre-culture treatment: $F_{1,36} = 15.0$, $P < 0.001$; plant origin: $F_{1,36} = 10.0$, $P < 0.01$; Pre-culture Treatment × Plant Origin: $F_{1,36} = 3.55$, $P = 0.07$). Interestingly, native *C. odorata* did not show positive inoculation effects, although plants in non-native-range soil had relatively more biomass when the soil was pre-cultured with *P. maximum* rather then with *C. odorata*. This result indicates an

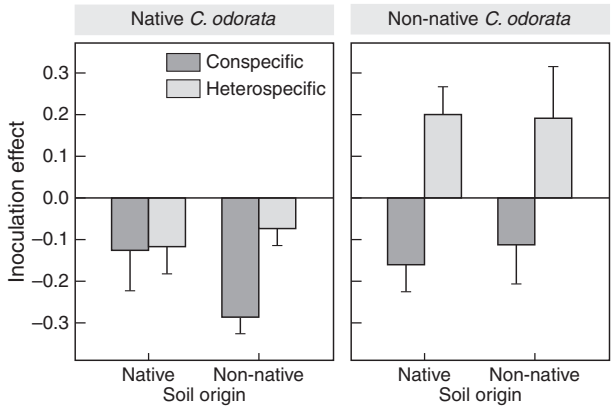

Fig. 2. Experiment 2. Inoculation effects of *Chromolaena odorata* from native (left panel) and non-native (right panel) ranges. All plants were grown in soil from the native (Puerto Rico) and non-native range (South Africa), as indicated on the *x*-axis. Soil was pre-cultured with conspecific (dark bars) or heterospecific (light bars) plants. Mean values (+SE) are shown. Negative values indicate reduced plant performance; positive values indicate increased plant performance. Soil inoculation effects were calculated as the change in total biomass relative to sterile soil from the same soil treatment.

enemy release response in heterospecific soils from which non-native *C. odorata* is able to benefit most.

NATIVE VERSUS NON-NATIVE *C. ODORATA* POPULATIONS (EXPERIMENTS 1 AND 2)

When comparing native and non-native *C. odorata* populations to test the potential for EICA, both experiments showed the same patterns. Contrary to EICA predictions, total biomass did not differ between plants from native and non-native ranges ($F_{1,16} = 0.36$, $P = 0.56$; $F_{1,5} = 0.07$, $P = 0.80$, for experiments 1 and 2 respectively). However, in both experiments there were consistent differences in biomass allocation. Native-range-plants invested significantly more biomass into leaves (leaf biomass: $F_{1,16} = 15.8$, $P = 0.001$; $F_{1,5} = 22.7$, $P < 0.01$; LWR: $F_{1,16} = 7.89$, $P = 0.01$; $F_{1,5} = 21.4$, $P < 0.01$, for experiments 1 and 2 respectively) and secondary shoots ($F_{1,5} = 41.4$, $P = 0.001$, experiment 2), while non-native range plants invested significantly more biomass into stems and stem elongation (stem biomass: $F_{1,16} = 62.9$, $P < 0.001$; $F_{1,5} = 21.4$, $P < 0.01$; SWR: $F_{1,16} = 252$, $P < 0.001$; $F_{1,5} = 292$, $P < 0.001$; height: $F_{1,16} = 27.4$, $P < 0.001$; $F_{1,5} = 23.8$, $P < 0.01$; internode length: $F_{1,16} = 57.8$, $P < 0.001$, $F_{1,5} = 17.6$, $P < 0.01$, for experiments 1 and 2 respectively). As a result, native-range plants were shorter and more densely branched, whereas non-native-range plants were taller and more erect. Moreover, the increased stem allocation of non-native *C. odorata* when grown in non-native-range soils further amplified these differences in growth form (Fig. 1A). Interestingly, in experiment 2, we found that non-native *C. odorata* plants performed better when grown in soils pre-cultured with the heterospecific grass *P. maximum* as compared to soil pre-cultured with conspecifics (Fig. 2). This could be indicative of enemy release in heterospecific soils. We did not find significant changes in SLA between the two *C. odorata* populations.

ACCUMULATION OF LOCAL PATHOGENS (EXPERIMENT 2)

Based on the ALP hypothesis we expected growth of *P. maximum* to be negatively affected when grown in soil pre-cultured with non-native *C. odorata* plants. Interestingly, we did not observe this, but found the opposite pattern. *Panicum maximum* performed better when grown in soil that was pre-cultured with non-native *C. odorata* (Fig. 3). For *C. odorata* we found the same pattern, as it performed better when grown in soil that was pre-cultured with *P. maximum* than with a conspecific (Species × Pre-culture Treatment: $F_{1,19} = 9.52$, $P < 0.01$). Hence, *C. odorata* does not hamper growth of the native species *P. maximum* in non-native South African soils.

Interestingly, root colonization by arbuscular mycorrhizal fungi significantly differed between ranges and between the two plant species. In South African soil non-native-range *C. odorata* plants had 35.1% (±1.44%) of their root length colonized with AMF, whereas in Puerto Rican soil native-range *C. odorata* had 61.3% (±4.81%) colonization. *Panicum maximum* roots had far lower colonization rates, 6.2% (±1.92%) vs. 15.8% (±0.11%) in South African versus Puerto Rican soils (range: $F_{1,4} = 89.7$, $P < 0.001$; species: $F_{1,4} = 385$, $P < 0.001$).

Discussion

Our experiments did not support the enemy release hypothesis that the high abundance of *C. odorata* in its non-native South

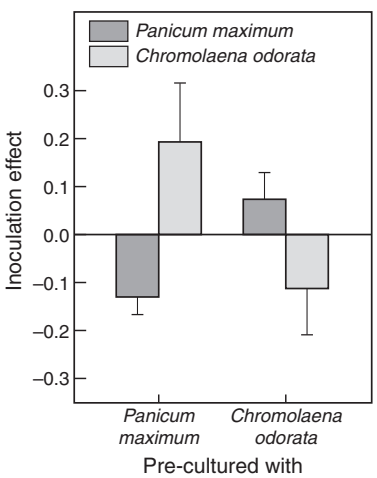

Fig. 3. Experiment 2. Inoculation effects of *Panicum maximum* (native, dark bars) and *Chromolaena odorata* (non-native, light bars). Data are shown for non-native range soils (South Africa). Plants were grown in soil pre-cultured with *Panicum maximum* or *Chromolaena odorata*, as indicated on the *x*-axis. Mean values (±SE) are shown. Negative values indicate reduced plant performance; positive values indicate increased plant performance. Soil inoculation effects were calculated as the change in total biomass relative to sterile soil from the same soil treatment.

African range is due to reduced negative effects from the soil community on plant performance. If *C. odorata* has escaped from native soil pathogens, it may have encountered novel pathogens in the non-native range (Beckstead & Parker 2003; Knevel *et al.* 2004). Alternatively, in the non-native range the mutualistic soil organisms may have a lower benefit to the plants than in the native range. We analysed root colonization by arbuscular mycorrhizal fungi and showed that plants from the non-native range had half the amount of root colonization compared to plants from the native range. Although root colonization is not necessarily indicative of mycorrhizal effectiveness, it could be that there is a lower arbuscular mycorrhizal benefit in the non-native range of *C. odorata*. A lower mycorrhizal benefit in combination with a lower pathogen pressure could still lead to a net negative effect of the soil community on plant performance. Therefore, enemy release cannot be completely excluded.

Interestingly, there were substantial shifts in biomass allocation in response to the soil biota. Non-native-range *C. odorata* plants had a greater allocation to stem biomass and height growth when confronted with soil communities from the non-native range, which is a well-described plastic response of plants that allows them to be more successful when competing for light (Valladares *et al.* 2000; Valladares 2007). Allocation responses have also been found when confronting clonal plants with arbuscular mycorrhizal fungi (Streitwolf-Engel *et al.* 1997) or soil pathogens (D'Hertefeldt & Van der Putten 1998). In *C. odorata*, these allocation effects might have a genetic component, as there was a difference between plants originating from native and non-native ranges and all plants were grown under equal conditions, presumed that there were no maternal effects (Bossdorf *et al.* 2005). Our results suggest that plants from the non-native range have responded to soil biota from that same range by investing more in traits, such as stem elongation, that allow these plants to be more successful in competing for light. Whether these traits are under selection in the non-native range cannot be concluded from this experiment.

Soil organism-driven allocation effects have been overlooked in the invasive plant literature thus far, as previous studies on responses of invasive species to the soil communities in their native and non-native ranges mostly have considered total biomass (Reinhart *et al.* 2003; Callaway *et al.* 2004; Reinhart & Callaway 2004). Although the differences in allocation patterns are no direct test of the EICA hypothesis, they point towards evolutionary changes that may play a role in the invasion of *C. odorata* in South Africa. Several studies have shown that shifts in allocation patterns other than increased size may promote a competitive advantage of the invasive species (Pattison, Goldstein & Ares 1998; Feng, Wang & Sang 2007; Morrison & Mauck 2007; Meyer & Hull-Sanders 2008). Therefore, interactions of *C. odorata* with soil biota from the non-native range may have lead to the selection of genotypes with a competitive advantage for light interception in mixed stands with native species. Light competition is extremely important in moist and nutrient-rich habitats along river courses and forest margins, where *C. odorata* occurs (Goodall & Erasmus 1996; Witkowski & Wilson 2001). Furthermore, being a heliophyte (Gautier 1992), *C. odorata* does not reproduce in shaded conditions (Witkowski & Wilson 2001). Interestingly, these soil organism-driven allocation patterns did not become expressed in the SLA.

Contrary to the ALP hypothesis, non-native-range *C. odorata* did not appear to accumulate local soil pathogens, as there was no detrimental effect of pre-culture with *C. odorata* on the co-occurring native grass species *P. maximum*. ALP has been suggested for *C. odorata* in Asia (Mangla, Inderjit & Callaway 2008), suggesting context dependence of this phenomenon. Differences in plant–soil interactions between similar species invading different novel ranges may occur more often (Levine, Adler & Yelenik 2004; Wolfe & Klironomos 2005). For example, the net effect of plant–soil interactions for the dune grass *Ammophila arenaria* varied from neutral to negative between soils from different non-native populations (Knevel *et al.* 2004). In soil from the non-native range of *C. odorata*, *P. maximum* shows increased biomass production in soils pre-cultured by *C. odorata*. This is in line with our personal field observations in South Africa that 2–3 months after clearing dense *C. odorata* stands, *P. maximum* successfully establishes and becomes the most abundant species.

Our results show that non-native *C. odorata* is not able to cultivate a soil community that has a net beneficial effect on its own growth, as was described in previous studies on invasive exotic plants (Klironomos 2002; Reinhart *et al.* 2003). However, *C. odorata* does increase its performance when grown in soil pre-cultured by *P. maximum*, which is native to the invaded range. We argue that this might be a valuable strategy for plants that reproduce prolifically and hence have little difficulty in dispersing to adjacent habitats. Interestingly, the positive effect of the heterospecific soil community will only aid *C. odorata* in the establishment phase. As soon as the species is established, it will start cultivating a soil community that negatively affects its growth. At that point in its life history other factors might promote its invasive behaviour, for example rapid growth rate, high SLA, prolific seed production and high sprouting ability (Kushwaha, Ramakrishnan & Tripathi 1981; Ramakrishnan & Vitousek 1989; Devendra, Chavan & Ramachandra Prasad 1998). The positive effect on plant performance in soil pre-cultured by *P. maximum* was strongest for plants from non-native *C. odorata* populations, which were overall experiencing a less negative interaction with the soil community than plants from the native range. This suggests that there may be selection operating on plants from the non-native range allowing the plants to better cope with their soil environment. Such selection may promote, for example, higher plasticity in allocating energy towards roots, as was detectable by comparing plants in non-native-range soil in con- and heterospecific soils. The mechanisms through which *C. odorata* interacts with the soil community are still to be clarified. Previous studies have shown that pyrrolizidine alkaloids are present in roots of *C. odorata* (Biller *et al.* 1994; Thoden 2007). These compounds are known to play a role in the defence against generalist herbivores (Joshi & Vrieling 2005; Macel *et al.* 2005). However, whether they play a role in herbivore defence in *C. odorata* as well requires further study.

Our data show that, in the case of *C. odorata*, soil biota from the native versus non-native range influenced plant biomass allocation between roots and stems, whereas soil biota of conspecific versus heterospecific rhizopheres influenced the direction of dynamic plant–soil interactions. These results suggest that there are two different processes that operate on different spatial and temporal scales (Bever 2003; Van der Putten 2003; Levine *et al.* 2006). On a large scale, when plants are transported between different continents, they encounter new soil communities with new below-ground interactions, which may change, or select for, allocation patterns and hence ecological strategy and performance. This process is most likely acting on a relatively long time scale, because most invasive species experience a lag phase between arrival and becoming dominant in their novel range. This is in line with enemy release- and EICA-type processes. On a local scale, however, dynamic plant–soil interactions become more important, leading to differences in soil communities between conspecific and heterospecific rhizospheres that have either positive, negative or neutral effects on the overall performance of invading plant species. These processes, like ALP, may act on a relatively short time scale and have been suggested as a possible mechanism promoting the invasion of exotic species (Reinhart *et al.* 2003; Reinhart & Callaway 2004; Eppinga *et al.* 2006).

Positive effects of the soil community on the plants alone is not enough for a species to become invasive in its new environment (Levine *et al.* 2006; Reinhart & Callaway 2006). However, positive soil effects could lead to high abundance of plants (Klironomos 2002). Our results suggest that dynamic interactions between individual plants and their soil communities could select for changes in allocation patterns of perennial invaders, which will indirectly influence the competitive ability or, in the case of a heliophytic species like *C. odorata* (Gautier 1992; Witkowski & Wilson 2001), the reproductive potential of an invader. Enhanced amounts of propagules available for invasive spread in a species' new environment will promote invasiveness. We propose that plant–soil feedback needs to be considered in the context of all other interactions of invasive species with native species and the abiotic environment. We conclude that soil communities may indirectly play an important role in shifting the competitive balance between native and invasive species through changed allocation patterns. Understanding of complex interactions between plants and soil communities in a more evolutionary context (Macel *et al.* 2007) is needed for the development of a comprehensive view on plant invasions.

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