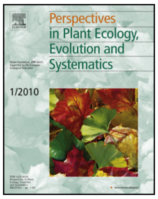
Perspectives in Plant Ecology, Evolution and Systematics 17 (2015) 87–95

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

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



Research article

Invasive plant species do not create more negative soil conditions for other plants than natives

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A R T I C L E   I N F O

Article history:
Received 6 June 2014
Received in revised form 12 February 2015
Accepted 12 February 2015
Available online 19 February 2015

Keywords:
Allelopathy
Biological invasions
Multi-species experiment
Novel weapons hypothesis
Soil biota

A B S T R A C T

A major task in ecology is to establish the degree of generality of ecological mechanisms. Here we present results from a multi-species experiment that tested whether a set of invasive species altered the soil conditions to the detriment of other species by releasing allelopathic compounds or inducing shifts in soil biota composition, and whether this effect was more pronounced relative to a set of closely related native species.

We pre-cultivated soil with 23 exotic invasive, 19 related native and 6 related exotic garden species and used plain soil as a control. To separate allelopathy from effects on the soil biota, we sterilized half of the soil. Then, we compared the effect of soil pre-cultivation and sterilization on germination and growth of four native test species in two experiments.

The general effect of soil sterilization was positive. The effect of soil pre-cultivation on test species performance was neutral to positive, and sterilization reduced this positive effect. This indicates general absence of allelopathic compounds and a shift toward a less antagonistic soil biota by cultivation species. In both experiments, pre-cultivation effects did not differ systematically between exotic invasive, exotic garden or native species.

Our results do not support the hypothesis that invasive plants generally inhibit the growth of others by releasing allelopathic compounds or accumulating a detrimental soil biota.

Introduction

Several mechanisms have been proposed to explain the success of plant invaders. Many of them involve natural enemies (e.g., Keane and Crawley, 2002) or other interspecific interactions (e.g., Mitchell et al., 2006), changes in the competitive balance between plants (e.g., Blossey and Notzold, 1995), or changes in resource availability (Davis et al., 2000). During recent years, several studies have highlighted the critical role of soil ecology for the study of plant invasions and the importance of belowground mechanisms for plant invasion success has been increasingly recognized (Callaway and Aschehoug, 2000; Inderjit and van der Putten, 2010; van der Putten et al., 2007; Wolfe and Klironomos, 2005). This has led to the formulation of two major hypotheses.

The first hypothesis is the novel weapons hypothesis, which states that invasive plants release biochemical compounds, so-called allelopathic compounds, which are harmful to native species (Callaway and Ridenour, 2004; Rabotnov, 1981). This hypothesis assumes that allelopathic effects of invasive plant species are especially important in the invaded range as the recipient community's species are not adapted to the biochemical compounds of plant invaders (Hierro and Callaway, 2003). To have a long-term effect, these allelopathic compounds must be persistent in the soil, resulting in a legacy effect (Kaur et al., 2009). Evidence for this mechanism relies on a few single species experiments. For instance, *Centaurea diffusa* and *Ageratina adenophora* exert stronger allelopathic effects on plant species from their invaded than from their native range (Callaway and Aschehoug, 2000; Inderjit et al., 2011). Another example is *Alliaria petiolata* exhibiting stronger allelopathic effects in the invaded than in the native range, both by harming other plants directly (Prati and Bossdorf, 2004) and indirectly by disrupting mycorrhizal associations in the invaded range (Callaway et al., 2008). Such biogeographical comparisons are important to understanding the role of co-evolution in plant invasions. However, this approach neglects the fact that native species might exert the same effects on other native species. Such a comparison is crucial to understand which processes contribute to the success of invasive over native

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http://dx.doi.org/10.1016/j.ppees.2015.02.002
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species (Hamilton et al., 2005), but a systematic comparison of allelopathy in invasive and native species is still lacking.

A second hypothesis is the accumulation of local pathogens, stating that invasive species alter the soil microbial community to the disadvantage of native species (Eppinga et al., 2006). This hypothesis makes the same prediction of outcome as the novel weapons hypothesis but assuming a different underlying mechanism. It is well known that plant species can influence the structure and composition of the soil microbial community, resulting in unique soil communities under different plant species (Bever et al., 1997; Bezemer et al., 2006; van der Putten et al., 2007). These soil communities may differ in density or composition of mutualistic or pathogenic microorganisms and thereby affect the performance of other plant species (Bever, 2003; Mangla et al., 2008). This idea has received a lot of attention in invasion ecology. However, evidence that invasive species accumulate pathogens that harm native species relies on only a few study systems (de la Pena et al., 2010; Mangla et al., 2008), not all of which show the same pattern (te Beest et al., 2009).

A major task in ecology is to establish the degree of generality of a mechanism. Although details of the mechanisms differ between the two above mentioned hypotheses, they both predict that invasive plants affect the soil to the detriment of native species, either directly or indirectly. Furthermore, these mechanisms are not restricted to invasive species and may play important roles during range expansion and competition among native species. In invasion ecology, many studies focused either on the effect of a single invasive species, or the response of a single native species, although native species have been shown to differ in sensitivity to belowground alterations, both in terms of allelopathic compounds and the soil microbial community (Abhilasha et al., 2008; Gomez-Aparicio and Canham, 2008). Thus, the general importance of both the novel weapons and the accumulation of local pathogens hypotheses in explaining invasions remains unclear. To assess the generality of a hypothesis, meta-analytical approaches are often used, which combine different studies that often vary considerably in the details of methods (Kulmatiski et al., 2008). Multi-species experiments offer an alternative to meta-analyses by comparing the response of several species in a common experiment and thereby reducing the heterogeneity among studies commonly associated with meta-analyses (Schlaepfer et al., 2010). Furthermore, these experiments allow estimating the variation among species groups more accurately than meta-analyses as they are unaffected by publication bias.

Most studies on mechanisms of plant invasions have focused on invasive plants without testing if native plants exert the same effects on other plants as invasives. Thus, one way to study the relative importance of allelopathy and accumulation of local pathogens is to compare the effect of invasive species with that of closely related native species. Even though closely related species may not always occupy the same habitat type or directly compete with each other, the strength of this method is that it accounts for phylogenetic interdependence among species (van Kleunen et al., 2010; Westoby et al., 1995).

Here, we tested the common prediction of the novel weapons and the accumulation of local pathogen hypotheses, that invasive species generally create more negative soil conditions for native plants compared with their native congeners. Specifically, we asked the following questions: (1) Do invasive species generally exert a stronger allelopathic effect on native plants compared to the invasives' native congeners? (2) Do invasive species generally promote a soil community more harmful to native plants compared with the invasives' native congeners? (3) Do native species respond consistently to soil pre-cultivation with invasive and closely related native species?

To answer these questions, we used the soil pre-cultivation approach, which allows assessing the net effect of changes in the soil microbial community composition caused by plant species (Bever et al., 1997; Wolfe and Klironomos, 2005). We pre-cultivated soil with invasive and native species and then compared the performance of plants with that of plants in control soil that was not pre-cultivated. This soil pre-cultivation approach has been acknowledged as the most useful to investigate the role of the soil microbial community in plant invasion success (Wolfe and Klironomos, 2005). Additionally, we compared the effect of soil pre-cultivation in sterilized and unsterilized soil to separate effects of soil microbial community composition and allelopathy.

Methods

Investigated plant species

To test the role of the soil microbial community and allelopathy in plant invasion success, we pre-cultivated soil with 48 plant species, which we call cultivation species hereafter. Among these, 23 were invasive in Europe, 19 were closely related natives and 6 were closely related exotic species cultivated in gardens (Appendix Table S1). The 23 invasive species are established in more than 40% of the European countries (DAISIE, 2008) and most of them appear on the 'black list' of noxious plant invaders in Switzerland (CPS/SKEW, 2007). To account for possible phylogenetic effects, we selected for each invasive species a congeneric or confamiliar native species or a closely related non-invasive exotic garden species to compare their pre-cultivation effect.

To test the effect of the cultivation species on the soil, we assessed germination and growth of four native species, which we call test species hereafter (Appendix Table S1). Our test species include three herbs (*Campanula rotundifolia*, *Capsella bursa-pastoris*, *Daucus carota*) and one grass (*Poa annua*), which all have a broad ecological range (Landolt, 2010). We chose test species with different phylogenetic backgrounds to test potential allelopathic and microbial effects of cultivation species. Moreover, test species are not closely related to any cultivation species. Furthermore, all test species often co-occur with our cultivation species, thus, representing species actually interacting with the cultivation species in the field.

Soil pre-cultivation and sterilization

For soil pre-cultivation, we grew the 48 cultivation species in 20 L pots in a greenhouse near Berne, Switzerland, from May to October 2010. Depending on the size of the species, we planted 1–5 individuals in each pot and replaced dead plants during the first 2 weeks. As a control, we placed pots containing only bare soil in the same greenhouse (non-cultivated soil). The substrate used (N_{total}: 1.5 g/kg, P_{total}: 40 mg/kg, K_{total}: 188 mg/kg) was a 3:1 mixture of sand and soil collected from an area that did not contain any plant species used in this study in Switzerland, the introduced range for the invaders. We replicated cultivation species and control pots 4 times each, resulting in a total pot number of $(48 + 1) \times 4 = 196$. Pots were randomly arranged in the greenhouse and regularly watered with tap water.

We harvested soil from all cultivation species and from the control at the end of October. The aboveground parts of plants were cut at soil level and soil was freed from roots by sieving with a 1 cm mesh. Above- and belowground biomass of cultivation species was dried at 80 °C and weighed. Plants in four pots of three cultivation species died during soil pre-cultivation (*Quercus palustris*, *Pseudotsuga menziesii*, two *Senecio jacobea*) and soil was replaced