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Exotic plant invasions: importance of functional traits for soil characteristics and plant-soil feedback

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Summary

Exotic plant invasions are causing profound changes to ecosystems around the world. However, it is difficult to predict their effects on ecosystem properties, since these vary according to the traits of the invading species, and the properties of the invaded vegetation and habitat. Furthermore, Effects on nutrient cycling or soil biota can result in plant-soil feedback loops that reinforce the success of invasive species. Although such effects have been demonstrated for individual species, it is not yet clear how common they are. Comparing the plant functional traits of exotic and native species in invaded vegetation may help in understanding invasions and their effects on biotic and abiotic ecosystem properties. In this dissertation, it was investigated whether and how exotic invasive plants in Switzerland differ from native species in plant functional traits and effects on nutrient cycling and soil biota. The effects of one invasive forb, *Solidago gigantea*, were studied in more detail to test whether they depend on the species composition of the invaded vegetation or on soil properties.

In Switzerland and other European countries, the main herbaceous plant invaders are forbs, whereas the native herbaceous vegetation can be dominated by forbs or graminoids. In a pot experiment with two nutrient levels and competition treatments, we compared the six most abundant exotic invasive forbs in Switzerland to six native forbs and six native graminoids. Invasive forbs had functional traits similar to those of native forbs, but differed from native graminoids in producing e.g. more rapidly decomposing litter. This suggests that invasive forbs are more likely to alter vegetation and ecosystem properties of native grasslands than of native forb stands. Invasive forbs had lower leaf chlorophyll contents than native forbs and graminoids (while not having lower nitrogen concentrations), which might indicate their ability to grow in a broader range of habitats of differing light intensity. Whereas invasive forbs did not benefit more from high nutrient supply and were not less affected by the presence of competitors than native forbs or graminoids, they tended to show stronger allelopathic effects upon a native grass than the native species.

The exotic invasive forb *Solidago gigantea* invades both fertile and infertile habitats. In a field survey, we investigated the effects of *S. gigantea* on vegetation and ecosystem properties by comparing invaded and uninvaded patches at 14 sites of varying productivity. The invasion of *S. gigantea* generally increased above-ground biomass production of the vegetation and soil carbon content, while reducing nutrient concentrations in biomass and nitrogen availability in soil. These results suggested that a conservative nutrient-use strategy allows *S. gigantea* to invade a broad range of habitats, and that its invasion success is not linked to an increase in soil nutrient availability. The observed effects did not vary according to the productivity of the native vegetation, but some were more pronounced at the phosphorus-rich sites.

The effects of *Solidago gigantea* on soil properties were further studied by simulating its invasion into three wetland plant communities. Mesocosms were planted with representative plant species of the three community types, either including or excluding *S. gigantea*. To investigate the nature of any feedbacks that may influence growth, we used soil from field sites both with and without *S. gigantea*. *S. gigantea* was more successful in invading the *Molinion* community, i.e. *S. gigantea* produced more biomass and took up more nutrients than in the more productive communities (*Magnocaricion* and *Filipendulion*). Compared to 'uninvaded' mesocosms, those with *S. gigantea* had lower soil bacterial biomass but tended to have a greater soil fungal biomass, organic matter and ß-glucosidase activity. Effects of *S. gigantea* on bacteria were similar in the three plant communities, though the biomass of *S. gigantea* differed. It is suggested that *S. gigantea* exudes antibacterial metabolites into the soil that are effective at low concentrations, even before *S. gigantea* becomes dominant. No differences were measured in nitrogen or phosphorus cycling between mesocosms with and without *S. gigantea*. Unexpectedly, *S. gigantea* produced less biomass in mesocosms inoculated with soil where it had grown before, indicating there was some kind of negative feedback upon growth.

Three general points emerge from this dissertation. Firstly, it is important to take account of functional traits and growth-form when comparing how native and invasive species affect ecosystem properties. Secondly, to draw general conclusions about the impacts of an exotic invasive plant, it is necessary to examine a broad range of invaded habitats. Thirdly, to improve our understanding of plant invasions, we need to pay more attention to how invasive plants affect soil microbial communities, and how these in turn affect plant growth, both in the short and long term.

Zusammenfassung

Invasive Neophyten verursachen oftmals tiefgreifende Veränderungen in Ökosystemen. Es ist jedoch schwierig solche Veränderungen vorherzusagen, da Richtung und Ausmaß meist art- und habitat-spezifisch sind. Veränderungen der Nährstoffkreisläufe oder Bodenfauna können wiederum das Wachstum der Neophyten begünstigen, und durch solche Pflanzen-Boden-Interaktionen können sich invasive Neophyten in einer Vegetation ausbreiten. Obwohl solche, den Neopyten begünstigende Veränderungen für manche Neophytenarten nachgewiesen wurden, ist noch nicht bekannt wie verbreitet diese sind. Ein besseres Verständnis von Neophyteninvasionen und den daraus resultierenden Veränderungen der Ökosystemeigenschaften kann durch den Vergleich funktioneller Merkmale zwischen invasiven Neophyten und nativen Arten einer betroffenen Vegetation erreicht werden, da die Merkmale einer Art ihren Einfluss auf biotische und abiotische Eigenschaften von Ökosystemen bestimmen. Im Mittelpunkt der vorliegenden Dissertation standen die Fragen ob und wie sich invasive Neophyten in der Schweiz von nativen Arten in funktionellen Merkmalen sowie in Auswirkungen auf Nährstoffkreisläufe und die mikrobielle Bodengemeinschaft unterscheiden. Die Auswirkungen eines Neophyten, *Solidago gigantea*, wurden detaillierter untersucht um herauszufinden ob diese von den Eigenschaften der nativen Vegetation oder des Bodens abhängen.

In der Schweiz und anderen europäischen Ländern sind die am häufigsten vorkommenden invasiven Neophyten in krautiger Vegetation Kräuter, wobei die dominanten nativen Arten Kräuter oder Gräser sein können. Wir untersuchten daher die sechs in der Schweiz häufigsten Neophytenkräuter und verglichen diese mit sechs nativen Kräutern und sechs nativen Gräsern in einem Topfexperiment, in welchem die Pflanzen mit zwei Nährstoffniveaus und mit oder ohne Konkurrenz kultiviert wurden. Die Neophytenkräuter waren den nativen Kräutern in den meisten funktionellen Merkmalen ähnlich, unterschieden sich aber von den nativen Gräsern, z.B. durch eine deutlich höhere Abbaurate der Blattstreu. Es ist daher wahrscheinlicher, dass diese Neophyten Ökosystemeigenschaften verändern werden wenn sie in grasreiche als wenn sie in krautreiche Vegetation einwandern. Die Neophyten fielen durch niedrigere Chlorophyllgehalte in den Blättern im Vergleich zu den nativen Gräsern und Kräutern auf (während sich die Stickstoffkonzentrationen nicht unterschieden), was auf ihre Fähigkeit hindeuten könnte ein größeres Spektrum an Habitaten mit unterschiedlicher Lichtintensität zu besiedeln. Die Neophyten reagierten nicht stärker auf eine Erhöhung der Nährstoffverfügbarkeit und wurden nicht weniger durch Konkurrenz beeinträchtigt als die nativen Gräser und Kräuter; sie wirkten aber tendenziell stärker allelopathisch auf eine native Grasart als die nativen Arten.

Die invasive Neophytenstaude *Solidago gigantea* besiedelt sowohl nährstoffarme, wenig produktive als auch nährstoffreiche, produktive Habitate. In einer Feldstudie untersuchten wir den Einfluss von *S. gigantea* auf Ökosystemeigenschaften indem wir an 14 unterschiedlich produktiven Standorten jeweils Vegetation mit und ohne *S. gigantea* verglichen. Die Invasion von *S. gigantea* steigerte generell die oberirdische Biomasseproduktion der Vegetation und erhöhte den C-Gehalt im Boden, reduzierte die Nährstoffkonzentration in der Biomasse und

die Stickstoffverfügbarkeit im Boden. Diese Ergebnisse legen nahe, dass *S. gigantea* mithilfe einer Strategie der konservierenden Nährstoffnutzung ein breites Spektrum an Habitaten besiedeln kann, und dass der Invasionserfolg von *S. gigantea* nicht mit einer Erhöhung der Nährstoffverfügbarkeit im Boden zusammenhängt. Der Einfluss von *S. gigantea* auf Vegetation und Boden hing nicht von der Produktivität der nativen Vegetation ab, jedoch waren manche Effekte ausgeprägter an Standorten mit hoher Phosphorverfügbarkeit.

Der Einfluss von *Solidago gigantea* auf Bodeneigenschaften wurde außerdem unter kontrollierten Bedingungen untersucht, indem die Invasion der Neophytenstaude in drei unterschiedlich produktive Feuchtgebiets-Pflanzengemeinschaften simuliert wurde. Dazu wurden Mesokosmen mit typischen Arten der drei Pflanzengemeinschaften bepflanzt, und zur Hälfte wurde *S. gigantea* hinzugefügt. Um herauszufinden ob das Wachstum von *S. gigantea* durch Pflanzen-Boden-Interaktionen beeinflusst wird, wurde zusätzlich eine Behandlung mit Boden von *S. gigantea*-Beständen und nativer Vegetation durchgeführt. *S. gigantea* wanderte erfolgreicher in die Pflanzengemeinschaft mit niedrigerer Produktivität ein (*Molinion*) d.h. *S. gigantea* produzierte dort mehr Biomasse und nahm mehr Nährstoffe auf als in den produktiveren Pflanzengemeinschaften (*Magnocaricion* and *Filipendulion*). Die Anwesenheit von *S. gigantea* führte zu einer Reduktion der bakteriellen Biomasse im Boden und einer tendenziellen Erhöhung der pilzlichen Biomasse im Boden, der organische Substanz und der ß-glucosidase Aktivität. Der Einfluss von *S. gigantea* auf die bakterielle Biomasse war ähnlich in allen drei Pflanzengemeinschaften, obwohl die Biomasse von *S. gigantea* unterschiedlich war. Dieses Ergebnis lässt vermuten, dass *S. gigantea* antibakterielle Stoffe über die Wurzeln ausscheidet welche schon bei niedrigen Konzentrationen wirken, noch bevor *S. gigantea* dominant wird. Wir stellten keine Veränderungen der Nährstoffkreisläufe in den Gemeinschaften mit oder ohne *S. gigantea* fest. Wir beobachteten jedoch, dass *S. gigantea* weniger Biomasse produzierte und weniger Nährstoffe aufnahm in einem Boden, in dem der Neophyt zuvor gewachsen war, als in einem Boden in dem bisher native Arten gewachsen waren. Der Einfluss von *S. gigantea* scheint daher zu negativen, das Wachstum des Neophyten beeinträchtigenden, Pflanzen-Boden-Interaktionen zu führen.

Drei wesentliche Schlussfolgerungen lassen sich aus dieser Dissertation ableiten. Erstens, funktionelle Merkmale und die Lebensform von Arten sollten berücksichtigt werden wenn es darum geht die Auswirkungen von nativen Arten und invasiven Neophyten auf Eigenschaften von Ökosystemen zu vergleichen. Zweitens, um allgemeine Aussagen über den Einfluss eines invasiven Neophyten treffen zu können, ist es wichtig ein breites Spektrum von besiedelten Habitaten zu untersuchen. Drittens, für ein detaillierteres Verständnis von Neophyteninvasionen sollte den kurz- und langfristigen Veränderungen der mikrobiellen Bodengemeinschaften und den daraus resultierenden Auswirkungen auf das Pflanzenwachstum mehr Beachtung geschenkt werden.

General Introduction

Exotic plant invasions are causing profound changes to ecosystems around the world (Vitousek 1990; Ehrenfeld 2003; Güsewell et al. 2006). However, it is difficult to generalise about their effects on ecosystem properties, since these vary according to the traits of the invading species, and the properties of the invaded vegetation and habitat. Yet, knowing the inherent functional traits of an exotic invasive plant could improve understanding of its invasion success and impact, since plant traits affect ecosystem properties such as throughfall distribution, soil temperature and nutrient cycling (Westoby & Wright 2006). The knowledge of the distribution of functional traits within the native plant community in comparison to the traits of the invader help to identify the mechanisms by which an exotic invasive plant is able to alter ecosystem properties and processes.

1. Plant functional traits

1.1. *Definition and relevance*

Plant functional traits are morphological, physiological or phenological traits - for example, specific leaf area, tissue nutrient concentrations or flowering period - which reflect plant performance (Violle et al. 2007). By screening for many plant functional traits and species, Grime et al (1997) concluded that traits are not randomly distributed across plant species but occur in combinations according to the specialisation of plants. Foremost, species of nutrient-rich habitats differ from those of nutrient-poor habitats by having high relative growth and nutrient acquisition rates in combination with high nutrient concentrations in leaves and short tissue life spans (Grime et al. 1997; Aerts 1999; Lavorel & Garnier 2002; Diaz et al. 2004). Hence, the habitat fertility determines specialisation in plants and therefore also certain trait combinations (Fig. 1). Further trait combinations distinguish monocotyledonous from dicotyledonous and annual from perennial species (Grime et al. 1997). Species with similar trait combinations are expected to have similar functions within a plant community or ecosystem, respectively (Lavorel et al. 1997).

Plant species not only respond to environmental conditions; they also modify them. Furthermore, species with similar responses to environmental changes do not necessarily have the same effects on ecosystem properties and *vice versa* (Chapin et al. 1997; Lavorel & Garnier 2002; Reich et al. 2003). Therefore, in order to understand the significance of a particular species

for ecosystem processes it is necessary to determine how that species interacts with both its biotic and abiotic environment, including both how the species responds to environmental factors, and the effect that this species has on those factors (Wardle et al. 1998). Within the group of functional traits, one can therefore distinguish between the measurement of effect- and response-traits. Response traits are traits such as life span, growth rate, or shoot height, whose attributes vary according to resource availability or disturbance (Violle et al. 2007). Effect-traits are traits, such as litter decomposability, which determine the effects of a plant on plant community or ecosystem processes. Some traits can be of an affecting as well as a responding character, e.g. traits involved in biogeochemical cycling (Lavorel & Garnier 2002). It requires different experimental approaches to measure responses to environmental changes or to measure effects on ecosystem processes; e.g. comparing species under varying or constant environmental conditions.

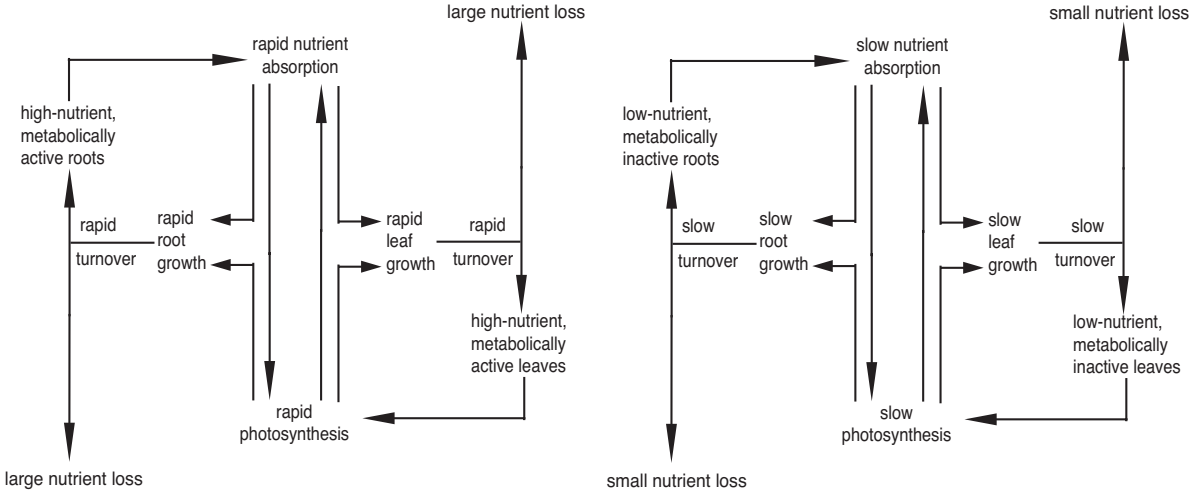

Figure 1. Scheme comparing some of the main functional traits related to nutrient cycling of plants from nutrient-rich habitats (left) with those of species from nutrient-poor habitats (right). Redrawn after Grime (2001).

1.2. *Importance for ecosystem processes*

In order to be able to affect ecosystem processes such as biotic interactions and resource supply, plant species need to maintain themselves in a community and compete with other species for resources and space. Traits conferring existence differ according to the physical environment such as habitat fertility, but most traits vary widely across species within existing communities at one site (Eviner 2004; Westoby & Wright 2006). Hence, even though environmental factors frame the conditions for competition and filter for some trait values and species, a variety of ecological strategies can still be successful at one site (Westoby & Wright 2006); i.e. species can respond to ecosystem processes individually.

Plants can affect nutrient cycling through biomass production and the quality of their litter. With increasing biomass production, plants take up more nutrients and biomass, especially root biomass, is therefore the major factor governing nutrient uptake (Lambers et al. 1998). Litter decomposition is a key process in nutrient cycling, since it regulates the nutrient supply of plants: slow litter decomposition coincides with low nutrient availability in soil, whereas rapid decomposing litter of high quality results in enhanced soil nutrient availability (Grime 2001; Chapin 2003). Functional leaf traits, such as life span, tensile strength, nitrogen and lignin concentrations, control leaf litter decomposition rates (Wardle et al. 1998; Aerts et al. 1999; Cornelissen 1999).

Plant species differ in nutrient acquisition strategies, thereby affecting nutrient cycling individually through differences in physiological, morphological or phenological functional traits such as N_2-fixation, rooting depth, cluster root formation, mycorrhizal symbioses, specific root lengths or periods of physiological activity; these, in turn, contribute to differences in plant nutrient uptake and soil nutrient availability (Chapin et al. 1997; Chapman et al. 2006).

Root exudates of plants can affect soil nutrient availability both directly and indirectly. Organic acids and the enzyme phosphatase secreted by roots act directly upon P availability in soil by solubilizing phosphate from inorganic and organic compounds (Lambers et al. 1998). Indirect effects arise through the effects of exudates upon soil biota: secondary metabolites can stimulate or inhibit microbial growth in the rhizosphere as well as rhizobial or mycorrhizal symbioses (Gregory 2006). The relationship may be a mutualistic one, with carbon compounds such as sugars, amino acids and organic acids stimulating the growth of microbes in exchange for their help in resource uptake and pathogen defence (Morgan et al. 2005). In consequence, the stimulation of microbial growth via exudation of carbon compounds generally also leads to increased numbers of protozoa and nematodes in the soil, which feed on microbes and therefore enhance mineralization and nutrient availability for plants by releasing nutrients into the soil that would otherwise have been immobilized in microbes (Gregory 2006). Thus, plant species may alter nutrient cycling via acquisition strategies, litter quality and root exudation.

1.3. *Plant-soil feedback*

Plant-soil feedback is a concept describing the possibility that the performance of plants is determined by soil abiotic and biotic conditions, which these plants create themselves. Plant performance can be influenced directly by a plants effect on nutrient availability, and indirectly if this effect on nutrient availability has a stronger effect on neighbouring species than on the initiating species (Evans et al. 2001). Interactions with soil biota seem to be more species-specific than interactions with nutrient cycling (Bezemer et al. 2006). It is assumed that plant species build up their "own" soil microbial community, probably via species-specific root exudates

(Eom et al. 2000; Kourtev et al. 2002; Porazinska et al. 2003; Broeckling et al. 2008). The soil community contains beneficial (mycorrhiza, rhizobia) as well as pathogenic (e.g. species of *Fusarium*, *Pythium*) microbes, and the feedback for plants can therefore be positive, neutral or negative (Bever et al. 1997; Wardle et al. 2004). More indirectly, the detrital food web can also have an effect on plant performance by liberating nutrients locked up in dead organic matter or in microbes, thus increasing nutrient availability for certain plants (Wardle et al. 2004).

Plant-soil feedback is investigated experimentally by determining the difference in plant growth of a species between soils pregrown or not pregrown by that species (Bever et al. 1997). Within a plant community, the net feedback can vary depending on the soil community beneath neighbouring species and their effects on plant growth (see Fig. 2). Dominant species have been shown to be associated with positive feedbacks, whereas rare species tend to experience negative feedback (Klironomos 2002). Negative feedbacks probably play a role in maintaining species diversity, whereas positive feedbacks rather lead to a loss of diversity (Bever et al. 1997). Negative feedbacks have also been shown to be involved in succession in early stages of plant communities by enhancing species replacement, with all pioneer species experiencing negative feedback (Kardol et al. 2007; Kulmatiski et al. 2008), whereas established or late-successional communities seem to exist longer due to more positive feedbacks (Kulmatiski et al. 2008). A meta-analysis of feedback studies carried out showed differences in feedback for plant functional types: grasses seem to experience more frequently negative feedback than forbs (Kulmatiski et al. 2008).

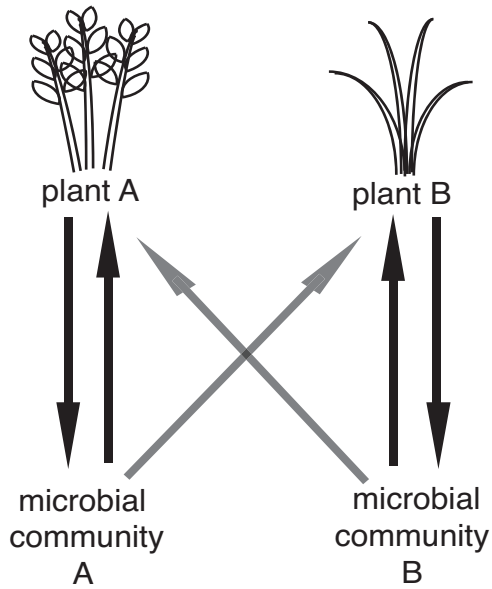

Figure 2. Scheme of plant-soil community feedback: plant species A and B influence the soil community species-specifically, creating soil community A and B, respectively. The direct feedback of the soil communities on the plant species is represented by black arrows and indirect effects of soil community A and B on the plant species are represented by grey arrows. Redrawn after Bever et al (1997).

2. Exotic invasive plants

"Biological invasions involve exotic species that have been introduced accidentally or incidentally from one region into another region separated by geographical barriers, such as oceans or mountain ridges and which become non-proportionally abundant in their new range." (Williamson 1996; Van der Putten 2007). In this sense, I investigated exotic invasive plants within this thesis and refer to them also in the simplified term as 'invasive plants' or 'invaders'. While many external factors contribute to the spread and establishment of invasive plants (e.g. human dispersal, vegetation disturbance, nutrient enrichment, enemy release), the trait equipment of a plant species is crucial for determining its impact on vegetation and ecosystem properties (Wardle et al. 1998; Levine et al. 2003; McIntyre et al. 2005). The comparison of traits between coexisting invasive and native plant species can therefore help understanding invasion success and impact (Thompson et al. 1995; Funk & Vitousek 2007).

2.1. *Importance of functional traits in invasion success*

In attempts to identify a set of traits that confer invasive ability or invasive potential to an exotic plant a variety of plant functional traits has been screened (Sutherland 2004; Hamilton et al. 2005; Küster et al. 2008; Thompson & McCarthy 2008). It has become evident that 'successful' plant functional traits are context-, scale- and species-dependent (Thompson et al. 1995; Daehler 2003; Hamilton et al. 2005; Moles et al. 2008). Dramatic invasions often happen when the invader differs functionally from the native species and introduces a new function, such as N_2-fixation, C_4-photosynthesis, annual growth form, or new allelochemicals, which has not been present in the native vegetation before (Vitousek et al. 1987; Hierro & Callaway 2003; Emery 2007; Moles et al. 2008). The introduction of a function that was formerly absent may give the invader an advantage either by using resources which the resident species were unable to use, or by suppressing resident species. The introduction of new allelochemicals can indeed confer an advantage upon invasive plants, since it strengthens the competitive ability of the invader by directly suppressing native species (Ridenour & Callaway 2001; Prati 2004; Vivanco et al. 2004; Inderjit et al. 2008). Even if not all native species are similarly affected by the allelochemicals of an invader (Abhilasha et al. 2008), 'new' root exudation traits can certainly contribute to the invasion success.

If species do not introduce a new function, variations in continuous traits among native and invasive species may still be important. In particular, traits promoting high reproduction rates and rapid spread, e.g. in annuals, are decisive for the colonisation of open habitats and those promoting fast growth and resource acquisition are most important for the ability to

establish, dominate and displace the resident vegetation (Pysek et al. 1995; Grotkopp et al. 2002; Lavorel & Garnier 2002; Dietz & Edwards 2006). Therefore, the most successful invaders among the species not introducing a new function are often species with high SLA, high relative growth rates and rather high nutrient turnover (Smith & Knapp 2001; Hamilton et al. 2005; James & Drenovsky 2007; Leishman et al. 2007). These traits are characteristic of a competitive-ruderal strategy according to Grime et al (2001). Invaders therefore tend to have an advantage over native species under high nutrient supply (Kolb et al. 2002; Daehler 2003; Rickey & Anderson 2004; Blumenthal & Hufbauer 2007), whereas nutrient-poor conditions do generally not favour plant invasions.

Invasive plants have been shown to benefit from changes in environmental conditions such as disturbance and nutrient enrichment, whereas native plants adapted to conditions prior to changes and are less likely to benefit (Moles et al. 2008). If the invasive species has a broad ecological niche, it might be better able than native species to increase its fitness under favourable conditions or maintain its fitness if conditions become unfavourable (Richards et al. 2006). Indeed, several studies have shown that invasive plants have a higher plasticity compared to native plants, especially in response to higher nutrient availability (Milberg 1999; Daehler 2003; Poulin et al. 2007; Drenovsky et al. 2008; Funk 2008). Phenotypic plasticity is not a cause of invasiveness, but it can help invasive plants to spread in a wider range of environments (Daehler 2003; Richards et al. 2006). It may also allow them to benefit most from climate change (Funk 2008), which implies that problems of undesirable exotic plant invasions may increase in future.

2.2. Effects on ecosystem properties

Among the ecosystem processes altered by invasive plants, nutrient cycling seems to be most prominent. By changing the period of nutrient uptake and release, by producing litter of different quality, or by introducing a different nutrient acquisition strategy, invasive plants can alter nutrient cycling compared to the native plant community (Evans et al. 2001; Mack et al. 2001; Blank & Young 2002; Chapuis-Lardy et al. 2006; Sala et al. 2007). Many studies have pointed towards a stimulation of nutrient cycling and increased nutrient availability (Ehrenfeld 2003), due to increased biomass production, increased nutrient pools as well as higher litter decomposition rates in invasive species. Generalizations are however difficult, since invasive plants vary widely in morphological and physiological traits, and reduced rates of nutrient cycling have also been observed for individual species (Evans et al. 2001; Scott et al. 2001; Drenovsky & Batten 2007).

Effects of invasive plants on soil biota might be as important as effects on nutrient cycling, but such effects only recently have been investigated. So far, effects of invasive plants on soil biota range from inhibition to stimulation of certain taxonomic groups of the soil community as well as the function of the soil community and a trend is not visible (Wolfe & Klironomos 2005).

The soil community composition is mostly studied by means of phospholipid fatty acid (PLFA) profiles and soil biota functioning by means of enzyme activities, N mineralization or litter decomposition rates (Kourtev et al. 2002; Belnap et al. 2005). Studies mainly found changes in bacterial or fungal abundance (Kourtev et al. 2002; Kourtev et al. 2003; Batten et al. 2006; Li et al. 2006), in which mycorrhiza were either stimulated (Kourtev et al. 2002; Batten et al. 2006) or inhibited (Stinson et al. 2006; Wolfe et al. 2008). The inhibiting effects indicate the exudation of antifungal secondary metabolites by the invasive plant, which not only directly harms the mycorrhizal fungi, but also has indirect negative effects on the growth of native plants that depend on the abundance of mycorrhiza (Stinson et al. 2006; Wolfe et al. 2008).

Exotic invasive plants are thought to create favourable growing conditions for themselves, which enable them to persist and spread (Callaway et al. 2004). Both changes in nutrient availability in soil and the shaping of the soil community can contribute to such positive plant-soil feedbacks. A change in the soil community composition does not necessarily result in a change of functioning of the soil community (Belnap et al. 2005) and effects on nutrient availability and soil community functioning are not necessarily related (Kourtev et al. 2002; Kourtev et al. 2003). One can therefore not unconditionally infer from effects on nutrient cycling to effects on soil biota or *vice versa*. Since both aspects (soil nutrients and soil biota) play a major role in plant-soil feedback, both need to be considered in order to understand and interpret these feedbacks.

2.3. *Do plant-soil feedbacks differ between invasive and native plants?*

Many exotic invasive plants have been shown to be associated with a positive feedback in interaction with soil biota and nutrients, enabling them to establish, invade and persist in a habitat (Klironomos 2002; Vinton & Goergen 2006). Feedbacks from interactions with soil biota in invasive plants are especially interesting, since some species show a positive feedback in their invaded range, whereas they experience negative feedback in their native range (Reinhart et al. 2003; Callaway et al. 2004; Reinhart & Callaway 2004). These results support the enemy release hypothesis (Keane & Crawley 2002), indicating that invasive species can also escape from their soil 'enemies' (pathogenic fungi, bacteria or nematodes) and therefore grow better. This is supported by studies showing that invasive plants experience positive feedback or less negative feedback compared to native species in the invaded range (Klironomos 2002; Van Grunsven et al. 2007). However, not all invasive plants escape their enemies and some are successful despite negative interactions with the soil biota (Beckstead & Parker 2003; Nijjer et al. 2007). The complexity of interactions with soil biota is illustrated by studies showing that invasive species can accumulate soil pathogens but experience positive feedback due to enhanced mutualistic interactions in the invaded range that overrule the pathogenic effects (Reinhart & Callaway 2004).

The accumulation of soil pathogens can also act as a weapon against native species, when these pathogens harm the native species more than the accumulating invasive species (Mangla et al. 2008).

3. Thesis aim

The study presented in this thesis had two aims: a) distinguishing relevant functional traits of exotic invasive forbs in Switzerland, and their similarity or difference with functional traits of native forbs and native graminoids dominating the invaded vegetation, and b) investigating in detail the functional traits, effects on ecosystem properties and plant-soil feedback of a highly invasive species in Switzerland: *Solidago gigantea*. The first aim takes into account that the main herbaceous plant invaders in Switzerland and other European countries are forbs, whereas the native herbaceous vegetation is dominated by forbs or graminoids, which suggests the comparison of both functional groups with the invasive forbs. While grasses differ from forbs in several functional traits, these differences have never been integrated in a comparative multi-species study of native and invasive species so far. The second aim comprises a case study, which is more extensive than previous studies, accounting for the full range of habitats in which the invader persists, and studying the dependence of invasion effects on the habitat productivity, nutrient availability and microbial community.

3.1. Thesis outline

The project combined three experimental approaches: i) a growth experiment to compare functional traits of the six most frequent invasive forbs in Switzerland with six native forbs and six native graminoids; ii) a field survey to study variability in plant functional traits and effects on ecosystem properties between the invader *Solidago gigantea* and a range of native vegetations in Switzerland; and iii) a mesocosm experiment to study effects of *S. gigantea* on nutrient cycling, the soil microbial community and affiliated feedback by simulating invasion in three native wetland plant communities.

Chapter 1: "Invasive forbs differ functionally from native graminoids, but are similar to native forbs."
Invasive forbs, native forbs and native graminoids were compared in functional traits, and plasticity in response to competition and low *versus* high nutrient supply. Furthermore, we compared the 18 species in effect-traits, namely litter decomposability and allelopathy. To test for the validity of our experimental results, leaf traits were also measured for all species on leaves from field sites. This study highlights the importance of functional group and life-form for differences in functional traits.

Chapter 2: "The invasive alien plant species *Solidago gigantea* alters ecosystem processes across habitats with differing fertility."
We surveyed 14 sites in the lowlands of Switzerland where the exotic forb *S. gigantea* invaded native vegetation. These sites differed widely in biomass productivity and soil nutrient availability. We compared functional traits, biomass production and soil properties between the native and the invaded stands. Two environmental gradients were analysed in this survey, the biomass productivity of the native vegetation and the soil P availability of the native stands. The results indicate the importance of studying the full range of habitats of an invader.

Chapter 3: "Plant-microbe interactions and a negative feedback for the invasive plant *Solidago gigantea.*"
The impact of *S. gigantea* upon the microbial community was studied in a mesocosm experiment using three constructed native wetland plant communities (*Molinion*, *Magnocaricion*, *Filipendulion*). We examined effects of *S. gigantea* on N and P availabilities in soil, enzyme activities, as well as bacterial and fungal biomass in soil and whether these effects depended on the native plant community. Furthermore, by using soil from field sites with and without *S. gigantea,* it was possible to investigate the nature of any feedbacks that may influence the growth of *S. gigantea*. The results demonstrate the importance of considering plant-soil feedbacks when studying exotic plant invasions.

References

Abhilasha, D., Quintana, N., Vivanco, J. & Joshi, J. 2008. Do allelopathic compounds in invasive *Solidago canadensis s.l.* restrain the native European flora? *Journal of Ecology* 96: 993-1001.

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* 50: 29-37.

Aerts, R., Verhoeven, J.T.A. & Whigham, D.F. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology* 80: 2170-2181.

Batten, K.M., Scow, K.M., Davies, K.F. & Harrison, S.P. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biological Invasions* 8: 217-230.

Beckstead, J. & Parker, I.M. 2003. Invasiveness of *Ammophila arenaria*: release from soil-borne pathogens? *Ecology* 84: 2824-2831.

Belnap, J., Phillips, S.L., Sherrod, S.K. & Moldenke, A. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* 86: 3007-3017.

Bever, J.D., Westover, K.M. & Antonovics, J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology* 85: 561-573.

Bezemer, T.M., Lawson, C.S., Hedlund, K., Edwards, A.R., Brook, A.J., Igual, J.M., Mortimer, S.R. & Van der Putten, W.H. 2006. Plant species and functional group effects on abiotic and microbial soil properties and plant-soil feedback responses in two grasslands. *Journal of Ecology* 94: 893-904.

Blank, R.R. & Young, J.A. 2002. Influence of the exotic invasive crucifer, *Lepidium latifolium,* on soil properties and elemental cycling. *Soil Science* 167: 821-829.

Blumenthal, D.M. & Hufbauer, R.A. 2007. Increased plant size in exotic populations: a common-garden test with 14 invasive species. *Ecology* 88: 2758-2765.

Broeckling, C.D., Broz, A.K., Bergelson, J., Manter, D.K. & Vivanco, J.M. 2008. Root exudates regulate soil fungal community composition and diversity. *Applied and Environmental Microbiology* 74: 738-744.

Callaway, R.M., Thelen, G.C., Rodriguez, A. & Holben, W.E. 2004. Soil biota and exotic plant invasion. *Nature* 427: 731-733.

Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman, D. 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500-504.

Chapin, F.S. 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany* 91: 455-463.

Chapman, S.K., Langley, J.A., Hart, S.C. & Koch, G.W. 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytologist* 169: 27-34.

Chapuis-Lardy, L., Vanderhoeven, S., Dassonville, N., Koutika, L.S. & Meerts, P. 2006. Effect of the exotic invasive plant *Solidago gigantea* on soil phosphorus status. *Biology & Fertility of Soils* 42: 481-489.

Cornelissen, J.H.C. 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* 143: 191-200.

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

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Marti, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M.R. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* 15: 295-304.

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

Drenovsky, R.E. & Batten, K.M. 2007. Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. *Biological Invasions* 9: 107-116.

Drenovsky, R.E., Martin, C.E., Falasco, M.R. & James, J.J. 2008. Variation in resource acquisition and utilization traits between native and invasive perennial forbs. *American Journal of Botany* 95: 681-687.

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

Emery, S.M. 2007. Limiting similarity between invaders and dominant species in herbaceous plant communities? *Journal of Ecology* 95: 1027-1035.

Eom, A.H., Hartnett, D.C. & Wilson, G.W.T. 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. *Oecologia* 122: 435-444.

Evans, R.D., Rimer, R., Sperry, L. & Belnap, J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11: 1301-1310.

Eviner, V.T. 2004. Plant traits that influence ecosystem processes vary independently among species. *Ecology* 85: 2215-2229.

Funk, J.L. & Vitousek, P.M. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446: 1079-1081.

Funk, J.L. 2008. Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology* 96: 1162-1173.

Gregory, P.J. 2006. *Plant roots: growth, activity and interaction with soils*. Blackwell, Oxford.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., RossFraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. & Whitehouse, J. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79: 259-281.

Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley and Sons, Chichester, UK.

Grotkopp, E., Rejmanek, M. & Rost, T.L. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* 159: 396-419.

Güsewell, S., Jakobs, G. & Weber, E. 2006. Native and introduced populations of *Solidago gigantea* differ in shoot production but not in leaf traits or litter decomposition. *Functional Ecology* 20: 575-584.

Hamilton, M.A., Murray, B.R., Cadotte, M.W., Hose, G.C., Baker, A.C., Harris, C.J. & Licari, D. 2005. Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* 8: 1066-1074.

Hierro, J.L. & Callaway, R.M. 2003. Allelopathy and exotic plant invasion. *Plant and Soil* 256: 29-39.

Inderjit, Pollock, J.L., Seastedt, T.R., Callaway, R.M. & Kaur, J. 2008. Allelopathy and plant invasions: traditional, congeneric, and bio-geographical approaches. *Biological Invasions* 10: 875-890.

James, J.J. & Drenovsky, R.E. 2007. A basis for relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology & Management* 60: 395-400.

Kardol, P., Cornips, N.J., van Kempen, M.M.L., Bakx-Schotman, J.M.T. & van der Putten, W.H. 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. *Ecological Monographs* 77: 147-162.

Keane, R.M. & Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17: 164-170.

Klironomos, J.N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417: 67-70.

Kolb, A., Alpert, P., Enters, D. & Holzapfel, C. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* 90: 871-881.

Kourtev, P.S., Ehrenfeld, J.G. & Haggblom, M. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83: 3152-3166.

Kourtev, P.S., Ehrenfeld, J.G. & Haggblom, M. 2003. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biology & Biochemistry* 35: 895-905.

Kulmatiski, A., Beard, K.H., Stevens, J.R. & Cobbold, S.M. 2008. Plant-soil feedbacks: a meta-analytical review. *Ecology Letters* 11: 980-992.

Küster, E.C., Kuhn, I., Bruelheide, H. & Klotz, S. 2008. Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology* 96: 860-868.

Lambers, H., Chapin, F.S. & Pons, T.L. 1998. *Plant physiological ecology*. Springer, New York, USA.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution* 12: 474-478.

Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545-556.

Leishman, M.R., Haslehurst, T., Ares, A. & Baruch, Z. 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist* 176: 635-643.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society London Series B-Biological Sciences* 270: 775-781.

Li, W.H., Zhang, C.B., Jiang, H.B., Xin, G.R. & Yang, Z.Y. 2006. Changes in soil microbial community associated with invasion of the exotic weed, *Mikania micrantha* HBK. *Plant and Soil* 281: 309-324.

Mack, M.C., D'Antonio, C.M. & Ley, R.E. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C-4 grasses in Hawaii. *Ecological Applications* 11: 1323-1335.

Mangla, S., Inderjit & Callaway, R.M. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. *Journal of Ecology* 96: 58-67.

McIntyre, S., Martin, T.G., Heard, K.M. & Kinloch, J. 2005. Plant traits predict impact of invading species: an analysis of herbaceous vegetation in the subtropics. *Australian Journal of Botany* 53: 757-770.

Milberg, P. 1999. Survival and growth of native and exotic composites in response to a nutrient gradient. *Plant Ecology* 145: 125-132.

Moles, A.T., Gruber, M.A.M. & Bonser, S.P. 2008. A new framework for predicting invasive plant species. *Journal of Ecology* 96: 13-17.

Morgan, J.A.W., Bending, G.D. & White, P.J. 2005. Biological costs and benefits to plant-microbe interactions in the rhizosphere. *Journal of Experimental Botany* 56: 1729-1739.

Nijjer, S., Rogers, W.E. & Siemann, E. 2007. Negative plant-soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. *Proceedings of the Royal Society B-Biological Sciences* 274: 2621-2627.

Porazinska, D.L., Bardgett, R.D., Blaauw, M.B., Hunt, H.W., Parsons, A.N., Seastedt, T.R. & Wall, D.H. 2003. Relationships at the aboveground-belowground interface: plants, soil biota, and soil processes. *Ecological Monographs* 73: 377-395.

Poulin, J., Sakai, A.K., Weller, S.G. & Nguyen, T. 2007. Phenotypic plasticity, precipitation, and invasiveness in the fire-promoting grass *Pennisetum setaceum* (*Poaceae*). *American Journal of Botany* 94: 533-541.

Prati, D. 2004. Allelopathic inhibition of germination by *Alliaria petiolata* (*Brassicaceae*). *American Journal of Botany* 91: 285-288.

Pysek, P., Prach, K. & Smilauer, P. 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora. *Plant Invasions* 39-60.

Reich, P.B., Buschena, C., Tjoelker, M.G., Wrage, K., Knops, J., Tilman, D. & Machado, J.L. 2003. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. *New Phytologist* 157: 617-631.

Reinhart, K.O., Packer, A., Van der Putten, W.H. & Clay, K. 2003. Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecology Letters* 6: 1046-1050.

Reinhart, K.O. & Callaway, R.M. 2004. Soil biota facilitate exotic Acer invasions in Europe and North America. *Ecological Applications* 14: 1737-1745.

Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. & Pigliucci, M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981-993.

Rickey, M.A. & Anderson, R.C. 2004. Effects of nitrogen addition on the invasive grass *Phragmites australis* and a native competitor *Spartina pectinata*. *Journal of Applied Ecology* 41: 888-896.

Ridenour, W.M. & Callaway, R.M. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* 126: 444-450.

Sala, A., Verdaguer, D. & Vila, M. 2007. Sensitivity of the invasive geophyte *Oxalis pes-caprae* to nutrient availability and competition. *Annals of Botany* 99: 637-645.

Scott, N.A., Saggar, S. & McIntosh, P.D. 2001. Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. *Ecological Applications* 11: 1311-1322.

Smith, M.D. & Knapp, A.K. 2001. Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *International Journal of Plant Sciences* 162: 785-792.

Stinson, K.A., Campbell, S.A., Powell, J.R., Wolfe, B.E., Callaway, R.M., Thelen, G.C., Hallett, S.G., Prati, D. & Klironomos, J.N. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *Plos Biology* 4: 727-731.

Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia* 141: 24-39.

Thompson, K., Hodgson, J.G. & Rich, T.C.G. 1995. Native and alien invasive plants: more of the same? *Ecography* 18: 390-402.

Thompson, K. & McCarthy, M.A. 2008. Traits of British alien and native urban plants. *Journal of Ecology* 96: 853-859.

Van Grunsven, R.H.A., Van der Putten, W.H., Bezemer, T.M., Tamis, W.L.M., Berendse, F. & Veenendaal, E.M. 2007. Reduced plant-soil feedback of plant species expanding their range as compared to natives. *Journal of Ecology* 95: 1050-1057.

Vinton, M.A. & Goergen, E.M. 2006. Plant-soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems* 9: 967-976.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882-892.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Muellerdombois, D. & Matson, P.A. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238: 802-804.

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

Vivanco, J.M., Bais, H.P., Stermitz, F.R., Thelen, G.C. & Callaway, R.M. 2004. Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. *Ecology Letters* 7: 285-292.

Wardle, D.A., Barker, G.M., Bonner, K.I. & Nicholson, K.S. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology* 86: 405-420.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H. & Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304: 1629-1633.

Westoby, M. & Wright, I.J. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21: 261-268.

Wolfe, B.E. & Klironomos, J.N. 2005. Breaking new ground: soil communities and exotic plant invasion. *Bioscience* 55: 477-487.

Wolfe, B.E., Rodgers, V.L., Stinson, K.A. & Pringle, A. 2008. The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. *Journal of Ecology* 96: 777-783.

Chapter 1

Invasive forbs differ functionally from native graminoids, but are similar to native forbs

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Abstract

Invasive exotic plant species are generally fast-growing plants with effective resource acquisition. These properties allow them to dominate or displace the native vegetation and often cause them to alter ecosystem processes. Effects on ecosystems are likely to occur if invasive plants are functionally different from the native vegetation. In Northern Switzerland, the main herbaceous plant invaders are forbs, whereas the native herbaceous vegetation can be dominated by forbs or graminoids. We therefore investigated whether the most abundant invasive forbs differ functionally from native forbs or graminoids, and whether this leads to different effects on the soil. In a garden pot experiment, 18 species (six invasive forbs with six native forbs and six native graminoids) were grown alone or in competition and with low or high nutrient supply. We measured leaf and whole-plant traits, plasticity in response to nutrients and competition, litter decomposition rate, effects on soil nutrient availability and allelopathy. Leaf traits were also measured at natural field sites for comparison. The invasive forbs differed clearly from the native graminoids: their leaves had a lower tissue density and a shorter life span, their leaf litter decomposed faster, they produced less biomass, and they had a lower nitrogen-use efficiency than the native graminoids. Invasive forbs differed from native forbs only in having lower P concentrations in roots. The specific leaf area did not differ between the three investigated plant groups in the pot experiment but tended to be higher in invasive forbs at field sites. The invasive forbs did not show more plastic responses to nutrient enrichment than native graminoids or forbs, and their growth was reduced similarly by root competition from a native grass. Nutrient availability in soil was similarly affected by all three plant groups. The growth rate of native grass seedlings in substrate taken from the experimental pots did not differ among the three plant groups, but the addition of activated charcoal had a more positive effect on seedling growth in the substrate pre-grown by the invasive forbs, suggesting a stronger allelopathic effect. Our results show that the invasive forbs have the potential to alter ecosystem properties especially when invading native grasslands but not when they invade forb stands. This highlights the importance of taking into account the life-form in the comparison of native and invasive species.

Introduction

Functional traits determine the ecological strategy of plants, their response to site conditions and their influence on ecosystems (Lavorel & Garnier 2002; Garnier et al. 2007; Suding et al. 2008). The study of functional traits therefore plays an important role in research on the ecology of exotic plant invasions. While many external factors contribute to the spread and establishment of invasive plants (e.g. human dispersal, vegetation disturbance, nutrient enrichment), the trait equipment of plant species is crucial for their impact on vegetation and ecosystem properties (Wardle et al. 1998; Levine et al. 2003; McIntyre et al. 2005). The comparison of traits between coexisting invasive and native plant species can therefore help understanding invasion success and impact (Thompson et al. 1995; Funk & Vitousek 2007).

Associations between plant functional traits and either invasiveness or invasion impact have been reported in many studies (McIntyre et al. 2005; Küster et al. 2008). However, there are also studies that found no relationship (Hastwell & Panetta 2005). Many traits may contribute to invasion success (life form, phenology, seed size, polyploidy level etc.) and the significance of individual traits is often context-dependent or species-specific (Thompson et al. 1995; Moles et al. 2008). In particular, traits promoting high reproduction rates and rapid spread are decisive for the colonisation of open habitats while those promoting fast growth and resource acquisition are most important for the ability to establish, dominate and displace the resident vegetation (Lavorel & Garnier 2002; Dietz & Edwards 2006). Therefore, the most successful invaders are often species with high SLA, high relative growth rates and rather high nutrient turnover (Smith & Knapp 2001; Hamilton et al. 2005; Leishman et al. 2007); these traits are characteristic of a competitive-ruderal strategy in the sense of Grime et al (2001). Invaders therefore tend to have an advantage over native species under high nutrient supply (Kolb et al. 2002; Rickey & Anderson 2004; Blumenthal & Hufbauer 2007), whereas nutrient-poor conditions do generally not favour plant invasions.

Phenotypic plasticity in functional traits can allow invasive plants to benefit from changing environmental conditions, either by greatly increasing their performance under resource-rich conditions or by maintaining their performance under resource-poor conditions (Richards et al. 2006). Some studies found invasive species to be particularly performant in acquiring and using nutrients under nutrient-poor conditions (Funk & Vitousek 2007; Muth & Pigliucci 2007). More often, however, invasive species showed a more plastic response to nutrient enrichment than native species (Milberg 1999). A possible reason is higher root plasticity, which allows for a more rapid capture of nutrients in soil (Callaway et al. 2003).

The effects of invasive plants on the soil are also variable. Invasive species have been found to increase or decrease soil nutrient availability (Ehrenfeld 2003), to exert allelopathic

effects (Callaway et al. 2005) or to alter the soil microbial community (Belnap et al. 2005), but none of these effects is ubiquitous. Apparently, effects on the soil are not the condition for plants to be invasive, but rather a consequence of the traits conferring invasiveness in competitive vegetation.

Effects on ecosystem processes are most likely to occur if invasive plants are functionally different from the native vegetation. In Northern Switzerland, the main herbaceous plant invaders are forbs, whereas the native herbaceous vegetation can be dominated by forbs or graminoids. In this case, ecosystem processes are likely to be changed when invasive forbs displace native graminoids, since grasses differ functionally from forbs above- and below-ground. Grasses have tougher leaves with a longer life span and lower litter decomposition rates (Cornelissen & Thompson 1997; Grime et al. 1997; Craine et al. 1999; Dorrepaal et al. 2005), while having similar or higher specific leaf areas (SLA) (Cornelissen 1999; Craine et al. 2002) than forbs. Grass roots are also thinner and grow denser than forb roots (Craine et al. 2002). In terms of growth, grasses seem to be more competitive than forbs under fertile conditions (Thompson et al. 2001; Pywell et al. 2003), but equal to forbs under nutrient-poor conditions (Craine et al. 2002). Accordingly, growth responses of forbs to fertilization have been reported to be lower or equal to grasses (Reich et al. 2001; Reich et al. 2003). These functional differences might play an important role in the evaluation of invasion effects, since native vegetations are frequently invaded by exotic species of a different functional group (Grant et al. 2003; LeJeune et al. 2006). However, these differences have never been integrated in a comparative multi-species study of native and invasive species so far.

The goal of this study was to compare invasive and native species in functional traits, plasticity, and effects on soil under controlled conditions. We included the invasive forbs occurring most frequently in the lowlands of Switzerland, as well as six native graminoids and six native forbs that are abundant in moist to wet herbaceous vegetation and are often found at sites colonized by the invasive species. We subjected all species to grow with or without competition and supplied a low and a high nutrient treatment.

We hypothesized that:

1) Invasive and native species differ in leaf traits and nutrient acquisition; in particular we hypothesized invasive forbs to have a higher SLA than native forbs and higher or equal SLA compared to native graminoids. Native forbs were supposed to take up more nutrients than native forbs and equal or lower amounts than native graminoids.

2) Invasive forbs have a higher competitive ability (referred to as biomass production in competition with a native grass) than native forbs, but equal to native graminoids at high nutrient supply. At low nutrient supply, we expected invasive forbs to have equal or lower competitive

ability compared to native species (graminoids and forbs).
Invasive forbs have a higher plasticity in biomass production than native forbs and respond similar as native graminoids to a high nutrient supply compared to a low nutrient supply.
3) Invasive forbs differ from the native species (especially graminoids) in effects on soil nutrient availability and having stronger allelopathic effects than both native plant groups.

Materials and Methods

Investigated plant species

The invasive species selected for our study are abundant throughout the lowlands in Switzerland. They are all forbs, three perennials (*Solidago gigantea*, *Solidago canadensis*, *Fallopia japonica*) and three annuals (*Impatiens glandulifera*, *Impatiens parviflora*, *Erigeron annuus*). We compared the invasive forbs to six native perennial forbs and to six native graminoids (see Table 1). We selected four different native species (two graminoid and two forb species) in each of the following plant communities: *Molinion* (mesotrophic), *Magnocaricion* (meso- to eutrophic) and *Filipendulion* (eutrophic) in Northern Switzerland. These communities are vulnerable to plant invasions in Switzerland if they are not regularly managed or flooded.

Table 1.
Species list for the three plant groups investigated in this study, their family and their native range.

Plant group	Species	Family	Life form	Native range*
Native graminoids	*Molinia caerulea*	Poaceae	perennial	Europe
	Carex panicea	Cyperaceae	perennial	Europe, East North America
	Calamagrostis epigejos	Poaceae	perennial	Europe, East North America
	Carex elata	Cyperaceae	perennial	Europe
	Phragmites australis	Poaceae	perennial	Europe, Atlantic Islands
	Carex acutiformis	Cyperaceae	perennial	Europe
Native forbs	*Succisa pratensis*	Dipsacaceae	perennial	Europe
	Centaurea angustifolia	Asteraceae	perennial	Europe
	Mentha aquatica	Lamiaceae	perennial	Europe, North America, West Asia
	Lythrum salicaria	Lythraceae	perennial	Europe, North Africa, Asia
	Filipendula ulmaria	Rosaceae	perennial	Europe
	Valeriana officinalis	Valerianaceae	perennial	Europe, North America
Invasive forbs	*Solidago gigantea*	Asteraceae	perennial	Northern America
	Solidago canadensis	Asteraceae	perennial	Northern America
	Impatiens glandulifera	Balsaminaceae	annual	Tropical Asia
	Impatiens parviflora	Balsaminaceae	annual	North East Asia
	Fallopia japonica	Polygonaceae	perennial	Temperate Asia
	Erigeron annuus	Asteraceae	annual	North America

* Sources: Weber (2003) Invasive plant species of the world. A reference guide to environmental weeds. Cabi Publishing, UK. Country occurrence data accessed by GBIF (global biodiversity information facility) data portal: www.gbif.net

Experimental design

The experiment was set up in an experimental garden in Zurich, Switzerland (47°24` N, 8°30`E at 520 m a.s.l.), and run for two growing seasons starting in May 2006. Four treatments were applied in the experiment, combining two nutrient levels (low and high) and two competition levels - with and without competition by *Holcus lanatus*. This perennial grass can be abundant in a wide range of herbaceous plant communities and was therefore expected to be a strong competitor at both the low and the high nutrient level. Each treatment was replicated three times for each species, resulting in a total number of 216 pots.

Plants were precultivated from seeds in a greenhouse for ten weeks, except for species with a low germination rate according to previous experiments (the *Carex* species, *Molinia caerulea*, and *Fallopia japonica*). Tillers of these species were sampled in the field, separated into single shoots and kept in tap water until they were transplanted when they had produced new roots. Plants were grown individually in 3-l pots filled with quartz sand (Carlo Bernasconi AG, Zurich, Switzerland, grain size 1-1.7 mm) and placed on saucers to ensure water availability and reduce nutrient losses through leaching. For the competition treatment, three tillers of *Holcus lanatus* were planted around the target plants. Pots were arranged on pallets in a randomized block design in the experimental garden. Each block consisted of 72 pots, i.e. one replicate of each species and treatment per block. Randomisation was repeated three times during the experiment, in September 2006, and March and June 2007. *Holcus lanatus* plants that died in winter 06/07, probably due to frost, were replaced in spring 2007.Plants were watered with tap water and fertilized with nutrient solutions in a biweekly interval during June to October in 2006 and April to October 2007. Plants received either 60 mg N pot^{-1} yr^{-1} or 300 mg N pot^{-1} yr^{-1}. The nutrient solutions had nutrient ratios of 0.7 (N:K), 3.0 (N:Mg), 3.5 (N:Ca), 10 (N:P), and 200-3000 for the micronutrients. Five stock solutions were prepared for fertilization: 1. $Ca(NO_3)_2$, 2. KNO_3 and KH_2PO_4, 3. $MgSO_4$, 4. $FeSO_4$ and 5. $MnCl_2$, H_3BO_3, $ZnSO_4$, Na_2MoO_4 and $CuSO_4$. Just before fertilization, appropriate amounts of each stock solution were added to 22 l of water, once for the "low" and once for the "high" fertilization level, and each pot was then fertilized with 200 ml of the diluted mix of nutrient solutions (low or high). In 2007, we replaced the $Ca(NO_3)_2$-solution by a NH_4NO_3-solution after measuring high pH concentrations (> 7) in some of the pots.

Measurements of plant traits

Leaf life span was determined by leaf tagging in all pots. Individual young (but fully developed) leaves were marked with light strings and their life span was recorded from July to December 2006. Leaves were counted as "dead" when 75% of the leaf was senesced or when it was dropped prior to 75% senescence. The life span of the leaves was corrected for the age of the leaves at time of tagging by recording the period until a new leaf was developed. This period was added to the

observed life span of the tagged leaves.

Acid root phosphatase activity and specific root length (SRL) were measured in October 2006. Roots were sampled from pots without competition to assure measurements at roots of the target species. With a small borer, soil cores (1 cm diameter, 0-10 cm depth) were taken in all pots, and stored at 4 °C until they were processed. Within 24 h after sampling, cleaned root pieces (100 mg) were incubated for 1 h at room temperature in reaction tubes with 5 ml of a 5 mM p-nitrophenyl phosphate (pNPP) solution buffered at pH 6 (Tabatabai & Bremner 1969). The reaction was stopped by adding 500 µl of the sample to 3 ml of 2 N NaOH. The absorbance of the solution was measured at 410 nm using a spectrophotometer (Uvi Light XT2, Secomam, Ales Cedex, France) and converted into the amount of *p*-nitrophenol released from the substrate as a measure of root phosphatase activity. For the determination of SRL, root subsamples (100 mg) were dispersed in a petri dish with a 1-cm^2-grid, and intersections of roots with gridlines in both directions were counted. Root length was estimated as the number of intersections x 11/14 according to Tennant (1975). Subsequently, SRL was calculated as the ratio between root length and root fresh mass.

In August 2007, leaf area was measured of one to six middle-aged leaves per plant, using a leaf area meter LI-3100 (LiCor, Lincoln, Nebraska, USA). The fresh leaf samples were weighed after measuring the area, dried at 75 °C for 24 h and weighed again. Specific leaf area (SLA) was calculated by dividing leaf area by dry leaf mass, tissue density was calculated as dry leaf mass divided by fresh leaf mass, and leaf thickness was determined as leaf fresh mass (roughly equal to leaf volume) divided by leaf area.

Leaf chlorophyll content was measured at three middle-aged leaves per plant in May 2007, using a chlorophyll-meter (SPAD-502, Konica Minolta, Tokyo, Japan). Three measurements were taken on each leaf, and the average of the nine SPAD-values was calculated for each plant.

Three times in 2006, all fresh leaf litter was collected from each pot and air-dried. A subsample of the litter was ground (1 mm). Litter C and N concentrations were measured using an elemental analyzer (CNS-2000, Leco Corporation, St. Joseph, USA). Phenolic compounds were extracted by shaking the litter with 50% Ethanol for one hour (Swain & Hillis 1959). Of these extracts, 100 µl were diluted with 5 ml H_2O before adding100 µl of the Folin-Ciocalteu reagent and 300 µl of 2 M Na_2CO_3. Absorbances were measured at 760 nm and converted into total phenolic concentrations using a tannic-acid-based calibration curve.

Leaf litter decomposition rates were determined in a 10-weeks laboratory incubation experiment. The litter was cut into < 2 cm pieces, and 100 mg subsamples were weighed into 5 x 5 cm nylon litterbags with 1-mm mesh size The litterbags were placed in trays on a 5-cm thick layer of a sand-soil mixture. The soil, collected from a nutrient-poor grassland, was added to the sand as a source of decomposers. To further improve microbial inoculation, the litterbags

were sprayed with a soil suspension (300 g fresh soil in 2 L of deionised water, left over night and filtered through a coarse paper filter) at the start of the incubation. The substrate was kept wet during the study and contact between substrate and litterbags was ensured by a lid loosely placed on the top of the litterbags. The incubation took place in a climate cabinet at 20 °C and 60% relative humidity. After 10 weeks, litterbags were removed from the substrate, cleaned and dried at 75 °C for 24 h. No contamination with soil was observed and leaf litter was therefore not washed before drying. The remaining litter was carefully separated from the bag and weighed to determine litter mass loss during incubation.

The above-ground biomass of all pots was harvested after two growing seasons in October 2007, and sorted into (i) living shoots of the target species, (ii) dead tissue of the target species, and (iii) competitor biomass. Root biomass was only harvested in pots without competition because it was unfeasible to separate roots of the target plants from those of the competitor in the pots with competition. Biomass samples were dried for 48-72 h at 75 °C, and weighed. Plant material of the three replicates was pooled for nutrient analyses, ground and digested for 1 h at 420 °C with concentrated H_2SO_4 and a K_2SO_4-$CuSO_4$ tablet (Foss Kjeltab). N and P concentrations in the digests were determined colorimetrically using a flow-injection analyser (FIAstar 5000, Foss Tecator, Höganäs, SE).

Allelopathy study

The sand from the pots without competition was used to study allelopathy. During the harvest, roots were separated from the sand with a 4-mm sieve, and the sand was kept at 4°C until it was processed (within two weeks). From each sand sample, we filled four 450-ml pots, and divided them among four treatments: with and without charcoal (2% activated charcoal or 18 g per 900 g sand), and with and without fertilizer supply. The fertilizer consisted in 8 mg N, 0.8 mg P, 12 mg K, 2.6 mg Mg and corresponding amounts of micronutrients per pot for the entire experimental period. One sixth of these amounts was supplied weekly as diluted solutions of a) NH_4NO_3, b) KNO_3 and KH_2PO_4, c) $MgSO_4$, d) $FeSO_4$ and e) $MnCl_2$, H_3BO_3, $ZnSO_4$, Na_2MoO_4 and $CuSO_4$. In addition to the harvested sand, pure, fresh quartz sand was subjected to the same four charcoal-fertilizer treatments as a control. All pots were planted with 3-week old seedlings of *Dactylis glomerata* and put in a greenhouse chamber with 16/8 hours light and 20/16 °C temperature as day/night cycle at 70% relative humidity. Plants were watered with deionised water twice a week. Shoot and root biomass of the *D. glomerata* plants was determined after six weeks.

Data analysis

All functional traits were analysed with mixed models including "plant group", "competition" and "nutrient level" as fixed factors and "species" as random factor nested in "plant group". For traits measured only in pots without or with competition (root traits, nutrient uptake, competitor biomass), the model was reduced by excluding the factor "competition".

The competitive ability of each species was calculated by dividing the above-ground biomass produced in competition by that produced without competition. Plasticity in response to nutrient supply was calculated for each species by dividing above-ground biomass produced at high nutrient level to that at low nutrient level. The log-transformed ratios were compared among plant groups and between treatments with mixed models as described above.

Allelopathic effects were calculated for each of the 18 species as the difference between the mean biomass produced by *Dactylis glomerata* with and without charcoal, adjusted for the difference in biomass production due to charcoal addition in the control sand. We only used data from the fertilized pots for these calculations, because charcoal addition negatively affected the biomass production of *D. glomerata* in the unfertilized pots, possibly by reducing nutrient availability (Lau et al. 2008).

All statistical analyses were performed in JMP 7.0.1 (SAS Institute Inc., USA).

Ancillary field sampling

To verify whether plant traits measured in our growth experiment under artificial conditions (plants grown in sand and exposed to full sunlight) correspond to those under natural conditions, we additionally sampled the 18 study species at their natural growth sites in the field. In three regions of Switzerland (cantons Zurich, Schaffhausen and Schwyz), we searched for the 18 study species in an effort to include their full range of habitats according to Lauber & Wagner (2007) and our experience. Each species was sampled at 3 to 11 sites (on average 6 sites). Species that occur in a broad range of habitats (dry or wet grasslands, road margin, river bank, forest edge, forest) were sampled at more sites than species with a narrow range.

To account for plastic responses in light conditions, we recorded the potential duration of insolation at each sampling site. This is the number of hours during which plants receive direct sunlight on a bright day in June, estimated on the basis of the surrounding structures (trees, buildings, topography) with a horizontoscope. Values varied from 0 (full shade in dense forest) to 16 (full sunlight in open, flat areas).

At each site we sampled 20 leaves of each study species that was present. Fully expanded, non-senescent leaves were taken at approximately half of the plant's height (or from rosettes for *Erigeron annuus*). The chlorophyll content of the leaves was measured immediately. Leaves were

taken to the laboratory between wet paper. Their specific leaf area, tissue density and nitrogen content were determined with the same methods as described above.

Differences in leaf traits among the three species groups measured in the ancillary field study were tested with mixed models including groups and insolation as fixed factors and species (nested within groups) as random factors. The group - insolation interaction was not significant for any of the variables and therefore excluded from the final model. To assess how traits in the field compared to those in the growth experiment, we calculated for each species the expected values of leaf traits at mean insolation (with analyses of covariance including species and insolation), and correlated these values with species means from the growth experiment.

Results

Comparison of functional traits among invasive and native species

In the pot experiment, invasive forbs differed from both native forbs and graminoids in two traits: leaf chlorophyll content (Fig. 1a) and the total pool of phosphorus in biomass, both lower in invasive than in native species (Table 2). Furthermore, invasive forbs had lower root phosphorus concentrations than native forbs (Table 2). No other trait differed between the two groups of forbs, but many traits differed among species within groups (Table 3). Many traits also differed between invasive forbs and native graminoids. The invasive forbs had shorter-lived leaves, and their leaves had a lower tissue density than the leaves of native graminoids (Table 2). Furthermore, invasive forbs produced less biomass, and they had a lower total nitrogen pool, lower nitrogen use efficiency, and higher nitrogen concentrations in roots than the native graminoids (Table 2).

In the field, the three plant groups differed significantly in leaf tissue density (lower in forbs than in graminoids) and chlorophyll content (lower in invasive forbs than in native graminoids; Table 4). The SLA and leaf nitrogen concentration did not differ significantly among the three groups despite a tendency (p = 0.09) for higher SLA in the invasive forbs (Table 4). The tissue density, SLA and chlorophyll content of the 18 species correlated well between field samples and the growth experiment (R = 0.6-0.9, Table 4). The N concentration of leaves in the field correlated with the N concentration of roots in the growth experiment (Table 4). Its absence of correlation with the N concentration in shoots may be due to variation in leaf-to-stem ratio in the growth experiment. Overall, these correlations support the validity of plant traits measured in the growth experiment.

Table 2. Plant functional traits, measures of plasticity and effects on soil properties and processes are compared between three plant groups, native graminoids, native forbs and invasive forbs. Means ± SE for the three plant groups were determined from six species per group, grown in pots in an experimental garden under two nutrient levels and with or without competition. Differences between plant groups are derived from three-way ANOVA (see table 3) and Tukey post-hoc test. Mean values sharing letters are not significantly different (α = 0.05).

Traits	Variables	Native graminoids	Native forbs	Invasive forbs
Leaf trait	SLA ($cm^2 g^{-1}$)	129.17 ± 10.74	140.91 ± 12.04	167.44 ± 24.02
Leaf trait	Tissue density	0.43 ± 0.01 a	0.28 ± 0.02 b	0.28 ± 0.03 b
Leaf trait	Leaf thickness (mg cm^{-2})	19.11 ± 1.57 b	27.71 ± 1.96 a	24.46 ± 1.92 ab
Leaf trait	Leaf life span (d)	127.50 ± 1.92 a	101.61 ± 2.37 b	107.61 ± 1.42 b
Leaf trait	Leaf chlorophyll content (SPAD)	30.38 ± 1.53 a	29.63 ± 1.54 a	22.37 ± 1.93 b
Leaf trait	Leaf litter C (%)	44.47 ± 0.34	43.07 ± 0.39	42.93 ± 0.67
Leaf trait	Leaf litter N (%)	1.53 ± 0.17	1.68 ± 0.15	2.02 ± 0.38
Leaf trait	Leaf litter C:N	54.54 ± 4.14	49.69 ± 4.13	52.30 ± 9.23
Leaf trait	Leaf litter phenolics (mg g^{-1})	12.94 ± 1.77	26.36 ± 9.69	19.73 ± 4.59
Whole-plant trait	Shoot biomass (g)	5.66 ± 0.62	4.51 ± 1.73	1.93 ± 0.41
Whole-plant trait	Litter biomass (g)	2.10 ± 0.45 a	1.85 ± 0.22 ab	0.80 ± 0.28 b
Whole-plant trait	Below-ground biomass (g)	44.12 ± 7.99 a	15.92 ± 3.63 b	12.34 ± 5.92 b
Whole-plant trait	Total biomass (g)	56.10 ± 8.28 a	26.68 ± 5.01 ab	17.26 ± 7.04 b
Whole-plant trait	Root mass ratio (%)	77.24 ± 3.28	59.15 ± 7.81	52.60 ± 10.81
Whole-plant trait	Shoot N concentration (mg g^{-1})	8.46 ± 1.43	10.87 ± 2.77	9.02 ± 2.31
Whole-plant trait	Shoot P concentration (mg g^{-1})	0.45 ± 0.07	0.67 ± 0.16	0.62 ± 0.23
Whole-plant trait	Root N concentration (mg g^{-1})	3.19 ± 0.28 b	6.08 ± 1.01 ab	6.88 ± 1.04 a
Whole-plant trait	Root P concentration (mg g^{-1})	0.49 ± 0.04 b	0.87 ± 0.12 a	0.56 ± 0.04 b
Whole-plant trait	Total N pool (mg)	201.15 ± 19.65 a	132.78 ± 13.90 ab	93.24 ± 26.01 b
Whole-plant trait	Total P pool (mg)	25.67 ± 5.13 a	15.68 ± 2.24 a	7.99 ± 2.25 b
Whole-plant trait	Nitrogen use efficiency (g biomass g^{-1} N)	281.73 ± 21.46 a	198.46 ± 38.35 ab	146.57 ± 26.79 b
Whole-plant trait	Phosphorus use efficiency (g biomass g^{-1} P)	2314.16 ± 192.76	1664.76 ± 314.88	1814.77 ± 306.26
Whole-plant trait	Specific root length (m g^{-1})	47.45 ± 11.56	33.04 ± 5.70	16.30 ± 1.79
Plasticity	Response to nutrients	3.46 ± 0.50	3.41 ± 0.34	3.52 ± 0.30
Plasticity	Response to competition	0.31 ± 0.09	0.19 ± 0.04	0.11 ± 0.01
Effects on soil	Litter decomposability (% mass loss)	26.54 ± 1.79 b	37.69 ± 2.88 a	34.73 ± 3.51 ab
Effects on soil	Root phosphatase activity (μM $g^{-1}h^{-1}$)	2.14 ± 0.35	1.61 ± 0.15	1.43 ± 0.54
Effects on soil	Soil total phenolics (μg g^{-1})	34.43 ± 3.10	36.21 ± 1.28	32.19 ± 1.76
Effects on soil	Soil N (mg kg^{-1} soil)	0.80 ± 0.10	0.52 ± 0.09	0.84 ± 0.11
Effects on soil	Soil P (μg kg^{-1} soil)	91.67 ± 19.22	105.00 ± 16.68	135.00 ± 19.79

Note: Some means include both nutrient and competition treatments and some include only nutrient treatments, because these traits were only measured in pots without competition (see Table 3).

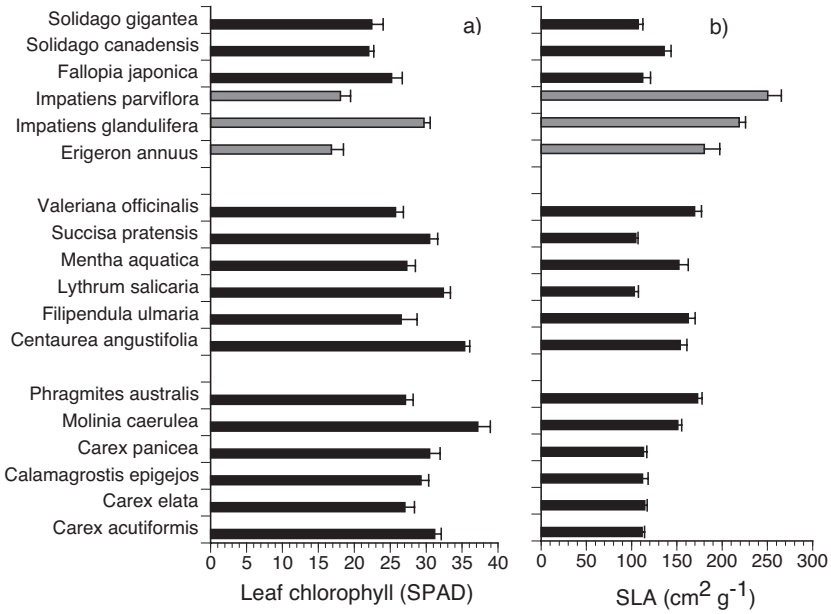

Figure 1. Comparison of functional leaf traits between native and invasive species grown in a pot experiment: means + s.e. (n = 12) of (a) leaf chlorophyll contents and (b) specific leaf area for the six investigated species in each group. In the group of invasive forbs, the three annual species are marked in grey compared to perennials in black.

Plasticity in traits: response to nutrients and competition

Both nutrient level and competition substantially affected plant growth and traits in general (Table 3). The higher nutrient supply significantly increased above- and below-ground biomass production of the 18 species and nutrient pools. Higher nutrient supply had no effect on nutrient concentrations in shoot and root biomass, and leaf chlorophyll content but decreased leaf litter C:N ratios (data not shown).

Plasticity in response to nutrient supply was similar for the three plant groups (no significant group*nutrient interactions in Table 3). On average, plants produced 3.46 times more biomass with the higher nutrient supply, and invasive forbs were not more plastic than the two other groups (Fig. 2a).

Competition by *Holcus lanatus* substantially decreased above-ground biomass production and nutrient concentrations in the biomass. Plants grown in competition also had a higher SLA due to reduced leaf thickness, as well as lower leaf chlorophyll content and litter N concentrations than plants grown without competition (data not shown).

The reduction in biomass production due to competition did not differ significantly among the three groups but varied widely among species within groups (Table 3), especially within native graminoids (Fig. 2b). Individual species produced between 1.6 and 34.6 times less above-ground biomass with competition. The nutrient level had no significant effect on the response to competition, nor did differences among plant groups depend on nutrient supply (Table 3).

Plant groups, however, responded differently to competition in two functional traits (Table 3): litter biomass production was reduced more in the native forbs than in the invasive forbs and native graminoids, and nitrogen concentrations in shoots were reduced only in the invasive forbs (Fig. 3a). This trend was similar for the shoot P concentrations, but not significant ($p = 0.21$, Fig. 3b).

Table 3. Anova results for the effects of plant species (within groups), groups, nutrient level and competition on plant functional traits, plasticity in these traits and on traits affecting soil properties and processes. Plant species were tested as random factor nested in plant group. For each effect, F-ratios and significance levels from the split plot Anova are shown (*** P <0.001, ** P <0.01, * P < 0.05, no sign P ≥ 0.05).

Traits	Species (within Group)	Group	Nutrients	Competition	G*N	G*C	N*C	G*N*C
SLA ($cm^2\ g^{-1}$)	32.04***	1.26	0.93	8.94**	0.70	1.66	2.28	1.80
Tissue density	38.17***	15.51***	0.23	0.05	0.13	1.31	0.17	1.64
Leaf thickness (mg cm^{-2})	61.57**	6.45*	0.82	15.72***	0.27	3.64	2.60	0.34
Leaf chlorophyll content (SPAD)	12.47**	8.64**	32.18***	29.49***	0.65	0.10	1.73	1.41
Leaf life span (d)	0.27	49.20***	0.00	0.00	0.59	2.60	1.20	0.08
Leaf litter C (%)	16.28***	1.44	10.71**	0.15	0.55	1.72	2.63	0.22
Leaf litter N (%)	10.50***	0.26	15.13***	8.01**	0.60	1.11	0.39	0.45
Leaf litter C:N	15.17***	0.07	17.28***	9.13**	0.10	1.82	0.03	0.30
Leaf litter phenolics (mg TAE g^{-1})	9.57***	1.07	2.36	0.27	0.68	0.41	0.14	4.58*
Shoot biomass (g)	1.56	3.08	33.49***	36.90***	1.81	1.27	30.15***	0.94
Litter biomass (g)	5.40***	4.12*	114.52***	110.25***	0.71	3.93*	18.44***	1.49
Below-ground biomass (g)	11.35***	7.86**	86.21***		3.51			
Total biomass (g)	23.74***	6.94**	193.77***		0.22			
Root mass ratio (%)	44.64***	2.59	5.54*		1.36			
Shoot N concentration (mg g^{-1})	27.42**	0.92	2.04	7.98*	0.02	5.36*	0.12	0.53
Shoot P concentration (mg g^{-1})	5.56**	1.21	0.26	4.74*	0.48	1.74	5.89*	1.32
Root N concentration (mg g^{-1})	29.51***	5.15*	0.00		2.37			
Root P concentration (mg g^{-1})	4.45**	6.86**	0.48		0.15			
Total N pool (mg)	21.29***	6.15*	504.69***		0.03			
Total P pool (mg)	13.16***	8.28**	177.68***		1.53			
Nitrogen use efficiency (g biomass g^{-1} N)	27.23***	5.46*	0.11		2.95			
Phosphorus use efficiency (g biomass g^{-1} P)	7.73***	1.84	1.15		0.77			
Specific root length (m g^{-1})	38.69***	2.90	0.06		0.54			
Response to nutrients	0.67	0.33		4.67*		0.28		
Response to competition	4.20**	1.06	2.83		0.33			
Litter decomposability (% mass loss)	1.25	3.99*	0.43	0.00	0.29	0.86	0.12	0.96
Root phosphatase activity (μM $g^{-1}h^{-1}$)	4.69**	1.20	0.04		3.10			
Allelopathic effects (shoot biomass) *	1.62	3.42	2.89		0.36			
Phytometer growth (shoot biomass) †	1.81	6.08*	1.37		0.96			
Soil total phenolics (μg g^{-1})	2.55*	0.85	10.14**		0.48			
Soil N (mg kg^{-1} soil)	0.96	2.29	0.22		0.94			
Soil P (μg kg^{-1} soil)	2.48*	1.59	72.38***		0.01			

* Allelopathic effects refer to differences in biomass production of the phytometer species between soils (pregrown by the study species) amended with fertilizer and with or without the addition of activated charcoal.

† Phytometer growth refers to the biomass production of the phytometer species in soil (pregrown by the study species) to which neither fertilizer nor activated charcoal was added.

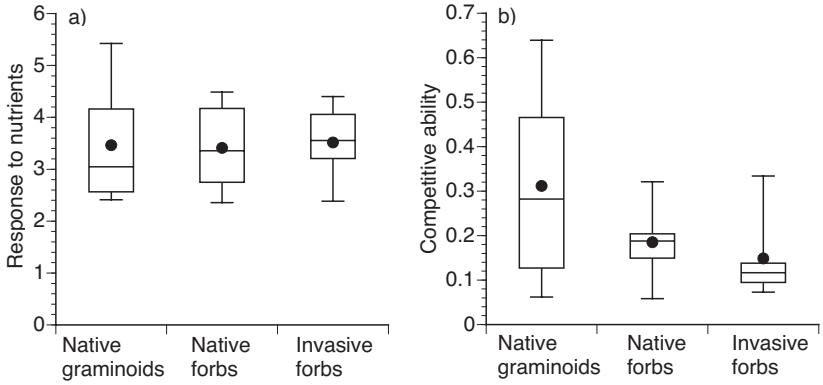

Figure 2. Plasticity of native graminoids, native forbs and invasive forbs: means and data distribution from six species per group for above-ground biomass produced at high compared to a low nutrient level (a) and in competition compared to no competition (b).

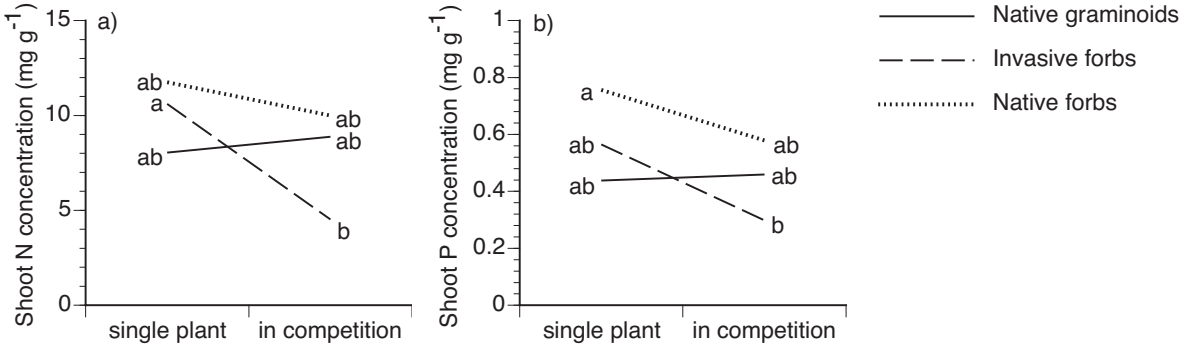

Figure 3. Response of native graminoids, native forbs and invasive forbs to competition in shoot nitrogen (a) and phosphorus concentrations (b). Means are derived from six species per group. Effects are interactions of plant group with competition from three-way anova with post-hoc Tukey test (α = 0.05).

Table 4. Comparison of leaf traits measured in the ancillary field study between native graminoids, native forbs and invasive forbs. Means ± SE were determined from the same six species per group that we used for the experiment. Measurements were conducted at on average six sites per species. The effects of species (nested within plant group), plant group and insolation were tested with mixed models. Differences between plant groups were determined with Tukey post hoc test (α = 0.05); values sharing the same letter are not significantly different. Correlations between field data and experimental data (mean values per species) are shown in the last column.

	Means and SE per group			Test of effects (F, p)		Correlation
	Native graminoids	Native forbs	Invasive forbs	Group	Insolation	*(R, p)*
Tissue density (%)	35.2 ± 2.3[a]	22.6 ± 2.3[b]	21.3 ± 2.1[b]	11.5***	41.6***	0.944***
SLA ($cm^2\ g^{-1}$)§	179.9 + 26.9	214.6 + 31.0	278.7 + 36.3	2.8	67.7***	0.745***
Leaf N concentration ($mg\ g^{-1}$)§	19.5 + 2.8	20.4 + 2.8	24.6 + 3.0	1.0	31.4***	#0.622**
Chlorophyll (SPAD)	38.9 ± 2.1[a]	33.0 ± 2.1[ab]	28.5 ± 1.8[b]	7.0**	2.7	0.620**

Note: test results for the random factor species [group] are not shown.

§ Calculated with log-transformed data; standard errors for positive deviations are given.

Correlation with the N concentration of roots in the growth experiment

Effects on soil

Leaf litter decomposition rates were lowest for the native graminoids, intermediate for the invasive forbs and highest for the native forbs (Table 2).

Allelopathic effects tended to be higher in invasive forbs than in native plant groups ($p = 0.06$). This tendency was only pronounced regarding the shoot biomass of the phytometer *Dactylis glomerata* (Fig. 4), it was not observed for root or total biomass (results not shown). In the pots without fertilization or activated charcoal, biomass production of *D. glomerata* was higher in the soil where invasive forbs had grown than where native forbs had grown, but there was no significant difference to the control pots (Fig. 5).

Root phosphatase activity, concentrations of soluble phenolics and availabilities of N and P in the soil did not differ between the plant groups (Table 2).

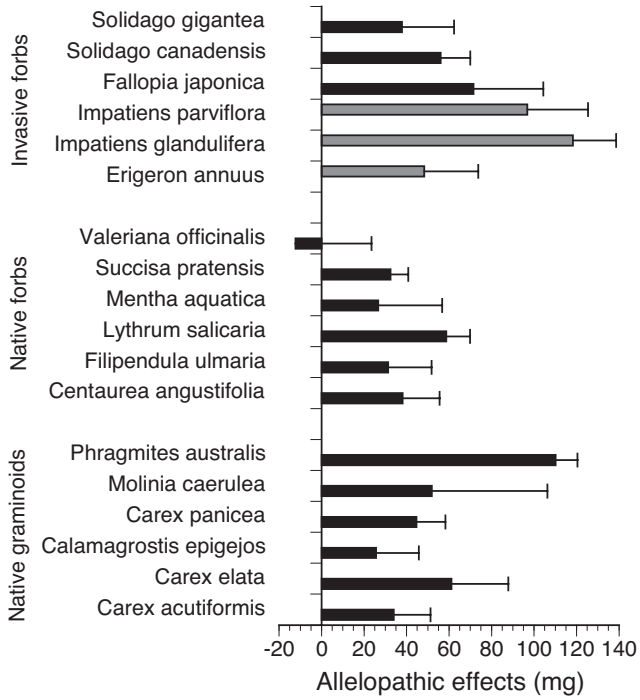

Figure 4. Comparison of allelopathic effects between the 18 investigated species. Allelopathic effects were measured as the differences in shoot biomass production of the phytometer Dactylis glomerata between pre-grown substrates with and without the addition of activated charcoal.

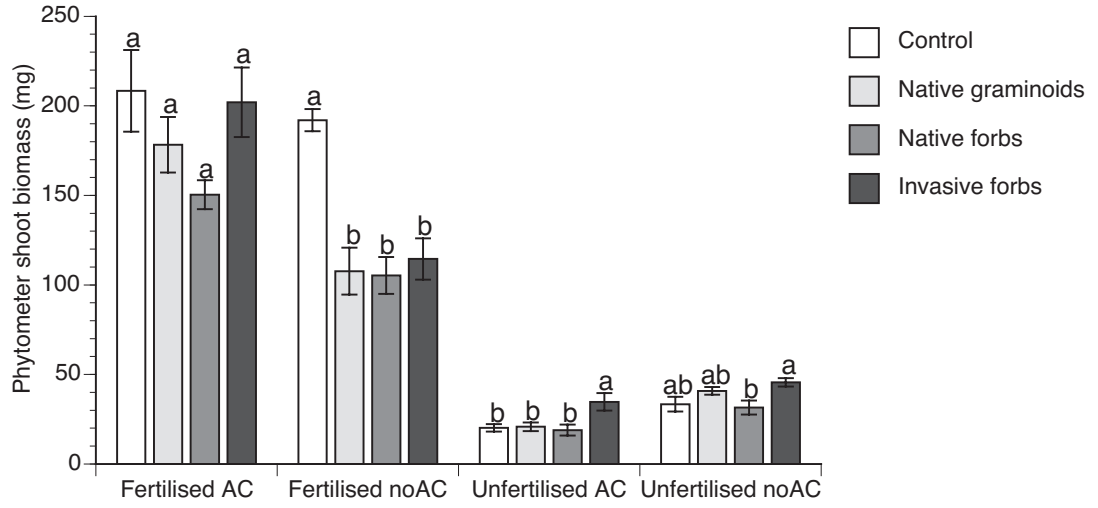

Figure 5. Comparison of phytometer shoot biomass production in pure sand or in sand pre-grown by native graminoids, native forbs or invasive forbs. The pre-grown sand was either fertilised or unfertilised, and activated charcoal (AC) was added to half of the samples to assess allelopathic effects. Letters are from one-way anova and post-hoc Tukey test ($\alpha = 0.05$) comparing plant groups and the control within treatments.

Discussion

Differences in plant traits between invasive and native species

We hypothesized that the invasive forbs would differ from the native species in functional traits, particularly in having higher specific leaf area (SLA), as observed in previous field studies (Smith & Knapp 2001; Grotkopp et al. 2002; Lake & Leishman 2004; Hamilton et al. 2005). However, the invasive species investigated in this study did not have higher SLA than the native forbs or graminoids, neither in the pot experiment nor in the ancillary field survey. In the leaves from the field sites there was a tendency for invasive forbs to have higher SLA than native species (especially graminoids), but light conditions were more important for SLA than the plant group. SLA is one of the most important traits mentioned in studies differentiating between native and invasive species. A high SLA is characteristic of ruderal, short-lived species (McIntyre et al. 2005). In our experiment, the annual invasive forbs *Impatiens glandulifera* and *Impatiens parviflora* had a SLA twice as high (97.9% higher) as the three perennial invasive forbs (cf. Fig. 1b). Similarly, Smith et al (2001) found that an exotic biennial forb had the highest SLA in a comparison with native and exotic legumes and grasses. This could mean that a higher SLA reported for invasive exotic species could partly be due to differences in life-cycle between these invaders and the native species. However, a higher SLA has also sometimes been found for invasive exotic perennials compared to native perennials (Grotkopp et al. 2002; Leishman et al. 2007). The absence of such a difference in the present study probably reflects the fact

that several native forbs were also fast-growing species occurring naturally at nutrient-rich or nutrient-enriched sites.

We also hypothesized that the invasive forbs would have a higher nutrient uptake than native forbs, since invasive species are generally thought to be proficient in nutrient acquisition (Baruch & Goldstein 1999), so that they often increase the nutrient pools in the biomass in comparison to the native vegetation (Ehrenfeld 2003; Vanderhoeven et al. 2006; Dassonville et al. 2007). In contrast, we found that the invasive forbs had 50-70% lower N and P pools in biomass than the native forbs and graminoids. This difference was largely caused by a lower root biomass in comparison to graminoids, especially due to the low root biomass of the annual *Impatiens* species. These results concur with the observation that the *Impatiens* species colonize only nutrient-rich sites, naturally dominated by forbs (Andrews et al. 2005; Hejda & Pysek 2006), whereas the two perennial *Solidago* species are also found in nutrient-poor grasslands (Güsewell et al. 2005; this thesis, Chapter 2).

Leaf chlorophyll content was one of the few functional traits that differed between invasive forbs and native forbs with invasive forbs having lower contents. This was not associated with lower N concentration because chlorophyll content was measured per unit leaf area, and N concentrations measured per leaf mass. This might indicate that invasive species spread their chlorophyll over a larger leaf area. Such a strategy might help plants to grow in a wide range of light environments as it reduces the risk of light inhibition in full sunlight while reducing self-shading when light is scarce. We are not aware of any other study comparing chlorophyll content per leaf area between native and invasive exotic species.

Overall the invasive forbs in our study hardly differed in functional traits from the native forbs but clearly differed from the native graminoids. This difference, which primarily reflects the growth form and anatomy of the species (Cornelissen & Thompson 1997; Grime et al. 1997; Cornelissen 1999), may be of ecological relevance when alien forbs invade ecosystems dominated by graminoids, as this will substantially change the functional trait composition of the vegetation, and potentially also its effect on soil processes (Pokorny et al. 2005; Chapuis-Lardy et al. 2006; Garnier et al. 2007; Suding et al. 2008).

Differences in plasticity; response to nutrients and competition

Invasive species did not increase their biomass more than native species in response to increased nutrient supply, nor were they more plastic in response to nutrient enrichment for any other trait. This differs from previous studies where invasive species responded stronger to nutrient enrichment than native species (Milberg 1999; Craine & Lee 2003). One possible reason is the generally low nutrient availability in our pots, even at the higher nutrient level. Even though nutrient supply was comparable to other experiments (Güsewell et al. 2006; Drenovsky et al.

2008), part of the nutrients probably leached out of the pots due to rainfall and watering. Total nutrient uptake was on average 82% of the supply in graminoids, with an extensive root system, but only 40% in the forbs with their reduced root system. Accordingly, the N and P concentrations were on average 46% lower in the native graminoids and 66% lower in the native forbs in this study compared to N and P concentrations reported from field measurements for these species (Güsewell & Koerselman 2002). Root mass ratios were hardly changed between low and high nutrient treatments (- 3%), indicating low nutrient conditions even with our "high" nutrient level (Aerts & Chapin 2000). However, low nutrient conditions do not have to impair the results of our study. Plant functional traits compared between field and pot measurements for 14 grassland species were found to correlate stronger when plants were grown under unfertilised compared to fertilised conditions in the pots (Mokany & Ash 2008).

The three plant groups also responded similarly to competition by *Holcus lanatus*, which does not support our hypothesis that invasive forbs would be less affected by competition than native species at the high nutrient level. Furthermore, their ability to suppress the competitor was not greater than the ability of the native forbs and tended to be lower than the ability of the native graminoids (*H. lanatus* produced a shoot biomass of 6.6 ± 0.6 g in pots of invasive forbs, 6.1 ± 0.6 g in pots of native forbs and 4.9 ± 0.7 g in pots of native graminoids; $F = 3.54$, $p = 0.055$). Competition reduced the shoot N concentrations of the invasive forbs but not that of the native forbs and grasses. Together with the similar biomass responses, this suggests that the N uptake of invasive forbs was reduced more by competition, although data for roots would be needed for a full assessment. At any event, results suggest a lower, rather than higher, competitive ability of forbs under the generally nutrient-poor conditions of the experiment.

Do the invasive forbs differ in impact on soil processes from native species?

On average leaf litter of invasive forbs decomposed faster in our experiment than that of native graminoids, but not than that of native forbs. This is in agreement with previous studies finding on average faster decomposition for forbs than for graminoids, mainly due to the tougher structure of graminoid leaves (Cornelissen 1996; Cornelissen 1999; Dorrepaal et al. 2005). Since decomposition is a major process for the release of nutrients in soil, the invasion of a grassland by invasive forbs with their shorter-lived and faster decomposing leaves could alter ecosystem nutrient cycling processes (Garnier et al. 2007; Suding et al. 2008). And indeed, alterations in nutrient cycling of habitats after the invasion of an exotic species were related to differences in litter decomposition rates in some studies (Emery & Perry 1996; Ashton et al. 2005; Drenovsky & Batten 2007). Absence of nutrient effects in soil between forbs and graminoids in our study might be due to relatively low nutrient conditions, where every available nutrient was probably immediately absorbed by the plants.

With the exception of one native forb, *Valeriana officinalis,* all investigated species exerted allelopathic effects (Fig. 4). The invasive forbs tended (P = 0.06) to exert stronger allelopathic effects on the shoot growth than the native plant groups. This tendency was due to the strong allelopathic effects of the two annual *Impatiens* species (Fig. 4). *Impatiens glandulifera* is known to be a competitive ruderal (Grime 2001; Andrews et al. 2005), but we are unaware of other studies reporting allelopathic effects for these two species. Nevertheless, this characteristic may certainly contribute to their potential to invade and dominate native vegetations. *Phragmites australis* was the only native species with a similar high allelopathic effect as the two *Impatiens* species. *Phragnites australis* is a competitive invader in North American coastal wetlands from where it is also described to have strong negative allelopathic effects on the growth of co-occuring plants (Zou et al. 2006). So far, most invasive plants described as allelopathic in literature were perennials. In addition to reports for the annuals *Alliaria petiolata* (Prati 2004) and *Parthenium hysterophorus* (Singh 2003) our study shows that two annual invasive *Impatiens* species can be very allelopathic. Thus, life form does not seem to be decisive for the presence or absence of allelopathic effects.

The higher biomass production of the phytometer *Dactylis glomerata* in unfertilized sand pre-grown with invasive forbs compared to native forbs (Fig. 5) might reflect a slight positive effect of invasive forbs on nutrient availability, which compensated any allelopathic effects. However, the difference was small, and accordingly, we did not find differences in soil nutrient availability or soluble phenolics between the plant groups. The reason may be that all measurements were close to the detection limit.

Conclusions

Differences in functional traits seemed to primarily depend on life form and functional group, since the largest differences were found between annual invasive forbs and perennial native graminoids. Exotic invasive plants are therefore most likely to alter ecosystem processes when they displace native species of a differing life form and functional group, respectively (Allison & Vitousek 2004). Often, invasive plants benefit from disturbances in ecosystems for the establishment phase. The ability of invasive plant species to exist and spread once they have established in a habitat (broad niche), might be due to similarities in nutrient use between native and invasive species (in Switzerland). This could also explain, why effects on soil nutrients were not different between these groups (Lavorel & Garnier 2002).

References

Aerts, R. & Chapin, 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.M. 2004. Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. *Oecologia* 141: 612-619.

Andrews, M., Maule, H.G., Raven, J.A. & Mistry, A. 2005. Extension growth of *Impatiens glandulifera* at low irradiance: importance of nitrate and potassium accumulation. *Annals of Botany* 95: 641-648.

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.

Baruch, Z. & Goldstein, G. 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. *Oecologia* 121: 183-192.

Belnap, J., Phillips, S.L., Sherrod, S.K. & Moldenke, A. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* 86: 3007-3017.

Blumenthal, D.M. & Hufbauer, R.A. 2007. Increased plant size in exotic populations: a common-garden test with 14 invasive species. *Ecology* 88: 2758-2765.

Callaway, R.M., Pennings, S.C. & Richards, C.L. 2003. Phenotypic plasticity and interactions among plants. *Ecology* 84: 1115-1128.

Callaway, R.M., Ridenour, W.M., Laboski, T., Weir, T. & Vivanco, J.M. 2005. Natural selection for resistance to the allelopathic effects of invasive plants. *Journal of Ecology* 93: 576-583.

Chapuis-Lardy, L., Vanderhoeven, S., Dassonville, N., Koutika, L.S. & Meerts, P. 2006. Effect of the exotic invasive plant *Solidago gigantea* on soil phosphorus status. *Biology and Fertility of Soils* 42: 481-489.

Cornelissen, J.H.C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* 84: 573-582.

Cornelissen, J.H.C. & Thompson, K. 1997. Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytologist* 135: 109-114.

Cornelissen, J.H.C. 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* 143: 191-200.

Craine, J.M., Berin, D.M., Reich, P.B., Tilman, D.G. & Knops, J.M.H. 1999. Measurement of leaf longevity of 14 species of grasses and forbs using a novel approach. *New Phytologist* 142: 475-481.

Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. 2002. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* 16: 563-574.

Craine, J.M. & Lee, W.G. 2003. Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. *Oecologia* 134: 471-478.

Dassonville, N., Vanderhoeven, S., Gruber, W. & Meerts, P. 2007. Invasion by *Fallopia japonica* increases topsoil mineral nutrient concentrations. *Ecoscience* 14: 230-240.

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

Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallen, B. & Van Logtestijn, R.S.P. 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *Journal of Ecology* 93: 817-828.

Drenovsky, R.E. & Batten, K.M. 2007. Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. *Biological Invasions* 9: 107-116.

Drenovsky, R.E., Martin, C.E., Falasco, M.R. & James, J.J. 2008. Variation in resource acquisition and utilization traits between native and invasive perennial forbs. *American Journal of Botany* 95: 681-687.

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

Emery, S.L. & Perry, J.A. 1996. Decomposition rates and phosphorus concentrations of purple Loosestrife (*Lythrum salicaria*) and cattail (*Typha spp*) in fourteen Minnesota wetlands. *Hydrobiologia* 323: 129-138.

Funk, J.L. & Vitousek, P.M. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446: 1079-1081.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.P., Thebault, A., Vile, D. & Zarovali, M.P. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* 99: 967-985.

Grant, D.W., Peters, D.P.C., Beck, G.K. & Fraleigh, H.D. 2003. Influence of an exotic species, *Acroptilon repens* (L.) DC. on seedling emergence and growth of native grasses. *Plant Ecology* 166: 157-166.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., RossFraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. & Whitehouse, J. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79: 259-281.

Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley and Sons, Chichester, UK.

Grotkopp, E., Rejmanek, M. & Rost, T.L. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* 159: 396-419.

Güsewell, S. & Koerselman, M. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspectives in Plant Ecology, Evolution and Systematics* 5: 37-61.

Güsewell, S., Zuberbühler, N. & Clerc, C. 2005. Distribution and functional traits of *Solidago gigantea* in a Swiss lakeshore wetland. *Botanica Helvetica* 115: 63-75.

Güsewell, S., Jakobs, G. & Weber, E. 2006. Native and introduced populations of *Solidago gigantea* differ in shoot production but not in leaf traits or litter decomposition. *Functional Ecology* 20: 575-584.

Hamilton, M.A., Murray, B.R., Cadotte, M.W., Hose, G.C., Baker, A.C., Harris, C.J. & Licari, D. 2005. Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* 8: 1066-1074.

Hastwell, G.T. & Panetta, F.D. 2005. Can differential responses to nutrients explain the success of environmental weeds? *Journal of Vegetation Science* 16: 77-84.

Hejda, M. & Pysek, P. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological Conservation* 132: 143-152.

Kolb, A., Alpert, P., Enters, D. & Holzapfel, C. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* 90: 871-881.

Küster, E.C., Kuhn, I., Bruelheide, H. & Klotz, S. 2008. Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology* 96: 860-868.

Lake, J.C. & Leishman, M.R. 2004. Invasion success of exotic in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* 117: 215-226.

Lau, J.A., Puliafico, K.P., Kopshever, J.A., Steltzer, H., Jarvis, E.P., Schwarzlander, M., Strauss, S.Y. & Hufbauer, R.A. 2008. Inference of allelopathy is complicated by effects of activated carbon on plant growth. *New Phytologist* 178: 412-423.

Lauber, K. & Wagner, G. 2007. *Flora Helvetica*. Haupt Verlag, Bern, Switzerland.

Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545-556.

Leishman, M.R., Haslehurst, T., Ares, A. & Baruch, Z. 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist* 176: 635-643.

LeJeune, K.D., Suding, K.N. & Seastedt, T.R. 2006. Nutrient availability does not explain invasion and dominance of a mixed grass prairie by the exotic forb *Centaurea diffusa* Lam. *Applied Soil Ecology* 32: 98-110.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society London Series B-Biological Sciences* 270: 775-781.

McIntyre, S., Martin, T.G., Heard, K.M. & Kinloch, J. 2005. Plant traits predict impact of invading species: an analysis of herbaceous vegetation in the subtropics. *Australian Journal of Botany* 53: 757-770.

Milberg, P. 1999. Survival and growth of native and exotic composites in response to a nutrient gradient. *Plant Ecology* 145: 125-132.

Mokany, K. & Ash, J.L. 2008. Are traits measured on pot grown plants representative of those in natural communities? *Journal of Vegetation Science* 19: 119-126.

Moles, A.T., Gruber, M.A.M. & Bonser, S.P. 2008. A new framework for predicting invasive plant species. *Journal of Ecology* 96: 13-17.

Muth, N.Z. & Pigliucci, M. 2007. Implementation of a novel framework for assessing species plasticity in biological invasions: responses of *Centaurea* and *Crepis* to phosphorus and water availability. *Journal of Ecology* 95: 1001-1013.

Pokorny, M.L., Sheley, R.L., Zabinski, C.A., Engel, R.E., Svejcar, T.J. & Borkowski, J.J. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13: 448-459.

Prati, D. 2004. Allelopathic inhibition of germination by *Alliaria petiolata* (*Brassicaceae*). *American Journal of Botany* 91: 285-288.

Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L.I.Z., Walker, K.J. & Rothery, P. 2003. Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* 40: 65-77.

Reich, P.B., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M.G., Knops, J., Wedin, D., Naeem, S., Bahauddin, D., Goth, J., Bengtson, W. & Lee, T.D. 2001. Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO_2 and N availability regimes? A field test with 16 grassland species. *New Phytologist* 150: 435-448.

Reich, P.B., Buschena, C., Tjoelker, M.G., Wrage, K., Knops, J., Tilman, D. & Machado, J.L. 2003. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. *New Phytologist* 157: 617-631.

Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. & Pigliucci, M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981-993.

Rickey, M.A. & Anderson, R.C. 2004. Effects of nitrogen addition on the invasive grass *Phragmites australis* and a native competitor *Spartina pectinata*. *Journal of Applied Ecology* 41: 888-896.

Singh, H.P. 2003. Assessment of allelopathic properties of *Parthenium hysterophorus* residues. *Agriculture, Ecosystems & Environment* 95: 537-541.

Smith, M.D. & Knapp, A.K. 2001. Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *International Journal of Plant Sciences* 162: 785-792.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125-1140.

Swain, T. & Hillis, W.E. 1959. The phenolic constituents of *Prunus domestica*. I - The quantitative analysis of phenolic constituents. *Journal of Science, Food and Agriculture* 10: 63-68.

Tabatabai, M.A. & Bremner, J.M. 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. *Soil Biology and Biochemistry* 1: 301-307.

Tennant, D. 1975. Test of a modified line intersect method of estimating root length. *Journal of Ecology* 63: 995-1001.

Thompson, K., Hodgson, J.G. & Rich, T.C.G. 1995. Native and alien invasive plants: more of the same? *Ecography* 18: 390-402.

Thompson, K., Hodgson, J.G., Grime, J.P. & Burke, M.J.W. 2001. Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *Journal of Ecology* 89: 1054-1060.

Vanderhoeven, S., Dassonville, N., Chapuis-Lardy, L., Hayez, M. & Meerts, P. 2006. Impact of the invasive alien plant *Solidago gigantea* on primary productivity, plant nutrient content and soil mineral nutrient concentrations. *Plant and Soil* 286: 259-268.

Wardle, D.A., Barker, G.M., Bonner, K.I. & Nicholson, K.S. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology* 86: 405-420.

Zou, J., Rogers, W., DeWalt, S. & Siemann, E. 2006. The effect of Chinese tallow tree (*Sapium sebiferum*) ecotype on soil-plant system carbon and nitrogen processes. *Oecologia* 150: 272-281.

Chapter 2

The invasive alien plant species *Solidago gigantea* alters ecosystem properties across habitats with differing fertility

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Abstract

Invasive alien plants can have effects upon biomass production and rates of biogeochemical cycling ranging from positive to negative. We hypothesised that the direction and intensity of such effects depend not only upon functional traits of native and alien species, but also upon properties of the invaded habitat, with the same alien species having differing impacts in different habitats. To test this hypothesis, we surveyed fourteen grassland and wetland sites in Switzerland invaded by the alien forb *Solidago gigantea*, which differed widely in biomass production and soil phosphorus availability. To determine whether the impact of the species was related to site fertility, we compared the invaded and uninvaded vegetation in terms of biomass, species composition, plant traits and soil properties. *S. gigantea* generally increased the above-ground biomass production of the vegetation and soil C content, while reducing nutrient concentrations in biomass and N availability in soil. However, it had no significant effect on plant species richness, below-ground biomass, soil respiration, soil pH and P availability. Leaves of *S. gigantea* had a higher C content than those of native species; other leaf traits and root phosphatase activity did not differ significantly. These results suggest that a conservative nutrient-use strategy allows *S. gigantea* to invade a broad range of habitats, and that this also determines its impact on biogeochemical cycling. The observed effects of invasion did not vary according to biomass production of the invaded sites, but some effects did depend on soil P availability, being more pronounced at more P-rich sites. Effects upon soil C:N ratio ranged from a decrease at P-poor sites to an increase at P-rich sites. Thus, the full range of invaded habitats should be considered in studying the potential impact of plant invasions on ecosystem processes.

Introduction

The displacement of native plant species by invasive plants is a major concern for nature conservation managers. To tackle this problem, the mechanisms underlying the impacts of invasive plants on the invaded communities need to be understood (Parker et al. 1999; Levine et al. 2003). Besides direct competitive exclusion, invasive plants may reduce native species diversity indirectly by changing soil processes so as to create a positive feedback-loop that promotes the growth and spread of the invader (Miki & Kondoh 2002; Ehrenfeld 2003). For example, invasive plants can influence nutrient cycles by changing the timing of nutrient uptake and nutrient release, by producing litter of different quality, by introducing different nutrient acquisition strategies (N_2-fixation, mycorrhiza, deep rooting), or by having higher or lower nutrient use efficiency than the established plant community (Evans et al. 2001; Mack et al. 2001; Blank & Young 2002; Windham & Ehrenfeld 2003; Chapuis-Lardy et al. 2006; Sala et al. 2007). Studies investigating impacts of invasive plants on soil processes have mainly pointed towards a stimulation of nutrient cycling and increased nutrient availability, although opposite effects have also been observed for individual species (Ehrenfeld 2003).

The overall tendency of plant invasions to stimulate nutrient cycling and to increase site fertility reflects the typical traits of successful plant invaders. Phenotypic plasticity, relative growth rate, specific leaf area (SLA) and nutrient concentrations in plant biomass and litter tend to be higher in invasive plants than in co-occurring native plant species (Grotkopp et al. 2002; Daehler 2003; Ehrenfeld 2003; Hamilton et al. 2005; Leishman et al. 2007). However, not all invasive plants exhibit these traits, and the impacts on ecosystems of plants with contrasting functional traits may differ (Vila et al. 2006). For example, Yelenik et al. (2007) found that two invasive legumes both increased nitrogen availability through N_2-fixation, but only the perennial woody species, due to its more refractory litter, caused a build-up of organic nitrogen. Thus, studying the functional traits of invasive plants helps to better understand the changes in ecosystem processes associated with their invasion (Eviner 2004; Gurvich et al. 2005; Suding et al. 2008).

The impacts of invasive plants may also depend on properties of the invaded ecosystem, with site fertility being particularly important (Funk & Vitousek 2007). According to initial site fertility, invasive plant species may increase or decrease nutrient concentrations in soil, as has just been recently shown for highly invasive species in Belgium (Dassonville et al. 2008). The 'typical' plant traits associated with invasiveness (see above) generally confer a competitive advantage upon a species at nutrient-rich sites (Aerts 1999; Leishman et al. 2007), and nutrient enrichment has indeed been found to promote plant invasions (Daehler 2003; Lake & Leishman 2004). However, nutrient-poor ecosystems may also be invaded, usually by species that use

resources more conservatively (Monaco et al. 2005; Funk & Vitousek 2007) or are more plastic than the native species (Richards et al. 2006; Schumacher et al. 2009). Nutrient-limiting growth conditions can lead to different or weaker effects of invasive species on soil properties and processes (Kueffer et al. 2008). We might therefore expect plant species that invade both nutrient-poor and nutrient-rich sites to have varying impacts, especially if the relevant functional plant traits vary according to site fertility.

An ideal species to test this hypothesis is the perennial rhizomatous forb *Solidago gigantea* (Asteraceae). It was amongst the earlier neophyte invaders in Central Europe, spreading extensively between 1850 and 1889 (Weber & Jakobs 2005), and nowadays it occupies a large variety of habitats, ranging from dry to wet and from nutrient-rich to nutrient-poor (Güsewell et al. 2005; Weber & Jakobs 2005). Studies in grasslands in Belgium revealed higher aboveground production, P uptake and labile P concentrations in invaded than uninvaded sites (Vanderhoeven et al. 2005; Chapuis-Lardy et al. 2006; Vanderhoeven et al. 2006). These results pointed to an increased P turnover in *S. gigantea* stands (Vanderhoeven et al. 2006; Herr et al. 2007). Such an effect would be a matter for concern, since it could potentially displace native plant species adapted to low P availability (Wassen et al. 2005) and promote further spread of invasive plants. However, the sites studied were ruderal grasslands with relatively high P concentrations in plants and soil, and it remains uncertain whether *S. gigantea* has undesirable effects in nutrient-poor ecosystems, these being of particular conservation interest.

In this study, we surveyed fourteen sites naturally invaded by *S. gigantea* and representing a wide range of habitat types of differing fertility. Our aim was to answer two main questions: (i) Does *S. gigantea* affect ecosystem properties across a broad range of habitats? and (ii) Do invasion effects depend on site fertility prior to invasion?

Materials and methods

Site selection

In summer 2006, fourteen sites with semi-natural vegetation invaded by *Solidago gigantea* were selected in northern and western Switzerland (46-47°N, 6-9°E), ranging from 350 to 500 m a.s.l. Criteria for site selection were that (i) the native plant community should be well established (no recently invaded sites) and visually homogeneous, (ii) *Solidago* invasion should not be associated with obvious heterogeneities in soil or terrain, or with previous disturbance, (iii) the survey should include a range of habitats from dry or semi-dry, nutrient-poor grasslands to highly productive wetlands and agricultural old-fields (established several years ago and with a dense vegetation cover).

The selected sites varied widely in the density of *S. gigantea* stands, ranging from 45 to 280 stems m^{-2}. At all sites, *S. gigantea* stands formed distinct patches of one to several meters diameter within the native vegetation. Sampling mostly took place in summer 2006, but some additional measurements were made in spring and autumn 2007 (as described below). In the following, we refer to areas without *S. gigantea* as "uninvaded patches", and to their plant communities as "native vegetation". Stands of *S. gigantea* are called "invaded patches" of "invaded vegetation", although they also contained native species. By analogy, the soil found under the native or invaded vegetation is called "native soil" and "invaded soil", respectively.

Vegetation description

Within an area of 50-100 m^2 at each site, three plots of 40 x 40 cm^2 (in total 0.5 m^2) were located in the native vegetation (uninvaded patches) and three plots in stands of *Solidago* (invaded patches). In July 2006, the height of the vegetation was recorded in all plots, and the shoot number of *S. gigantea* was counted in the invaded plots. The species composition of each plot was recorded (without abundance data) and used to establish two pooled species lists for each site, one for the native vegetation and one for the invaded vegetation (see Appendix 1). Species numbers as well as average ecological indicator values for moisture (F) and nutrients (N) (Ellenberg et al. 1997) were calculated for the total area of 0.5 m^2 in the native as well as in the invaded vegetation of each site. *S. gigantea* was excluded from these calculations, which were intended to detect how the presence of this species influenced floristic composition.

The above-ground biomass of the plots was harvested, dried for 48 h at 75 °C, and weighed. Below-ground biomass samples were collected at four sites (wetlands) in summer 2006 from an area of 20 x 20 cm^2 and a depth of 0-15 cm within the selected plots. Roots and rhizomes were cleaned from soil and these samples were also dried and weighed. The dried plant material (above- and below-ground) was ground to 1 mm prior to chemical analyses. Kjeldahl-nitrogen and phosphorus concentrations were determined in the dried plant material by acid digestion, where ground plant material was digested with concentrated H_2SO_4 and a Kjeltab (3.5 g K_2SO_4 / 0.4 g $CuSO_4$, FOSS Analytical AB, Höganäs, Sweden) at 420 °C for 1 h. N and P concentrations of the digests were analysed using a flow injection analyser FIASTAR 5000 (FOSS Tecator AB, Höganäs, Sweden).

Species properties

To determine differences or similarities in leaf traits between the invader *S. gigantea* and dominant native species, we sampled ten to 20 leaves from *S. gigantea* and from two or three dominant species of the adjacent native vegetation at each site in July 2006. Leaves of native species were sampled in the uninvaded patches. Samples were kept between wet paper to saturate

leaf tissue with water until they were processed later in the same day. Leaf area was measured using a leaf area meter LI-3100 (LiCor, Lincoln, Nebraska, USA), and the samples were then weighed, dried at 75 °C for 24 h and weighed again. The measurements were used to calculate the specific leaf area (SLA; leaf area divided by dry mass), tissue density (dry mass divided by fresh mass), and leaf thickness (fresh mass - approximately equal to leaf volume - divided by leaf area). Carbon and nitrogen concentrations of the dried leaf material were measured using an elemental analyzer (CN-2000, Leco Corporation, St.Joseph, USA).

Additionally, root phosphatase activity was determined with root samples obtained from soil cores (4 cm diameter) taken in the uninvaded and invaded patches (n = 5 cores). In the invaded patches, only roots of *S. gigantea* were collected; in the uninvaded patches, all roots were collected but no attempt was made to identify the species. Within 24 h after soil core sampling, cleaned roots (100 mg) were incubated for 1 h at room temperature in reaction tubes with 5 ml of a 5 mM *p*-nitrophenyl phosphate (pNPP) substrate solution buffered at a pH of 6 (Tabatabai & Bremner 1969). The reaction was stopped by adding 500 µl of the samples to 3 ml of 2 N NaOH. The absorbance of the solution was measured at 410 nm using a photometer Uvi Light XT2 (Secomam, Ales Cedex, France) and used to calculate the amount of *p*-Nitrophenol released from the substrate as a measure of root phosphatase activity.

Soil properties

Immediately after the biomass had been harvested, five soil cores (4 cm diameter, 0-15 cm depth) were taken in the uninvaded and invaded patches and kept at 4 °C until they could be processed. Fresh soil samples were analysed for pH, availability of N and P, and phosphatase activity within 48 h after sampling. Soil pH was determined in distilled water. Ammonium and nitrate availability were determined with 0.2 M potassium chloride extractions, by shaking 20 g of fresh soil in 100 ml of KCl for 1 h. Phosphate availability (Olsen-P) was assessed with 0.5 M sodium bicarbonate extractions, by shaking 10 g of fresh soil in 100 ml $NaHCO_3$ (pH 8.5) for 1 h (Allen 1989). N and P concentrations in the soil extracts were measured using the flow injection analyser FIASTAR 5000. Phosphatase activity in soil was determined using modification of the *p*-Nitrophenyl phosphate (pNPP) method of Tabatabai (1969). Two grams of fresh soil were mixed with 5 ml of a 200 µM pNPP substrate solution and gently shaken for 1 h at room temperature (pH was not manipulated). After the addition of 200 µl of 2 N NaOH to the samples, the absorbances were measured at 410 nm using the photometer Uvi Light XT2. Soil samples were dried at 105 °C for 24 h to determine the dry weight percentage. They were subsequently ground in a mortar to analyse total C and N concentrations using the elemental analyzer CN-2000.

In spring 2007 (April), when soil biota were assumed to be very active, soil respiration was measured at six of the sites (four semi-dry grasslands and two wetlands) in three replicate patches per vegetation type (uninvaded or invaded). For this purpose, we used a soil respiration chamber (991 cm^3 volume) attached to a portable infrared gas analyser (Li 6400, LiCor, Lincoln, Nebraska, USA). To minimise effects of soil disturbance, the PVC collars (10.5 cm diameter) were inserted into the soil 24 h before the measurements began. In the same plots, soil temperature and soil moisture at 5 cm depth were measured using a contact thermometer (testo 112, testo AG, Mönchaltorf, Switzerland) and a TDR probe (HH2 Moisture Meter, Delta-T Devices Ltd, Cambridge, UK).

Nutrient availabilities in the soil under native and invaded vegetation were investigated *in situ* using ion-exchange resin (IER) bags in October 2007, when litter decomposition processes were supposed to take place. Each IER bag consisted of 2 g mixed-bed ion-exchange resin (Amberlite IRN 150, H^+- and OH^--form, Sigma-Aldrich, Switzerland), which was filled in 5 x 5 cm^2 bags made of fine nylon fabric (60 µM mesh width, Sefar Nitex 03- 60/35, Sefar AG, Thal, Switzerland). Before use, the IER bags were shaken twice for 30 min with 1 M KCl to saturate exchange sites with K^+ and Cl^- ions. Six IER bags were inserted 1-2 cm below soil surface in each of the two vegetation types (native or invaded) within an area of 50-100 m^2 at each site. IER bags were removed from soil after one month, cleaned with deionised water and extracted in 50 ml of 0.5 M HCl by shaking for 1 h. IER-extracts were analysed for ammonium and nitrate concentrations using a flow injection analyser FIASTAR 5000. Phosphate concentrations were determined in the IER-extracts by the acid molybdate blue method (Murphy & Riley 1962), and absorbance was measured at 880 nm using the photometer Uvi Light XT2.

Data analysis

To test whether ecosystem properties differ between native and invaded vegetation (Question 1) and whether these differences depend on site fertility (Question 2), we first carried out two-way analyses of variance with the factors "invasion" (fixed) and "site" (random). These analyses revealed significant invasion*site interactions for most variables, confirming that invasion effects vary among sites (results not shown in this paper). We then performed analyses of covariance with "invasion" as fixed factor and site fertility as covariable to test for shifts in the direction or intensity of invasion effects along fertility gradients. To select the variable(s) describing site fertility (prior to invasion), we performed a principal component analysis (PCA) on correlations of vegetation and soil properties measured in the native vegetation. This analysis revealed two main gradients, which together explained 61% of the variation among sites. The first PCA axis (35% of variation), referred to as "productivity gradient", correlated positively with above-ground biomass, vegetation height, soil C and N contents and KCl-extrated N, but

negatively with IER-N. We chose to represent it by above-ground biomass because this variable is most easily compared across studies. Correlations between biomass and the other variables are shown in Table 1. The second PCA axis (28% of variation), referred to as "P availability gradient", correlated positively with IER-P, the P concentration and P pool of the vegetation and the Ellenberg N indicator value (Table 1). We represented this axis by Olsen-P in data analysis. Given the complementary character of the two gradients across the investigated habitats, both were included in the analyses. All variables were thus analysed with linear mixed models including the invasion effect (uninvaded vs. invaded patches) as fixed factor, productivity and P availability as covariables, and sites as random factor. Variables measured at only four sites (below-ground biomass and root mass ratio) were analysed without covariables because of the small site number.

Functional leaf traits were compared between *S. gigantea* and native plant species, with an additional distinction being made between native grasses and forbs to account for differences between these functional groups. A two-way anova was performed, with species group (*S. gigantea*, native forbs, native grasses) and site as factors.

All statistical analyses were performed with R (Version 2.5., R Foundation for Statistical Computing, Vienna, Austria).

Table 1. Correlations of the two site fertility gradients, above-ground biomass productivity (Prod) and soil P availability (Olsen extraction; Pav), with measured vegetation and soil properties of the native vegetation from 14 studied sites. Shown are Pearson's correlation coefficients and significance levels (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, no sign $P \geq 0.05$).

	Prod §	Pav §
Aboveground biomass	–	0.242
Vegetation height	0.839***	0.127
N pool in biomass	0.823***	0.135
Soil N availability (KCl)	0.618*	0.238
Soil N availability (IER)	-0.695*	0.103
Soil N_t	0.737**	0.049
Soil C_t	0.869***	-0.008
Root phosphatase activity	0.710**	0.021
Soil phosphatase activity	0.447	-0.448
N concentration in biomass	-0.006	-0.176
Leaf N conc	0.477	0.417
Species number	-0.477	-0.571*
Nutrient indicator value (N)	0.238	0.814***
SLA	-0.321	-0.663*
P concentration in biomass	-0.012	0.814***
P pool in biomass	0.576*	0.739**
Soil P availability (IER)	-0.041	0.778**

Note: § Data were log-transformed prior to analysis

Results

Vegetation and species properties

Native plant species richness in uninvaded patches at the 14 investigated sites ranged from four to 16 species (within a total area of 0.5 m^2) and was not significantly changed by the invasion of *Solidago gigantea* (Table 2); differences ranged from –82% to +40% at individual sites. Ellenberg moisture indicator values of the vegetation ranged from rather dry (4.1) to wet (8.6), and nutrient indicator values ranged from nutrient-poor (3.0) to nutrient-rich (7.8) across sites; invaded and native vegetations did not differ.

Above-ground biomass ranged from 0.19 to 1.26 kg m^{-2} in the native patches and was significantly increased (on average by 87%) by the invasion of *S. gigantea* (Table 2, Fig. 1a). Vegetation in the invaded plots was also taller (Table 2). Below-ground biomass (at four of the sites) did not differ significantly between the invaded and the native vegetation, so that below-ground parts represented a smaller fraction of total biomass in the invaded vegetation (Table 2).

Nitrogen and phosphorus concentrations in the above-ground biomass were lower in the invaded vegetation than in the native vegetation (Fig. 1c-d, Table 2). The reduction in P concentration was most pronounced at sites with high P availability (Fig. 2d; I*Pav interaction in Table 2). The P pool in the above-ground biomass was 1.3 times higher in invaded than in native vegetation (Table 2), but there was no difference between the N pools.

Table 2. Vegetation properties compared between native vegetation and adjacent invaded vegetation (*Solidago gigantea*) at four to fourteen semi-natural sites in Switzerland. Means ± SE of native and invaded vegetation were calculated from n sites based on the total of three plots (for species number), the means of three plots, or the means of five root samples (for root phosphatase activity). Effects of invasion, dependence on site productivity (Prod) and P availability (Pav), as well as interactions were tested using linear mixed models, with sites as random factor. For each effect, F ratios and significance levels are shown (*** P < 0.001, ** P < 0.01, * P < 0.05, no sign P ≥ 0.05).

		Mean ± SE		Tests of effects (F, P)				
Variable	n	Native	Invaded	Invasion	Prod	I x Prod	Pav	I x Pav
Species number	14	9.71 ± 0.89	8.21 ± 1.30	2.7	1.9	0.6	5.2*	1.1
Moisture indicator value (F)	13	6.62 ± 0.35	6.37 ± 0.33	2.5	5.1*	0.0	6.4*	1.9
Nutrient indicator value (N)	13	5.02 ± 0.23	5.25 ± 0.29	0.0	1.8	0.2	7.4*	0.7
Aboveground biomass (kg m^{-2})	14	0.56 ± 0.06	0.98 ± 0.09	29.5***	59.0***	2.4	1.6	2.1
Vegetation height (m)	13	0.79 ± 0.07	1.18 ± 0.06	18.3**	27.7***	0.8	0.3	2.7
N conc in biomass (mg g^{-1})	14	9.62 ± 0.63	6.89 ± 0.60	23.1***	0.0	0.0	1.0	0.4
P conc in biomass (mg g^{-1})	14	1.04 ± 0.09	0.76 ± 0.05	20.1***	0.2	0.5	29.9***	16.0**
N pool in biomass (g m^{-2})	14	5.36 ± 0.77	6.55 ± 0.87	2.0	21.0***	0.2	0.2	0.0
P pool in biomass (g m^{-2})	14	0.57 ± 0.09	0.76 ± 0.10	9.7**	9.8**	0.0	14.2**	0.7
Root phosphatase activity (μM g^{-1} h^{-1})	12	2.90 ± 0.22	1.99 ± 0.19	3.6	19.0**	0.3	1.9	0.4
Belowground biomass (kg m^{-2}) §	4	1.38 ± 0.20	1.30 ± 0.36	0.1				
Root mass ratio §	4	0.59 ± 0.03	0.48 ± 0.03	36.0**				

§ Invasion effects were analysed without covariables due to reduced site number.

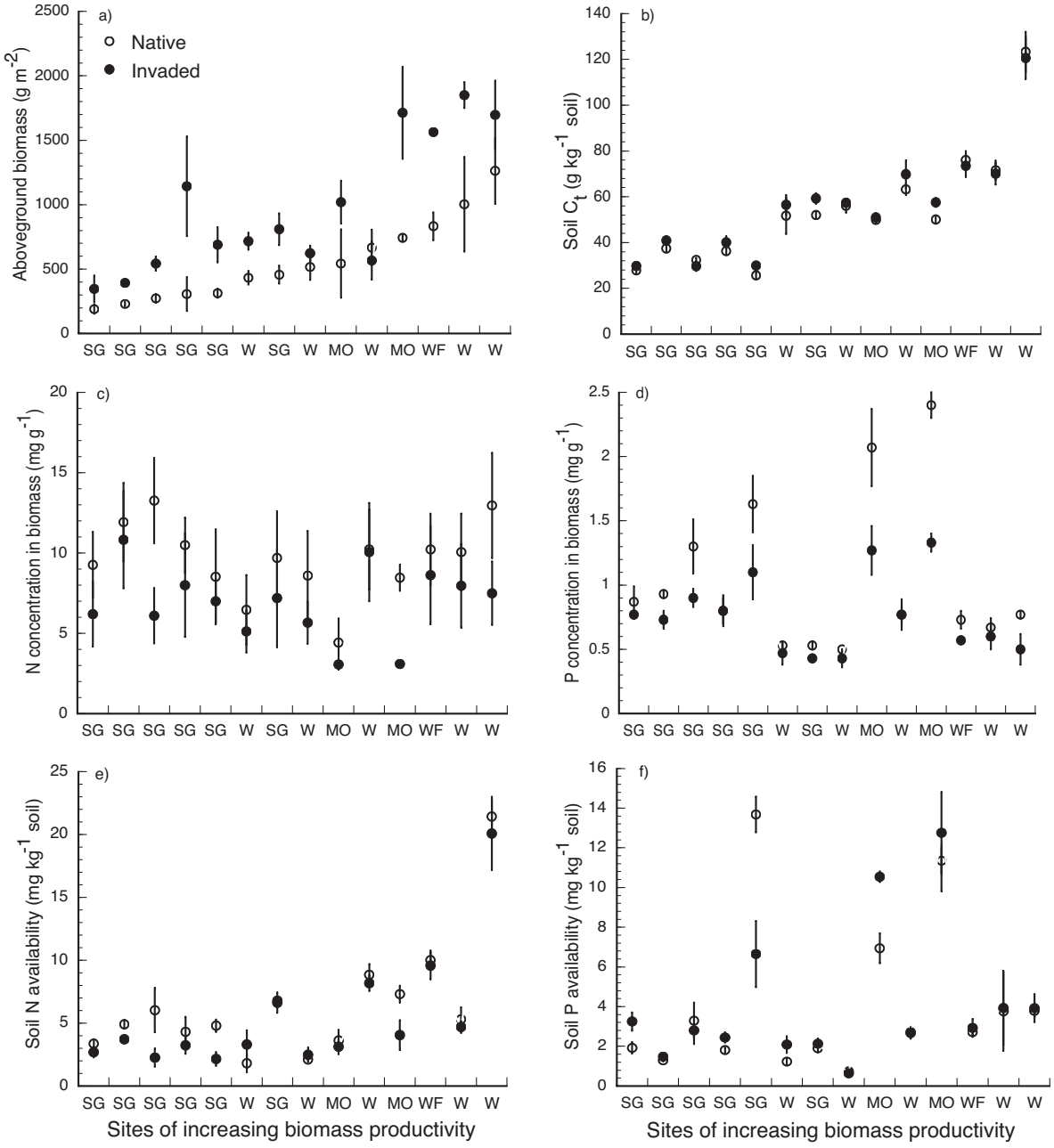

Figure 1. Traits and associated soil properties of native and invaded (*Solidago gigantea*) vegetations along the biomass productivity gradient of fourteen sites in Switzerland: above-ground biomass production (a), total soil carbon concentration (b), N and P concentrations in the above-ground biomass (c, d) and soil N and P availabilities determined by soil extractions (e, f). Shown are means ± se of three plots (a-d) or five soil samples (e, f) per vegetation type. Sites were grouped as follows: SG = Semi-dry grassland, W = Wetland, MO = Moist old-field, WF = Wet forest skirt.

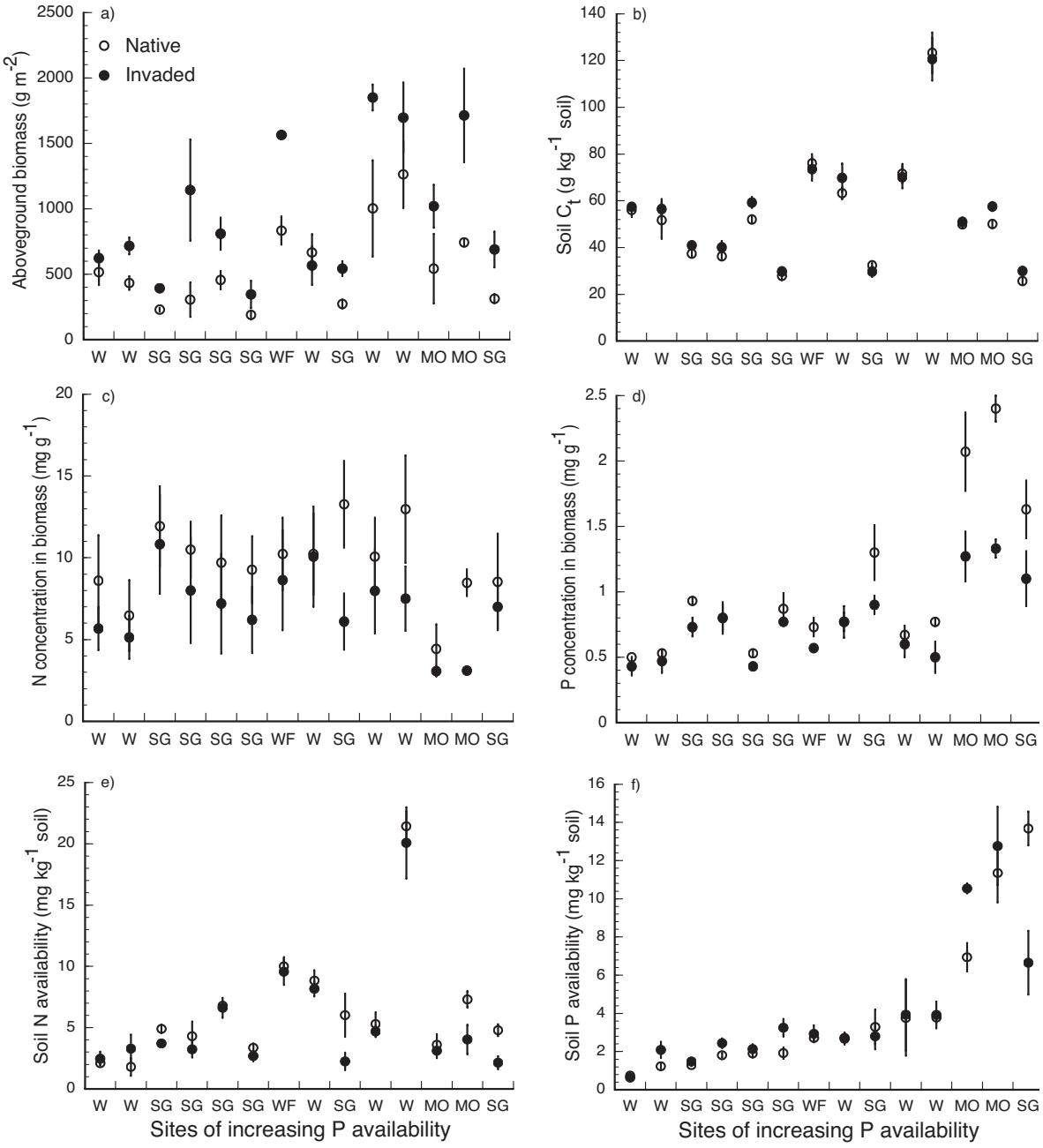

Figure 2. Traits and associated soil properties of native and invaded (*Solidago gigantea*) vegetations along the soil P availability gradient of fourteen sites in Switzerland: above-ground biomass production (a), total soil carbon concentration (b), N and P concentrations in the above-ground biomass (c, d) and soil N and P availabilities determined by soil extractions (e, f). Shown are means ± se of three plots (a-d) or five soil samples (e, f) per vegetation type. Sites were grouped as follows: SG = Semi-dry grassland, W = Wetland, MO = Moist old-field, WF = Wet forest skirt.

Leaves of *S. gigantea* had a higher C concentration than leaves of the dominant native species (Fig. 3a). Other leaf traits (SLA, leaf thickness, leaf tissue density, leaf nitrogen concentration or C:N ratio) did not differ significantly between *S. gigantea* and native species (Fig. 3). When functional groups were distinguished, *S. gigantea* and native forbs had lower leaf tissue densities than native grasses (Fig. 3d). The root phosphatase activity of *S. gigantea* tended to be lower than that of the native vegetation, but the difference was not significant (p = 0.09, Table 2).

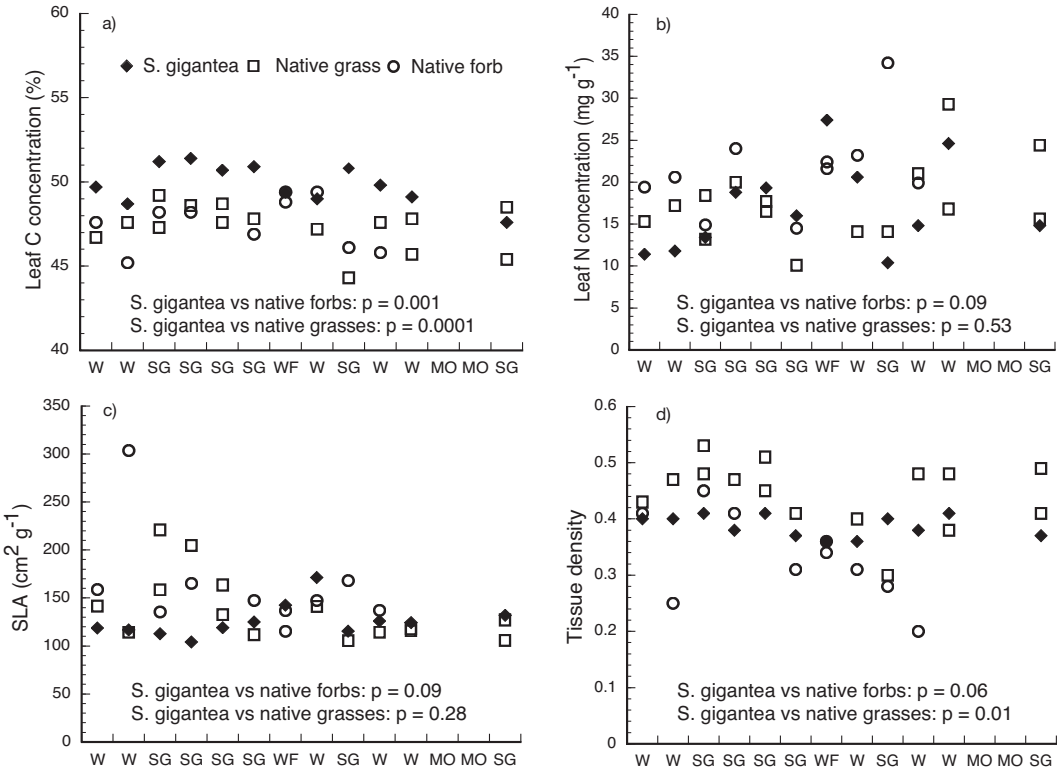

Fig. 3. Leaf traits comparison between the invader *Solidago gigantea* and dominant native grass and/or forb species along the soil P availability gradient of fourteen sites. Shown are means of leaf C and N concentrations (a+b), specific leaf area (c), and leaf tissue density (d, determined as dry leaf mass divided by fresh mass). Results are from two-way anova including site and species as factors. Sites are ordered according to the P availability gradient (cf. Fig. 2) and were grouped as follows: MO = Moist old-field, SG = Semi-dry grassland, W = Wetland, WF = Wet forest skirt.

Soil properties

The soils at the various sites ranged from loam to peat, and all soil properties also varied widely among sites. However, only few variables appeared to be influenced by *S. gigantea*. Total carbon concentrations, which ranged from 25.7 to 123.3 g kg^{-1}, were on average 6% higher in nvaded soils (Fig. 1b, 2b, Table 3). Total nitrogen concentrations ranged from 1.2 to 10.3 g kg^{-1} and did not differ between native and invaded plots (Table 3). For the soil C:N ratio, differences depended on soil P availability (significant interaction): the soil C:N ratio was reduced under invaded vegetation at sites with low P availability, and increased at sites with higher soil P availability.

Inorganic N concentration (ammonium + nitrate) was 16% lower in invaded plots than in the native ones (Fig. 1e, 2e and Table 3). Both nitrate and ammonium concentrations were reduced similarly, although the effect was only significant for nitrate (Table 3). These differences depended also on soil P availability, with greater reductions in soil N and nitrate concentrations at sites with higher P availabilities (Table 3, Fig. 2e). The phosphate concentration (Olsen-P) varied widely among sites (0.6-13.7 mg P kg^{-1} soil), but was not significantly affected by *Solidago* invasion (Table 3, Fig. 1f, 2f). Also, there was no interaction between P availability in the native vegetation and the effect of *Solidago* invasion on soil phosphate concentration (Table 3).

Nutrient availability as assessed by IER burial (14-103 µg N g^{-1} IER and 0.8-24.6 µg P g^{-1} IER) was not significantly affected by *Solidago* invasion, nor did any differences depend on productivity or soil P availability (Table 3). Soil pH, soil phosphatase activity, soil respiration rate, moisture and temperature also did not differ between uninvaded and invaded patches (Table 3).

Table 3. Soil properties and processes compared between soil under native vegetation and adjacent invaded vegetation (*Solidago gigantea*) at six to fourteen semi-natural sites in Switzerland. Means ± SE for native and invaded vegetations were determined from n sites, based on the means of five soil samples, six ion-exchange resin (IER) bags, or three measurement plots (for respiration measurements) per site. Effects of invasion, dependence on site productivity (Prod) and P availability (Pav), as well as interactions were tested using linear mixed models, with sites as random factor. For each effect, F ratios and significance levels are shown (*** P < 0.001, ** P < 0.01, * P < 0.05, no sign P ≥ 0.05).

		Means ± *SE*		Tests of effects (*F, P*)				
Variable	*n*	Native	Invaded	Invasion	Prod	I x Prod	Pav	I x Pav
C_t (g kg^{-1} soil)	14	53.81 ± 3.20	56.21 ± 3.06	5.1 *	46.6 ***	0.7	3.2	0.1
N_t (g kg^{-1} soil)	14	3.34 ± 0.31	3.48 ± 0.30	2.4	14.7 **	0.5	0.8	3.2
C/N ratio	14	19.03 ± 0.80	18.62 ± 0.68	0.4	0.5	0.1	0.3	6.1*
P_{Olsen} (mg kg^{-1} soil)	14	4.16 ± 0.51	4.22 ± 0.48	0.0	2.8	0.4	71.4***	1.7
N_{KCl} (mg kg^{-1} soil)	14	6.57 ± 0.64	5.52 ± 0.65	13.7**	8.2*	0.5	0.0	11.7**
$NO_{3\ KCl}^-$ (mg kg^{-1} soil)	14	3.98 ± 0.56	3.38 ± 0.55	22.8***	7.3*	8.7*	0.1	18.2**
$NH_{4\ KCl}^+$ (mg kg^{-1} soil)	14	2.59 ± 0.28	2.15 ± 0.25	2.6	1.0	4.3	0.7	2.5
P_{IER} (µg g^{-1} IER)	12	8.72 ± 1.15	5.62 ± 0.81	1.2	0.1	0.3	45.8***	1.3
N_{IER} (µg g^{-1} IER)	12	42.52 ± 4.93	29.56 ± 4.82	1.2	5.8*	1.3	1.0	0.3
$NO_{3\ IER}^-$ (µg g^{-1} IER)	12	25.58 ± 4.06	19.96 ± 3.83	0.6	2.5	0.7	0.0	0.7
$NH_{4\ IER}^+$ (µg g^{-1} IER)	12	12.81 ± 2.54	7.52 ± 1.61	1.0	1.0	0.9	5.2*	0.1
pH (H_2O)	14	7.62 ± 0.09	7.60 ± 0.08	0.2	0.2	0.0	2.1	1.5
Phosphatase activity	12	0.13 ± 0.01	0.15 ± 0.01	0.7	2.7	0.1	3.9	0.0
Respiration rate	6	4.73 ± 0.47	5.48 ± 0.43	1.6	237.6***	0.5	51.5**	0.0

Soil phosphatase activity is given in µM g^{-1} h^{-1}, and soil respiration rate in µmol CO_2 m^{-2} s^{-1}.

Discussion

Are ecosystem properties affected by S. gigantea *across a broad range of habitats?*

The 14 study sites varied widely in biomass production and soil P availability as well as in disturbance history (old-fields, semi-natural grasslands, natural wetlands) and present management (part of the sites are mown). Despite this variation, the effects of *S. gigantea* on many vegetation properties and on some soil properties were qualitatively consistent across sites, although the size of the effects differed among sites. Thus, invasion at all or most sites was associated with increases in above-ground biomass, vegetation height, P pools and soil C content, and decreases in nutrient concentrations in biomass and in N availability in soil. Most of these effects were also reported in previous studies in Belgium (Chapuis-Lardy et al. 2006; Vanderhoeven et al. 2006), suggesting that *S. gigantea* has fairly consistent effects on ecosystem properties across a broad range of habitats.

Greater biomass production is one of the effects most frequently associated with plant invasions worldwide (Ehrenfeld 2003), and the invasion of *Solidago gigantea* conforms to this pattern. The ability of invasive species to increase biomass production can be due to (i) faster inherent growth rate, (ii) the exploitation of nutrient sources that are unavailable to the native species (Yelenik et al. 2004; Dassonville et al. 2007), or (iii) a more efficient use of nutrients for biomass production (Fiala et al. 2004; Funk & Vitousek 2007). Our comparison of leaf traits did not support the first mechanism for *S. gigantea*, since it did not have a greater SLA or higher nutrient concentrations in leaves than the cooccurring dominant native species. A greater SLA is typically found in fast-growing plants that invade nutrient-rich sites (Daehler 2003; Leishman et al. 2007). Accordingly, *S. gigantea* did not grow consistently faster than a subset of the native species in a common garden experiment (Chapter 1). A different nutrient acquisition strategy from the native species is as well rather unlikely for *S. gigantea*. We found a lower biomass allocation to roots and a tendency to lower root phosphatase activity and *S. gigantea* has a similar rooting depth as native species in Belgian stands (Herr et al. 2007). Thus, the high biomass production of *S. gigantea* is probably largely due to a more efficient use of acquired nutrients.

Biomass N and P concentrations of the invaded vegetation were lower than those of the native vegetation in our study, apparently due to the production of nutrient-poor stems, which can make up 70% of the above-ground biomass of *S. gigantea* in late summer, as Herr et al (2007) determined in Belgian stands. Lower nutrient concentrations mean that more biomass can be produced per unit of N or P taken up. However, this alone does not explain the greater biomass production of the invaded vegetation, since it contained a larger absolute amount of P than the

native vegetation. This may have been due to reduced pools of P in below-ground parts during the growing season and/or to more efficient nutrient conservation during the winter. Herr et al. (2007) showed that *S. gigantea* outperformed native species in nutrient resorption from senescing shoots and nutrient accumulation in below-ground parts during the autumn. In pot experiments, we also found that nutrients stored in roots and rhizomes at the end of the growing season were conserved throughout the winter (S. Güsewell and C. del Fabbro, unpublished data). Nutrient accumulation in rhizomes during the winter is an effective competitive strategy at both nutrient-poor and nutrient-rich sites (Grime 2001). It may therefore explain why *S. gigantea* is able to invade the vegetation and increase its above-ground biomass across sites with widely varying fertility.

Despite the greater biomass production, native plant species richness was not consistently reduced by *S. gigantea*, contrary to the negative effects reported from Belgian sites (Vanderhoeven et al. 2006). This contradiction can be resolved by considering that the effect of *S. gigantea* on species richness was related to its effect on biomass: thus, when the effect of *S. gigantea* on above-ground biomass was small the native species number tended to increase, while it decreased when the biomass effect was large (more than + 0.25 kg m^{-2}). Our results are therefore consistent with those in the Belgian study, in which *S. gigantea* increased the above-ground biomass by more than 0.25 kg m^{-2} (Vanderhoeven et al. 2006). The absence of a clear negative effect of *S. gigantea* on species richness may be due to its late phenology: shoots only start growing in late April, leaving niches for the growth of native species in early spring, especially when its stem density is not very high. Differences in phenology between native and invasive species might explain why some invasive species do not reduce native species diversity (Güsewell & Edwards 1999; Vila & Gimeno 2007)

An increase in soil organic matter (C) content under stands of invasive plants has been reported in many previous studies (Scott et al. 2001; Caldwell 2006; Fickbohm & Zhu 2006; Heneghan et al. 2006; Vila et al. 2006), and has been attributed to increased biomass production and litterfall (Yelenik et al. 2004) or to reduced litter decomposition rates (Ogle et al. 2003). In the case of *S. gigantea*, both mechanisms might have contributed to the increase in soil C. Biomass production was increased, but the leaves of *S. gigantea* also had a higher mean carbon concentration than those of native species (+ 2.6%), suggesting higher content of lignin or other refractory compounds. Furthermore, the nutrient-poor stems probably decompose more slowly than leaves of *S. gigantea* or native species The effect of *S. gigantea* on soil C was, however, very small compared to effects reported for other species (Yelenik et al. 2007), and no significant increase in soil C was found under *S. gigantea* in Belgium (Vanderhoeven et al. 2006).

N availability in soil is often increased under invasive plants (Ehrenfeld 2003), but reduced

N availability has also been found, for example for *Hieracium pilosella* in tussock grasslands of New Zealand (Scott et al. 2001) and *Bromus tectorum* in an arid grassland in the Western USA (Evans et al. 2001). The latter effect was typically attributed to the production of nutrient-poor litter, leading to slower N mineralization (Evans et al. 2001; Drenovsky & Batten 2007). Since the vegetation invaded by *S. gigantea* had lower nutrient concentrations in standing biomass (this study) and litter (Herr et al. 2007), nitrogen immobilisation in decomposing plant litter with a high C:N ratio might have caused the lower N availability in soil under *S. gigantea*. By causing low N supply rates through reduced mineralization rates, plants with a conservative nitrogen-use strategy can reinforce their superiority over native species (Wedin & Tilman 1990; Evans et al. 2001; Drenovsky & Batten 2007). It remains to be investigated whether *S. gigantea* benefited from reduced N mineralization. For the likewise invasive congeneric *S. canadensis,* (Rebele 2000) e.g. did observe a greater competitive ability relative to native species under low-nutrient conditions.

P availability in soil was not increased by *S. gigantea* invasion in our study. In contrast, increased P availability was reported for Belgian sites, where it was attributed to a higher P turnover due to *S. gigantea* taking up more P in its biomass and releasing more P through litter mineralization (Chapuis-Lardy et al. 2006). Since the invaded vegetation in Belgium had higher P concentrations than at our Swiss sites, it is possible that the Swiss litter with a higher C:P ratio released P more slowly and therefore did not increase soil P availabilities. Soil acidification, as partly found to be associated with increased soil P availability in Belgium, also did not occur. Furthermore, acid soil phosphatase activity and soil respiration did not differ between native and invaded vegetation at our sites, whereas they were increased under *S. gigantea* in Belgium (Chapuis-Lardy et al. 2006). This further suggests that the greater litter input by *S. gigantea* stimulated nutrient release through microbial activity in Belgium, but not in Switzerland. Whether different nutrient concentrations in litter were really responsible would be a topic for further study.

How do effects of S. gigantea *differ along a P gradient?*

There were two largely independent gradients related to fertility across our sites: productivity and P availability. The productivity gradient was not clearly related to N availability, despite a strong positive correlation with KCl-extracted N, since productivity (i.e. above-ground biomass of the vegetation) correlated negatively with IER-N and did not correlate with N concentrations in biomass (Table 1). Productivity was also unrelated to soil moisture, as assessed by Ellenberg F indicator values. We found that that the effects of *S. gigantea* on ecosystem properties did not depend on productivity, but for several variables the magnitude and/or direction of the invasion effect was conditioned by P availability in soil.

The differences in P concentrations in the above-ground biomass between native and invaded vegetations were clearly strongest at the P-rich sites, which consisted of one grassland and the two old-field sites. This relationship might be linked to the native vegetation composition, as there was a strong positive correlation between the Ellenberg N indicator value and the soil P availability (R=0.81, cf. Table 1). Species with high Ellenberg N values generally have high P concentrations in biomass and a ruderal or competitive-ruderal strategy (Güsewell 2004), which implies a rapid cycling of nutrients. The more conservative nutrient-use strategy of *S. gigantea* would then contrast most strongly with properties of the native vegetation at sites with high soil P availability. The same reasoning may hold for the reduction in soil N availability, which was also more pronounced at the P-rich sites. Furthermore, the soil C:N ratio was generally reduced in the invaded patches, but it was increased at the most P-rich sites. The latter was due to higher soil C content and slightly lower soil N content, consistent with the proposed difference in nutrient use strategy between *S. gigantea* and native species at the P-rich sites.

The measured functional leaf traits of *S. gigantea* gave no clear explanation for the dependence of invasion effects on soil P availability. For the N concentration of vegetation biomass, the C and N concentrations of leaves, or plant height (which is related to the fraction of stem biomass), differences between the native and the invaded vegetation were unrelated to soil P availability. It is possible that differences in below-ground traits such as root nutrient concentrations and litter production were more important (Herr et al. 2007). Studies of seasonal changes in below-ground biomass and nutrient pools at a larger number of sites may be needed to better understand the observed invasion effects.

Our study was initially triggered by concern about the increase in soil P availability under *S. gigantea* reported from Belgium (Chapuis-Lardy et al. 2006). We wondered whether vegetation of high conservation value would be threatened by this effect, or whether it would be limited to rather fertile sites. Contrary to expectation, we found that *S. gigantea* had no consistent effect on soil P regardless of the productivity or P availability of the invaded site. There were considerable differences in Olsen P or IER-P between invaded and uninvaded plots at some of the sites, but these were either positive or negative. Absolute differences were largest at the most P-rich sites (Fig. 2f), but relative differences were also large at some of the P-poor sites (50–100% difference). A similar observation was actually made by Vanderhoeven et al. (2006), who found available P to be increased following invasion of *S. gigantea* at two of the five investigated sites and reduced at one site. Interestingly, the increase in available P occured at the least P-rich sites, and the decreased occurred at the most P-rich site, so that P availability varied less among the invaded patches than among the uninvaded ones (Vanderhoeven et al. 2006). Dassonville et al. (2008) recently proposed that such a negative relationship between initial nutrient availability and invasion effect on nutrient availability, leading to more homogeneous soil conditions, is

a general pattern. This was not confirmed by our study, in which the effects of *S. gigantea* on soil P showed no relationship to initial P availability. The labile soil P fractions were higher in Belgium than the Olsen-availability in our study, but soil P availabilities were determined with different methods in Belgium and a comparison is therefore difficult. Further examination of our data also revealed no relationship between invasion effects and soil moisture (Ellenberg F value) or soil pH. It is possible that site management plays a role by influencing organic matter inputs to the soil (cf. Chapuis-Lardy et al. 2006, Herr et al. 2007). Further research to explain the diverging effects of *S. gigantea* on soil P availability should therefore include long-term experiments manipulating both initial soil fertility and management.

Conclusions

Three main conclusions can be drawn from this study. First, our results have confirmed the ability of *S. gigantea* to modify ecosystem properties across a wide range of vegetation types, including regularly managed semi-natural vegetation. Our results also basically confirm the previous suggestion that the greater productivity and nutrient-use efficiency of *S. gigantea* compared to native species are decisive for its effect on ecosystem processes, whereas differing leaf traits typical of fast-growing invaders, such as higher SLA and nutrient concentrations, were not involved.

Second, the effects of *S. gigantea* on the invaded vegetation were less dramatic than those described from Belgium. Native plant species richness was not always reduced, and there was no increase in P availability. However, our results do not imply that invasion by *S. gigantea* is unproblematic for nature conservation; rather, they highlight of the need to keep the biomass and litter production of *S. gigantea* as low as possible through regular management.

Third, some effects of *S. gigantea* on soil properties were related to P availability but not to N availability or biomass production. It is therefore important to consider that there may be independent gradients related to nutrient availability, and that these may be of differing importance for the invasion effects. Accordingly, a multi-site approach is important in studying effects of invasive plants on ecosystems. Detailed investigations of soil processes at a single site (Herr et al. 2007) or at a small number of carefully selected sites (Chapuis-Lardy et al. 2006) are valuable for understanding how an invasive plant affects site conditions, while multi-site surveys are needed to assess the generality of such effects.

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References

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* 50: 29-37.

Allen, S.E. 1989. *Chemical analysis of ecological materials*. Blackwell Scientific Publications, Oxford, UK.

Blank, R.R. & Young, J.A. 2002. Influence of the exotic invasive crucifer, *Lepidium latifolium,* on soil properties and elemental cycling. *Soil Science* 167: 821-829.

Caldwell, B.A. 2006. Effects of invasive scotch broom on soil properties in a Pacific coastal prairie soil. *Applied Soil Ecology* 32: 149-152.

Chapuis-Lardy, L., Vanderhoeven, S., Dassonville, N., Koutika, L.S. & Meerts, P. 2006. Effect of the exotic invasive plant *Solidago gigantea* on soil phosphorus status. *Biology & Fertility of Soils* 42: 481-489.

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

Dassonville, N., Vanderhoeven, S., Gruber, W. & Meerts, P. 2007. Invasion by *Fallopia japonica* increases topsoil mineral nutrient concentrations. *Ecoscience* 14: 230-240.

Dassonville, N., Vanderhoeven, S., Vanparys, V., Hayez, M., Gruber, W. & Meerts, P. 2008. Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157: 131-140.

Drenovsky, R.E. & Batten, K.M. 2007. Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. *Biological Invasions* 9: 107-116.

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

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1997. *Zeigerwerte von Pflanzen in Mitteleuropa*. 2nd edition. Erich Goltze KG, Göttingen, Germany.

Evans, R.D., Rimer, R., Sperry, L. & Belnap, J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11: 1301-1310.

Eviner, V.T. 2004. Plant traits that influence ecosystem processes vary independently among species. *Ecology* 85: 2215-2229.

Fiala, K., Zahora, J., Tuma, I. & Holub, P. 2004. Importance of plant matter accumulation, nitrogen uptake and utilization in expansion of tall grasses (*Calamagrostis epigejos* and *Arrhenatherum elatius*) into an acidophilous dry grassland. *Ekologia Bratislava* 23: 225-240.

Fickbohm, S.S. & Zhu, W.X. 2006. Exotic purple loosestrife invasion of native cattail freshwater wetlands: effects on organic matter distribution and soil nitrogen cycling. *Applied Soil Ecology* 32: 123-131.

Funk, J.L. & Vitousek, P.M. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446: 1079-1081.

Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley and Sons, Chichester, UK.

Grotkopp, E., Rejmanek, M. & Rost, T.L. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* 159: 396-419.

Gurvich, D.E., Tecco, P.A. & Diaz, S. 2005. Plant invasions in undisturbed ecosystems: the triggering attribute approach. *Journal of Vegetation Science* 16: 723-728.

Güsewell, S. & Edwards, P.J. 1999. Shading by *Phragmites australis*: a threat for species-rich fen meadows? *Applied Vegetation Science* 2: 61-70.

Güsewell, S. 2004. N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164: 243-266.

Güsewell, S., Zuberbühler, N. & Clerc, C. 2005. Distribution and functional traits of *Solidago gigantea* in a Swiss lakeshore wetland. *Botanica Helvetica* 115: 63-75.

Hamilton, M.A., Murray, B.R., Cadotte, M.W., Hose, G.C., Baker, A.C., Harris, C.J. & Licari, D. 2005. Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* 8: 1066-1074.

Heneghan, L., Fatemi, F., Umek, L., Grady, K., Fagen, K. & Workman, M. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica*, L.) alters soil properties in Midwestern US woodlands. *Applied Soil Ecology* 32: 142-148.

Herr, C., Chapuis-Lardy, L., Dassonville, N., Vanderhoeven, S. & Meerts, P. 2007. Seasonal effect of the exotic invasive plant *Solidago gigantea* on soil pH and P fractions. *Journal of Plant Nutrition and Soil Science* 170: 729-738.

Kueffer, C., Klingler, G., Zirfass, K., Schumacher, E., Edwards, P.J. & Güsewell, S. 2008. Invasive trees show only weak potential to impact nutrient dynamics in phosphorus-poor tropical forests in the Seychelles. *Functional Ecology* 22: 359-366.

Lake, J.C. & Leishman, M.R. 2004. Invasion success of exotic in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* 117: 215-226.

Leishman, M.R., Haslehurst, T., Ares, A. & Baruch, Z. 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist* 176: 635-643.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society London Series B-Biological Sciences* 270: 775-781.

Mack, M.C., D'Antonio, C.M. & Ley, R.E. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C-4 grasses in Hawaii. *Ecological Applications* 11: 1323-1335.

Miki, T. & Kondoh, M. 2002. Feedbacks between nutrient cycling and vegetation predict plant species coexistence and invasion. *Ecology Letters* 5: 624-633.

Monaco, T.A., Johnson, D.A. & Creech, J.E. 2005. Morphological and physiological responses of the invasive weed *Isatis tinctoria* to contrasting light, soil-nitrogen and water. *Weed Research* 45: 460-466.

Murphy, J. & Riley, J.P. 1962. A modified single solution method for the determination of phosphorus in natural waters. *Analytica Chimica Acta* 27: 1-6.

Ogle, S.M., Reiners, W.A. & Gerow, K.G. 2003. Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist* 149: 46-58.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Holle, B., von Moyle, P.B., Byers, J.E. & Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3-19.

Rebele, F. 2000. Competition and coexistence of rhizomatous perennial plants along a nutrient gradient. *Plant Ecology* 147: 77-94.

Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. & Pigliucci, M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981-993.

Sala, A., Verdaguer, D. & Vila, M. 2007. Sensitivity of the invasive geophyte *Oxalis pes-caprae* to nutrient availability and competition. *Annals of Botany* 99: 637-645.

Schumacher, E., Kueffer, C., Edwards, P.J. & Dietz, H. 2009. Influence of light and nutrient conditions on seedling growth of native and invasive trees in the Seychelles. *Biological Invasions*. In press.

Scott, N.A., Saggar, S. & McIntosh, P.D. 2001. Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. *Ecological Applications* 11: 1311-1322.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125-1140.

Tabatabai, M.A. & Bremner, J.M. 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. *Soil Biology and Biochemistry* 1: 301-307.

Vanderhoeven, S., Dassonville, N. & Meerts, P. 2005. Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. *Plant and Soil* 275: 169-179.

Vanderhoeven, S., Dassonville, N., Chapuis-Lardy, L., Hayez, M. & Meerts, P. 2006. Impact of the invasive alien plant *Solidago gigantea* on primary productivity, plant nutrient content and soil mineral nutrient concentrations. *Plant and Soil* 286: 259-268.

Vila, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Medail, F., Moragues, E., Traveset, A., Troumbis, A.Y. & Hulme, P.E. 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography* 33: 853-861.

Vila, M. & Gimeno, I. 2007. Does invasion by an alien plant species affect the soil seed bank? *Journal of Vegetation Science* 18: 423-430.

Wassen, M.J., Venterink, H.O., Lapshina, E.D. & Tanneberger, F. 2005. Endangered plants persist under phosphorus limitation. *Nature* 437: 547-550.

Weber, E. & Jakobs, G. 2005. Biological flora of central Europe: *Solidago gigantea* Aiton. *Flora* 200: 109-118.

Wedin, D.A. & Tilman, D. 1990. Species effects on nitrogen cycling - a test with perennial grasses. *Oecologia* 84: 433-441.

Windham, L. & Ehrenfeld, J.G. 2003. Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. *Ecological Applications* 13: 883-896.

Yelenik, S.G., Stock, W.D. & Richardson, D.M. 2004. Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology* 12: 44-51.

Yelenik, S.G., Stock, W.D. & Richardson, D.M. 2007. Functional group identity does not predict invader impacts: differential effects of nitrogen-fixing exotic plants on ecosystem function. *Biological Invasions* 9: 117-125.

Appendix 1. Plant species list for the 14 investigated sites, separately listed for native and invaded vegetation at each site, without (-) and with *Solidago gigantea* (+, grey shaded columns). Sites are ordered according to soil P availability (Olsen extraction) at uninvaded patches (cf. to Fig. 2) and species are ordered according to their occurrence at sites with low (< 3 mg P kg^{-1} soil) or high (> 3 mg P kg^{-1} soil) soil P availability, or in both respectively. Species that occurred only at one site are not listed.

	W		W		SG		SG		SG		SG		WF		W		SG		W		W		MO		MO		SG	
	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
Soil P availability (Olsen)	0.74		1.23		1.29		1.81		1.90		1.92		2.71		2.72		3.29		3.76		3.78		6.94		11.4		13.7	
Angelica sylvestris																							•		•			
Origanum vulgare																							•	•	•			
Festuca arundinacea																	•				•	•						
Agrostis stolonifera																	•	•									•	•
Poa pratensis																	•	•	•	•								
Symphytum officinale															•				•	•								
Lychnis flos-cuculi			•														•					•						
Epilobium hirsutum		•																	•	•	•	•						
Deschampsia cespitosa			•																				•		•		•	
Galium album						•					•	•							•	•					•			•
Cirsium arvense					•						•	•			•		•	•			•						•	•
Phragmites australis						•	•	•							•		•	•					•				•	
Ajuga reptans											•	•			•		•	•				•						
Mentha aquatica					•	•					•								•	•		•						
Carex flacca						•	•										•	•										
Acer pseudoplatanus							•																					•
Achillea millefolium			•															•										
Carex acutiformis	•	•	•	•												•			•	•	•	•						
Calamagrostis epigejos									•	•			•		•	•			•	•	•	•						
Brachypodium pinnatum	•	•									•	•															•	•
Bromus erectus									•						•	•					•	•						
Potentilla reptans	•	•	•												•	•			•	•								
Lysimachia vulgaris					•	•					•				•	•											•	•
Lathyrus pratensis			•	•									•	•	•	•			•	•								
Festuca rubra			•		•				•						•	•			•	•								
Holcus lanatus	•	•		•	•	•		•								•				•								
Poa angustifolia					•				•		•	•					•											
Fraxinus excelsior		•	•	•							•	•	•															
Agrostis gigantea						•	•		•		•	•																
Phalaris arundinacea		•		•									•			•												
Lythrum salicaria					•	•	•	•																				
Dactylis glomerata	•		•	•																								
Filipendula ulmaria									•				•	•														
Plantago lanceolata					•	•					•																	
Prunella vulgaris							•				•	•																
Rubus caesius					•	•	•																					
Agropyron repens				•											•													
Carex gracilis		•		•																								
Carex hirta								•	•																			
Carex panicea							•									•												
Crataegus monogyna					•				•																			

Chapter 3

Plant-microbe interactions and a negative feedback for the exotic invasive plant *Solidago gigantea*

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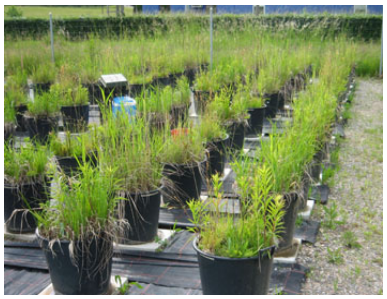
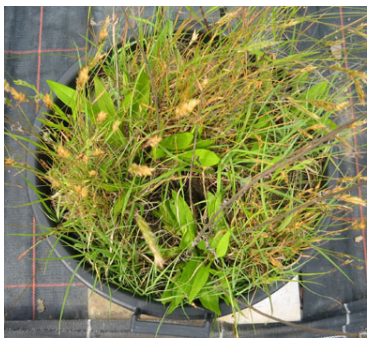


Mesocosm experiment



Molinion without *S. gigantea*

Molinion with *S. gigantea*

Abstract

There is increasing evidence that below-ground processes can play a critical role in plant invasions. For example, some exotic plants alter biotic and abiotic soil properties resulting in a positive feedback that favours the invading species. Previous studies often focused on the effects of exotic invasive plants on either abiotic or biotic soil components, whereas conclusions cannot be drawn from one component to the other. We investigated whether the exotic invasive species *Solidago gigantea* influences soil nutrient cycling and microbial communities, and whether this depends not only on the invader but also on properties of the invaded native vegetation. For this purpose, we performed a mesocosm experiment in which we simulated invasion of *S. gigantea* into three European wetland communities of different productivity (*Molinion*, *Magnocaricion*, and *Filipendulion*). To investigate possible feedback mechanisms due to alterations in nutrient availability or microbial community, we included an inoculation treatment with soil collected from invaded and non-invaded sites. *S. gigantea* was more successful in invading the *Molinion* than the more productive *Magnocaricion* and *Filipendulion* communities. It reduced the soil bacterial biomass and increased the fungal biomass, organic matter, and ß-glucosidase activity, but did not affect nitrogen or phosphorus cycling. The effects on soil did, however, not depend on the type of native plant community that got invaded. We hypothesise that *S. gigantea* exudes antibacterial compounds into the soil; and since the magnitude of the antibacterial effect was independent of biomass, we suggest that presence of the invader is more important than its abundance. Furthermore, we found evidence of a negative feedback, with *S. gigantea* producing less biomass in soil previously occupied by the same species. Our results add another species to the list of successful invaders, which - contrary to the prevalent theory - experience negative feedback.

Introduction

It is increasingly recognized that effects on below-ground processes can play a critical role for exotic plants invading natural plant communities (Van der Putten et al. 2007, Wardle et al. 2004). Exotic plants can, for example, influence soil nutrient availability (Ehrenfeld 2003), change the composition of microbial communities (Kourtev et al. 2002, Stinson et al. 2006)} and other components of the soil food web (Belnap et al. 2005, Callaway et al. 2004, Klironomos 2002), and directly affect native plants by releasing allelochemicals (Vivanco et al. 2004). Effects upon soil nutrient availability may be due to the differing quality and quantity of litter, changes in the release and uptake of nutrients by roots, and modified enzyme activities (Wardle et al. 2004). Root exudation of enzymes, as well as of allelochemicals, can also affect soil microbial communities (Broeckling et al. 2008, Stinson et al. 2006), and such community changes can, in turn, influence soil nutrient cycling. Thus, a range of interrelated below-ground processes complicate understanding of the effects of invasive plants on ecosystem properties and processes.

Effects of invasive species on ecosystem processes are not necessarily constant in direction and magnitude over time (Belnap et al. 2005) and can vary among habitats (Dassonville et al. 2008, Kueffer et al. 2008, Marler et al. 1999, Vila et al. 2006, Wolfe et al. 2008). These variations might not be idiosyncratic; exotic invasive plants were shown to increase nutrient concentrations in soil at sites of initially nutrient-poor status while reducing soil nutrient concentrations at initially nutrient-rich sites in Belgium (Dassonville et al. 2008), suggesting that invasive plants contribute to a homogenisation of soil nutrient states. Alternatively, the correlation of invasion effects with initial site conditions may be related to the properties of the native plant communities, which differed according to habitat fertility. Impacts on ecosystem processes are likely to be stronger at sites where traits of the invader differ substantially from those of native species (Levine et al. 2003, Mack et al. 2001, Moles et al. 2008). However, no studies have yet investigated how the effect of an invader varies according to the characteristics of the native vegetation (e.g. differences in productivity or nutrient-use efficiency).

The success of some invasive plants has been attributed to plant-soil feedback mechanisms. There are various examples of positive feedbacks by which exotic invasive plants alter soil conditions in ways that stimulate biomass production of the invading species: such conditions include altered (generally increased) nutrient availability (Dassonville et al. 2007, Ehrenfeld 2003, Vinton and Goergen 2006), and the promotion of beneficial microbes in the rhizosphere, such as mycorrhiza or rhizobia (Bever et al. 1997, Callaway et al. 2004, Klironomos 2002, Reinhart et al. 2003). However, positive feedbacks appear not to be a prerequisite for invasion success, since there are also examples of negative feedback, where soil pathogens accumulating in the rhizosphere restrain growth of successful plant invaders (Beckstead and Parker 2003, Nijjer et

al. 2007, Packer and Clay 2000).

Wetlands are ecosystems of high conservation value, and *Solidago gigantea* is a frequent invader of these ecosystems in Europe (Weber and Jakobs 2005). In Switzerland, the species invades wetland communities of both low (e.g. *Molinion*) and high (e.g. *Filipendulion*) productivity (Güsewell et al. 2005). Formerly, the success of *S. gigantea* as an invader was attributed to its high reproductive capacity, both vegetatively and by seed (Weber and Jakobs 2005) and otherwise appeared to be functionally similar to native species (Güsewell et al. 2005), but it was recently found to have the potential to increase as well as decrease soil nutrient availability (Chapuis-Lardy et al. 2006). Whether such effects on nutrient cycling involve alterations in the soil microbial community, possibly leading to a positive plant-soil feedback, has not previously been studied.

The aim of this study was to (i) evaluate the effects of *S. gigantea* on soil C, N and P cycling, as well as on the activity of specific enzymes and soil microbial biomass; (ii) assess whether invasion success and effects of this invasive plant on nutrient cycling and microbial communities depend on the native plant community, and (iii) determine whether the growth of this exotic invader is affected by plant-soil feedback related to microbial and/or nutrient conditions which this species creates itself.

We hypothesized that *S. gigantea* (i) alters nutrient cycling and microbial community composition; (ii) alters these ecosystem properties in dependence of the productivity of plant communities, i.e. increasing rates of nutrient cycling in the low-productive and decreasing rates of nutrient cycling in the high-productive plant community; (iii) favours its own growth by effects on nutrient cycling and microbial community, thereby triggering a positive feedback effect for itself.

Materials and methods

Native plant communities

We studied *S. gigantea* as an invader of three wetland plant community types which under natural conditions form a productivity gradient: a mesotrophic *Molinion*, an intermediate *Magnocaricion*, and a eutrophic *Filipendulion* community. The native plant species associated with these communities differ in their nutrient requirements, but all three communities are invaded by *S. gigantea*. We assembled these plant communities experimentally in mesocosms, each being represented by three native graminoids and two native forbs characteristic for the respective community (Table 1). Most plants were grown from seeds for ten weeks in a greenhouse. However, species that were difficult to germinate (*Carex* species and *Molinia caerulea*) were collected in the field, separated into single shoots, and kept in tap water until they had produced new roots, at which point they were transplanted.

Experimental design

The experiment was set up in May 2006 in an experimental garden at ETH Zurich, Switzerland (47°24` N, 8°30` E, 520 m a.s.l.) and ran for three growing seasons until July 2008. Six treatments were applied in the experiment, combining two invasion levels (with and without *S. gigantea*) and several soil inoculum types (invaded and native soils from paired field sites, and a neutral control soil) (Fig.1). Specifically, we used soil from sites covered by *Molinion* (close to Chabrey: 46°56` N, 6°59` E), *Magnocaricion* (close to Yverdon: 46°47` N, 6°41` E) and *Filipendulion* communities (close to Zurich: 47°28` N, 8°32` E). At each of these, we collected 'invaded soil' from stands of *S. gigantea* and 'native soil' in nearby native vegetation without *S. gigantea* and used these soils for inoculation with the assembled *Molinion*, *Magnocaricion* or *Filipendulion* communities in the experiment (Fig. 1). The paired sites for native and invaded soil were less than 20 m apart to minimize differences in soil characteristics caused by factors other than *S. gigantea* invasion. To separate effects of *S. gigantea* on soil properties related to the plant communities from influences of the specific native and invaded soil, we also used a neutral control soil collected at a site close to Zurich (47°22' N, 8°28' E) which showed aspects of all three communities (i.e. presence of *Molinia arundinacea, Carex panicea, Lythrum salicaria, Filipendula ulmaria,* and *Carex acutiformis*) and was not invaded by *S. gigantea*. For simplicity, we refer hereafter to only three types of soil inocula (invaded, native, and control). Each treatment was replicated four times for each plant community, resulting in a total of 72 experimental pots.

Plastic buckets with a capacity of 35 litres were filled with 30 litres of a mixture of 90% sand (Carlo Bernasconi AG, Zurich, Switzerland, grain size 1-1.7 mm) and 10% soil (air-dried

and sieved (4-mm mesh size) prior to inoculation). Each mesocosm was planted with three individuals per species, resulting in 15 individuals in mesocosms without *S. gigantea* and 18 individuals in mesocosms with *S. gigantea*. These 15 or 18 individuals were planted in three concentric pentagons or hexagons, so that all species occurred once in the outer, intermediate and central part of the penta- or hexagon, respectively. Pots were randomised twice during the duration of the experiment.

Plants were watered with tap water and fertilized with nutrient solutions at two-weekly intervals from June to September 2006 and from April to October 2007. All pots received the same amounts of nutrients. Five stock solutions were prepared for fertilization: 1. $Ca(NO_3)_2$, 2. KNO_3 and KH_2PO_4, 3. $MgSO_4$, 4. $FeSO_4$ and 5. $MnCl_2$, H_3BO_3, $ZnSO_4$, Na_2MoO_4 and $CuSO_4$. All pots received 800 mg N in the first year and 1600 mg N in the second year. The other nutrients were supplied in ratios of 0.7 (N:K), 3 (N:Mg), 3.4 (N:Ca), 10 (N:P), 25 (N:Fe) and 200-3000 for the micronutrients. In 2007, we replaced the $Ca(NO_3)_2$-solution by an NH_4NO_3-solution after measuring pH levels >7 in some of the pots. Pots were not fertilized in 2008.

Table 1. List of native species used for assembling the three native plant community types differing in productivity

Molinion	*Magnocaricion*	*Filipendulion*
Carex panicea	*Carex elata*	*Carex acutiformis*
Molinia caerulea	*Phragmites australis*	*Phalaris arundinacea*
Anthoxanthum odoratum	*Calamagrostis epigejos*	*Alopecurus pratensis*
Succisa pratensis	*Lythrum salicaria*	*Filipendula ulmaria*
Centaurea angustifolia	*Mentha aquatica*	*Valeriana officinalis*

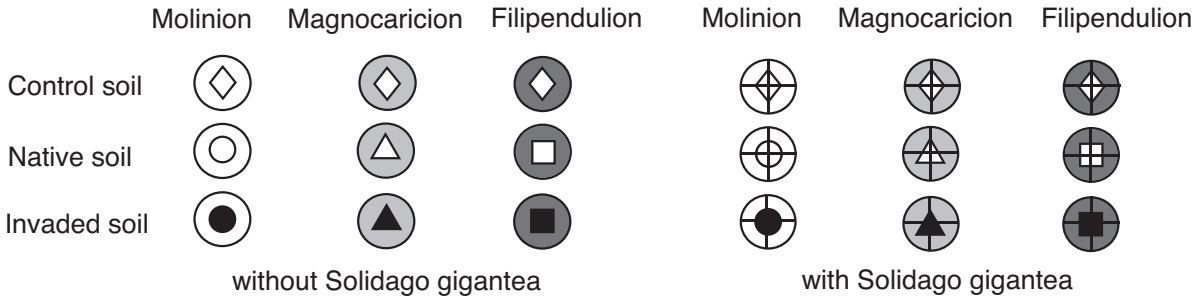


Figure 1. Experimental design to test for the effects of invasion (without and with *Solidago gigantea*), plant community type (*Molinion, Magnocaricion and Filipendulion*) and soil inoculum type (native, invaded and control soil). Communities were assembled with five native species per community type and *S. gigantea* was added to simulate invasion (crosses). Sand was used as growth substrate inoculated with the three different soil inoculum types. The control soil was the same for each plant community and invasion treatment (open diamond), whereas native and invaded soils were specific for each plant community (open and filled circles for *Molinion*, open and filled triangles for *Magnocaricion*, open and filled squares for *Filipendulion*).

Vegetation properties

The performance of *S. gigantea* in the different plant communities was assessed in June 2008 by recording the number and height of shoots. Above-ground biomass was harvested in July 2008 and separated per pot into i) living shoots of each species, ii) *S. gigantea* litter, and iii) pooled litter of all native species. Total below-ground biomass was determined in two of the four replicate pots (including roots of *S. gigantea*, since it was impossible to separate roots by species). Biomass samples were dried at 75 °C for 48-72 h, weighed and ground (1-mm mesh screen) for nutrient analyses.

Nitrogen and phosphorus concentrations were determined in shoots of *S. gigantea*, the above-ground biomass of the native species, and the total below-ground plant biomass, all after Kjeldahl digestion. Subsamples of 150 mg were digested with concentrated H_2SO_4 and a K_2SO_4-$CuSO_4$ tablet (FOSS Kjeltab) for 1 h at 420 °C. Concentrations in the digests were determined spectrophotometrically in a flow-injection analyser (FIAstar 5000, Foss Tecator, Höganäs, Sweden).

Soil properties

Bacterial numbers and biomass in soil samples pooled from 5 cores taken in November 2006 and June 2008 from each pot (0-10 cm depth, 1 cm diameter) were determined by epifluorescence microscopy. Four grams of fresh soil were preserved with 10 ml of a 2% formaldehyde solution buffered with $Na_4P_2O_7$ (3.8 mM l^{-1}). Samples were shaken and exposed to sonication (Branson Sonifier 250, SKAN AG, Basel, Switzerland) for 5 min in order to detach bacterial cells from soil particles (Buesing & Gessner 2002). Aliquots of the suspension were diluted (50-fold) and filtered through a 0.2 µM membrane filter (Anodisc 25, Whatman International Ltd., Maidstone, UK). Cells trapped on the filters were stained with 100 µl of 2.5% SYBR Green II solution (Molecular Probes, Eugene, OR, USA) and examined at 1000-fold magnification under a microscope (Zeiss Axioskop 2, Carl Zeiss AG, Feldbach, Switzerland) with an attached camera system (Sensys Digital CCD, Photometrics, Arizona, USA). Fifteen microscopic fields were photographed per filter and the bacterial numbers as well as bacterial size and shape on each field were determined using the program Metamorph 4.6r3 (Universal Imaging Corporation, West Chester, PA, USA). Length (l) and width (w) of the cells was used to calculate cell biovolume for elongate cells according to Bratbak (1993): $V = (\pi/4)*w^2*(l-w/3)$ and sphere volumes were calculated with $V = 4/3* \pi*r^3$. The calculated biovolumes were converted to bacterial carbon (C) according to the empirically determined relationship: $C = 89.6 \times V^{0.59}$ (Simon & Azam 1989).

Fungal biomass was determined as ergosterol in pooled samples from 5 soil cores taken per pot in November 2006 and June 2008 (Gessner & Schmitt 1996). Three grams of fresh soil were preserved with 10 ml of KOH in methanol (143 mM l^{-1}). Samples were heated for 30 min

in a water bath at 80 °C and subsequently allowed to cool down. The extract was passed over conditioned solid-phase cartridges (SepPak Vac RC tC18, 500mg, Waters Corporation, Milford, MA, USA) and successively rinsed with a washing solution (0.4 M KOH). Subsequently, the cartridges were dried under a stream of air before they were eluted with five portions of 0.35 ml isopropanol. The eluates were analysed for ergosterol content by a Jasco HPLC, using methanol as the mobile phase and measuring detection at 282 nm. Ergosterol concentrations in the soil samples were derived from standard curves prepared with pure ergosterol (Fluka Chemie GmbH, Buchs, Switzerland, >98% purity). For further details of the method see Gessner (2005). Ergosterol concentrations were converted to fungal carbon contents by using a conversion factor for fungal biomass of 5 mg ergosterol per gram mycelium dry mass (Gessner & Newell 2002) and assuming a fungal carbon content of 46% (Ruzicka et al. 2000).

Activities of β-glucosidase, β-N-acetylhexosaminidase (formerly β-glucosaminidase) and acid phosphatase, which are involved in the cycling of C, N and P, respectively (Sinsabaugh et al. 2008), were measured in samples pooled from 5 soil cores taken in July 2007 and July 2008 from each pot (0-10 cm depth, 1 cm diameter). Two g of fresh soil were mixed in a centrifuge tube with 4 ml buffer (Tris, pH 6.0, or Na-acetate-trihydrate, pH 5.5) and 1 ml of the appropriate substrate analogue (25 mM p-nitrophenyl-β-D-glucopyranoside, 10 mM p-nitrophenyl-N-acetyl-β-D-glucosamidine, or 10 mM p-nitrophenylphosphate) according to Parham & Deng (2000). After shaking for 1 h, 1 ml of 0.5 M $CaCl_2$ and 4 ml of alkaline buffer (Tris, pH 12, or 0.5 M NaOH) were added. The tubes were then centrifuged for 5 min at 3000 rpm before absorbance was measured at 410 nm. Standard solutions of p-nitrophenol spiked with 0.2 ml of 2 M NaOH were used for calibration. The amount of p-nitrophenol released by the enzymes was expressed in μmol per hour and g fresh soil.

Total phenolic concentrations were determined in fresh soil samples after harvesting the above-ground biomass in July 2008. Soil samples were kept at 4 °C until processed (three weeks). We used a modified method of Swain & Hillis (1959). One g of fresh soil was extracted by adding 5 ml of 50% ethanol and placing samples on a shaker (300 rpm) for 1 h. Samples were then centrifuged and a 3-ml aliqout of the extract was diluted with 2 ml H_2O and mixed with 100 μl Folin-Ciocalteu-reagent. After 8 min, 300 μl of 2 M Na_2CO_3 was added and absorbance at 760 nm measured after 1 h. Phenolic concentrations were determined with a standard curve of tannic acid and expressed as μg tannic acid per g fresh soil.

Total soil carbon concentrations were determined in air-dried soil samples (mix of 5 cores of 1cm diameter, 10 cm depth, taken after the harvest in July 2008), using a CN-analyser (CNS-2000, Leco Corporation, St. Joseph, MI, USA). N and P availability in soil was determined by measuring adsorption of nitrate, ammonium and phosphate to ion-exchange resins (IER) in all pots. Resins were exposed in soil during successive 2-month intervals between April 2007

and May 2008. For analysis, these successive measurements were subdivided into two periods, a fertilized (April-June, June-August, August-October, October-December) and an unfertilized period (December-February, February-March, March-May). One 25-cm^2 nylon bag per pot (60-µm mesh size, Sefar Nitex 03-60/35, Sefar AG, Thal, Switzerland) containing IER was placed at about 5 cm below the soil surface. Each bag contained 2 g mixed-bed IER (Amberlite IRN 150, H^+- and OH^--form, Sigma Aldrich, Switzerland). Before exposure, IER bags were shaken twice for 30 min with 1 M KCl to saturate exchange sites with K^+ and Cl^-. After exposure, nutrients were extracted from the IER by placing the bags in 50 ml of 0.5 M HCl for 1 h on a shaker. IER extracts were analysed for ammonium and nitrate using a flow injection analyser (FIAstar 5000). Phosphate concentrations were determined in the IER extracts by the acid-molybdate blue method (Murphy & Riley 1962) and measuring absorbance at 880 nm on a spectrophotometer (Uvi Light XT2, Secomam, Ales, France).

Data analysis

Most vegetation and soil data were analysed by three-way analysis of variance, with invasion, plant community type and soil inoculum type as factors. The effects of plant community type, soil inoculum type, and the interaction on the performance of *S. gigantea* was carried out by means of two-way ANOVAs (cf. Table 2). Soil N and P availabilities were analysed by means of repeated measures ANOVA for fertilized (four measurements) and unfertilized (three measurements) periods in the experiment. Variables were log-transformed prior to analyses if necessary to meet assumptions for normal distribution of the residuals. All analyses were performed with JMP 7.0.1 (SAS Institute Inc., USA).

Results

Growth and nutrient uptake of S. gigantea *and native plant communities*

The performance of *S. gigantea* was mainly affected by the plant community (Table 2). *S. gigantea* produced most shoots in the *Molinion* community, less in the *Magnocaricion*, and least in the *Filipendulion* community (Fig. 2a). It also produced significantly more shoot mass (Fig. 2b) and litter mass (data not shown) in the *Molinion* than in the *Magnocaricion* and *Filipendulion* communities. However, shoots grew taller in the *Filipendulion* and *Molinion* than in the *Magnocaricion* community (Appendix 1). N and P concentrations in *S. gigantea* shoots were higher in the *Filipendulion* than in the *Molinion* community (Fig. 2c, Appendix 1). In contrast, shoots of *S. gigantea* took up more N in the *Molinion* than in the *Magnocaricion* and *Filipendulion* communities (Fig. 2d), whereas the P pool in *S. gigantea* shoots did not significantly differ among

communities (Appendix 1).

Growth and nutrient uptake of *S. gigantea* was also affected by the kind of soil inoculum type (Table 2). *S. gigantea* produced more shoot biomass and took up more N and P when a native soil inoculum than when an invaded soil inoculum was present, and the biomass production and nutrient uptake was intermediate with the control soil (Fig. 5). On the other hand, native species produced more biomass and took up more N and P when the control soil inoculum was present than when native or invaded soil inocula were present (Fig. 5). The presence of *S. gigantea* reduced biomass production and nutrient uptake of the native species, but *S. gigantea* did not alter the total biomass production and nutrient uptake of the plant communities (Table 2).

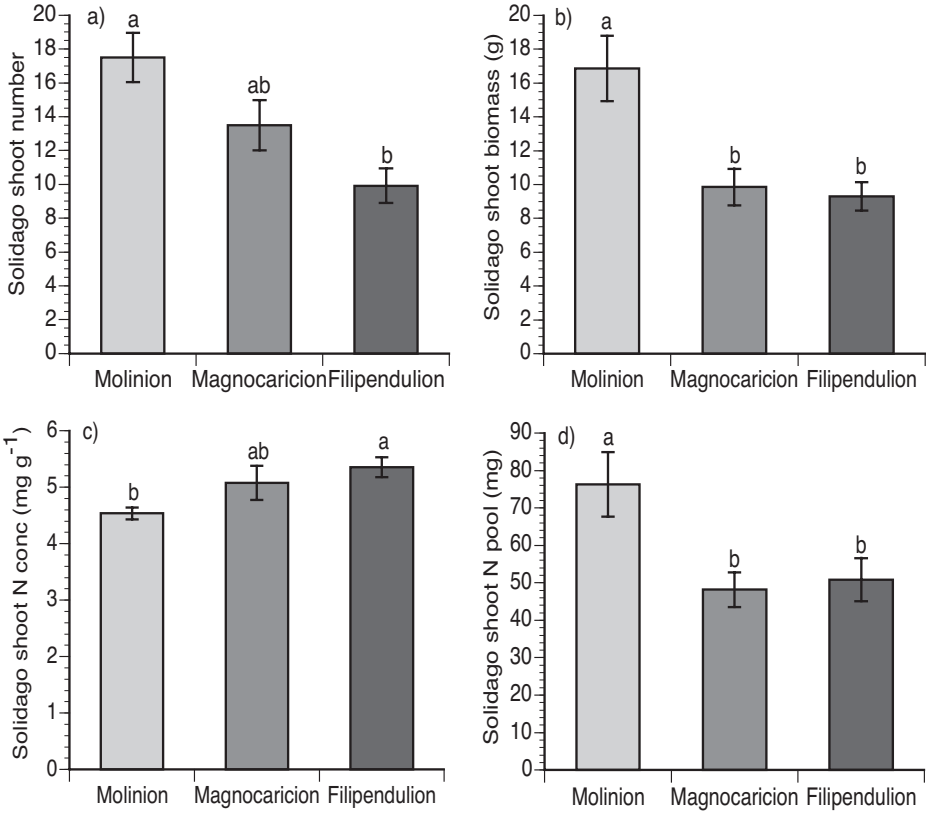


Figure 2. Characteristics of *Solidago gigantea* in dependence of three plant communities in mesocosms: shoot number (a), shoot biomass (b), nitrogen concentrations in shoots (c), and nitrogen pools in shoots (d). Shown are means ± SE per plant community type (n = 12). Results are from two-way ANOVA with post-hoc Tukey test (α = 0.05). Mean values sharing letters are not significantly different.

The three plant communities differed significantly in biomass productivity: the *Molinion* produced the lowest biomass (296.4±6.5 g), the *Magnocaricion* produced intermediate biomass (376.4±34.5 g) and the *Filipendulion* produced the highest biomass (559.4±54.4 g). While the *Filipendulion* community produced significantly more root biomass than *Molinion* and *Magnocaricion* communities, it was the *Magnocaricion* community that produced significantly more shoot biomass than the other two communities (Appendix 1).

Plant communities differed also in their capacity to capture the amount of nutrients supplied with fertiliser. The *Filipendulion* community took up most N and P of all three communities, whereas the *Molinion* community took up the least (Fig. 3, Appendix 1). The *Magnocaricion* community took up similar or higher amounts of nutrients as the *Molinion* community, except for the higher P pools in shoot biomass than the other two communities (Fig. 3, Appendix 1).

Table 2. Effects of invasion by *Solidago gigantea*, plant community type, soil inoculum type, and their interactions on characteristics of the native species and total plant community (3-way ANOVA), as well as effects of plant community type, and soil inoculum type on characteristics of *S. gigantea* (2-way ANOVA). For each effect, the F-values and the significance levels are indicated (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, $P \geq 0.05$). The three-way interactions are not shown; they were not significant ($P > 0.1$).

Plants	Variable	Invasion (I)	Community (C)	Soil (S)	I x C	I x S	C x S
S. gigantea	shoot number		7.77**	1.67			0.34
S. gigantea	shoot max. height		4.15*	2.61			2.09
S. gigantea	shoot biomass		13.53***	6.00**			2.07
S. gigantea	shoot N pool		8.48**	6.88**			2.37
S. gigantea	shoot P pool §		3.54*	6.41**			1.82
Native species	shoot biomass	34.18***	52.34***	29.09***	1.31	0.27	6.97***
Native species	shoot N pool §	112.52***	83.23***	42.30***	4.56*	1.82	7.36***
Native species	shoot P pool	15.74***	139.37***	8.52***	1.03	0.24	6.89***
Plant community	shoot biomass	1.86	38.85***	26.19***	0.36	1.92	5.57***
Plant community	root biomass §	0.03	49.88***	8.73**	0.36	0.78	1.49
Plant community	total biomass §	0.00	36.53***	8.29**	0.48	1.26	1.44
Plant community	total N pool	0.06	26.06***	6.48**	0.17	1.88	0.81
Plant community	total P pool	1.74	10.69***	1.01	0.05	0.24	1.10

Note: Plant community-variables refer to the whole community including *S. gigantea*, whereas Natives-variables exclude *S. gigantea*.

§ Variables were log-transformed prior to analysis

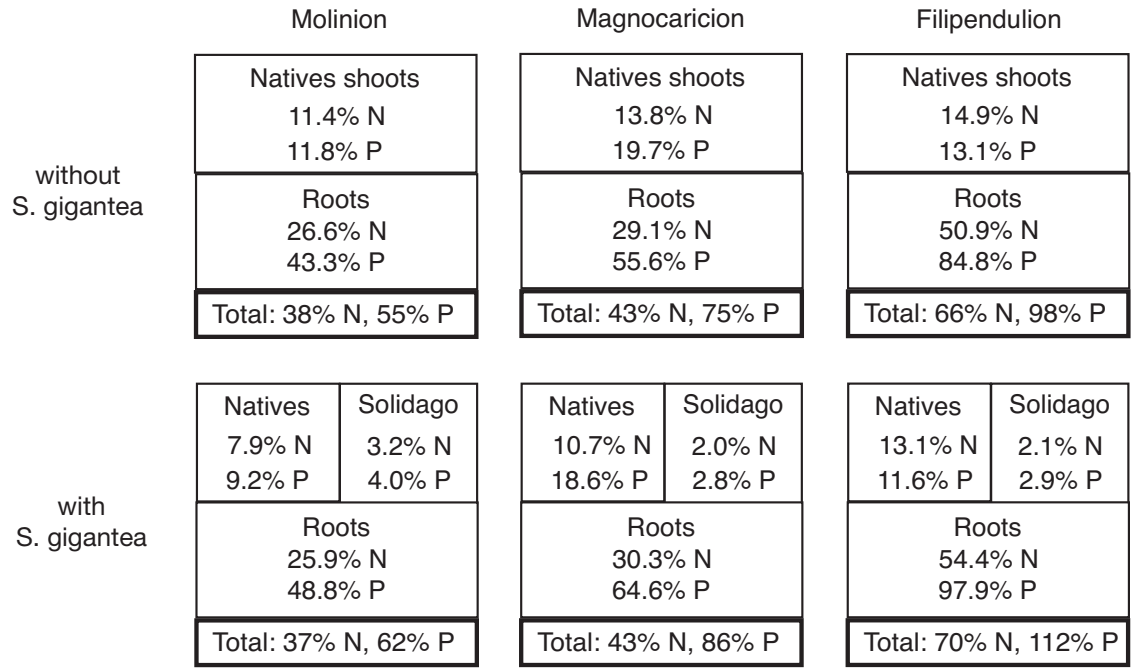


Figure 3. Recovery of supplied N and P for the three different wetland plant communities (*Molinion, Magnocaricion, Filipendulion*), expressed as the percentages of N and P found in shoots of native species and invasive *Solidago gigantea* and in the pooled roots of all plants. Each plant community received in total 2411 mg N and 242 mg P during the experiment. The >100% P recovery for the invaded *Filipendulion* could be due to initial P content in seedlings at time of planting and P release by the soil inocula, as well as low amounts of P in irrigation water and precipitation.

Effects of S. gigantea *on soil properties*

S. gigantea had no effect upon bacterial biomass in 2006 (Table 3), but had reduced bacterial numbers and biomass by 15% in soil after three growing seasons in 2008 (Fig. 4). In contrast to bacterial biomass, soil fungal biomass (measured as ergosterol) increased in response to presence of *S. gigantea* by 21% (Fig. 4) but this effect was detected only in 2008 (Table 3). Moreover, there was a strong interaction between invasion and soil inoculum type (Table 3, Fig. 4), with *S. gigantea* leading to a 65% greater fungal biomass in soil previously grown by this plant (invaded soil), but not in control or native soil.

Enzyme activities varied significantly among plant communities (Table 3), being mostly higher in the *Filipendulion* than in the *Magnocaricion* and *Molinion* communities (data not shown). In 2007, *S. gigantea* increased the β-glucosidase activity in soil, but a year later this effect was no longer evident (Table 3). *S. gigantea* had no effect on ß-N-acetylhexosaminidase and acid phosphatase activities in either year of assessment (Table 3).

Carbon concentration in the soil was mainly affected by plant community type, but invasion

Table 3. Effects of *Solidago gigantea*, plant community type, and soil inoculum type on soil properties, and the interactions of these factors. For each effect, the F-values and significance levels are indicated (*** P < 0.001, ** P < 0.01, * P < 0.05, ° P < 0.1). The three-way interactions are not shown; none of them was significant (P > 0.1). Means ± SE of uninvaded (- *S. gigantea*) and invaded (+ *S. gigantea*) vegetations were calculated from 36 pots, grown with three plant communities (*Molinion, Magnocaricion, Filipendulion*) and three soil inocula (control soil, native soil, invaded soil).

Soil property	Year of assessment	- S. gigantea	+ S. gigantea	Invasion (I)	Community (C)	Soil (S)	I x C	I x S	C x S
Bacterial abundance (10^{10} cells g^{-1} soil C)	2006	39.5 ± 1.6	41.3 ± 1.7	0.30	2.80	3.70*	0.15	1.19	3.10*
Bacterial abundance (10^{10} cells g^{-1} soil C)	2008	65.5 ± 3.1	55.1 ± 2.3	9.77**	21.16***	2.21	1.41	0.10	1.05
Bacterial C (mg g^{-1} soil C)	2006	10.8 ± 0.6	11.6 ± 0.6	0.76	2.81	2.06	0.02	0.43	3.32*
Bacterial C (mg g^{-1} soil C)	2008	16.9 ± 0.8	14.3 ± 0.6	7.86**	12.54***	0.50	1.13	0.09	1.97
Fungal C (mg g^{-1} soil C) §	2006	47.2 ± 5.3	41.0 ± 3.8	2.13	3.38*	38.97***	2.20	0.27	7.66***
Fungal C (mg g^{-1} soil C) §	2008	16.0 ± 1.24	19.3 ± 1.6	5.71*	10.03***	9.32**	0.06	4.94*	2.92*
β-glucosidase (μM g^{-1} h^{-1}) §	2007	0.90 ± 0.07	1.05 ± 0.05	8.45**	11.66***	2.25	2.47	0.09	3.86**
β-glucosidase (μM g^{-1} h^{-1}) §	2008	1.15 ± 0.05	1.24 ± 0.09	0.68	0.78	5.03**	0.40	0.41	0.89
β-N-acetylhexosaminidase (μM g^{-1} h^{-1}) §	2007	0.35 ± 0.02	0.33 ± 0.02	1.35	13.48***	1.63	2.41	0.74	2.18
β-N-acetylhexosaminidase (μM g^{-1} h^{-1}) §	2008	0.72 ± 0.13	0.74 ± 0.07	0.83	14.63***	2.54	0.15	0.80	2.90*
Acid phosphatase (μM g^{-1} h^{-1})	2007	3.14 ± 0.28	3.09 ± 0.15	0.10	16.16***	2.56	5.07**	0.06	0.86
Acid phosphatase (μM g^{-1} h^{-1})	2008	3.23 ± 0.16	3.03 ± 0.20	1.94	8.38***	0.81	0.13	1.62	3.84**
Phenolics 2008 (mg kg^{-1} soil)	2008	81.9 ± 8.9	81.85 ± 4.58	0.72	7.33**	0.93	1.55	0.98	0.37
Soil C (mg g^{-1})	2008	2.09 ± 0.10	2.28 ± 0.09	3.82°	21.67***	3.82*	0.69	0.67	4.11**
N availability in fertil. periods (μg g^{-1} IER)	2007	488.5 ± 67.9	567.9 ± 73.8	1.93	7.06**	6.97**	2.01	2.58°	3.04*
N availability in unfertil. periods (μg g^{-1} IER)	2008	16.9 ± 2.1	14.8 ± 1.7	1.20	3.02°	2.77°	0.88	1.85	0.91
P availability in fertil. periods (μg g^{-1} IER)	2007	74.7 ± 7.4	86.5 ± 8.2	3.37°	6.76**	8.11***	0.75	3.34*	1.56
P availability in unfertil. periods (μg g^{-1} IER)	2008	4.37 ± 0.49	5.12 ± 0.41	0.96	4.46*	4.12*	3.07°	0.32	0.71

Note: N and P availabilities were analysed with repeated-measures ANOVA, including four measurement dates in the fertilized period and three measurement dates in the unfertilized period.

§ Variables were log-transformed prior to analysis

by *S. gigantea* also tended to have an effect with an average of 9.5% higher C concentrations in soil of the invaded communities (P = 0.056, Table 3). Soil phenolic concentration was unaffected by *S. gigantea* (Table 3).

Nitrogen availability in soil was unaffected by the invasion of *S. gigantea* in both fertilised and unfertilised periods (Table 3), but differed among plant communities (Appendix 2) and soil inoculum types in the fertilised period (Table 3, data not shown). *S. gigantea* tended to increase phosphorus availability by 16% in the fertilized period (P = 0.07), but only in soil inoculated with native and invaded soil and not with control soil (I × S, Table 3, data not shown), and had no effect on P availability in the unfertilised period (Table 3). P availabilities differed among plant communities (Table 3, Appendix 2) and soil inoculum types (Table 3, data not shown) in both fertilised and unfertilised periods. For both N and P availability, there was no interaction with the measuring time and invasion of *S. gigantea* in both the fertilized and unfertilized periods, i.e. *S. gigantea* had also no seasonal effect on nutrient availability.

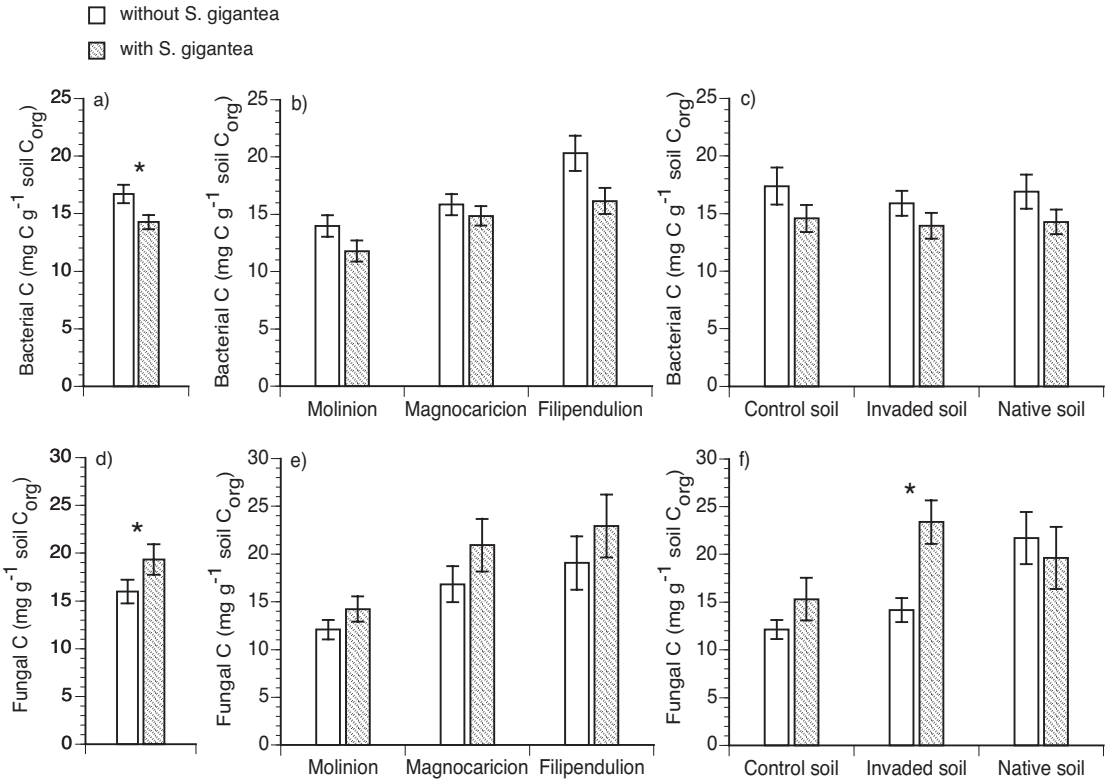


Figure 4. Effects of *Solidago gigantea* on bacterial and fungal biomass (determined as ergosterol concentrations) in soil in 2008 as such (a, d), in interaction with plant communities (b, e) and in interaction with three soil inoculum types (c, f). Control soil means that the same standard soil was used within all plant communities, whereas native and invaded soils were specific for *Molinion, Magnocaricion and Filipendulion*, respectively (cf. Fig. 1). Results are from 3-way ANOVA with post-hoc Students t-test (a, d) and Tukey test (b+c, e+f, α = 0.05). Shown are means ± SE. Mean values sharing letters are not significantly different.

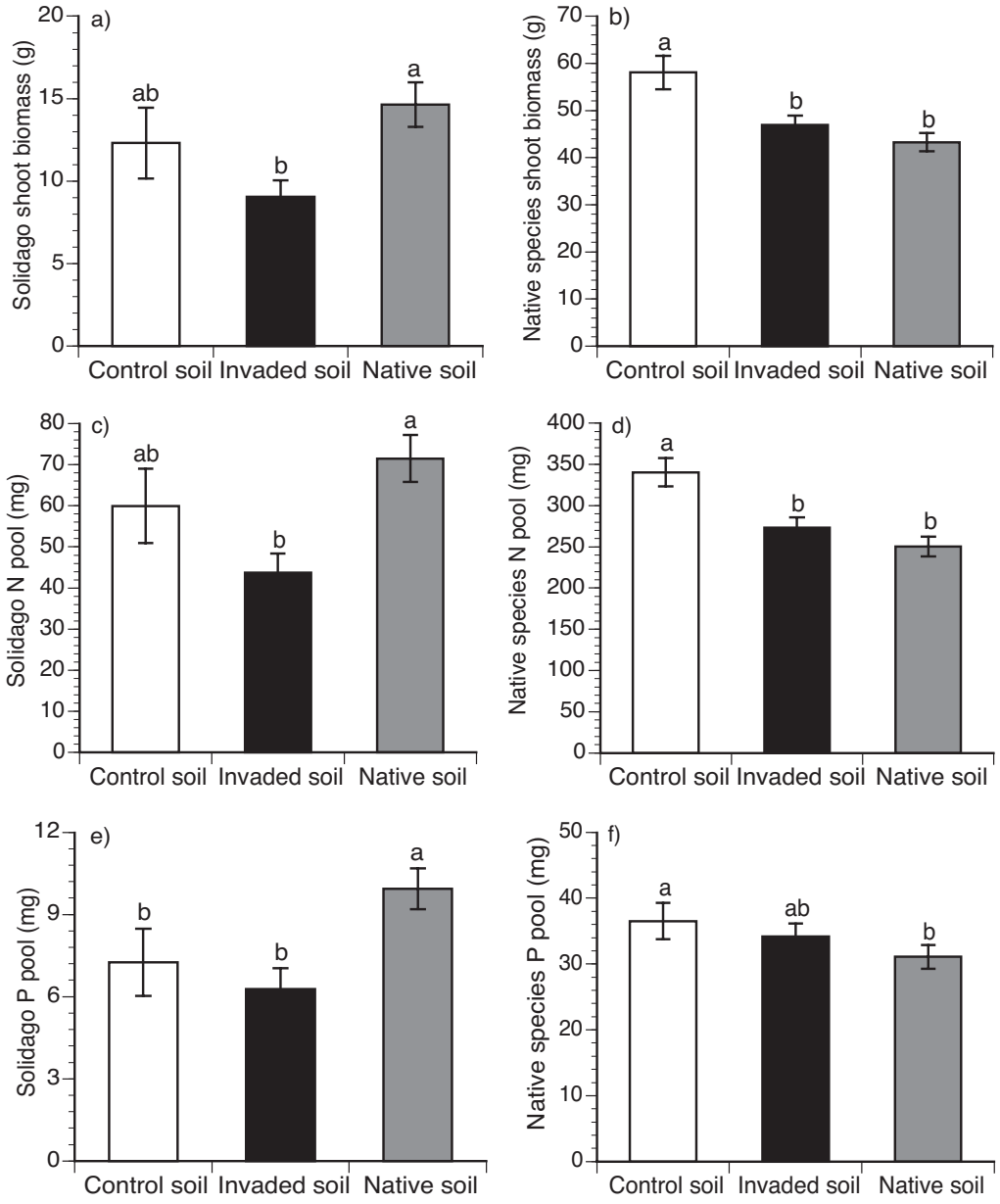


Figure 5. Characteristics of *Solidago gigantea* and native species in dependence of soil inoculum type: shoot biomass (a, b), nitrogen pools in shoots (c, d), and phosphorus pools in shoots (e, f). Control soil means that the same standard soil was used for inoculation within all plant communities, whereas native and invaded soils were specific for the *Molinion, Magnocaricion* and *Filipendulion* community, respectively (cf. Fig. 1). Results are from 2-way ANOVA for S. gigantea and 3-way ANOVA for the native species, respectively, with post-hoc Tukey test ($\alpha = 0.05$). Shown are means ± SE per soil inoculum type (n = 12 for *S. gigantea* and n = 24 for native species). It made no difference for the response of native species to the soil inoculum types, whether *S. gigantea* was present or not. Mean values sharing letters are not significantly different.

Discussion

Effects of S. gigantea *on soil microbial biomass and C, N and P cycling*

Within three growing seasons, *S. gigantea* significantly decreased bacterial biomass and increased fungal biomass. However, these shifts in the microbial community were not accompanied by any significant effect of *S. gigantea* on N and P cycling, as assessed by measuring potential activities of three complementary enzymes. The fact that there were changes in the number and size of bacteria suggests that *S. gigantea* may have altered the bacterial community structure, although changes in metabolic state are also conceivable. We conclude that effects on the microbial community prevail over those on soil nutrients, although we cannot exclude the possibility that *S. gigantea* alters nutrient cycling in later stages of invasion or under more nutrient-rich conditions. This effect of invasive *S. gigantea* upon the soil microbial community has not been previously reported, but otherwise our results are consistent with studies showing changes in plant – microbe interactions during the course of a plant invasion (Wardle et al. 2004; Wolfe & Klironomos 2005; Reinhart & Callaway 2006; Van der Putten et al. 2007).

The reduction in bacterial abundance, size and biomass which we observed in the soil of the invaded communities could be related to a change in fungal biomass, increased competition with plants, substrate limitation, or chemical inhibition (Lodhi & Killingbeck 1980; Lipson et al. 2000; Bais et al. 2004; Broeckling et al. 2008). Indeed, there was a higher fungal biomass in the soils of invaded communities, but especially in pots inoculated with invaded soil (cf. Fig. 4); thus, the decreased bacterial biomass is not fully explained by changes in the fungal biomass. At first sight, the increased competition with plants seems relevant because of the additive design of the experiment (*S. gigantea* plants were added to a constant number of native plants), but by the time of harvesting the overall biomass of plants, as well as the total N and P uptake by plants, was not affected by the presence of *S. gigantea* (Table 2). Furthermore, we have no indications of a reduced substrate availability for bacteria through *S. gigantea*, because in that case we might have expected to observe a reduced ß-glucosidase activity (DeForest et al. 2004), but this was not the case. We suspect, therefore, that chemical inhibition probably has been involved in the reduction of the bacterial biomass.

Whereas shoots of *S. gigantea* are known to contain secondary plant compounds (sesquiterpenes) with antimicrobial and antiherbivoral activity (Kalemba & Thiem 2004; Johnson et al. 2007), there appear to be no reports of antimicrobial activities of the roots or rhizomes. In a previous pot experiment, we found evidence of an allelopathic effect of *S. gigantea* upon the growth of a native grass species (this thesis, chapter 1), though this effect was not greater than that produced by other native forbs and grasses. It could nevertheless have specific antimicrobial root exudates that influence the soil biota. To our knowledge, there is no other study about

chemical inhibition of bacteria by an exotic invasive plant. There are some studies which found a relationship between invasive plants and chemical inhibition of arbuscular mycorrhizal fungi (Stinson et al. 2006; Wolfe et al. 2008) or chemical stimulation of pathogenic fungi, respectively (Mangla et al. 2008). For example, allelochemicals produced by the congeneric species *Solidago canadensis* were recently shown to reduce the mycorrhizal colonization of three native plants in China (Zhang et al. 2007). It is therefore likely that root exudation plays a role in the effects of *S. gigantea* on the microbial biomass.

Carbon concentrations in soil of our experiment tended to be increased by *S. gigantea* (P = 0.056). Although differences were small and not statistically significant, it could be a general effect of *S. gigantea* on invaded ecosystems, since we observed the same effect under field conditions (this thesis, chapter 2). In the field, we explained the effect on soil C by the increased biomass production in vegetations invaded by *S. gigantea.* In this experiment, however, we found no increase in biomass production in communities invaded by *S. gigantea* compared to uninvaded communities (Table 2). An increase in soil carbon concentrations can also be caused by the input of low-quality plant litter with high C:N ratio (Ogle et al. 2004). And indeed, *S. gigantea* shoots had lower nitrogen concentrations than the shoots of the native species (5.0±0.2 *vs.* 5.9±0.5 mg g^{-1}, P = 0.03), which could explain the slight increase in soil carbon. Furthermore, the increased ß-glucosidase activity in soils of invaded communities in 2007 indicated an increase of organic C in the soil compared to the uninvaded communities, although this difference in ß-glucosidase activity was no longer observed in 2008. Increases in soil organic matter (C) are a relatively frequent observation with plant invasions and have been attributed to increased biomass production and litterfall (Scott et al. 2001; Fickbohm & Zhu 2006; Heneghan et al. 2006; Vila et al. 2006). Irrespective of the effects of *S. gigantea* on soil C, we found a relatively strong negative relationship between carbon concentrations and bacterial biomass: the bacterial biomass declined with increasing carbon concentrations in soil (R^2 = 0.50, t = -8.42, P < 0.0001).

A variety of invasive species have been found, or assumed, to increase soil N availability (Ehrenfeld 2003; Allison & Vitousek 2004; Fickbohm & Zhu 2006; Dassonville et al. 2007). However, based on the results from our field study about *S. gigantea* (chapter 2), we would have expected to see a decrease in soil N availability in the presence of *S. gigantea*. In our experiment, soil N availability or factors related to N cycling such as ß-N-acetylhexosaminidase activity, were not altered by *S. gigantea.* Also, we did not see a seasonal difference in N availability in association with invasion of *S. gigantea.* Although the presence of *S. gigantea* reduced the N pool of the native species, the community as a whole did not differ in the N pool among treatments with or without *S. gigantea* (Table 2). In our field study, we assumed that the low quality of the litter probably led to nitrogen immobilisation in the decomposition process and therefore to reduced N availability in soil of invaded stands (chapter 2). Our experiment may simply have

been too short to detect such effects.

Alterations in P cycling and soil P availability due to plant invasions have been less frequently reported, and may indeed be less common, than effects on N cycling. However, increases have been found, particularly in combination with changes in soil pH (Mitchell et al. 1997; Blank & Young 2002; Sala et al. 2007; Rodgers et al. 2008). Although *S. gigantea* tended to increase P availability in soil in the fertilized period, the effect was only evident when native and invaded soil inocula were present, and not when control soil was present. Since neither community P pools nor acid phosphatase activity in soil were changed by *S. gigantea*, and we found no clear direction in effects on soil P availability in the field survey (chapter 2), we conclude that *S. gigantea* scarcely alters P cycling, if at all. In contrast, in Belgian grasslands *S. gigantea* was found to increase as well as decrease soil P availability (Chapuis-Lardy et al. 2006; Dassonville et al. 2008). Since the invaded vegetation in Belgium had higher P concentrations than in our experiment and also compared to field sites in Switzerland, it seems that the effect of *S. gigantea* on soil P availability depends on local conditions and the P status of the invaded soil.

Did the invasion success of S. gigantea and its effects on soil depend on the invaded plant community type?

Contrary to our hypothesis, the effects of *S. gigantea* on soil processes did not depend on the plant community type. We did observe that biomass production of *S. gigantea* was higher when it invaded in the *Molinion* community than in the other communities and *S. gigantea* also took up more nitrogen. Surprisingly, the effects on soil properties (bacteria, ß-glucosidase activity, soil C, fungal biomass) were not different between the plant communities. Furthermore, hypothesized effects on nutrient cycling were not observed, *S. gigantea* did not alter N and P availability, related enzyme activities, nor N and P pools. Sporadically occurring interactive effects between plant communities and *S. gigantea* were not related to significant invasion effects (e.g. acid phosphatase activity).

The higher biomass of *S. gigantea* in the *Molinion* community may be explained simply by a overall lower nutrient uptake capacity of the native *Molinion* vegetation (Fig. 3); thus, more nutrients were left for *S. gigantea*, whereas the competition for nutrients between native and invasive species was much higher in the *Magnocaricion* and *Filipendulion* communities. Our results suggest that *S. gigantea* influences the soil microbial community independently from the productivity of the native vegetation. The surprising result that the presence of *S. gigantea* did affect soil microbial biomass, but the abundance (biomass) of *S. gigantea* did not, could be a further indication for chemical inhibition involved in the effects of *S. gigantea* on the soil microbial community.

Does S. gigantea *benefit from positive plant-soil feedback?*

We hypothesized *S. gigantea* to alter soil properties in order to promote its spread and growth, and hence to show signs of a positive feedback of invasion as was shown for some other species (Callaway et al. 2004; Van Grunsven et al. 2007). However, we found evidence of a negative feedback, with growth of *S. gigantea* being inhibited by substrate inoculated with soil where it had grown before (Fig. 5). In contrast, native species were unaffected by whether or not *S. gigantea* had grown in the soil before (Fig. 5), suggesting that there was no difference in nutrient availability between invaded and uninvaded soil inocula. We note here that for the feedback mechanims we focused on the comparison between native and invaded soil, and not on the control soil; the latter was not directly comparable and was only included in the experiment to compare invasion effects among plant communities. The negative feedback may indicate an accumulation of *S. gigantea*-specific pathogens in soil of *S. gigantea* stands. Since we found a much higher fungal biomass in invaded soil when *S. gigantea* grew on it compared to when only native species (cf. Fig. 4), we speculate that pathogenic fungi could be the source of inhibition, but this obviously requires further investigation. A negative feedback was also observed for other exotic invading plants (Packer & Clay 2000; Beckstead & Parker 2003; Nijjer et al. 2007), but not for *S. gigantea* or related species. It also remains to investigate whether *S. gigantea* experiences positive or negative feedback in its native range, since positive feedback was described for the congeneric species *Solidago canadensis* in its native range (Klironomos 2002), and this species is similarly invasive in Europe as *S. gigantea*.

How can we explain that exotic invasive plants, and *S. gigantea* in particular, experience a negative feedback? By regulating the density of species, negative feedback processes generally contribute to the maintenance of species diversity in a plant community (Bever et al. 1997; Packer & Clay 2000). A negative feedback could therefore trigger the dispersal of an invader, by forcing offspring not to grow too densely, when they are not able to control the pathogens (Van der Putten et al. 2001). However, this hypothesis does not seem to hold for a clonal species such as *S. gigantea* which can form monospecific stands in nutrient-rich habitats. Alternatively, it could be hypothesized that the negative feedback in *S. gigantea* is only evident under rather nutrient-poor conditions, and is masked under nutrient-rich conditions. Nutrient addition can modify plant-soil feedbacks (Manning et al. 2008), but whether this mechanism modifies the direction of feedback in *S. gigantea* needs further investigation. Whatever the mechanism of the negative feedback, our results support the theory that the success of invasive plants depends not only upon positive feedbacks or enemy release mechanisms (Beckstead & Parker 2003).

References

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

Bais, H.P., Park, S.W., Weir, T.L., Callaway, R.M. & Vivanco, J.M. 2004. How plants communicate using the underground information superhighway. *Trends in Plant Science* 9: 26-32.

Beckstead, J. & Parker, I.M. 2003. Invasiveness of *Ammophila arenaria*: release from soil-borne pathogens? *Ecology* 84: 2824-2831.

Belnap, J., Phillips, S.L., Sherrod, S.K. & Moldenke, A. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* 86: 3007-3017.

Bever, J.D., Westover, K.M. & Antonovics, J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology* 85: 561-573.

Blank, R.R. & Young, J.A. 2002. Influence of the exotic invasive crucifer, *Lepidium latifolium,* on soil properties and elemental cycling. *Soil Science* 167: 821-829.

Bratbak, G. 1993. Microscope methods for measuring bacterial biovolume: epifluorescence microscopy, scanning electron microscopy, and transmission electron microscopy. In: Kemp, P.F., Sherr, B.F., Sherr, E.B. & Cole, J.J. (eds.), *Handbook of methods in aquatic microbial ecology*, pp. 309-317. Lewis Publishers, Boca Raton, Florida, USA.

Broeckling, C.D., Broz, A.K., Bergelson, J., Manter, D.K. & Vivanco, J.M. 2008. Root exudates regulate soil fungal community composition and diversity. *Applied and Environmental Microbiology* 74: 738-744.

Buesing, N. & Gessner, M.O. 2002. Comparison of detachment procedures for direct counts of bacteria associated with sediment particles, plant litter and epiphytic biofilms. *Aquatic Microbial Ecology* 27: 29-36.

Callaway, R.M., Thelen, G.C., Rodriguez, A. & Holben, W.E. 2004. Soil biota and exotic plant invasion. *Nature* 427: 731-733.

Chapuis-Lardy, L., Vanderhoeven, S., Dassonville, N., Koutika, L.S. & Meerts, P. 2006. Effect of the exotic invasive plant *Solidago gigantea* on soil phosphorus status. *Biology and Fertility of Soils* 42: 481-489.

Dassonville, N., Vanderhoeven, S., Gruber, W. & Meerts, P. 2007. Invasion by *Fallopia japonica* increases topsoil mineral nutrient concentrations. *Ecoscience* 14: 230-240.

Dassonville, N., Vanderhoeven, S., Vanparys, V., Hayez, M., Gruber, W. & Meerts, P. 2008. Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157: 131-140.

DeForest, J.L., Zak, D.R., Pregitzer, K.S. & Burton, A.J. 2004. Atmospheric nitrate deposition, microbial community composition, and enzyme activity in northern hardwood forests. *Soil Science Society of America Journal* 68: 132-138.

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

Fickbohm, S.S. & Zhu, W.X. 2006. Exotic purple loosestrife invasion of native cattail freshwater wetlands: effects on organic matter distribution and soil nitrogen cycling. *Applied Soil Ecology* 32: 123-131.

Gessner, M.O. & Schmitt, A.L. 1996. Use of solid-phase extraction to determine ergosterol concentrations in plant tissue colonized by fungi. *Applied and Environmental Microbiology* 62: 415-419.

Gessner, M.O. & Newell, S.Y. 2002. Biomass, growth rate, and production of filamentous fungi in plant litter. In: Hurst, C.J. (ed.) *Manual of environmental microbiology*, pp. 390-408. ASM Press, Washington D.C, USA.

Gessner, M.O. 2005. Ergosterol as a measure of fungal biomass. In: Graça, M.A.S., Bärlocher, F. & Gessner, M.O. (eds.), *Methods to study litter decomposition: a practical guide*, pp. 189-196. Springer, Dordrecht, The Netherlands.

Güsewell, S., Zuberbühler, N. & Clerc, C. 2005. Distribution and functional traits of *Solidago gigantea* in a Swiss lakeshore wetland. *Botanica Helvetica* 115: 63-75.

Heneghan, L., Fatemi, F., Umek, L., Grady, K., Fagen, K. & Workman, M. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica*, L.) alters soil properties in Midwestern US woodlands. *Applied Soil Ecology* 32: 142-148.

Johnson, R.H., Hull-Sanders, H.M. & Meyer, G.A. 2007. Comparison of foliar terpenes between native and invasive *Solidago gigantea*. *Biochemical Systematics and Ecology* 35: 821-830.

Kalemba, D. & Thiem, B. 2004. Constituents of the essential oils of four micropropagated *Solidago* species. *Flavour and Fragrance Journal* 19: 40-43.

Klironomos, J.N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417: 67-70.

Kourtev, P.S., Ehrenfeld, J.G. & Haggblom, M. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83: 3152-3166.

Kueffer, C., Klingler, G., Zirfass, K., Schumacher, E., Edwards, P.J. & Güsewell, S. 2008. Invasive trees show only weak potential to impact nutrient dynamics in phosphorus-poor tropical forests in the Seychelles. *Functional Ecology* 22: 359-366.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society London Series B-Biological Sciences* 270: 775-781.

Lipson, D.A., Schmidt, S.K. & Monson, R.K. 2000. Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. *Soil Biology & Biochemistry* 32: 441-448.

Lodhi, M.A.K. & Killingbeck, K.T. 1980. Allelopathic inhibition of nitrification and nitrifying bacteria in a ponderosa pine (*Pinus ponderosa* Dougl.) community. *American Journal of Botany* 67: 1423-1429.

Mack, M.C., D'Antonio, C.M. & Ley, R.E. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C-4 grasses in Hawaii. *Ecological Applications* 11: 1323-1335.

Mangla, S., Inderjit & Callaway, R.M. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. *Journal of Ecology* 96: 58-67.

Manning, P., Morrison, S.A., Bonkowski, M. & Bardgett, R.D. 2008. Nitrogen enrichment modifies plant community structure via changes to plant-soil feedback. *Oecologia* 157: 661-673.

Marler, M.J., Zabinski, C.A. & Callaway, R.M. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology* 80: 1180-1186.

Mitchell, R.J., Marrs, R.H., Le Duc, M.G. & Auld, M.H.D. 1997. A study of succession on lowland heaths in Dorset, Southern England: changes in vegetation and soil chemical properties. *Journal of Applied Ecology* 34: 1426-1444.

Moles, A.T., Gruber, M.A.M. & Bonser, S.P. 2008. A new framework for predicting invasive plant species. *Journal of Ecology* 96: 13-17.

Murphy, J. & Riley, J.P. 1962. A modified single solution method for the determination of phosphorus in natural waters. *Analytica Chimica Acta* 27: 1-6.

Nijjer, S., Rogers, W.E. & Siemann, E. 2007. Negative plant-soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. *Proceedings of the Royal Society B-Biological Sciences* 274: 2621-2627.

Ogle, S.M., Ojima, D. & Reiners, W.A. 2004. Modeling the impact of exotic annual brome grasses on soil organic carbon storage in a northern mixed-grass prairie. *Biological Invasions* 6: 365-377.

Packer, A. & Clay, K. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404: 278-281.

Parham, J.A. & Deng, S.P. 2000. Detection, quantification and characterization of beta-glucosaminidase activity in soil. *Soil Biology & Biochemistry* 32: 1183-1190.

Reinhart, K.O., Packer, A., Van der Putten, W.H. & Clay, K. 2003. Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecology Letters* 6: 1046-1050.

Reinhart, K.O. & Callaway, R.M. 2006. Soil biota and invasive plants. *New Phytologist* 170: 445-457.

Rodgers, V.L., Wolfe, B.E., Werden, L.K. & Finzi, A.C. 2008. The invasive species *Alliaria petiolata* (garlic mustard) increases soil nutrient availability in northern hardwood-conifer forests. *Oecologia* 157: 459-471.

Ruzicka, S., Edgerton, D., Norman, M. & Hill, T. 2000. The utility of ergosterol as a bioindicator of fungi in temperate soils. *Soil Biology & Biochemistry* 32: 989-1005.

Sala, A., Verdaguer, D. & Vila, M. 2007. Sensitivity of the invasive geophyte *Oxalis pes-caprae* to nutrient availability and competition. *Annals of Botany* 99: 637-645.

Scott, N.A., Saggar, S. & McIntosh, P.D. 2001. Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. *Ecological Applications* 11: 1311-1322.

Simon, M. & Azam, F. 1989. Protein content and protein synthesis rates of planktonic marine bacteria. *Marine Ecology Progress Series* 51: 201-213.

Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R. & Zeglin, L.H. 2008. Stoichiometry of soil enzyme activity at global scale. *Ecology Letters* 11: 1252-1264.

Stinson, K.A., Campbell, S.A., Powell, J.R., Wolfe, B.E., Callaway, R.M., Thelen, G.C., Hallett, S.G., Prati, D. & Klironomos, J.N. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *Plos Biology* 4: 727-731.

Swain, T. & Hillis, W.E. 1959. The phenolic constituents of *Prunus domestica*. I - The quantitative analysis of phenolic constituents. *Journal of Science, Food and Agriculture* 10: 63-68.

Van der Putten, W.H., Vet, L.E.M., Harvey, J.A. & Wackers, F.L. 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology & Evolution* 16: 547-554.

Van der Putten, W.H., Klironomos, J.N. & Wardle, D.A. 2007. Microbial ecology of biological invasions. *ISME Journal* 1: 28-37.

Van Grunsven, R.H.A., Van der Putten, W.H., Bezemer, T.M., Tamis, W.L.M., Berendse, F. & Veenendaal, E.M. 2007. Reduced plant-soil feedback of plant species expanding their range as compared to natives. *Journal of Ecology* 95: 1050-1057.

Vila, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Medail, F., Moragues, E., Traveset, A., Troumbis, A.Y. & Hulme, P.E. 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography* 33: 853-861.

Vinton, M.A. & Goergen, E.M. 2006. Plant-soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems* 9: 967-976.

Vivanco, J.M., Bais, H.P., Stermitz, F.R., Thelen, G.C. & Callaway, R.M. 2004. Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. *Ecology Letters* 7: 285-292.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H. & Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304: 1629-1633.

Weber, E. & Jakobs, G. 2005. Biological flora of central Europe: *Solidago gigantea* Aiton. *Flora* 200: 109-118.

Wolfe, B.E. & Klironomos, J.N. 2005. Breaking new ground: soil communities and exotic plant invasion. *Bioscience* 55: 477-487.

Wolfe, B.E., Rodgers, V.L., Stinson, K.A. & Pringle, A. 2008. The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. *Journal of Ecology* 96: 777-783.

Zhang, Q., Yao, L.J., Yang, R.Y., Yang, X.Y., Tang, J.J. & Chen, X. 2007. Potential allelopathic effects of an invasive species *Solidago canadensis* on the mycorrhizae of native plant species. *Allelopathy Journal* 20: 71-77.

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Appendix 1. Comparison of biomass and nutrient characteristics among three wetland plant communities differing in productivity (*Molinion, Magnocaricion* and *Filipendulion*), as well as among *Solidago gigantea* plants within these communities. Means ± SE for the three communities were determined from plants grown with three soil inoculum types and with or without *S. gigantea* and compared by three-way ANOVA. Means ± SE for *S. gigantea* within the three communities were calculated across the three soil inoculum types and compared by two-way ANOVA and Tukey's post-hoc test (α = 0.05). Mean values sharing superscript letters are not significantly different.

Plants	Variable	*Molinion*	*Magnocaricion*	*Filipendulion*
S. gigantea	Shoot max. height (cm)	37.6 ± 2.9^{ab}	32.9 ± 1.3^{c}	38.0 ± 1.8^{a}
S. gigantea	Shoot P conc (mg g^{-1})	0.58 ± 0.03^{b}	0.70 ± 0.01^{a}	0.70 ± 0.07^{a}
S. gigantea	Shoot P pool (mg)	9.7 ± 1.7	6.9 ± 0.7	6.9 ± 1.6
Native species	Shoot biomass (g)	42.0 ± 3.2^{b}	61.2 ± 5.9^{a}	45.1 ± 2.4^{b}
Native species	Shoot N conc (mg g^{-1})	5.5 ± 0.1^{b}	4.8 ± 0.2^{c}	7.6 ± 0.2^{a}
Native species	Shoot N pool (mg)	232.0 ± 19.5^{c}	294.9 ± 31.9^{b}	337.3 ± 23.4^{a}
Native species	Shoot P conc (mg g^{-1})	0.61 ± 0.02^{c}	0.77 ± 0.03^{a}	0.68 ± 0.04^{b}
Native species	Shoot P pool (mg)	25.4 ± 1.9^{c}	46.4 ± 2.8^{a}	30.0 ± 1.0^{b}
Plant community	Shoot biomass (g)	50.4 ± 1.8^{b}	66.2 ± 5.5^{a}	49.8 ± 1.8^{b}
Plant community	Root biomass (g)	202.9 ± 5.6^{b}	252.5 ± 27.7^{b}	461.3 ± 49.6^{a}
Plant community	Root N conc (mg g^{-1})	3.1 ± 0.1^{a}	2.8 ± 0.1^{b}	2.8 ± 0.1^{b}
Plant community	Root N pool (mg)	633.1 ± 23.1^{b}	715.1 ± 69.7^{b}	1268.1 ± 146.0^{a}
Plant community	Root P conc (mg g^{-1})	0.55 ± 0.03^{ab}	0.59 ± 0.05^{a}	0.48 ± 0.03^{b}
Plant community	Root P pool (mg)	111.5 ± 5.8^{b}	145.5 ± 11.7^{b}	221.2 ± 22.0^{a}
Plant community	Total N pool (mg)	911.1 ± 26.2^{b}	1042.1 ± 94.3^{b}	1633.4 ± 152.6^{a}
Plant community	Total P pool (mg)	141.9 ± 6.3^{b}	196.1 ± 13.6^{ab}	254.5 ± 22.5^{a}

Note: Plant community-variables refer to the whole community including *S. gigantea*, whereas Natives-variables exclude *S. gigantea*.

Appendix 2. Comparison of N and P availabilities in soil measured by ion-exchange resins (IER) between the wetland plant communities *Molinion, Magnocaricion* and *Filipendulion* over seven bi-monthly fertilised or unfertilised periods. Means ± SE for the three communities were determined from vegetation grown with three soil inoculum types and with or without S. gigantea. Results are from three-way ANOVA (see Table 3) with Tukey post-hoc test (α = 0.05). Mean values sharing letters are not significantly different.

Nitrogen (μg g^{-1} IER)	Fertilisation	*Molinion*	*Magnocaricion*	*Filipendulion*
April-June	Fertilised	709.5 ± 129.4^{ab}	1014.6 ± 123.8^{a}	472.2 ± 76.8^{b}
June-August	Fertilised	325.1 ± 72.2	452.2 ± 95.1	419.2 ± 79.2
August-October	Fertilised	302.1 ± 69.0^{b}	584.0 ± 100.1^{a}	509.0 ± 86.6^{ab}
October-December	Fertilised	498.0 ± 57.4^{ab}	668.3 ± 64.0^{a}	383.9 ± 53.6^{b}
December-February	Unfertilised	9.0 ± 0.9^{c}	20.9 ± 2.5^{a}	13.5 ± 0.9^{b}
February-March	Unfertilised	17.3 ± 3.6	20.7 ± 3.9	24.2 ± 5.2
March-May	Unfertilised	12.0 ± 0.7	13.7 ± 0.9	11.6 ± 0.8
Phosphorus (μg g^{-1} IER)				
April-June	Fertilised	89.5 ± 12.0^{a}	113.5 ± 12.6^{a}	55.5 ± 8.3^{b}
June-August	Fertilised	83.9 ± 10.3	87.0 ± 12.1	76.3 ± 9.9
August-October	Fertilised	82.3 ± 8.6	111.2 ± 8.2	97.6 ± 9.1
October-December	Fertilised	57.7 ± 6.5^{ab}	72.3 ± 7.2^{a}	40.3 ± 5.7^{b}
December-February	Unfertilised	1.7 ± 0.2^{b}	2.8 ± 0.4^{a}	2.9 ± 0.4^{a}
February-March	Unfertilised	2.2 ± 0.3^{b}	7.0 ± 0.2^{a}	4.5 ± 0.9^{a}
March-May	Unfertilised	6.4 ± 0.7	8.9 ± 1.1	6.3 ± 0.5

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Publications

Scharfy, D., Eggenschwiler, H., Olde Venterink, H., Edwards, P.J., Güsewell, S. (submitted) The invasive alien plant species *Solidago gigantea* alters ecosystem properties across habitats with differing fertility. *Journal of Vegetation Science*.

Conference contributions

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