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L. Chapuis-Lardy · S. Vanderhoeven · N. Dassonville · L.-S. Koutika · P. Meerts

Effect of the exotic invasive plant *Solidago gigantea* on soil phosphorus status

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Abstract Invasions by exotic plant species can modify biogeochemical cycles and soil properties. We tested whether invasion by early goldenrod (*Solidago gigantea*, Asteraceae) modifies soil phosphorus pools at three sites in Belgium. Aboveground phytomass and soil samples (0–10 cm) were collected in early goldenrod patches and in adjacent, uninvaded, grassland vegetation. Soil P fractions varied between the three sites in line with corresponding differences in organic matter, carbonate and clay contents. In addition to site-specific impacts, plots invaded by goldenrods generally had higher concentrations of labile P [i.e. resin-extractable inorganic P (Pi) and bicarbonate-extractable Pi and organic P]. Soil CO_2 release and alkaline and acid phosphomonoesterase activities were also higher in invaded plots, suggesting that the increase in labile Pi was due to enhanced mineralization. Phosphorus uptake by vegetation was 1.7–2.1 times higher in invaded plots, mostly due to the higher annual yield of *S. gigantea*. Altogether, the results indicate that *S. gigantea* enhances P turnover rates in invaded ecosystems.

Keywords Biological invasion · Early goldenrod · Phosphomonoesterase activity · Sequential phosphorus fractionation · Soil phosphorus availability

L. Chapuis-Lardy · S. Vanderhoeven · N. Dassonville · L.-S. Koutika · P. Meerts
Laboratory of Plant Genetics and Ecology,
Université Libre de Bruxelles,
1160 Brussels, Belgium

L. Chapuis-Lardy (✉)
Institute for Research and Development (IRD),
BP 64501, 34394 Montpellier, France
e-mail: lydie.lardy@mpl.ird.fr
Tel.: +33-4-67416228
Fax: +33-4-67416294

Introduction

Over the past two decades, invasions by exotic plants have been recognized as a serious cause of biodiversity loss and natural habitat degradation (Vitousek et al. 1997; Levine et al. 2003). In addition to their impacts on biodiversity and community structure, invasions by exotic plants might also modify ecosystem functioning in a more subtle way. The possibility for plants to be able to modify soil properties and biogeochemical cycles is well recognized. Plant-induced heterogeneity in soil properties has been recognized in many types of ecosystems (Hobbie 1992; Van Breemen and Finzi 1998; Ehrenfeld 2003), and the structure of soil microbial communities has been shown to differ in soils beneath different species of plants (e.g. Westover et al. 1997; Kourtev et al. 2002). The functional capacity of the soil microbial community, as reflected in the activities of enzymes involved in nutrient mineralization processes, also varied among soils under the canopy of different plant species (Kourtev et al. 2002; Chen et al. 2004). The indirect effects of plants on microbial processes can equal or exceed the direct effects of plant uptake on nutrient retention (Hooper and Vitousek 1998). Vitousek (1990) first pointed out that, like other plants, exotic species could modify soil processes.

To our knowledge, only two studies have examined the effects of exotic plants that are invasive in Europe (Plichta et al. 1997; Mitchell et al. 1997). Recently, Ehrenfeld (2003) and Levine et al. (2003) reviewed 79 and 30 papers, respectively, dealing with the effects of invasive exotic plant on soil nutrient cycling processes. Most published studies have focused mainly on C and N cycling, whereas effects on P were only rarely examined (Ehrenfeld 2003). Only quantitative changes in total or exchangeable P were reported, and no data exist on the impacts of exotic plants on P dynamics. Phosphorus is essential for the basic processes in plants that sustain growth and development. Sequential P fractionation method (Hedley and Stewart 1982, modified by Tiessen and Moir 1993) has been and is still widely used to characterise soil inorganic (Pi) and organic (Po) P forms based on their extractability in spe-

cific reagents, which could be related to their availability and chemical forms. Pi removed by anion exchange resin and 0.5 M sodium bicarbonate constitutes a highly available Pi pool in soil (Hedley and Stewart 1982). Diluted NaOH extracts more slowly the available Pi associated with Fe and Al compounds. The weak alkaline bicarbonate extraction removes easily hydrolysable organic compounds such as ribonucleic acids and glycerophosphate (Bowman and Cole 1978), while the stronger alkaline NaOH solution extracts less labile Po associated with humic and fulvic acids. Diluted acid extracts Pi from apatite or octocalcium phosphate (Frossard et al. 1995). Hot concentrated acid extracts more stable pools of Pi and Po, some of which may come from particulate organic matter (POM) and may therefore be potentially bioavailable (Tiessen and Moir 1993). The fractionation residue is unlikely to contain anything but highly recalcitrant P. Soil Po represents between 20 and 80% of total P (Pt) in the surface layers of soils (Dalal 1977), and it also contributes to the P nutrition of plants primarily after being mineralized into Pi. The rate of P mineralization depends on microbial activity and on the activity of micro-organism- and plant-synthesized enzymes (Dalal 1977). Among the phosphatases, phosphomonoesterases (PME) form an important group of enzymes catalysing the hydrolysis of Po monoesters (i.e. mainly inositol phosphates that may account for up to 60% total soil Po; Halstead and McKercher 1975) to orthophosphate, potentially available to both microbes and plants. Plant roots induce several chemical processes that may modify the mobility and bioavailability of P ions in the rhizosphere, namely, root-induced depletion/accumulation of P ions, acidification/alkalinisation and the exudation of organic acids/anions (Hinsinger 2001).

Solidago gigantea (early goldenrod), a native of northern America, was introduced into Western Europe as an ornamental plant, and the first observations of naturalization were reported in the middle of the nineteenth century (Wagenitz 1964). *S. gigantea* considerably increased its range during the twentieth century and has become one of the most serious invaders in Europe (Jakobs et al. 2004). In the present study, we examined its impacts on soil P pools and bioavailability in three sites with contrasting soil properties in Belgium.

Materials and methods

The invasive species

S. gigantea (Asteraceae) is a rhizomatous perennial forb with a height of up to 2.5 m. Its shoots are erect and unbranched except within the inflorescence. Within established stands, population growth occurs almost exclusively vegetatively (rhizomes), as has been shown for the closely related *Solidago altissima* (Meyer and Schmid 1999). Due to this clonal growth, the species can form dense stands that exclude almost all other species. In Europe, goldenrod species are not attacked by herbivores that could control population growth and density, and their growth performance and competitive ability were apparently better than in their native range (Jakobs et al. 2004).

Site selection

Three sites were selected (Table 1) in the central part of Belgium based on the following criteria: (1) a well-established (i.e. at least 10 years old) and still increasing population of the target species that has formed at least 5 m^2 monospecific patches clearly distinct from the surrounding vegetation, (2) adjacent (i.e. only few metres apart) zones of uninvaded vegetation consisting of herbaceous native species and (3) a soil auger investigation that suggested a relatively homogenous soil cover in the whole area (i.e. no apparent topsoil difference between invaded stands and uninvaded zones). According to the Food and Agriculture Organization of the United Nations (FAO) classification, soils were eutric or calcic regosols with anthropic origin (FAO/UNESCO 1990).

Vegetation and soil sampling

Within each site, six 1-m^2 plots were randomly located within stands of the target species, and six 1-m^2 plots were selected between invaded patches in closely adjacent, uninvaded herbaceous vegetation. Aboveground vegetation was harvested at the peak of biomass production in August.

Table 1 Description of the selected sites invaded by *S. gigantea*

Site	Place in Belgium	Site type	Dominating plant species in uninvaded zones[a]
Sg1	Woluwe-St-Lambert	Waste land in urban area	*Dactylis glomerata* (G), *Arrhenatherum elatius* (G), *Heracleum sphondylium* (F), *Festuca rubra* (G), *Pastinaca sativa* (F), *Carex hirta* (G), *Agrostis stolonifera* (G), *Rubus* sp. (S)
Sg2	Kraainem	Rough grassland in urban area	*Agrostis stolonifera* (G), *Pulicaria dysenterica* (F), *Holcus lanatus* (G), *Epilobium hirsutum* (F), *Cirsium arvense* (F), *Leucanthemum vulgare* (F), *Festuca rubra* (G), *Achillea millefolium* (F)
Sg3	Saint-Ghislain	Rough grassland in nature conservation area	*Calamagrostis epigeios* (G), *Achillea millefolium* (F), *Epilobium angustifolium* (F), *Phragmites australis* (G), *Rubus* sp. (S), *Potentilla reptans* (F), *Cirsium arvense* (F)

[a]Growth habit (USDA-NRCS 2004) in parentheses: *G* graminoid, *F* forb/herb, *S* subshrub

The material (all organs pooled) was oven-dried at 60°C for 72 h, weighed and finely ground (<150 μm) prior to analysis.

A bulk soil sample, consisting of six cores (diameter 4 cm, depth soil borer 0–10 cm), was also collected in each 1-m^2 plot. The 12 composite bulk samples per site were air-dried and sieved to 2 mm before analysis. Subsamples were dried at 105°C to constant weight to express chemical characteristics on a dry soil weight basis. Another subsample was finely ground (<150 μm) prior to the determination of total C and N. Selected chemical and physical properties of the topsoils are summarized in Table 2. Hereafter, the term 'Solidago soil' refers to soils in invaded situations, i.e. under the canopy of *S. gigantea*, whereas 'control soil' refers to soil of the corresponding uninvaded situations.

Plant and soil chemical analyses

Dried plant tissue was prepared for P analysis by calcination at 550°C for 5 h and digestion of the resulting ash in 1 N HCl. Phosphorus concentrations were determined on digests by inductively coupled plasma optical emission spectometry (ICP-OES). Results were expressed as Pt concentration [mg P g^{-1} plant dry matter (DM)] and converted into P uptake per unit area (mg P m^{-2}) using the plant aboveground biomass data.

Soils were analysed for total C and total N using a Carbo Erba model NC2100 elemental analyser. Soil P was fractionated sequentially with three replicates per treatment, following the modified method of Hedley and Stewart (1982) as described in Tiessen and Moir (1993), with HCO_3-saturated resin strips (BDH #55164-2S, 9×62 mm), followed by 0.5 M $NaHCO_3$ (bicarb-P), 0.1 M NaOH (OH-P), 0.5 M cold HCl (acid-P) and concentrated hot HCl (hcHCl-P) at 80°C for 10 min. The shaking period for each of the first four steps was 16 h at 20°C, followed by centrifugation for 15 min at approximately 10,000×*g* and followed by filtration. The procedure involved 0.5 g of soil extracted in centrifuge tubes using 30 ml of each extractant. The methods used for the regeneration of the anion exchange strips, the removal of organic matter from the extracts for Pi determination (by flocculation following acidification with H_2SO_4) and the determination of Pt in the solution by oxidation with ammonium persulfate were as described by Tiessen and Moir (1993). The residue containing the most chemically stable P forms (residual-P) was digested using concentrated H_2SO_4 + H_2O_2. Phosphorus in extracts and digests was determined colorimetrically using the ascorbic acid/molybdenum blue method (John 1970). Po in appropriate extracts was calculated by subtracting Pi from Pt (Po = Pt − Pi). Labile Pi refers to available Pi pools, i.e. those removed by resin strips and extracted by sodium bicarbonate (resin-Pi + bicarb-Pi).

Soil CO_2 release and phosphomonoesterase activities

Ten grams of soil was moistened with 2 ml of deionised water and kept for 7 days. Thereafter, the soil was placed in 150-ml sealed plastic jars along with 10 ml of 0.1 M NaOH in a small plastic container. The jars were incubated at 28°C, and carbon dioxide (CO_2) trapped in NaOH was measured by titration with 0.1 M H_2SO_4 on the Radiometer TIM 900 Titration Manager pH meter using an ABU 901 Autoburette after 7 and 14 days.

Phosphomonoesterase activity was measured in a soil solution buffered at pH 6.5 [acid PME (Ac-PME), EC 3.1.3.2] and pH 11 [alkaline PME (Alk-PME), EC 3.1.3.1], with disodium *p*-nitrophenylphosphate tetrahydrate as enzyme substrate (Tabatabai 1982). The soil samples were incubated for 1 h at 37°C, the reaction terminated by alkalinisation and the absorbance determined spectrophotometrically at 410 nm. Controls were processed on each sample to determine the non-enzymatic hydrolysis of the substrate and to correct for background coloration. Enzymatic activities are expressed as the concentration of the hydrolysis product [μg *p*-nitrophenol (NP) g^{-1} soil h^{-1}]. These results were converted to μmol NP g^{-1} soil h^{-1} for easier comparison with literature data (using the molecular weight of *p*-nitrophenol, 139.11 g mol^{-1}).

Table 2 Properties of the topsoil (0–10 cm) in invaded and uninvaded situations at the three sites (means with standard deviations in parentheses, *N*=6)

Site		pH (H_2O)	CEC (cmol kg^{-1})	CO_2 release (mg CO_2–C g^{-1} 14 $days^{-1}$)	Total C (%)	Total N (%)	$CaCO_3$(%)	Clay (%)
Sg1	Uninvaded	7.2 (0.2)	43.5 (18.8)	2.4 (0.3)	3.01 (0.8)	0.17 (0.05)	0.4 (0.1)	12.8 (3.4)
	Invaded	7.1 (0.1)	44.6 (10.7)	2.8 (0.3)	3.91 (0.9)	0.22 (0.04)	0.4 (0.2)	12.6 (2.1)
	P	ns	ns	*	ns	ns	ns	ns
Sg2	Uninvaded	6.5 (0.4)	8.3 (0.9)	2.0 (0.2)	1.48 (0.16)	0.14 (0.01)	0.0	2.5 (0.5)
	Invaded	5.9 (0.3)	8.4 (1.2)	2.5 (0.4)	1.80 (0.54)	0.15 (0.02)	0.0	2.4 (0.4)
	P	*	ns	*	ns	ns	ns	ns
Sg3	Uninvaded	7.1 (0.1)	39.2 (14.0)	2.7 (0.2)	9.36 (1.30)	0.36 (0.05)	1.4 (0.7)	17.0 (7.8)
	Invaded	7.2 (0.0)	59.9 (19.2)	2.9 (0.2)	8.51 (1.21)	0.36 (0.05)	1.3 (0.4)	14.1 (5.0)
	P	ns	ns	ns	ns	ns	ns	ns

ns Not significant (*t* test), *CEC* cation exchange capacity
*$P<0.05$ (*t* test)

Data analysis

All data are presented as means of six plant samples or six composite bulk soil samples per situation (i.e. invaded vs uninvaded within a site). Standard deviations are shown in parentheses or as bars. Randomly selected soil samples were analysed in triplicate, and the analytical error is shown to be relatively small (mean coefficient of variations of 2% for Pt, 7.8% for P fractions and 8.5% for PME activities). All statistical analyses were performed using the Statistica software package (StatSoft 2003). Data were log-transformed when necessary to improve the homogeneity of variances, and the significance level was $P<0.05$ unless otherwise stated. Invaded and uninvaded plots were compared by means of paired *t* tests. Comparisons among sites were performed by means of one-way analysis of variance (ANOVA) and post hoc (least significant difference) tests. A two-way ANOVA was also performed with "site" and "plant cover" (invaded vs uninvaded) as the fixed main effects for selected soil parameters. Pearson correlation coefficients and principal components analysis (PCA) were used to assess relationships between selected soil variables.

Results

Biomass production and P content of aboveground vegetation

The aboveground phytomass of Solidago patches, ranging from 760 to 917 g DM m^{-2}, was significantly higher than that of the native vegetation (from 252 to 438 g DM m^{-2}, depending on the species composition of the uninvaded situations at the three sites; Tables 1 and 3). There was no significant variation of Solidago phytomass among sites [ANOVA; $F(2)=2.0$, $P=0.167$]. It should be noted that the aboveground biomass of the native vegetation (forb-rich grassland) did not vary significantly among sites either [ANOVA; $F(2)=2.8$, $P=0.095$] despite contrasting floristic composition (Table 1). Phosphorus concentrations in the aboveground components of Solidago were significantly lower than those of the native vegetation in the Sg1 and Sg2 sites, whereas no change was observed for Sg3 situations (Table 3). For all sites, Solidago significantly took up 1.7–2.1 times more P per unit area (1,211–1,713 mg m^{-2}) than did native vegetation (574–878 mg m^{-2}; Table 3).

Soil chemical and physical characteristics of the different sites

There was a marked contrast between soils from the different study sites (Table 2). Sg2 soil was slightly acidic, whereas that of Sg1 and Sg3 were neutral (pH 7.1) and contained calcium carbonate (0.4% in Sg1 and 1.4% in Sg3 soil). Due to their high exchangeable calcium content, Sg1 and Sg3 soils presented a higher cation exchange capacity (CEC; average values between control and Solidago soils: 44.1 cmol kg^{-1} for Sg1 and 46.6 cmol kg^{-1} for Sg3) than did the topsoil of Sg2 [8.3 cmol kg^{-1}; ANOVA; $F(2,28)=34.2$, $P<0.001$]. Carbon concentrations ranged from 1.48 to 9.36% (Table 2), with highly significant differences between soils: Sg2<Sg1<Sg3 [ANOVA; $F(2,30)=175.3$, $P<0.001$]. A similar trend was observed for total N concentration, with average values of 0.14% in Sg2, 0.20% in Sg1 and 0.36% in Sg3 soil [$F(2,30)=89.9$, $P<0.001$]. Clay contents were significantly lower in the Sg2 soil (2.4% on average) compared with Sg1 (12.6%) or Sg3 (15.6%) soil [ANOVA; $F(2,29)=32.3$, $P<0.001$].

Within sites, comparisons of means (*t* tests, Table 2) revealed no significant difference between invaded patches and uninvaded plots for clay content, CEC and total C and N contents. At Sg2, the pH decreased slightly from 6.5 in the topsoil of uninvaded plots to 5.9 under the canopy of *S. gigantea*, whereas no significant change was observed in Sg1 and Sg3 (Table 2).

Sequentially extracted P fractions of soil

The sum of all P fractions [$Pt_{(sum)}$] ranged from 309 to 1,067 mg P kg^{-1} soil (Table 4), with significant differences between sites [ANOVA; $F(2,30)=102$, $P<0.001$] as follows: Sg2<Sg1<Sg3. Calcium-associated phosphates extractable with dilute HCl (acid-Pi) was 7.8 times lower in the non-calcareous (Sg2, ≈56 mg P kg^{-1} soil) than in the calcareous soil (Sg1 and Sg3; 417–470 mg P kg^{-1} soil). This fraction accounted for 16–18% of $Pt_{(sum)}$ at Sg2, but reached 40 to 60% at Sg1 and Sg3.

Table 3 Plant aboveground biomass and P concentration and uptake (phytomass × P concentration) in invaded and uninvaded situations at the three sites (means with standard deviations in parentheses, $N=6$)

Site		Phytomass (g DM m^{-2})	P concentration (mg g^{-1} DM)	P uptake (mg m^{-2})
Sg1	Uninvaded	357 (107)	2.4 (0.4)	848 (291)
	Invaded	917 (152)	1.9 (0.3)	1,713 (227)
	P	***	*	***
Sg2	Uninvaded	252 (126)	2.3 (0.2)	574 (287)
	Invaded	891 (102)	1.4 (0.2)	1,211 (244)
	P	***	***	**
Sg3	Uninvaded	438 (171)	2.0 (0.3)	878 (432)
	Invaded	760 (170)	2.0 (0.2)	1,544 (461)
	P	**	ns	*

ns Not significant (*t* test), *DM* dry matter
*$P<0.05$, **$P<0.01$, ***$P<0.001$ (*t* tests)

Table 4 Comparison of P fractions (mg P kg^{-1} soil) in invaded and uninvaded stands

Site		Resin-Pi	Bicarb		OH		Acid-Pi	hcHCl		Residual-P	$Pi_{(sum)}$	$Po_{(sum)}$	$Pt_{(sum)}$
			Pi	Po	Pi	Po		Pi	Po				
Sg1	Invaded	25.6	21.7	5.5	29.3	104.9	417.2	65.1	26.9	51.8	610.6	137.4	747.9
	Uninvaded	16.1	22.7	3.7	36.3	77.0	443.5	65.0	18.4	74.2	657.8	99.1	756.9
	P level	ns[a]	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Sg2	Invaded	28.1	23.0	12.5	42.0	44.6	55.1	53.1	20.6	59.7	261.0	77.7	334.1
	Uninvaded	19.3	19.0	11.0	38.1	36.8	57.0	51.8	15.8	60.1	245.3	63.6	308.9
	P level	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
Sg3	Invaded	91.5	81.0	14.3	118.9	160.5	421.8	100.1	9.6	69.8	883.0	184.4	1,066.9
	Uninvaded	61.2	57.9	11.3	98.0	121.0	469.7	96.6	6.1	98.0	881.	138.4	1,019.8
	P level	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns not significant (*t* test), *Pi* inorganic P, *Po* organic P, *Pt* total P
*$P<0.05$ (*t* test)
[a]Not significant at the 0.05 probability level, but note that, here, $P=0.06$

Resin-P (i.e. highly labile P) is significantly increased under the canopy of *S. gigantea* in all sites: 16.1 vs 25.6 mg P kg^{-1} soil for site Sg1 ($P=0.06$), 19.3 vs 28.1 mg P kg^{-1} for Sg2 ($P=0.03$) and 61.2 vs 91.5 mg P kg^{-1} for Sg3 ($P=0.02$) (Table 4). Bicarb-Pi, another fraction of labile Pi, was significantly higher in Solidago soil of site Sg3 (81 vs 57.8 mg P kg^{-1} in control soil; $P<0.05$; Table 4). In site Sg1, hcHCl-Po significantly increased from 18.4 mg P kg^{-1} in the control soil to 26.9 mg P kg^{-1} under the canopy of *S. gigantea* ($P<0.05$). The effect of *S. gigantea* is also noticeable on the sum of Po fraction [$Po_{(sum)}$] for Sg2 (Table 4; $P<0.05$). The organic fractions extracted by bicarbonate and soda (bicarb-Po and OH-Po, respectively) tended to be higher in soil under the cover of *S. gigantea*, but *t* tests did not show any significant differences for these fractions. When all sites were pooled, two-way ANOVA showed a highly significant site effect for all P fractions (Table 5). A significant (at least $P<0.05$) plant effect was found for resin-P, bicarb-Pi, bicarb-Po and hcHCl-Po (Table 5). For all of these variables, the invaded soils had higher mean values compared with the control. There was a significant site × plant interaction for bicarb-Pi, indicating contrasting impacts of the invasive species depending on the site.

Soil CO_2 release and phosphomonoesterase activities

Soil CO_2 release during wet incubation was significantly higher in soil under Solidago compared with native vegetation at Sg1 (2.8 vs 2.4 mg CO_2–C g^{-1} 14 $days^{-1}$, $t=-2.81$, $P=0.018$) and Sg2 (2.5 vs 2.0 mg CO_2–C g^{-1} 14 $days^{-1}$, $t=-2.83$, $P=0.017$), while there was no significant effect at Sg3 (Table 2). Enzymatic activities ranged from 140 to 336 μg NP g^{-1} soil h^{-1} for Ac-PME and 95 to 641 μg NP g^{-1} soil h^{-1} for Alk-PME (Fig. 1). ANOVA and post hoc tests showed a highly significant site effect ($P<0.001$; Table 5). The calcareous soils Sg1 and Sg3 had highest values for both Ac- and Alk-PME activities compared with the non-calcareous, less organic Sg2 (Fig. 1). Two-way ANOVA revealed a highly significant plant cover effect ($P<0.001$) on Ac-PME activity. The site × plant interaction was also significant ($P<0.05$), indicating that the impact of *S. gigantea* varied depending on the site (Table 5). Ac-PME activity was significantly higher ($P<0.05$) in soil under the canopy of the invasive species in sites Sg1 (336 vs 190 μg NP g^{-1} soil h^{-1}; $t=-3.53$) and Sg2 (211 vs 140 μg NP g^{-1} soil h^{-1}; $t=-3.52$), whereas no difference was observed for the calcareous soil Sg3 (circa 311 μg NP g^{-1} soil h^{-1}; Fig. 1). In the acidic soil of site Sg2, the Alk-PME activity of the soil was unchanged in the

Table 5 Results of two-way analyses of variance (ANOVA; *df*, *F* ratio and probability levels) for the effects of site and plant cover (uninvaded vs invaded) and the interactions on selected P fractions, phosphomonoesterase (PME) activities (Ac-PME and Alk-PME) and soil pH

Source	*df*	Resin-Pi	Bicarb		OH		Acid-Pi	hcHCl		PME		pH
			Pi	Po	Pi	Po		Pi	Po	Ac	Alk	
Site (A)	2	76.7 ***	85.2 ***	26.2 ***	58.9 ***	11.5 ***	174.5 ***	28.5 ***	23.6 ***	21.0 ***	148.1 ***	52.8 ***
Plant (B)	1	15.4 ***	6.2 *	4.8 *	0.9 NS	2.0 NS	1.6 NS	0.1 NS	9.9 **	16.3 ***	30.9 ***	4.7 *
A × B	2	2.9 NS	4.4 *	0.2 NS	1.6 NS	0.3 NS	0.5 NS	0.03 NS	0.7 NS	5.2 *	10.0 ***	4.2 *

Ac Acid, *Alk* alkaline
*$P<0.05$, **$P<0.01$, ***$P<0.001$

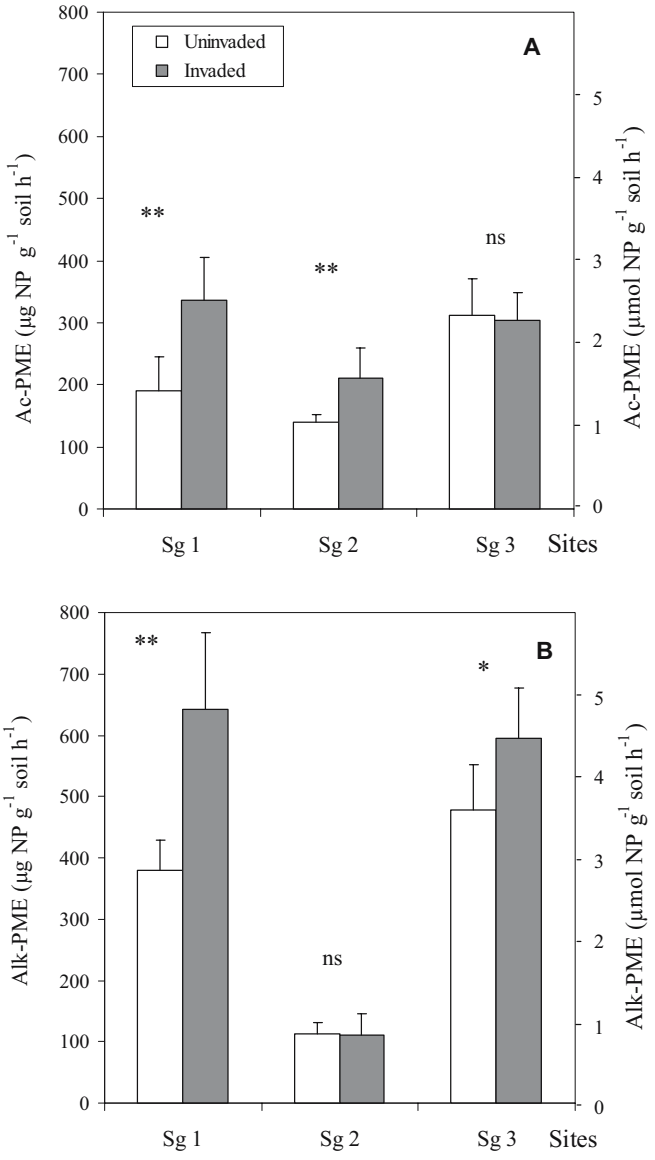

Fig. 1 Acid (**a**) and alkaline (**b**) phosphomonoesterase (PME) activities in topsoil of invaded and uninvaded situations. *Bars* indicate standard deviation

presence of *S. gigantea*. Calcareous soils in Sg1 and Sg3 presented higher Alk-PME activity under *S. gigantea* patches than in the control (Sg1: 641 vs 379 µg NP g^{-1} soil h^{-1}, t=−3.93; Sg3: 623 vs 477 µg NP g^{-1} soil h^{-1}, t=−3.75; P<0.05; Fig. 1). The two-way ANOVA also revealed highly significant (P<0.001) effects of plant cover and site × plant interaction for Alk-PME activity of topsoils.

Relationships between soil P fractions and other soil parameters

Resin-Pi was strongly and highly correlated with bicarb-Pi (r=0.97, P<0.001) and OH-Pi (r=0.093, P<0.001), with the latter being also highly correlated to bicarb-Pi (r=0.96, P<0.001; Table 6). These three forms of Pi were highly (P<0.001) but less strongly (0.71<r<0.85) correlated to OH-Po as well as to C and N content (Table 6). To a lesser extent (0.44<r<0.51), their relationships with bicarb-Po and Ac- and Alk-PME activities were also significant (Table 6). Ac- and Alk-PME activities were highly correlated with each other (r=0.83, P<0.001) and with OH-Po (r=0.74 and 0.70, respectively, P<0.001). Soil pH was correlated with bicarb-Pi (r=0.42, P<0.05), OH-Po (r=0.44, P<0.05) and Ac- and Alk-PME activities (r=0.45, P<0.01 and r=0.76, P<0.001, respectively) but not with resin-Pi, OH-Pi and bicarb-Po. In PCA, the first principal component (PCI) associated with 63.7% of the variance and displayed strong negative loadings (<−0.7) on several variables that could be grouped into three clusters according to their relative position in the plane defined by the two first principal components (data not shown): (i) OH-Po and PME activities, (ii) total C and N contents and (iii) Pi pools (resin-, bicarb- and OH-Pi). The second most important component (PC2)accounted for 19.3% of the total variance and targeted dominantly bicarb-Po and, secondarily, Alk-PME. Soil pH presented similar absolute correlation with PC1 and PC2.

Table 6 Pearson's correlation coefficients between selected P fractions and soil parameters (all sites pooled)

	Bicarb		OH		PME		Soil pH	Total N	Total C
	Pi	Po	Pi	Po	Ac	Alk			
Resin-P	**0.97*****	0.51**	**0.93*****	**0.71*****	0.56***	0.52**	NS	**0.72*****	**0.81*****
Bicarb-Pi		0.44*	**0.96*****	**0.73*****	0.54***	0.53**	0.42*	**0.78*****	**0.85*****
Bicarb-Po			0.51**	NS	NS	NS	NS	NS	NS
OH-Pi				**0.72*****	0.50**	0.43*	NS	**0.78*****	**0.82*****
OH-Po					**0.74*****	**0.70*****	0.44*	0.60***	0.62***
Ac-PME						**0.83*****	0.45**	0.56***	0.58***
Alk-PME							**0.76*****	0.61***	0.64***
Soil pH								0.54***	0.58***
Total N									**0.96*****

Coefficients higher than 0.70 are in bold
NS Not significant
*P<0.05, **P<0.01, ***P< 0.001

Discussion

Site effect on soil P dynamics

We investigated the impacts of the exotic invasive plant *S. gigantea* on soil P status at three different sites. The three study sites have contrasting soil properties that are likely to explain the large differences among them in soil P fractions and PME activities. Sg1 and Sg3 were neutral soils with calcium carbonate and higher clay and organic matter contents compared with Sg2. In the Sg1 and Sg3 soils, the largest pool of P is the $CaCO_3$-bound, acid-extractable P (acid-Pi), which may have partly originated from phosphate rocks or basic slag applications in the past. Despite the influence of calcium carbonates, P-sorption was also impacted by other soil properties such as clay and organic matter contents. The significant difference in clay contents between the studied sites (Sg2 < Sg1 = Sg3) may also be responsible for the differences in soil P-sorbing capacity (Frossard et al. 1995, 2000). The studied soils also differed in their C and N contents; this variability may also be responsible for differences in P fractions, as organic matter consists of various variable charge compounds. Moreover, organic matter mineralization produces organic acids that compete with P for sorption sites on soil minerals (López-Hernández et al. 1986; Frossard et al. 1995, 2000). Higher values of PME activities were found for soils with higher organic matter content and CO_2 release rate (Sg1 and Sg3). Such positive correlations have already been reported in the literature (Bonmati et al. 1991; Tarafdar and Claassen 1988). As expected, Ac-PME was predominant in the slightly acidic soils (Sg2) and Alk-PME was predominant in neutral soils (Sg1 and Sg3); the influence of soil pH on PME activities was described previously (e.g. Eivazi and Tabatabai 1977; Juma and Tabatabai 1978).

In-site soil conditions

A fundamental problem in invasion studies is the potential for pre-existing differences in soil properties that made certain areas more conducive to invasion. The experimental design does not allow us to exclude with complete certainty the possibility of such pre-existing differences between uninvaded and invaded zones. However, uninvaded plots were located close to the selected invaded patches, being separated only by a few metres. Moreover, preliminary field observations and samples analyses (e.g. texture and cationic exchange capacity) showed that soils of uninvaded and invaded zones did not differ significantly. It should also be noted that the *S. gigantea* patches are still expanding. In this context, the observed differences in P more probably resulted from the contrasting plant cover of the two types of plots, uninvaded vs invaded. Our failure to detect significant impacts at some sites (e.g. resin-Pi in Sg1) may be due to the relatively low sample size (n=6). Alternatively, the significant site × plant interactions may be due to the genuinely idiosyncratic impacts of the invasive species. Thus, pH was found to significantly decrease under the canopy of *S. gigantea* in site Sg2 but not in sites Sg1 and Sg3, where calcium carbonate probably enhances soil buffering capacity.

P uptake by vegetation

In our study, Solidago showed differences in plant growth. It produced 1.7–3.5 times more aboveground biomass and took up about twice as much P per unit area as the native plants did. Yearly P turnover will be consequently greater for Solidago than for native vegetation. This may explain the higher proportion of Po fractions in invaded patches. In line with its higher productivity, Solidago has deeper rooting systems compared with native vegetation (personal observation; USDA-NRCS 2004), which may result in an uplift of mineral nutrients from deeper soil layer to surface soil (Jobbagy and Jackson 2004). More specific mechanisms may also be involved in the higher P uptake of *S. gigantea*, including mycorrhizal processes, as documented for the closely related *Solidago canadensis* (Jin et al. 2004). Solidago might exploit its mycorrhizal symbiosis more effectively than might the native grassland species. Zabinski et al. (2002) demonstrated the importance of mycorrhiza in affecting the competitive ability of an invasive forb over native grassland species and suggested that part of its ability to invade grasslands depends on the ability of its mycorrhizal symbiont to increase tissue P concentration. However, in our study, plant P concentration was lower for Solidago than for native plants.

Geochemical and biochemical processes involved in soil P transformations

Acid extractable Pi pools, i.e. Ca-bound P, can be depleted by plant species (Hedley et al. 1983; Zoysa et al. 1997). However, in our study, this fraction did not appear to be significantly affected by the invasive species (Tables 4 and 5), suggesting that it was under geochemical rather then biological control. The presence of *S. gigantea* increased all topsoil labile P pools, i.e. resin-Pi, bicarb-Pi and bicarb-Po, probably because sparingly soluble forms of soil P were mobilised by roots through increased efflux of H^+ or exudation of organic acids (Hinsinger 2001 and references therein). The monospecific cover of *S. gigantea* significantly affected pH (ANOVA, Table 5) at one site, which probably indirectly affected the solubility of P-containing complexes in solution (Lindsay 1979; Hinsinger 2001). In addition to solubilization effect, and because of its high affinity for di- and trivalent cations, citrate and other organic acids can also displace P from humic-metal complexes, making it available for plant uptake (e.g. Frossard et al. 1995; Jones 1998). However, these processes can only partly explain the increase in labile Pi because desorption and release of P by organic acids generally requires high concentrations of organic acids (Jones 1998).

Biologically mediated processes involved in soil P transformations

Differences in soil P status between the control and invaded plots may also result from changes in soil microbiological activity, as soil CO_2 release and PME activities were significantly affected by the invasive species. Biological processes influence P distribution because most of the plant-available P is derived from soil organic matter (e.g. Cross and Schlesinger 1995; Frossard et al. 1995, 2000). In our study, increased Po content in topsoil may be related to higher litter inputs in invaded stands. An increase in bicarb-Po, i.e. highly hydrolysable Po, is indicative of root exudation or high microbial activity and/or microbe and root turnover. The hcHCl-Po was increased in topsoil under Solidago and may contain Po linked to POM. This macro-organic matter has been considered as an active organic matter pool that participates in the release of nutrients. Recent studies have indicated that the dynamics of POM can significantly influence P cycling in crop rotations with either legumes or natural fallow (Maroko et al. 1999; Salas et al. 2003), suggesting that P contained in this organic matter pool can have a significant influence on P availability. The linkage of labile Pi and Po is reflected in enzymatic activities, as Po may contribute to plant P supply after being mineralized by enzymes. The influence of plant species on Po mineralization has been reported previously in various ecosystems (e.g. Tarafdar and Claassen 1988; Giardina et al. 1995; Scott and Condron 2003). Labile Pi, i.e. resin- and bicarb-Pi, was highly correlated to OH-Po and Ac-PME activity.

Phosphomonoesterase activities in this study were in the range found in most other studies across a variety of ecosystems, 28–1,670 μg NP g^{-1} soil h^{-1} (i.e. 0.2–12 μmol NP g^{-1} soil h^{-1}; Nannipieri et al. 1978; Harrison 1983; Rojo et al. 1990; Bonmati et al. 1991; Amador et al. 1997). PME activities are correlated with OH-Po as expected because NaOH probably extracts compounds related to *ortho*-P monoesters (Robinson et al. 1998). Besides microorganisms, plant roots may represent an important source of Ac-PME in soils, while they show no alkaline phosphatase activity (Juma and Tabatabai 1978). Alk-PME has been attributed to soil bacteria and fungi (Tarafdar and Claassen 1988), and soil microorganisms have been shown to be a major factor in controlling organic and Pi solution concentrations in temperate grassland topsoils (Seeling and Zasoski 1993). Plant species composition through root activity (exudation) is likely to determine critically the biomass, the diversity and the functional capacities of microbial species (Kourtev et al. 2002; Johnson et al. 2003; Chen et al. 2004). In addition to root exudates (Hinsinger 2001), differences in the amount and quality (mineral nutrient concentration, C/N ratio and lignin and polyphenol contents) of organic debris between invasive species and resident vegetation may affect soil microbial community structure and function (Ehrenfeld 2003, Kourtev et al. 2002). Thus, in our studied situations, PME activities were affected by the presence of the invasive species, suggesting that the increase in the soil labile Pi pool under the cover of *S. gigantea* was linked to enhanced Po mineralization. The significantly greater soil CO_2 release (indicative of soil respiration rate) and PME activities may be due to enhanced soil microbial activity and diversity after invasion. Such a linkage among plant cover, soil microbiological activity and soil P availability has been suggested by others (e.g. Tarafdar and Claassen 1988; Spears et al. 2001; Scott and Condron 2003).

Conclusions

It has been recognized that exotic invasive species can modify C and N cycling (Ehrenfeld 2003). Our results provide one of the first demonstrations of the influence of an invasive species on P availability and dynamics in soil. The results point out enhanced P dynamics in soil invaded by *S. gigantea*, probably through biologically mediated processes. However, this effect may vary with soil type and invading plant. The results also highlight that the impacts of exotic plants may not be apparent where only the total soil pool is considered, as observed by Ehrenfeld (2003) for C and N in her recent review. It is clear that a comprehensive understanding of the impacts of exotic species on soil requires a functional approach of the bioavailability of specific nutrients, including P.

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