Seasonal effect of the exotic invasive plant *Solidago gigantea* on soil pH and P fractions§

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Abstract

Invasions by alien plants can alter biogeochemical cycles in recipient ecosystems. We test if Early Goldenrod (*Solidago gigantea*) alters P fractions. To that end, we compare invaded plots and adjacent, uninvaded resident vegetation for specific fractions of organic and inorganic P, phosphomonoesterase (PME) activity in topsoil, and immobilization of P in above- and belowground organs and in soil microbial biomass. Invaded plots had lower soil pH and 20%–30% higher labile P fractions (resin-P_i, bicarb-P_i, NaOH-Pi), and the difference was consistent across seasons. There was no difference in microbial P. Alkaline-PME activity was 30% lower in topsoil of invaded plots. Annual P uptake in aboveground phytomass was not markedly higher in *Solidago.* In contrast, P in belowground organs steadily increased in autumn in invaded plots, due to both increased biomass and increased P concentrations. This indicated higher net P immobilization in *Solidago*, far in excess of both resorption from senescing shoots and P requirements for aboveground biomass in subsequent year. Higher turnover rates of P in belowground organs and mobilization of sparingly soluble P forms through rhizosphere acidification may be involved in the observed differences in soil P status between invaded and uninvaded plots.

Key words: exotic-species effects / Early Goldenrod / soil-plant P cycling / soil phosphorus availability / microbial biomass P / phosphomonoesterase

1 Introduction

Biogeochemical cycling of nutrients is influenced by the species composition of plant communities (*Evans* et al., 2001; *Vitousek* et al., 1987). Invasions by exotic plant species may result in dramatic changes in the structure of plant communities (*Tyser* and *Key*, 1988). In some cases, exotic invasive plants are able to spread rapidly and build up monospecific stands in their new habitats. In addition to their effects on community structure, invasive plants can alter ecosystem function (*Vitousek*, 1990; *Ehrenfeld* et al., 2001). Thus, impacts of invasive plants on soil C and N were demonstrated. In general, exotic invasive species have higher net primary productivity and higher turnover rates of C and N, but the opposite pattern was also found (*Ehrenfeld*, 2003). These impacts are also mediated by alterations in soil microbial communities (*Hooper* and *Vitousek*, 1998; *Kourtev* et al., 2002).

In addition to N, P is the second-most limiting mineral nutrient to plants in natural habitats. Impacts of invasive species on P and other nutrients were rarely examined. Thus, increased soil-P fractions were found under the canopy of invasive N-fixing species (*Witkowski* and *Mitchell*, 1987) and of the crucifer *Lepidium latifolium* (*Blank* and *Young*, 2002). Plant species effects on soil P can be mediated by various mechanisms including alterations of rhizosphere pH, production of phosphoesterases, symbiotic interactions, and mobilization of sparingly soluble P forms by root exudates (*Hinsinger*, 2001 and references therein).

Early Goldenrod (*Solidago gigantea*), introduced from N America as an ornamental species, has spread rapidly in Europe, becoming one of the most widespread alien invasive species (*Jakobs* et al., 2004). Recently, *Güsewell* et al. (2005) failed to show a significant impact of invasion by Early Goldenrod (*Solidago gigantea*) on total soil P in Swiss wetlands. *Chapuis-Lardy* et al. (2006) did not also find impact on total soil P but found increased concentrations of readily available inorganic P in topsoil under *S. gigantea*, possibly due to increased phosphatase activity. However, in this study soil P was sampled on a single date and was determined on dried soil samples. Seasonal variation of soil labile P fractions and phosphatase activity may be quite large (*Chen* et al., 2003; *Grierson* and *Adams*, 2000; *Krämer* and *Green*, 2000). The possibility also exists that impacts on soil P vary throughout the year, due to phenological differences between Early Goldenrod and native vegetation. Finally, in order to better understand the mechanisms of the impacts, other important P fractions need to be quantified, including P in plant tissues and litter and soil microbial P.

In this study, in an effort to better understand the mechanisms by which Early Goldenrod may affect soil P, we examine seasonal variation of labile inorganic and organic soil-P fractions,

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microbial P, and phosphomonoesterase activity. All measurements were performed on fresh soil samples. In addition, P in standing biomass (above- and belowground) was also assessed.

2 Materials and methods

2.1 Invasive plant

Solidago gigantea (Asteraceae) (Early Goldenrod) is a geophytic rhizomatous perennial up 2 m in height. Due to clonal growth, the species can form dense, monospecific stands (*Jakobs* et al., 2004). Early Goldenrod is native to N America and was introduced to Europe in the 19th century as an ornamental species. In Europe, goldenrod species apparently don't suffer from herbivory and show increased vigor and competitive ability compared to populations from the native range (*Jakobs* et al., 2004).

2.2 Study site

The study site is located at Kraainem, a few km in the NE of the city of Brussels (Belgium). *Solidago gigantea* has established there for more than 20 y in an abandoned cultivated field. It forms dense, monospecific stands, ranging in size from a few to about 50 m^2, surrounded by native, herbaceous vegetation. Invaded patches are still extending. Native vegetation is a dense, mesic grassland 0.5–1 m in height. The most abundant species are: *Achillea millefolium, Agrostis stolonifera, Carex flacca, Cirsium arvense, C. palustre, Daucus carota, Festuca rubra, Holcus lanatus, Leucanthemum vulgare, Plantago lanceolata, Pulicaria dysenterica, Ranunculus repens, Senecio jacobaea.* In contrast to the resident vegetation, all aboveground organs of Early Goldenrod die off in November and are completely replaced in spring. According to the FAO classification, the soil is an Eutric Regosol with anthropic origin (*cf.*, deep cultivation) (*FAO-UNESCO*, 1990). A preliminary soil auger investigation suggested a relatively homogenous soil cover in the whole area (*i.e.*, no apparent topsoil difference between invaded stands and uninvaded zones). Selected characteristics of this silty-loam soil are given in Tab. 1. Invaded plots have lower pH and bulk density and higher concentrations of NH_4-acetate–extractable P (Tab. 1). There is no significant difference in other element concentrations or in clay content between the soils under invaded and native, uninvaded vegetation.

Table 1: Selected properties of the topsoil (0–10 cm in depth, $n = 6$) in invaded and uninvaded stands.

	Uninvaded	Invaded	***p*** (*t*-test)[b]
pH	6.5	5.9	*
CEC[a] ($cmol_c\,kg^{-1}$)	8.3	8.4	*ns*
K[a] ($cmol_c\,kg^{-1}$)	68.2	97.9	*ns*
Mg[a] ($cmol_c\,kg^{-1}$)	109.9	126.0	*ns*
P[a] ($mg\,kg^{-1}$)	2.6	4.6	*
Total C (%)	1.48	1.80	*ns*
Total N (%)	0.135	0.150	*ns*
Clays (%)	2.45	2.43	*ns*
Bulk density ($g\,cm^{-3}$)	1.21	1.13	*

[a] extracted by 1M ammonium acetate, pH 4.65
[b] *t*-tests: *ns*, not significant; * $p < 0.05$

2.3 Soil sampling

Soil samples were collected at five dates (July and September 2004; January, March, and May 2005) from ten 1 m^2–plots (five plots in uninvaded vegetation, five plots within invaded stands). Plots in uninvaded vegetation were located randomly and were at least 10 m apart from each other. Invaded plots were located within the different largest *Solidago* stands, where the density of *Solidago* shoots was highest. In each plot, six soil cores were collected (0–10 cm in depth, ∅ 4 cm; litter discarded) and pooled into a single bulk sample. Sampling was restricted to 10 cm in depth because phosphatase activity and microbial P are most elevated in that soil layer (*Chen* et al., 2003; *Spears* et al., 2001; *Chen*, 2003; *Grierson* and *Adams*, 2000). Fresh soil samples were used on account of the fact that air-drying may alter P chemical speciation, microbial immobilization, and phosphatase activity (*Bartlett* and *James*, 1980; *Brookes* et al., 1982; *Turner* et al., 2002a). Fresh soil samples were sieved (4 mm mesh), and root fragments were manually removed. Analyses were performed generally within 48 h of collection. Relative moisture content was determined by oven-drying (105°C).

2.4 Plant sampling

Above- and belowground-vegetation samples were collected at three dates corresponding to contrasted phenological states: (1) at the peak of aboveground biomass (August 2004), (2) after the start of senescence (November 2004), and (3) during aboveground-biomass production (May 2005). Vegetation-collection plots (*i.e.*, four in invaded and four in uninvaded vegetation; 0.5 m × 0.5 m for shoots and 0.3 × 0.3 m for roots) were located close to the corresponding soil-sampling plots (<1 m apart). Aboveground biomass of *Solidago* was divided in three parts: living leaves, living stems, and litter. Litter comprises organic debris on the ground and standing dead shoots from previous year. For the uninvaded vegetation, which is dominated by grasses, sorting living and dead organs was practically not feasible due to gradual senescence of grass leaves, and all aboveground parts were thus pooled. Belowground organs were excavated (depth: 0–20 cm) in August and November; no root collection in May 2005. The soil samples were sieved under running tapwater, and rhizomes and roots were carefully separated from the mineral fraction with a 2 mm sieve. Plant samples were oven-dried until constant weight at 50°C and ground (<0.12 mm) before analysis.

2.5 Soil and plant analyses

2.5.1 Soil analyses

Soil pH was measured with a glass electrode on a soil-water stiff paste (1:1 soil–to–distilled water ratio).

All P forms were assessed on fresh soil sample (sieved at 4 mm). Different extraction methods were used to assess specific fractions of P with contrasting bioavailability. Anion-exchange resins were used to assess readily available P forms. Methods for determining inorganic P extractable by anion-exchange resins follow *Kouno* et al. (1995). Three grams of soil samples were shaken in 30 mL demineralized water in presence of three strips (60 mm × 10 mm) of anion-exchange resins (B.D.H. Chemicals Ltd, Poole, UK) for 16 h. Resin strips were rinsed and shaken in 30 mL HCl 0.5 M for 1 h, and P was determined colorimetrically (*John*, 1970). Sodium bicarbonate–extractable fractions also comprise P that is considered as bioavailable in the short term. An amount of 5 g of fresh soil was shaken in 100 mL $NaHCO_3$ (0.5 M; pH 8.5; *Olsen* and *Sommers*, 1982) for 30 min. Sodium hydroxide–extractable fraction comprises P forms that are considered as more slowly available. An amount of 1 g of soil was shaken in 30 mL NaOH (0.1 M) for 16 h (*Bowman* and *Cole*, 1978). Bicarb-P and NaOH-P extracts were acidified and diluted for determination of inorganic P (bicarb-P_i and NaOH-P_i, respectively) as recommended by *Tiessen* and *Moir* (1993). Total P (P_{tot}) was also determined on the same extracts by oxidation in the autoclave in presence of NH_4-persulfate (*Tiessen* and *Moir*, 1993). Organic P (bicarb-P_o and Na OH-P_o, respectively) was determined as ($P_o = P_{tot} - P_i$). Phosphorus was determined colorimetrically in all extracts by the ascorbic acid–ammonium molybdate method (*John*, 1970).

A fumigation-extraction method was applied to determine microbially immobilized P (*McLaughlin* and *Alston*, 1986). Each soil sample was divided into three subsamples that were treated in parallel. In subsample A, P_i was extracted in 100 mL Na-bicarbonate (0.5 M, pH 8.5) for 30 min. Subsample B was subjected to fumigation using liquid chloroform for 36 h, followed by bicarbonate extraction after complete evaporation of chloroform. A correction coefficient K_p (0.40 at 25°C; *Brookes* et al., 1982) was applied to account for incomplete recovery of microbial P_o. Subsample C was extracted in Na-bicarbonate after addition of inorganic P (125 μg). This served to assess the magnitude of P_i sorption, expressed as the recovery coefficient R. All extracts were acidified and diluted (*Tiessen* and *Moir*, 1993), and P was determined colorimetrically as specified here above. All measurements were replicated thrice. Microbial biomass P was finally calculated as $[(B - A) \times 100 / (R \times K_p)]$ (*Kouno* et al., 1995). This analysis was not performed for the July samples.

Phophomonoesterases (PME) activity was determined by the para-nitrophenyl phosphate tetrahydrate (pNPP) method (*Tabatabai*, 1982). A fresh soil sample was incubated with pNPP at 37°C and pH 6.5 (acid phosphatases) or pH 11 (alkaline phosphatases). Reaction was stopped with NaOH 0.5 M and $CaCl_2$ 0.5 M. After filtration, the product of the reaction (pNP, para-nitrophenol) was determined colorimetrically at 410 nm. Each sample was replicated thrice. A blank was included to correct for nonenzymatic hydrolysis. Enzymatic activities are expressed as μg pNP (g soil)$^{-1}$ h^{-1}. Phosphomonoesterases (PME) are enzymes involved in hydrolysis of phosphomonoesters and are thus most important in mineralization of organic P. Acid phosphatases (ac-PME) are most abundant in acid soils (*Tabatabai*, 1982) and are produced by plant roots, microorganisms, and pedofauna. Alkaline phosphatases (alk-PME) are most abundant in neutral soil and are produced by soil bacteria, fungi, and animals only (*Krämer* and *Green*, 2000).

2.5.2 Phytomass analyses

Plant samples were ashed in a muffle furnace at 550°C for 8 h. Ashes were dissolved in concentrated HCl, and P was determined by ICP-OES (Varian Vista MPX).

2.6 Calculation of pools and fluxes

Soil P pools were calculated based on measurements of soil bulk density in invaded and uninvaded plots.

The amount of P that is resorbed in autumn from senescing shoots of *Solidago* was estimated as follows: [(P concentration at the peak of biomass – P concentration in senesced shoots) × aboveground biomass]. For the uninvaded vegetation, it was not possible to calculate resorption because senesced and living organs could not be separated due to gradual senescence of grass leaves. *Aerts* (1996) estimated average P-resorption efficiency of grasses as 71.6%. This figure was used to calculate a rough estimation of annual P resorption in the uninvaded vegetation. Phytomass harvested in August in the uninvaded vegetation mostly consists of living materials (personal observation).

A loss of P in root litter could not be measured directly, because belowground organs were collected at only two dates (August and November) and no attempt was made to separate living and dead roots. As *Solidago* patches in the studied sites have more than 15 y and vegetation samples were collected in their centre, *i.e.*, where shoot density was highest, we assume that standing biomass has reached a steady state (*i.e.*, no net biomass increase from year to year). Under this assumption, P losses in root litter can be estimated based on seasonal variation in the mass of belowground organs: (highest value of belowground P stock, November) – (lowest value of belowground P stock, August).

2.7 Data analysis

The results were expressed as arithmetic means with standard deviations. The data were analyzed by two-way analysis of variance with date and invasion as main fixed effects. Data were log-transformed when necessary to meet assumptions of analysis of variance. In this analysis, a significant date effect indicates seasonal variation, a significant invasion effect indicates significant difference between invaded and uninvaded plots, and a significant date × invasion interaction indicates that the difference between invaded and uninvaded plots changes with time. All statistical analyses were performed with Statistica software (StatSoft, Inc.).

3 Results

3.1 Soil parameters

3.1.1 Soil pH

Soil pH was consistently lower in invaded plots at all dates (annual mean for invaded: 5.94, uninvaded: 6.36). Seasonal variation was not significant in spite of slightly lower values in July compared to January. Date × invasion interaction was also not significant (Tab. 2).

Table 2: Two-way analyses of variance of seasonal variation of soil pH, soil P fractions, soil phosphatase activity in plots invaded by Early Goldenrod and adjacent, uninvaded plots. Degree of freedom (df), mean squares, and significance levels. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns not significant.

	Invasion (df = 1)	**Date** (df = 4)	**Date × invasion** (df = 4)	**Error** (df = 41)
pH	2.31***	0.26 ns	0.136 ns	0.177 ns
Resin-P	0.20***	0.010 ns	0.013 ns	0.0122 ns
Bicarb-P_i	0.26***	0.11***	0.0075 ns	0.015 ns
Bicarb-P_o	0.036 ns	0.25***	0.028 ns	0.018 ns
NaOH-P_i	0.37***	0.022 ns	0.0094 ns	0.019 ns
NaOH-P_o	0.024 ns	0.22***	0.0038 ns	0.0127 ns
Microbial P	0.0016 ns	1.015***	0.0063 ns	0.135 ns
Ac-PME	0.017 ns	0.12***	0.0029 ns	0.0103 ns
Alk-PME	0.055***	0.22***	0.0066 ns	0.0236 ns

3.1.2 Soil P fractions

Resin-P_i was systematically higher in invaded plots at all dates (Fig. 1) (annual mean for invaded: 6.4, uninvaded: 4.6 mg P (kg dry soil)$^{-1}$). The difference tended to be larger in summer (3.5 mg P (kg dry soil)$^{-1}$) compared to winter (1 mg P (kg dry soil)$^{-1}$), but neither date nor date × invasion interaction were significant (Tab. 2).

Bicarb-P_i was markedly higher in invaded plots (annual mean for invaded: 13.7 mg P (kg dry soil)$^{-1}$; uninvaded: 10.1 mg P (kg dry soil)$^{-1}$) (Fig. 2). Seasonal variation was significant

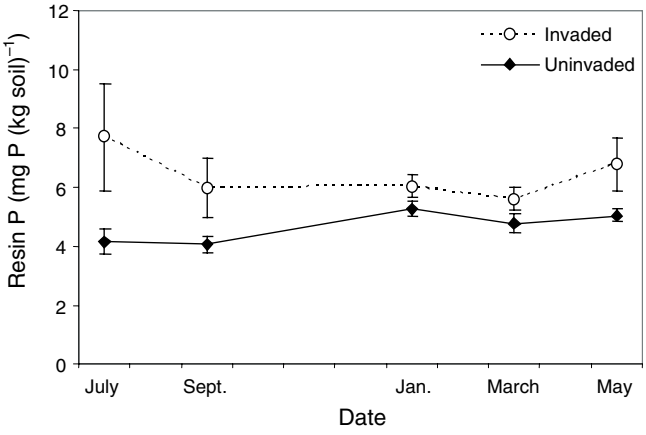

Figure 1: Seasonal variation of soil resin-P_i (0–10 cm) in plots invaded by Early Goldenrod and adjacent, uninvaded plots. Means (n = 6) and standard deviations.

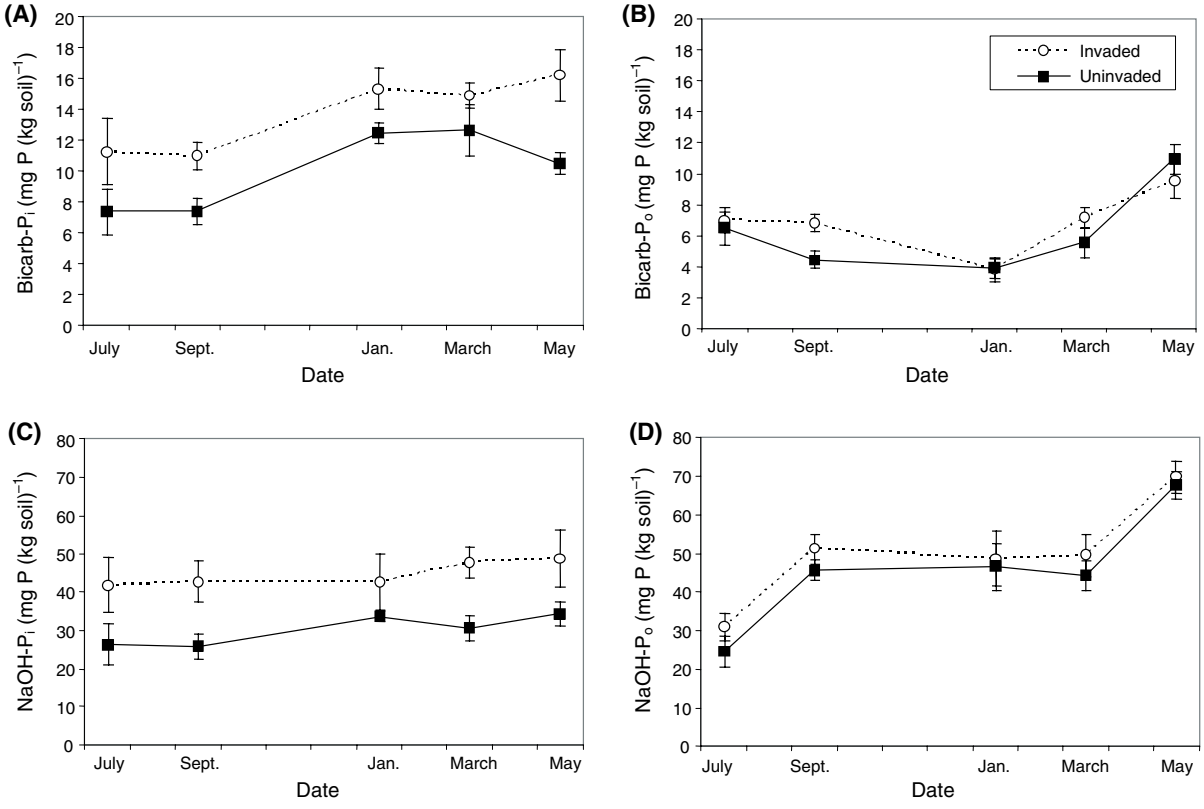

Figure 2: Seasonal variation of different soil P fractions (0–10 cm) in plots invaded by Early Goldenrod and adjacent, uninvaded plots. (A) bicarb-P_i, (B) bicarb-P_o, (C) NaOH-P_i, (D) NaOH-P_o. Means (n = 6) and standard deviations.

($p < 0.001$), with markedly higher values in winter compared to summer, but the date × invasion interaction was not significant (Tab. 2). Bicarb-P_o did not differ between invaded and uninvaded plots (annual mean for invaded: 7.8 mg P (kg dry soil)$^{-1}$; uninvaded: 7.0 mg P (kg dry soil)$^{-1}$) (Fig. 2).

Seasonal variation was significant ($p < 0.001$), with highest and lowest values in May and January, respectively. Date × invasion interaction was not significant (Tab. 2). NaOH-P_i was systematically higher in invaded compared to uninvaded plots (annual mean for invaded: 44.8 mg P (kg dry soil)$^{-1}$; uninvaded: 30.1 mg P (kg dry soil)$^{-1}$) (Fig. 2). Seasonal variation and date × invasion effects were not significant (Tab. 2). NaOH-P_o had slightly higher values in invaded stands, but the difference was not significant (annual mean: invaded: 50.0 mg P (kg dry soil)$^{-1}$; uninvaded: 45.8 mg P (kg dry soil)$^{-1}$; $p > 0.05$) (Fig. 2). The date effect was significant ($p < 0.001$), with the lowest and the highest values in July and May, respectively (Tab. 2).

3.1.3 PME activities

Both ac-PME and alk-PME activities were highest in July and steadily decreased from summer to the end of winter (Fig. 3). Ac-PME activity was generally somewhat higher in invaded stands, but the difference was not significant (annual mean for invaded: 222.4 μg pNP (g soil)$^{-1}$ h^{-1}, uninvaded: 197.9 μg pNP (g soil)$^{-1}$ h^{-1}). Alk-PME activity was ca. 50% lower in invaded stands at all dates, and the difference was highly significant (annual mean for invaded 124.1 μg pNP (g soil)$^{-1}$ h^{-1}, uninvaded: 176.4 μg pNP (g soil)$^{-1}$ h^{-1}; $p < 0.001$) (Fig. 3 and Tab. 2).

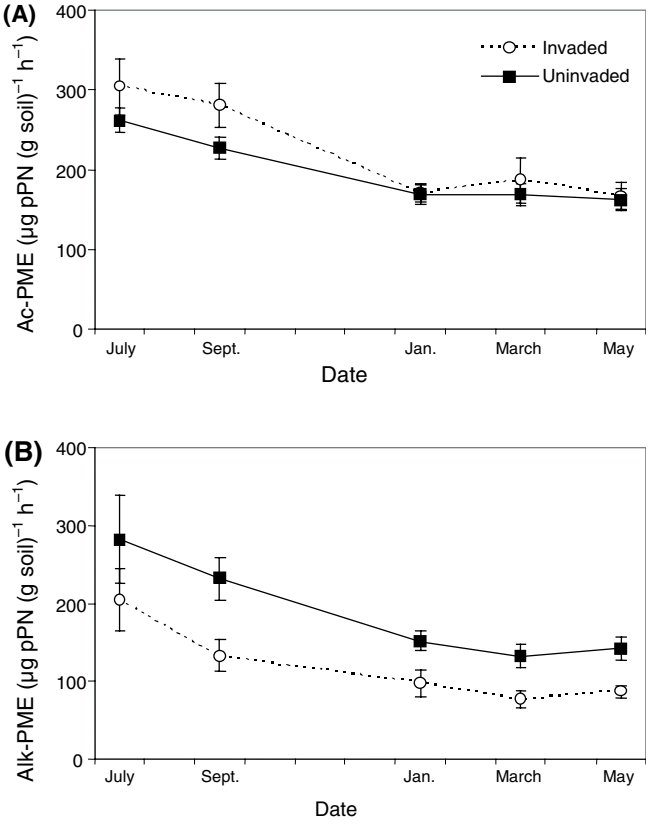

Figure 3: Seasonal variation of soil phosphomonesterase (PME) activity in plots invaded by Early Goldenrod and adjacent, uninvaded plots. (A) Ac-PME, (B) Alk-PME. Means ($n = 6$) and standard deviations.

3.1.4 Microbial P

Phosphorus immobilized in microbial biomass was highest in September and decreased until the end of the winter, where it was close to zero, and then increased again in the spring. The date effect was significant (Tab. 2). There was no significant difference between invaded and uninvaded stands (Fig. 4 and Tab. 2).

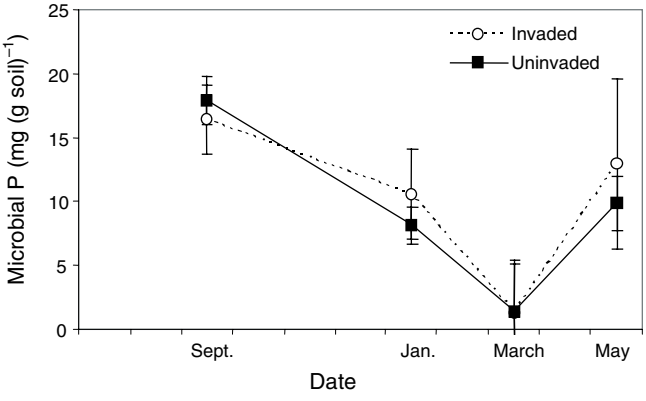

Figure 4: Seasonal variation of soil microbial P (0–10 cm) in plots invaded by Early Goldenrod and adjacent, uninvaded plots. Means ($n = 6$) and standard deviations.

3.2 Phosphorus concentrations and stocks in plants

3.2.1 Aboveground organs

Seasonal variation in aboveground biomass, P concentration, and stocks was much larger for *Solidago* compared to uninvaded stands, which resulted in highly significant date × invasion interaction for all these parameters. Aboveground biomass (including litter) of uninvaded plots showed little seasonal variation, ranging from 600 g m^{-2} in summer to 500 g m^{-2} in winter (Fig. 5). In contrast, aboveground biomass of *Solidago* showed a marked seasonal pattern, with highest values in August (1700 g m^{-2}) and lowest values in winter (800 g m^{-2}; that was close to zero if litter was not considered). When litter was pooled with living parts as presented in Fig. 5, phytomass was consistently higher in invaded compared to uninvaded stands.

Average concentrations of P in aboveground biomass (including litter) were lowest in winter and highest in spring in both types of stands. They were 2- to 4-fold higher in uninvaded than in invaded stands (annual mean, uninvaded: 1733 mg P (kg dry matter)$^{-1}$, invaded: 586 mg P (kg dry matter)$^{-1}$). Total-P stocks in aboveground biomass plus litter showed a marked seasonal pattern, most strikingly so for *Solidago*, with the highest values in summer, the lowest values in November, and intermediate

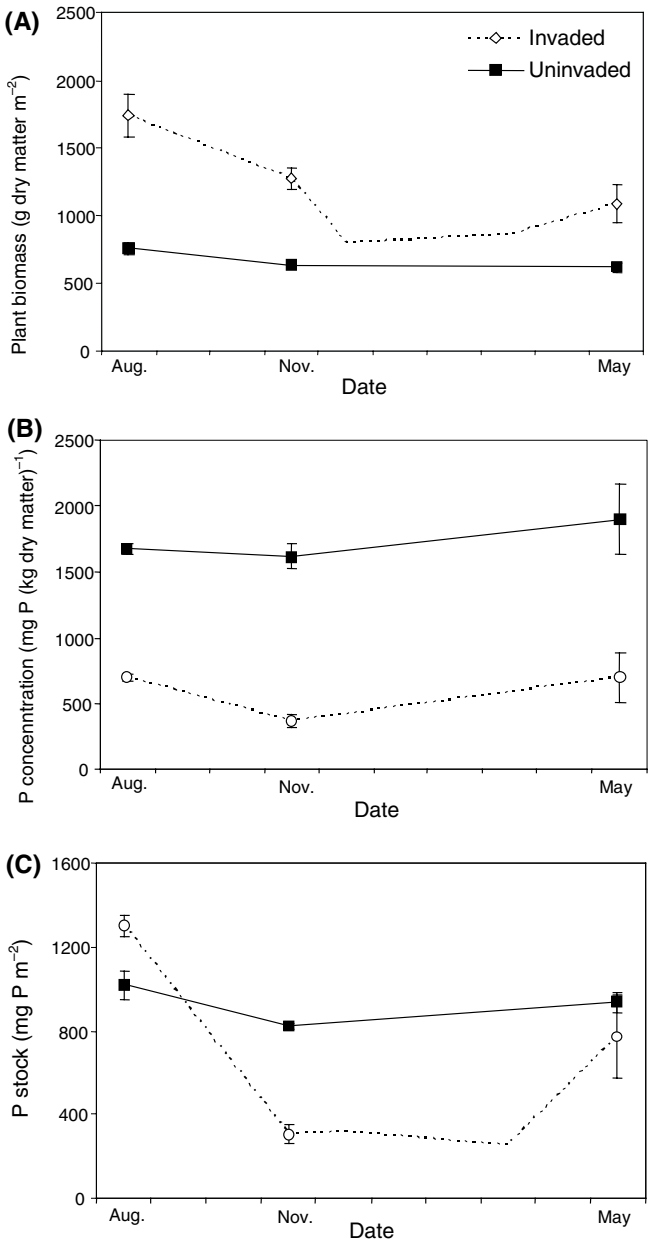

Figure 5: Seasonal variation of standing biomass (A), P concentration (B), and P pools in standing biomass (C) in plots invaded by Early Goldenrod and adjacent, uninvaded plots. Litter and dead shoots of *Solidago* included. Error bars are standard deviations.

values in spring. Invaded stands had lower aboveground stocks of P in autumn and winter and higher stocks in August, compared to uninvaded stands.

Concentrations and stocks of P in stems and leaves of *Solidago* are presented in Tab. 3. Phosphorus concentration of leaves was 2- to 4-fold higher than in stems. For both types of organs, P concentrations were highest in May and decreased steadily to November. Resorption efficiency, calculated as the ratio of P concentration in November to P concentration in August was 67% for stems and 39% for leaves. At the peak of total aboveground biomass, living biomass of

Table 3: Mass, P concentration, and P stocks of stems and leaves of *Solidago gigantea* at three dates.

		Mass (g m^{-2})	**P concentration** (mg (kg soil)$^{-1}$)	**P stock** (mg m^{-2})
August	Stems	750	680	510
	Leaves	350	1585	550
November	Stems	49	220	110
	Leaves	20	960	20
May	Stems	100	1390	150
	Leaves	90	4195	400

Table 4: Seasonal variation of average ($n = 4$) belowground biomass, P concentration, and stock in roots from plots invaded by early Goldenrod and adjacent, uninvaded plots.

	Biomass (g dry matter m^{-2})		**P concentration** (mg P (kg dry matter)$^{-1}$)		**P stock** (mg P m^{-2})	
	Aug.	**Nov.**	**Aug.**	**Nov.**	**Aug.**	**Nov.**
Uninvaded	1156	1822	1720	1811	1909	3271
Invaded	1399	2813	1400	1921	1926	5426
p level[a]	ns	**	ns	ns	ns	*

[a] Statistical significance for *t*-tests performed for a parameter within a date between uninvaded and invaded plots: ns, not significant; ** $p < 0.01$; * $p < 0.05$

Solidago consisted of 32% leaves and 68% stems. Figures for the uninvaded vegetation are not available, due to the difficulty to separate leaves from stems and senescing organs from living organs in grasses.

3.2.2 Belowground organs

Biomass of belowground organs was roughly similar for both types of stands in August (1156–1399 g m^{-2}) and steadily increased from August to November, most strikingly so for *Solidago.* In November, biomass of belowground organs of *Solidago* was ca. 35% higher compared to the control, and this difference was significant ($p < 0.01$). Concentrations of P in belowground organs were not significantly different for the two types of plots (Tab. 4, $p > 0.05$). For *Solidago*, it increased from August to November (1400–1921 mg P kg^{-1}), but the difference was not significant due probably to low sample size ($n = 4$). Phosphorus stocks in belowground organs increased from August to November in both types of stands. In August, they were similar for both types of stands, while P stocks were much higher in *Solidago* compared to the control in November (Tab. 4, 5426 *vs.* 3271 mg P m^{-2}).

4 Discussion

A striking result is the finding of systematic differences in P availability and pH between topsoil of closely adjacent invaded and uninvaded plots. Our sampling protocol was designed to reduce the possibility of pre-existing differences in soil conditions be-

tween plots. Thus, within site, homogeneity of soil texture and soil profile was checked. Moreover, *S. gigantea* is still expanding in this site, and uninvaded plots were located close to the front of expansion of invaded stands. Furthermore, *S. gigantea* occurs over a wide range of soil conditions (*Weber* and *Jakobs*, 2005). In Belgium, the following variation ranges were observed for *Solidago*-invaded sites: pH 5.9 to 7.2, resin-P_i: 25.6–91.5 mg P kg^{-1} (measured on air-dried soil samples), bicarb-P_i: 21.7–81.0 mg P_i kg^{-1}, C: 1.5%–6.4%, and clay: 2.4%–17.0% (*Chapuis-Lardy* et al., 2006). It is thus unlikely that fine-scale variation in soil chemistry is governing the present distribution of *S. gigantea* within our study site. We believe that plant-driven variation is the most likely mechanism explaining the observed spatial variation in soil conditions.

We have found increased concentrations of several forms of inorganic P (Resin-P_i, Bicarb-P_i, and NaOH-P_i) in invaded stands. All these fractions are considered as bioavailable at more or less short term (*Mallarino* and *Atia*, 2005; *Scott* and *Condron*, 2003; *Spears* et al., 2001). Increased availability of P under *Solidago* might be explained by one or a combination of the following mechanisms: nutrient uplift, enhanced mineralization, altered turn over of microbial community, a shift in the geochemical equilibria controlling P availability, and differences in the flux rates of P through the plant community. These hypotheses will be addressed in turn.

4.1 Nutrient uplift

Plants can increase availability of nutrients in topsoil by the mechanism of nutrient uplift (*Jobbágy* and *Jackson*, 2004), *i.e.*, net displacement of nutrients from deep layers to topsoil. This was shown for the alien invasive crucifer *Lepidium latifolium* (*Blank* and *Young*, 2002). However, *S. gigantea* does not have deeper rooting depth compared to the resident vegetation (personal observation). Moreover, nutrient uplift cannot be invoked to explain increased concentrations of a single nutrient.

4.2 Organic-P mineralization

Our results show a slight, nonsignificant increase of acid PME and a significant decrease of alkaline PME. These observations do not roughly support the hypothesis that increased concentrations of inorganic P in invaded stands would be due to enhanced mineralization by phosphomonoesterases. In spite of the large number of published studies, the relationships between PME activity and the rate of organic-P mineralization remain obscure (*Chen* et al., 2002). Negative correlations between spatial variation in availability of inorganic P and PME activity were sometimes documented (*Chen* et al., 2003). Higher concentrations of inorganic P in soils have shown to reduce phosphatase activity by feedback inhibition (*Tabatabai*, 1982; *Harrison*, 1983). Activity of PME is also very susceptible to pH (*Kang* and *Freeman*, 1999; *Dick* et al., 2000), and decreased alk-PME activity in invaded stands might be related to lower pH. Another hypothesis is the presence of functionally different organisms producing alkaline phosphatase in both plots (invaded *vs.* uninvaded). We did not characterize soil fungi that can be effective producers of alkaline PME (*Tarafdar* and *Chhonkar*, 1979). Moreover, phosphomonoesterases are not the sole enzymes involved in P mineralization (*Tabatabai*, 1982), and hydrolysis of complex organic P compounds may be more limiting (*Nakas* et al., 1987). A hypothesis could be the presence of other phosphate-releasing enzymes in the litter such as phosphodiesterases. *Turner* et al. (2002a, b) showed that only small amounts of both organic and condensed P compounds, in soil solution, were hydrolyzed by phosphomonoesterases alone, whilst a combination of phosphomonoesterases and phosphodiesterases hydrolyzed much greater proportions. Moreover, they have shown that diester forms of soil organic P were more labile and more readily mineralized than monoesters and thus play an important role in the transformations of P.

Similar topsoil C concentrations in both kinds of plots, in spite of higher primary productivity both above- and belowground in invaded stands, still point to higher decomposition rates in invaded stands. Litter-decomposition rate is strongly influenced by the C : N and C : P ratio (*Kwabiah* et al., 2003a, b). Dead leaves of *Solidago* have higher concentrations of P than aboveground biomass of the control, (960 mg P (g dry matter)$^{-1}$ *vs.* 480 mg P (g dry matter)$^{-1}$, respectively). It is well known that differences in litter quality can influence soil P status. Thus, *Nziguheba* et al. (1998) have observed increased resin-P_i, Bicarb-P_i, and NaOH-P_i in the soil after addition of leaf litter of the Asteraceae *Tithonia diversifolia* and no effect of leaf litter of maize.

4.3 Microbial immobilization

The microbial-P fraction was not different between invaded and uninvaded stands. Seasonal variations allow calculating the turnover rate of this fraction (turnover = annual mean of microbial P / cumulated losses of microbial P) (*Chen* et al., 2003). Turnover of microbial P is 1.76 y^{-1} and 1.47 y^{-1} in control and invaded plots, respectively. Thus, increased available-P fraction cannot be accounted for by higher turnover of microbial P. This conclusion must be taken with caution, however, because of the low sampling frequency of microbial P in our study. Differences in the composition of the bacteria and fungi communities might still be involved.

4.4 Influence on geochemical equilibria

Bioavailability of soil inorganic P is strongly affected by root-induced chemical changes (*Hinsinger*, 2001). Stands invaded by *S. gigantea* were found to have decreased pH values (5.9 *vs.* 6.5). pH is indeed one of the most important parameters determining adsorption/desorption equilibria of phosphate in soils (*Hinsinger*, 2001). It is quite possible that the observed half-a-unit decrease of pH might favor solubility of mineral P compounds as suggested by *Chapuis-Lardy* et al. (2006) in a former study that includes our study site. Decreased pH was also invoked as a possible mechanism for the increased P availability under the exotic invasive *Lepidium latifolium* (*Blank* and *Young*, 2002). Both increased and decreased pH under the canopy of invasive plants were documented (see *Ehrenfeld* (2003) for a review). Enhanced nitrification was

proposed as a likely explanation for decreased pH under the canopy of the invasive *Berberis thunbergii* and *Microstegium vimineum* in N American deciduous forests (*Ehrenfeld* et al., 2001; *Ehrenfeld*, 2003). Other possible mechanisms include shifts in N nutrition from predominantly NO_3^-- to NH_4^+-based, production of organic acids by roots (*Hinsinger* et al., 2003; *Vanderhoeven* et al., 2006). Acidification may enable *Solidago* to obtain P from fractions that are little available to the resident vegetation. Interestingly, the formation of mycorrhizae was largely reported in the literature for most of the native plants (*e.g.*, *Harley* and *Harley*, 1987) as well as for *Solidago canadensis*, which is also invasive in Europe (*Jin* et al., 2004). The ability in *S. Canadensis* to form mycorrhizae with different *Glomus* species was invoked to explain the ability of the species to colonize newly reclaimed habitats (*Jin* et al., 2004). More effective secretion of organic acids by roots or mycorrhizae might increase availability of P under *Solidago* (*Frossard* et al., 1995; *Geelhoed* et al., 1999).

4.5 Nutrient fluxes in plants

Solidago stands have much higher standing biomass in summer compared to control plots. However, due to low concentrations of P in stems (680 mg (kg dry matter^{-1}) compared to 1680 mg (kg dry matter^{-1}) in the control), P stocks in living aboveground biomass are roughly similar between invaded and uninvaded plots (1000 mg P m^{-2}). This result must be taken with caution, however, because the difference invaded *vs.* uninvaded in aboveground biomass apparently varies from year to year due to changes in control biomass. Thus, in the year 2003, aboveground biomass in the control plots was 250 g m^{-2}, *i.e.*, more than two times as much as in 2004 (*Chapuis-Lardy* et al., 2006). Based on the P-concentration difference between August and November, resorption of P from senescing shoots of *Solidago* can be estimated as about 550 mg P m^{-2}. Thus, resorption efficiency is 52%, *i.e.*, close to the average value for herbaceous dicots (*Aerts*, 1996). Resorption could not be measured in the resident vegetation, because aboveground-biomass samples comprised both living and senesced leaves. Using the average resorption efficiency for graminoids species (70%) as reported by *Aerts* (1996), resorption flux can be estimated as 700 mg P m^{-2}. Thus, annual loss rate of P by aboveground organs might be somewhat larger in *Solidago* patches compared to the control (about 500 mg P m^{-2} *vs.* 300 mg P m^{-2}). However, this difference cannot account for the difference in the stock of P in the NaOH-P_i fraction (2400 mg P m^{-2}).

Phosphorus stocks in belowground organs of *Solidago* show a more than 2-fold increase from August to November, mainly due to increased biomass. The autumnal increase in P stocks in belowground organs can be calculated as 3500 mg P m^{-2} in *Solidago* and 1300 mg P m^{-2} in the control. Resorption of P from aboveground organs (500 mg P m^{-2}) can account for only a small part this flux. Our data thus point to a massive root uptake of P by *Solidago* in autumn, probably coupled to fine-root production. This uptake is far in excess of P requirements for aboveground organs in subsequent year in *Solidago*, which were calculated as 1300 mg P m^{-2}. Although belowground biomass was not measured in spring, it is reasonable to assume a steady-state situation for biomass from year to year. It thus appears that most of the P that is absorbed and stored in belowground organs in autumn will be lost before next summer in belowground litter. Nutrient resorption from senescing roots is usually low (*Chapin*, 1980). Fast nutrient leaching and mineralization were already reported for roots, suggesting that root may play a major role in the cycling of nutrients (*Scheffer* and *Aerts*, 2000). Phosphorus is easily released from dying roots (*Eason* and *Newman*, 1990), and quick release of P from decomposing roots was invoked as a possible mechanism of P enrichment in the soil (*Campbell* et al., 1993).

Interestingly, the difference in P stock in belowground organs in autumn is quite similar to the difference in the stock of NaOH-P_i in the soil (2400 mg P m^{-2}). Intense mobilization of P by *Solidago* roots in autumn and restitution of easily mineralizable root debris in next spring may well contribute to the higher availability of P observed in invaded plots in this study.

Invasion by Early Goldenrod alters P fractions, pools, and fluxes in the study site. Higher concentrations of bioavailable P in the topsoil might be due to a combination of enhanced P-turnover rates in belowground organs and rhizosphere acidification. It would be interesting to test if enhanced P availability results in a positive feed-back, *i.e.*, an aggravation of the competitive superiority of Early Goldenrod over the resident vegetation.

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References

Aerts, R. (1996): Nutrient resorption from senescing leaves of perennials: are there general patterns? *J. Ecol.* 84, 597–608.

Bartlett, R., James, B. (1980): Studying dried, stored soil samples–some pitfalls. *Soil Sci. Soc. Am. J.* 44, 721–724.

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

Bowman, R. A., Cole, C. V. (1978): An exploratory method for fractionation of organic phosphorus from grassland soils. *Soil Sci.* 125, 95–101.

Brookes, P. C., Powlson, D. S., Jenkinson, D. S. (1982): Measurement of microbial biomass phosphorus in soil. *Soil Biol. Biochem.* 14, 319–329.

Campbell, C. A., Lafond, G. P., Biederbeck, V. O., Winkleman, G. E. (1993): Influence of legumes and fertilization on deep distribution of available phosphorus (Olsen-Pi) in a thin black chernozomic soil. *Can. J. Soil Sci.* 73, 555–565.

Chapin, F. S. (1980): The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11, 233–260.

Chapuis-Lardy, L., Vanderhoeven, S., Dassonville, N., Koutika, L. S., Meerts, P. (2006): Effects of the invasive plant *Solidago gigantea* on soil phosphorus. *Biol. Fertil. Soils* 42, 481–489.

Chen, H. (2003): Phosphatase activity and P fractions in soils of an 18-year-old chinese fir (*Cunninghamia lanceolata*) plantation. *Forest Ecol. Manage.* 178, 301–310.

Chen, C. R., Condron, L. M., Davis, M. R., Sherlock, R. R. (2002): Phosphorus dynamics in the rhizosphere of perennial ryegrass (*Lolium perenne* L.) and radiata pine (*Pinus radiata* D. Don.). *Soil Biol. Biochem.* 34, 487–499.

Chen, C. R., Condron, L. M., Davis, M. R., Sherlock, R. R. (2003): Seasonal changes in soil phosphorus and associated microbial properties under adjacent grassland and forest in New Zealand. *Forest Ecol. Manage.* 177, 539–557.

Dick, W. A., Cheng, L., Wang, P. (2000): Soil acid and alkaline phosphatase activity as pH adjustment indicators. *Soil Biol. Biochem.* 32, 1915–1919.

Eason, W. R., Newman, E. I. (1990): Rapid loss of phosphorus from dying ryegrass roots: the chemical components involved. *Oecologia* 82, 432–436.

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

Ehrenfeld, J. G., Kourtev, P., Huang, W. (2001): Changes in soil functions following invasions of exotic understory plant in deciduous forests. *Ecol. Appl.* 11, 1287–1300.

Evans, R. D., Rimer, R., Sperry, L., Belnap, J. (2001): Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecol. Appl.* 11, 1301–1310.

FAO-UNESCO (1990): Soil map of the world, Revised legend. World Soil Resources Report 60. FAO, Rome, p. 119.

Frossard, E., Brossard, M., Hedley, M. J., Metherell, A. (1995): Reactions controlling the cycling of P in soils, in Tiessen H.: SCOPE 54, Phosphorus in the global environment. J. Wiley & Sons Ltd., Chichester, pp. 107–137.

Geelhoed, J. S., Van Riemsdijk, W. H., Findenegg, G. R. (1999): Simulation of the effect of citrate exudation from roots on the plant availability of phosphate adsorbed on goethite. *Eur. J. Soil Sci.* 50, 379–390.

Grierson, P. F., Adams, M. A. (2000): Plant species affect acid phosphatase, ergosterol and microbial P in a Jarrah (*Eucalyptus marginata* Donn ex Sm.) forest in south-western Australia. *Soil Biol. Biochem.* 32, 1817–1827.

Güsewell, S., Zuberbuhler, N., Clerc, C. (2005): Distribution and functional traits of *Solidago gigantea* in a Swiss lakeshore wetland. *Bot. Helv.* 115, 63–75.

Harley, J. L., Harley, E. L. (1987): A check-list of mycorrhiza in the British flora. *New Phytol.* 105, 1–102.

Harrison, A. F. (1983): Relationship between intensity of phosphatase activity and physic-chemical properties in the woodland soils. *Soil Biol. Biochem.* 15, 93–99.

Hinsinger, P. (2001): Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil* 237, 173–195.

Hinsinger, P., Plassard, C., Tang, C., Jaillard, B. (2003): Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. *Plant Soil* 248, 43–59.

Hooper, D. U., Vitousek, P. M. (1998): Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* 68 , 121–149.

Jakobs, G., Weber, E., Edwards, P. J. (2004): Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than cospecifics in the native range. *Divers. Distrib.* 10, 11–19.

Jin, L., Gu, Y. G., Xiao, M., Chen, J. K., Li, B. (2004): The history of *Solidago canadensis* invasion and the development of its mycorrhizal associations in newly-reclaimed land. *Funct. Plant Biol.* 31, 979–986.

Jobbágy, E. G., Jackson, R. B. (2004): The uplift of soil nutrients by plants: Biogeochemical consequences across scales. *Ecology* 85, 2380–2389.

John, M. K. (1970): Colorimetric determination of phosphorus in soil and plant materials with ascorbic acid. *Soil Sci.* 109, 214–220.

Kang, H., Freeman, C. (1999): Phosphatase and arylsulphatase activities in wetland soils: annual variation and controlling factors. *Soil Biol. Biochem.* 31, 449–454.

Kouno, K., Tuchiya, Y., Ando, T. (1995): Measurement of soil microbial biomass phosphorus by an anion exchange membrane method. *Soil Biol. Biochem.* 27, 1353–1357.

Kourtev, P. S., Ehrenfeld, J. G., Huang, W. Z. (2002): Enzyme activities during litter decomposition of two exotic and two native plant species in hardwood forests of New Jersey. *Soil Biol. Biochem.* 34, 1207–1218.

Krämer, S., Green, D. M. (2000): Acid and alkaline phosphatase dynamics and their relationship to soil microclimate in a semiarid woodland. *Soil Biol. Biochem.* 32, 179–188.

Kwabiah, A. B., Stoskopf, N. C., Palm, C. A., Voroney, R. P. (2003a): Soil P availability as affected by the chemical composition of plant materials : implications for P-limiting agriculture in tropical Africa. *Agric. Ecosyst. Environ.* 100, 53–61.

Kwabiah, A. B., Stoskopf, N. C., Palm, C. A., Voroney, R. P., Rao, M. R., Gacheru, E. (2003b): Phosphorus availability and maize response to organic and inorganic fertilizer inputs in a short term study in western Kenya. *Agric. Ecosyst. Environ.* 95, 49–59.

Mallarino, A. P., Atia, A. M. (2005): Correlation of a resin membrane soil phosphorus test with corn yield and routine soil tests. *Soil Sci. Soc. Am. J.* 69, 266–272.

McLaughlin, M. J., Alston, A. M. (1986): Measurement of phosphorus in the soil microbial biomass: a modified procedure for field soils. *Soil Biol. Biochem.* 18, 437–443.

Nakas, J. P., Gould, W. D., Klein, D. A. (1987): Origin and expression of phosphatase activity in a semi-arid grassland soil. *Soil Biol. Biochem.* 19, 13–18.

Nziguheba, G., Palm, C. A., Buresh, R. J., Smithson, P. C. (1998): Soil phosphorus fractions and adsorption as affected by organic and inorganic sources. *Plant Soil* 198, 159–168.

Olsen, S. R., Sommers, L. E. (1982): Phosphorus in Methods of Soil Analysis, in Page, A. L., Miller, R. H., Keeney, D. R.: Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties. American Society of Agronomy, Madison, WI., pp. 421–422.

Scheffer, R. A., Aerts, R. (2000): Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems. *Oikos* 91, 541–549.

Scott, J. T., Condron, L. M. (2003): Dynamics and availability of phosphorus in the rhizosphere of a temperate silvopastoral system. *Biol. Fertil. Soils* 39, 65–73.

Spears, J. D. H., Lajtha, K., Caldwell, B. A., Pennington, S. B., Vanderbilt, K. (2001): Species effects of *Ceanothus velutinus* versus *Pseudotsuga menziesii*, Douglas-fir, on soil phosphorus and nitrogen properties in the Oregon cascades. *Forest Ecol. Manage.* 149, 205–216.

Tabatabai, M. A. (1982): Soil enzymes, in Page, A. L., Miller, R. H., Keeney, D. R.: Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties. American Society of Agronomy, Madison, WI., pp. 903–948.

Tarafdar, J. C., Chhonkar, P. K. (1979): Phosphatase production by microorganisms isolated from diverse types of soils. *Zentralbl. Bakteriol. Naturwiss.* 134, 119–24.

Tiessen, H., Moir, J. O. (1993): Characterization of available P by sequential extraction, in Carter, M. R.: Soil sampling and methods of analysis. Lewis Publishers, Boca Raton, FL., pp. 75—86.

Turner, B. L., McKelvie, I. D., Haygarth, P. M. (2002a): Characterisation of water-extractable soil organic phosphorus by phosphatase hydrolysis. *Soil Biol. Biochem.* 34, 27–35.

Turner, B. L., Baxter, R., Whitton, B. A. (2002b): Seasonal phosphatase activity in three characteristic soils of the English uplands polluted by log-term atmospheric nitrogen deposition. *Environ. Pollut.* 120, 313–317.

Tyser, R. W., Key, C. H. (1988): Spotted knapweed in natural area fescue grasslands: an ecological assessment. *Northwest Sci.* 62, 151–160

Vanderhoeven, S., Dassonville, N., Chapuis-Lardy, L., Hayer, M., Meerts, P. (2006): Impact of the invasive *Solidago gigantea* on primary productivity and topsoil chemistry. *Plant Soil,* 286, 259–268.

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

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

Weber, E., Jakobs, G. (2005): Biological flora of Central Europe: *Solidago gigantea* Aiton. *Flora* 200, 109–118.

Witowski, E. T. F., Mitchell, D. T. (1987): Variations in soil phosphorus in the fynbos biome, South Africa. *J. Ecol.* 75, 1159–1171.

