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Impact of the invasive alien plant *Solidago gigantea* on primary productivity, plant nutrient content and soil mineral nutrient concentrations

**Sonia Vanderhoeven · Nicolas Dassonville ·
Lydie Chapuis-Lardy · Matthieu Hayez ·
Pierre Meerts**

Abstract Invasion by alien plants can alter ecosystem processes and soil properties. In this study, we compared aboveground productivity, nutrient pools in standing biomass and topsoil (0–0.10 m) mineral nutrient concentrations between plots invaded by Early Goldenrod (*Solidago gigantea*) and adjacent, uninvaded, vegetation at five sites in Belgium. The five sites were characterised by a resident perennial herbaceous vegetation and spanned a wide range in soil fertility level and floristic composition. Invaded stands consistently had higher (2–3-fold) aboveground productivity and lower mineral element concentrations in standing phytomass. Nutrient pools (calculated as concentration × phytomass) was ca. twice higher in invaded plots, suggesting that *S. gigantea* might enhance nutrient cycling rates. Impacts on topsoil chemistry were surprisingly modest, with slightly higher nutrient concentrations under the invader. A noticeable exception was phosphorus, which showed higher concentrations of ammonium acetate-extractable fraction in invaded plots in four of five sites. It appears that *S. gigantea* does not significantly contribute to nutrient uplift from deep soil layers to topsoil, possibly because it does not root much deeper compared to resident vegetation.

Keywords Invasive alien species · Soil nutrients · Nutrient pools · Phosphorus · *Solidago gigantea*

Abbreviations
CEC Cation exchange capacity
Bs base saturation rate

Equally contributing authors: S. Vanderhoeven and
N. Dassonville

S. Vanderhoeven · N. Dassonville ·
L. Chapuis-Lardy · M. Hayez · P. Meerts
Laboratory of Plant Genetics and Ecology, Free
University of Brussels, 1850, chaussée de Wavre,
B-1160, Bruxelles, Belgium

S. Vanderhoeven (✉)
Laboratory of Ecology, Gembloux
Agricultural University, Passage des Déportés,2,
B-5030 Gembloux, Belgium
e-mail: sonia.vanderhoeven@belgacom.net

Introduction

Besides the well-documented alteration of community composition and dynamics, exotic plant invasions are known to modify key ecosystem processes in subtle way (Ehrenfeld 2003; Levine et al. 2003). As plant traits and ecosystem processes are closely connected (Chapin et al. 2002; Hobbie 1992; Van Breemen and Finzi 1998), the substitution of dominant exotics for native species may result in alterations in biogeochemical

cycles and soil chemistry (Ehrenfeld and Scott 2001).

In her review focussing on soil nutrient cycling processes, Ehrenfeld (2003) pointed out that invasive species often increased biomass and net primary productivity of ecosystems, increased N availability, altered N fixation rates and produced litter with higher decomposition rates than co-occurring native species. Besides the existence of general patterns, direction and amplitude of impacts depend on local abiotic conditions as well as on the composition of the native community (Bolton et al. 1990; Evans et al. 2001; Scott et al. 2001). However, most published work has examined impacts of exotics at a single site (but see Hook et al. 2004). Moreover, studies have been mainly concerned with carbon and nitrogen and comparatively less attention has been paid to other elements (but see Blank and Young 2002, 2004; Vanderhoeven et al. 2005). It is still well known that plants can influence the availability of other elements, including P, by species-specific processes (Chapin et al. 2002; Grierson and Adams 2000; Mitchell et al. 1997).

Belgium and neighbouring countries have suffered from invasion by exotic plants, which have dramatically increased their range in the last 30 years (Muller 2000; Verloove 2002). *Solidago gigantea* Aiton (Early Goldenrod) is one of the most troublesome invaders in this area. It is a rhizomatous perennial herb native of North America. It was introduced in Europe in the 18th century as an ornamental and melliferous plant and became invasive some 100 years later (Wagenitz 1964). It is known to have a broad tolerance to light, temperature, soil moisture and chemical properties (Weber and Jakobs 2005). It has high invasive success in ruderal and riverside habitats, forming dense mono-specific patches (Weber 1998) and preventing the establishment of native species (Weber 2003). Moreover, along a latitudinal gradient in Europe, it shows clinal variation in phenology and life-history traits (Weber and Schmid 1998).

As proposed by Walker and Smith (1996), the most realistic way to measure the impact of an invader is to compare invaded sites with nearby control sites with similar vegetation, soil, geology, climate and land-use history. In one of the first evaluations of impacts of alien invasive plants on soil in Europe, Vanderhoeven et al. (2005) found higher concentrations of bioavailable nutrients in topsoil under five invasive plants. *S. gigantea* was one of the five target species but the assessment of its own impact was of relative extent as only one site was considered. On the other hand, Chapuis-Lardy et al. (in press) showed increased P availability in three sites invaded by *S. gigantea* but they did not considered neither the effects on other soil nutrients nor the nutrient contents and pools in the phytomass. Recently, Güsewell et al. (2005) focussed on one ecosystem of high conservation value, a lakeshore wetland, where they did not find any impact of *S. gigantea* on total soil N and P.

In this paper, we examine the effects of the invasion of *Solidago gigantea* on topsoil chemistry, primary productivity and nutrient pools in standing biomass. The comparison is replicated in five sites spanning contrasting floristic composition of the resident vegetation in Belgium. We addressed the following questions: (1) What are the impacts of *S. gigantea* on mineral nutrient concentrations in soil? (2) Are impacts on soil correlated with impacts on nutrients pools in the standing biomass? (3) Do impacts differ in direction and amplitude according to invaded site?

Materials and methods

Site selection

The 5 selected sites are *Kra* (Kraainem, 50°51′40″ N–4°28′33″ E), *For* (Brussels, 50°47′10″ N–4°25′33″ E), *Gul* (Brussels, 50°47′10″ N–4°25′07″ E), *Ghi* (St-Ghislain, 50°27′30″ N–3°50′25″ E) and *Mar* (Marche-les-Dames, 50°27′30″ N–3°50′25″ E). Selected sites fulfilled all the following conditions: (1) well-established, and still increasing populations of *S. gigantea*, (2) sufficiently homogeneous soil, (3) dense patches of *S. gigantea* surrounded by uninvaded vegetation (invaded patches ranged from 25 m^2 to more than 100 m^2). Within site homogeneity of soil was checked by comparing soil profiles topsoil texture between invaded and uninvaded patches.

Moreover, uninvaded control plots were located as close as possible to the front of expansion of the invader. Thus, site selection sought to minimise the probability of pre-existing differences in soil properties. The same comparative approach was successfully applied to investigate impacts of alien invasive plants by McIntosh et al. (1995), Ehrenfeld et al. (2001), Scott et al. (2001) or more recently by Hook et al. (2004).

In each site, we selected six 1-m^2 plots in invaded patches and six 1-m^2 plots in adjacent, uninvaded vegetation. In each plot, the abundance of all vascular plant species was estimated according to Braun–Blanquet scale (5: 75–100% abundance, 4: 50–75%, 3: 25–50%, 2: 5–25%, 1: 1–5%, + : <1%). The mean abundance of each species was calculated for invaded and uninvaded plots, based on the median value of each class (i.e. 87.5, 62.5, 37.5, 15, 3 and 0.5%). Mean abundance was then back-transformed into Braun–Blanquet coefficients.

Soil sampling and analyses

Soil was sampled from February to April before vegetation period. In each plot, five soil cores (0–0.10 m depth, litter discarded) were collected with a soil borer (0.04 m in diameter). One core was taken at each corner and one core at the centre of the square. The five cores were then mixed up into a single bulk sample for each plot. In the uninvaded patches, cores were not taken under any particular species. Rather, they were collected under the multispecies vegetation. Soil samples were air-dried until constant weight, and sieved (<0.002 m). The following parameters were assessed for each sample: soil pH (stiff paste soil-H_2O and stiff paste soil-KCl), exchangeable acidity and exchangeable aluminium (1 M KCl extraction; derivative titration curve for H^+ and Al^{3+} for acidic soils), exchangeable cations, available P and trace elements (1 M CH_3COONH_4 pH 4.65 extraction), ICP-AES determination of Ca (except for carbonated soils) Mg, K, Mn, P, Cu and Zn. Cation exchange capacity (CEC = $[Ca^{2+}] + [K^+] + [Mg^{2+}] + [H^+] + [Al^{3+}]$) and base saturation rate (Bs) were thereafter computed (Bs = $([Ca^{2+}] + [K^+] + [Mg^{2+}])/CEC$) except for carbonated soils. Total C and N were assessed using a dry combustion C/N analyser (NC-2100, Carlo Erba Instruments, Italy). $CaCO_3$ content was assessed after calcination of organic matter at 450°C (dry combustion, Ströhlein dosimeter). Organic C content (C_{org}) was calculated as (total C–carbonate C). Organic matter content (OM) was then calculated as $2 \times C_{org}$. Potential nitrogen availability was assessed by in vitro mineralisation: fresh soil samples (sieved at 4 mm) were incubated for 6 weeks, at 28°C and soil hydratation was kept near field capacity (Lemée 1967). NO_3–N and NH_4–N were extracted with 1 N KCl and determined colorimetrically with a Technicon analyser.

Aboveground biomass sampling and analyses

Aboveground biomass was harvested in invaded and uninvaded 1 m^2 plots in August. Biomass (whole shoot) was oven-dried, weighted and ground with a mill (ZM 100, Retsch, Germany). The samples were ashed in a muffle furnace. Ashes were then dissolved in 1 M HCl and mineral element concentrations were determined by ICP-AES (Varian Vista MPX). N and C were assessed using a dry combustion C/N analyser (NC-2100, Carlo Erba instruments, Italy). For each element, aboveground nutrient pool was calculated as biomass × element concentration in the biomass.

Statistical analyses

For nutrients in soils (Ca, Mg, K, Mn, Zn, Cu and P), χ^2 tests were used to compare the proportion of cases showing greater versus lower values in invaded plots with the proportion expected (50–50%) under the null hypothesis that invasion has no systematic impact. For each variable, a two-way ANOVA was performed with 'site' and 'invasion' as main effects. In this analysis, a significant 'site × invasion' interaction indicates that impact of invasion differs according to site. Logarithmic transformation was applied when necessary prior to ANOVA. In case of significant 'invasion' effect or significant 'site × invasion' interaction, mean values for each site were compared between invaded and uninvaded plots by means of t-tests. Bonferroni correction was

applied based on the number of simultaneous tests for each variable ($n = 5$ sites). Statistical analyses were performed with *Statistica 6.1* software (StatSoft Inc. 2003).

Results

Species composition of vegetation

Solidago gigantea showed an abundance of at least 75% in invaded plots of all sites. Species composition differed between invaded and uninvaded plots. The number of species in the community was consistently higher in uninvaded (*Kra* = 40; *For* = 5; *Gul* = 17; *Ghi* = 21; *Mar* = 13) compared to invaded plots (*Kra* = 11; *For* = 4; *Gul* = 2; *Ghi* = 10; *Mar* = 5). In site *For*, however, uninvaded plots were dominated by *Urtica dioica*.

Soil chemical properties

The five study sites spanned a broad range of soil chemical conditions (Fig. 1). Thus, concentrations of P, NO$_3$–N and K were 40, 20 and 4× higher at

Fig. 1 Soil chemical composition of invaded and uninvaded plots. Mean values and standard errors for soil pH, exchangeable nutrients (mg kg^{-1}), organic matter (OM: %), N content (%), C/N ratio, NH$_4^+$ and NO$_3^-$ (mg kg^{-1}). Notice log scale for P. H$^+$, Al^{3+}, Ca, CEC and Bs are not considered here, as they were determined for <5 sites. The diagonal black line denotes equal value for invaded and uninvaded plots. Stars refer to significant difference between invaded and uninvaded plots in *t*-tests (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Boxes show the *F*-ratios of the two-way ANOVA performed for the 5 sites with site and invasion (Inv) as main effects (df: site = 4; Inv = 2; Site × Inv = 4)
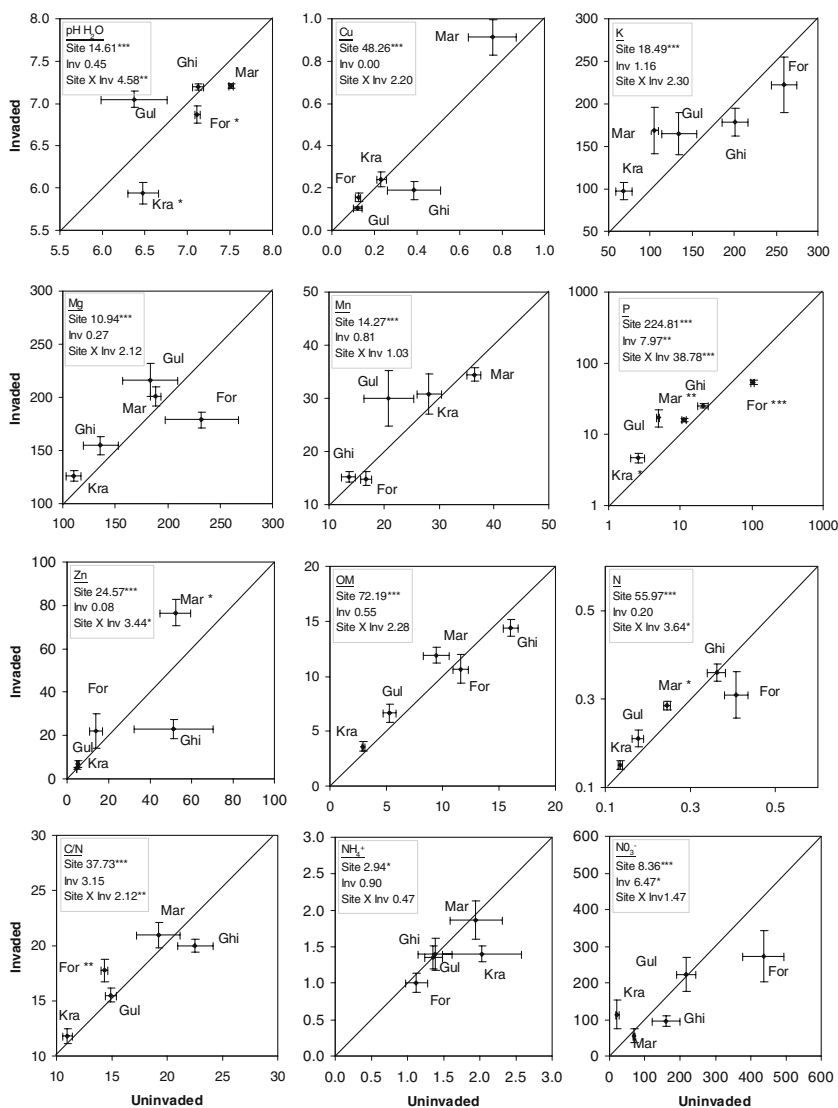
site *For* compared to site *Kra*, respectively (Fig. 1). The variation within site due to invasion is low in comparison with variation across the 5 sites. Higher concentrations of nutrients in invaded plots were significantly more frequent than lower concentrations (21 increases of 31 cases; $\chi^2 = 3.90$, $P < 0.05$). The two-way ANO-VAs performed on pooled sites (Fig. 1) showed a significant invasion effect for P ($P < 0.001$) and NO_3^- ($P < 0.01$). The 'site' effect was significant for all variables. For 5 variables out of 12 (pH_{H2O}, P, Zn, N, C/N), there was a significant 'site × invasion' interaction, indicating that the impact of invasion varied according to site. The most significant interaction was for P. In contrast to all other sites, site *For* had significantly lower concentrations of P under *S. gigantea*.

Impacts can also be expressed as the ratio of invaded to univaded plots (I/U ratio). On average, this ratio was higher than 1 for all nutrients (Fig. 2), but this was only significant for P (I/U = 1.70). In contrast, concentrations of NO_3–N after incubation were lower in invaded plots (I/U = 0.82).

Primary productivity and nutrients in standing biomass

In all sites, aboveground biomass was significantly higher in invaded plots compared to uninvaded plots (Table 1; Fig. 3). *Solidago gigantea* was from 70% (*Ghi*) to 260% (*Kra*) more productive than the surrounding native vegetation.
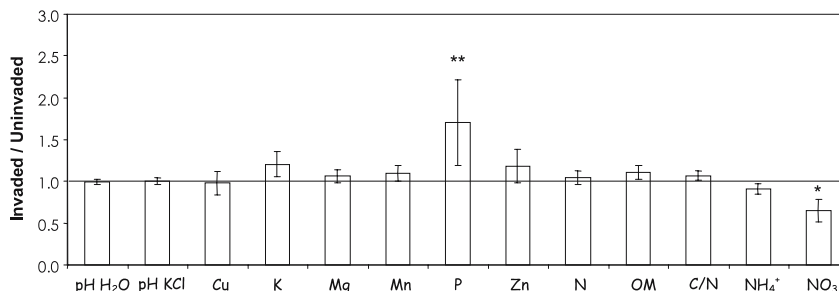
The two-way ANOVA (Table 2) showed significant invasion effects for all element concentrations in plant tissues (except for K and Zn), C/N ratio, and nutrients pools in the standing biomass (Fig. 3). Moreover, a significant 'site × invasion' interaction also existed for all nutrient concentrations and nutrient pools except for Cu, Zn and N, with different degree of response according to site. *t*-tests showed 11 significant differences in 45 comparisons (after Bonferroni correction) for nutrients concentrations in plant tissues. With only few exceptions, mineral nutrient concentrations in biomass were lower in invaded plots than in the resident vegetation. On average over all sites (Fig. 3), nutrient concentrations in invaded plots were 10–20% lower compared to uninvaded plots except for K and Zn. C content was significantly higher in invaded plots in three sites whereas in two sites, N content was significantly lower compared to uninvaded plots. As a result, C/N ratio of standing biomass was always higher in invaded plots. For nutrients pools in standing biomass, *t*-tests showed 30 significant differences on 45 comparisons (after Bonferroni correction). All significant differences consisted in greater values in invaded plots, except Ca in site *For*.

Discussion

Solidago gigantea can form monospecific stands in sites with widely different resident vegetation

Fig. 2 Ratio of mean value of invaded plots on mean value of uninvaded plots (I/U ratio) for soil pH, exchangeable nutrients (mg kg^{-1} except Al^{3+}, H$^+$: meq 100 g^{-1}), organic matter (OM: %), N content (%) and C/N ratio. Ca, CEC and Bs are not considered, as they were determined for <5 sites. Whiskers are standard errors. The horizontal line (I/U = 1) denotes equal value for invaded and uninvaded plots. Stars indicate significant invasion effect in the two-way ANOVA (*$P < 0.05$; **$P < 0.01$)

Table 1 Minimum–maximum range of invaded and uninvaded plots for biomass (kg m⁻²) nutrient concentrations in the biomass (mg kg⁻¹), aboveground nutrient pool (g m⁻²) and C/N ratio (5 sites)

Concentrations in plant tissue (mg kg⁻¹)

	Ca	Cu	K	Mg	Mn	P	Zn	C	N	C/N
Invaded min–max	7302–9499	4.83–6.69	12164–19133	1250–1428	21.27–30.28	1358–2124	26.82–75.61	43.95–45.37	0.64–1.03	44.52–70.36
Uninvaded min–max	6311–22072	6.52–8.62	12165–121717	1036–2502	23.38–102.19	1988–3677	24.90–75.80	41.25–43.96	1.02–1.37	30.62–42.43

Biomass (kg m⁻²) and Nutrient pools in standing biomass (g m⁻²)

	Biomass (kg m⁻²)	Ca	Cu	K	Mg	Mn	P	Zn	C	N
Invaded min–max	0.76–1.48	6680–11746	4.31–9.04	10880–27041	953.3–1195.8	24.44–78.91	1211–3136	15.94–84.56	336.7–651.8	
Uninvaded min–max	0.25–0.84	2181–18186	2.29–5.47	4035–18052	432.9–1370	10.22–33.99	574.7–3074	10.33–31.15	115.8–346.2	

and soil chemical composition, e.g. pH ranging from 5.9 to 7.2, organic matter content from 4 to 14%, C/N from 12 to 22, exchangeable P from 2 to 100 mg kg⁻¹. This result is in line with earlier reports of a broad ecological niche of this species in Europe (Weber and Jakobs 2005). It suggests that *S. gigantea* can achieve high invasive success across a wide range of soil fertility levels. Interestingly, aboveground phytomass of invaded stands also showed a two-fold variation range roughly matching differences in soil nutrient status among sites. Thus, the site *For*, with the highest values of P, K, Mg and nitrate in soil, also had by far the highest productivity.

In all five sites, invaded stands had much higher aboveground productivity (on average 2.4 times higher) compared to the resident vegetation. Higher productivity in communities invaded by alien exotic plants has often been reported: *Berberis thunbergii*, 4–44-fold increase (Ehrenfeld et al. 2001); *Lepidium latifolium*, 3-fold increase (Blank and Young 2002); *Phragmites australis*, 3-fold increase (Windham 2001).

For all elements except for Zn and K, nutrient concentrations in plant tissues were lower in invaded compared to resident vegetation. Functional differences between *S. gigantea* and the resident vegetation may account for this difference. Lower N and P concentrations in the standing biomass, may arguably point to higher nutrient use efficiency, defined as the amount of synthesised dry matter per unit mineral nutrients allocated to shoot (Vitousek 1982). Lower nutrient concentrations in shoots may be due to higher biomass allocation to stems, which are poor in nutrients, compared to the resident vegetation often dominated by grass-like species. Impacts of alien invasive species on element concentrations in phytomass have quite rarely been tested except for C and N content. The exotic crucifer *Lepidium latifolium* differed considerably from the native *Elytrigia elongata* with greater Ca, Mg, K and S content in the aboveground tissue of the invader (Blank and Young 2002), whereas Vanderhoeven et al. (2005) found lower nutrient concentrations in the biomass of *Fallopia japonica*, compared to the native vegetation.

However, higher productivity is not at all compensated for by lower nutrient concentrations,
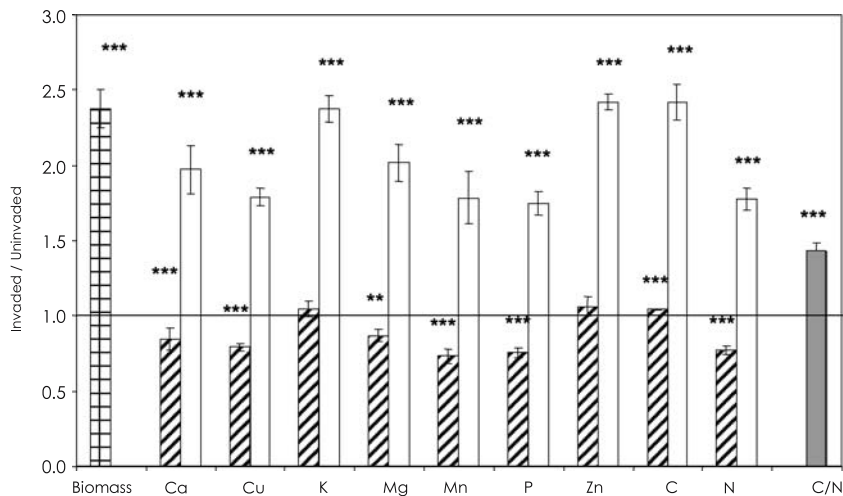
Fig. 3 Ratio of mean value of invaded plots on mean value of uninvaded plots (I/U ratio) for standing biomass (cross-rule), nutrient concentrations in biomass (hatched), aboveground nutrient pools (white boxes) and C/N ratio of biomass (grey box). Whiskers are standard errors. The horizontal line (I/U = 1) denotes equal value for invaded and uninvaded plots. Stars indicate significant invasion effect in the two-way ANOVA (*P < 0.05; **P < 0.01; ***P < 0.001)

resulting in 1.8–2.5 times higher mineral nutrient pool in invaded stands. Although nutrient resorption has not been measured in this study, preliminary data comparing nutrient returns in the litter indicate higher potential P return for the invader (500 mg m^{-2}) in comparison with the control vegetation (300 mg m^{-2}) (Herr et al. unpublished data). It would therefore be reasonable to assume that higher nutrient allocation to shoots also results in higher nutrient losses in litter fall. Thus, our results suggest enhanced nutrient turnover in plots invaded by *S. gigantea*, a result that has also been found for many other alien invasive species worldwide (Allison and Vitousek 2004; Ehrenfeld 2003).

In view of these consistent trends, it is surprising that only few significant impacts have been detected in soil. Our failure to detect impacts in soil may be due, in part, to low sample size (*n* = 6). Invasions may also be too recent for soils to have responded to altered vegetation cover. Other alien invasive plants also have limited impacts on soil, including the highly successful *Centaurea maculosa* (Hook et al. 2004).

On average across all sites, mineral element concentrations in topsoil were only slightly higher in invaded plots. Phosphorus stands out as a

notable exception, with 70% higher concentrations. In three sites, significantly higher concentrations of extractable P were found in invaded stands. In a previous study (Vanderhoeven et al. 2005) focusing on five invasive plants, we found higher concentrations of bioavailable nutrients in the topsoil. *S. gigantea* was one of the five target species but the assessment of its own impact was of relative extent per se as only one site was considered. The result of this single site was however consistent with the present study performed on 5 sites as it exhibited significant differences for soil P and pH between invaded and uninvaded plots. Another recent study by Güsewell et al. (2005) was conducted in eight sites of a Swiss lakeshore wetland and focused on total soil N and P. In this ecosystem, *S. gigantea* was shown to be functionally similar to the resident vegetation. Our results are in agreement with their observation showing that total soil N concentrations under *S. gigantea* did not differ from those under uninvaded vegetation. However, we cannot infer about P status because this study assessed total P while we assessed more available P (ammonium acetate-extractable fraction).

Nutrient uplift from deep soil layers is a well-known mechanism by which plants can increase

mineral nutrient concentration in topsoil (Jobbagy and Jackson 2004). However, this mechanism cannot explain the elevation of only a single nutrient, phosphorus. Moreover, *S. gigantea* does not seem to root considerably deeper than resident vegetation with 85% of the belowground biomass concentrated in the upper 6 cm vs. 80% for the resident vegetation (Dassonville et al. unpubl. obs.). Therefore, enhanced nutrient uptake rates found in *S. gigantea* cannot per se result in higher nutrient concentrations in topsoil. An alternative hypothesis is that *S. gigantea* specifically alters soil P availability. Recently, Chapuis-Lardy et al. (in press) found higher pools of plant available P (resin- and bicarbonate-exchangeable) under *S. gigantea*. These were correlated to increased activities of phosphomonoesterase and increased soil respiration rate. The authors suggested that it may be due to enhanced soil microbial activity and/or diversity, as already observed for other invaders (Hawkes et al. 2005; Kourtev et al. 2002, 2003). Thus, enhanced P mineralisation rates may well be involved in the increased pools of bioavailable P in the topsoil. *S. gigantea* may also be able to use P pools that are less available for plants compared to the surrounding vegetation. The importance of mycorrhizae in the competitive ability of invasive plants has been demonstrated for *Centaurea maculosa* (Zabinski et al. 2002). Part of the invasive success depends on the ability of the mycorrhizal symbiont to increase tissue P concentrations. Jin et al. (2004) documented that the total number of arbuscular mycorrhizal fungi associated with the closely related invasive *S. canadensis* increased with time of invasion. Topsoil plant available P pools may also be increased as a result of increased effluxes of H^+ or exudation of organic acids by roots (Hinsinger 2001). This hypothesis cannot be either rejected as we observed significant acidification under *S. gigantea* compared to uninvaded plots in three sites.

The impact on soil P varied depending on site, as shown by the significant invasion × site interaction, with different responses (higher vs. lower P concentrations) and different degrees of response (from 21 to 258% higher P concentrations) according to site. The only exception to

Table 2 *F*-values of the two-way ANOVA performed on biomass, nutrient concentrations in the biomass, aboveground nutrient pool and C/N ratio

	df	Biomass	Concentrations in plant tissue										Nutrient pools in standing biomass								
			Ca	Cu	K	Mg	Mn	P	Zn	C	N	C/N	Ca	Cu	K	Mg	Mn	P	Zn	C	N
Site	4	18.94 ***	13.02 ***	1.79	16.25 ***	9.22 ***	42.12 ***	25.28 ***	35.39 ***	4.96 **	2.72 *	3.07 *	31.80 ***	11.42 ***	30.43 ***	15.86 ***	15.38 ***	38.09 ***	27.36 ***	16.81 ***	20.38 ***
Invasion	1	153.20 ***	16.41 ***	27.77 ***	0.33	9.47 **	16.36 ***	88.81 ***	0.15	58.72 ***	32.62 ***	43.48 ***	51.82 ***	46.20 ***	130.59 ***	62.31 ***	25.59 ***	58.61 ***	117.74 ***	161.42 ***	50.52 ***
Site × invasion	4	4.16 **	15.94 ***	4.09 **	15.38 ***	6.13 ***	4.73 **	10.54 ***	5.19 **	3.80 **	4.01 **	4.30 **	10.77 ***	0.83	2.67 *	3.59 *	5.50 ***	3.64 *	0.50	3.33 *	2.40

Analyses were performed for 5 sites

P < 0.05; **P* < 0.01; ***P* < 0.001

higher P concerned site *For*. This site also had by far the highest soil P levels prior to invasion. In this highly eutrophicated site, the resident vegetation consists of monospecific stands of *Urtica dioica*, a nutrient rich, highly productive species. In this single site, pools of P in standing biomass were similar in invaded and uninvaded plots. Varying impacts of exotics depending on site were observed for *Hieracium pilosella* (Scott et al. 2001), *Bromus tectorum* (Belnap and Philips 2001) and *Centaurea maculosa* (Hook et al. 2004). This suggests that environmental factors including soil nutrients and floristic composition of the invaded community may influence the response of soil to invasions (Ehrenfeld 2003).

In conclusion, our study indicated that the impact of *S. gigantea* on topsoil chemistry was quite modest with a slight increase in mineral nutrient concentrations. An essential exception was phosphorus which showed higher concentrations in invaded plots compared to uninvaded soils. Humble impacts on soil properties contrasted with the high aboveground productivity and nutrient pools of the invader. The impacts differed according to site in different responses and different degrees of response to the invasion of *S. gigantea*.

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