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Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium

Sonia Vanderhoeven[1,2], Nicolas Dassonville[1,2,3] & Pierre Meerts[1]
[1]*Laboratoire de Génétique et Ecologie végétales, Université Libre de Bruxelles, 1850, chaussée de Wavre, B-1160 Bruxelles, Belgium.* [2]*Equally contributing authors.* [3]*Corresponding author**

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Abstract

Exotic invasive plants can alter ecosystem processes. For the first time in Europe, we have analysed the impacts of exotic invasive plants on topsoil chemical properties. At eight sites invaded by five exotic invasive species (*Fallopia japonica*, *Heracleum mantegazzianum*, *Solidago gigantea*, *Prunus serotina* and *Rosa rugosa*), soil mineral element composition was compared between invaded patches and adjacent, uninvaded vegetation. We found increased concentrations of exchangeable essential nutrients under the canopy of exotic invasive plants, most strikingly so for K and Mn (32% and 34% increase, respectively). This result fits in well with previous reports of enhanced N dynamics in invaded sites, partly due to higher net primary productivity in exotic invasive plants compared to native vegetation.

Abbreviations: CEC – Cation exchange capacity; Bs – base saturation rate.

Introduction

Invasions by exotic species represent a major challenge to biodiversity conservation (D'Antonio and Kark, 2002; D'Antonio and Meyerson, 2002). Belgium and neighbouring countries have suffered from invasion by exotic plants, some of which have dramatically increased their range in the last 30 years (Muller, 2000; Verloove, 2002). Much research on exotic plant invasions has focused on traits that favour invasiveness (Grotkopp et al., 2002; Rejmánek and Richardson, 1996) and on attributes that make an ecosystem susceptible to invasion (Alpert et al., 2000). The impacts of invasive plants on ecosystem functioning are receiving increasing attention (Levine et al., 2003). Ehrenfeld (2003) recently reviewed the effects of invasive plants on biogeochemical cycling. She concluded 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.

The possibility that invasive species alter soil properties has not often been tested (Ehrenfeld and Scott, 2001). Most published work has focused on the effects of a particular species at a single site and has been mainly concerned with carbon and nitrogen. Ehrenfeld (2003) emphasized that soil pools of C, N and nutrients often respond to invasions but the direction and magnitude of the impacts are probably determined by the composition of the invaded community and local soil conditions. However, assuming that successful invaders share a number of functional

* FAX No: + 32-2-6509170. E-mail: ndassonv@ulb.ac.be

traits and that ecosystems susceptible to invasions also share common attributes (Alpert et al., 2000), it might be possible to identify recurring patterns in the impacts of invasive plants on soil properties.

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, soils, geology, climate and land-use history. In this paper, we examine the impacts of invasion on topsoil chemistry in eight sites invaded by five of the most successful invasive plant species in Belgium. We compare invaded and uninvaded plots for 17 variables characterising chemical topsoil properties, not only C and N as is most often done. To our knowledge, this study represents the first attempt to assess the impact of exotic invasive plants on soil in Europe.

Materials and methods

We selected five exotic invasive species (*Fallopia japonica* (Houtt.) Ronse Decraene, *Solidago gigantea* Ait., *Prunus serotina* Ehrh., *Heracleum mantegazzianum* Somm. et Lev., *Rosa rugosa* Thunb.), the first four of which rank amongst the most successful invaders in Belgium and neighbouring countries (Muller, 2000; Saintenoy-Simon, 2003; Verlaque et al., 2002; Verloove, 2002). We included *R. rugosa* because it is a successful invader of maritime sand dunes, a priority habitat for nature conservation in Western Europe (EU Habitats Directive, 1992). A short description of the species is given in Table 1. All of them usually form dense monospecific stands at invaded sites and can thus be considered as 'transformers' according to the terminology of Pyšek et al. (2004), that is a subset of invasive plants that change the character, condition, form or nature of ecosystems over a substantial area. These species represent contrasting life forms, including two perennial geophytes (*F. japonica*, *S. gigantea*), a perennial monocarpic hemicryptophyte (*H. mantegazzianum*), a deciduous tree (*P. serotina*) and a shrub (*R. rugosa*). We selected eight sites that fulfilled all of the following conditions: (1) having well-established, and still increasing populations of one of the target species, (2) having sufficiently homogeneous soil, (3) having dense patches of the target exotic surrounded by uninvaded vegetation consisting of native species (invaded patches ranged from 25 m^2 to more than 100 m^2). Thus, site selection sought to minimise the probability of pre-existing differences prior to the invasion event. To that end, we performed comparisons of soil profiles on three invaded and three uninvaded plots. If the profiles of invaded and control situations were similar (same texture and same colour of the parent material), the site was selected. Moreover, we selected the uninvaded control plots as close as possible to the front of expansion of the invader. The sample consisted of three sites invaded by *F. japonica*, two by *H. mantegazzianum*, one by *P. serotina*, one by *S. gigantea* and one by *R. rugosa*. A larger number of sites were sampled for *F. japonica* on account of the abundance of that species in Belgian landscapes (Saintenoy-Simon, 2003; Verloove, 2002). We do not have precise information about the history of the selected sites but according to local naturalists, most of them have been invaded for at least 10 years. All sites are located in the vicinity of Brussels (<10 km) except the *R. rugosa* site, which is located at the coast. The localisation of the selected sites and a short description of the invaded habitats are given in Table 2. 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, we conducted phytosociological relevés. Ground cover of all vascular plant species was

Table 1. Characterisation of the studied species

Species	Family	Life form	Height on the field
Solidago gigantea	Asteraceae	Perrenial geophyte	05–1.5 m
Prunus serotina	Prunaceae	Deciduous tree	3–15 m
Rosa rugosa	Rosaceae	Shrub	0.5–2 m
Fallopia japonica	Polygonaceae	Perrenial geophyte	1–2.5 m
Heracleum mantegazzianum	Apiaceae	Perrenial monocarpic Hemicryptophyte	1.5–3 m

Table 2. Localisation and characterisation of the study sites

Site	Species	Locality	Habitat
Sg	*Solidago gigantea*	Kraainem	Oldfield/grassland
Ps	*Prunus serotina*	Uccle	Old sand quarry/wasteland
Rr	*Rosa rugosa*	Nieuwpoort	Coastal sand dune
Fj1	*Fallopia japonica*	Watermael-Boitsfort	Beech forest
Fj2	*F. japonica*	Haren	Oldfield/Wasteland
Fj3	*F. japonica*	Watermael Boitsfort	Pond bank
Hm1	*Heracleum mantegazzianum*	Ganshoren	Grassland
Hm2	*H. mantegazzianum*	Watermael-Boitsfort	Willow scrub on wet soil

estimated according to Braun-Blanquet's (1972) scale (5: 75–100% cover, 4: 50–75%, 3: 25–50%, 2: 5–25%, 1:1–5%, +: <1%). The mean cover 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%, 0.5%). Mean cover was then back-transformed into Braun-Blanquet's coefficients.

In the same plots, soil was sampled from February to April. In each plot, we collected five soil cores (0–0.10 m depth, litter discarded) with a soil borer (0.04 m in diameter). We collected one core at each corner of the square and one core at the centre of the square and then homogenised them 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 multispecific 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 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 the difference of total C and carbonate C. Organic matter content was then calculated as $2 \times C_{org}$.

At three sites (*F. japonica*: 2 sites, *S. gigantea*: 1 site), aboveground biomass was harvested in invaded and uninvaded 1-m^2 plots in August. Biomass was oven-dried, weighted and ground. The samples were mineralised in a muffle furnace. Ashes were then dissolved in 1 *M* HCl. Mineral element concentrations were determined by ICP-AES. N content in the biomass was assessed using a dry combustion C/N analyser (NC-2100, Carlo Erba instruments, Italy). For each element, aboveground nutrient stock was calculated as the product of biomass × concentration in the biomass.

At each site, we compared mean values of all soil parameters between invaded and uninvaded plots by means of t-tests. A Bonferroni correction was applied to the t-tests based on the number of simultaneous tests for each variable ($n = 8$ sites except for Ca, CEC, Bs: 6 and H^+, Al^{3+}: 5). Secondly, for essential nutrients only (Ca, Mg, K, Mn, Zn, Cu, P) a χ^2 test was used to compare the proportion of cases showing increased vs. decreased concentrations of exchangeable mineral nutrients with the expected proportion (50–50%) under the null hypothesis of no systematic impact of invasive species. This test was performed for all sites and species pooled. A two-way ANOVA was performed on all sites and species pooled, with 'site' and 'invasion' as main effects. In this analysis, invasion (invaded vs. uninvaded) was considered as a fixed factor, and site was considered as a random factor. As we wanted to highlight the general impact of invasive species on soil properties (whatever the species and invaded site), species was not included as a factor in the ANOVA. Finally, a Discriminant Analysis (DA) was performed using concentration of exchangeable mineral nutrients (except Ca) with invaded vs. uninvaded plots as *a priori* groups. Logarithmic transformation was applied prior to ANOVA and DA for all variables except pH. Statistical analyses were performed with *Statistica 6.1* software (StatSoft Inc., 2003).

Results

Floristic data revealed differences in species composition between invaded and uninvaded plots (Table 3). The alien species was dominant in the vegetation of all invaded plots and in five sites, it was the only species with soil cover in excess of 10%. In six of eight sites, the total number of species was higher in the uninvaded plots compared to the invaded plots. In the *R. rugosa* site, the uninvaded area consisted of large bare ground zones with scattered patches of *Carex arenaria* L. In *H. mantegazzianum* 2, the uninvaded vegetation was composed of only three species (*Urtica dioica* L., *Rubus* sp. and *Petasites hybridus* (L.) P. Gaertn., B. Mey. et Scherb.).

T-tests revealed several significant differences in soil chemical parameters between invaded and uninvaded plots for all investigated sites and species (17 significant differences on 119 tests) (Table 4). The number of significant differences ranged from one to four, depending on site. Significant differences were observed twice for pH, K and P, and once for Ca, Cu, Mg, Zn, Al, CEC, Bs, OM and N (Table 5). All species showed at least one significant difference. When Bonferroni correction was applied (based on eight simultaneous tests), three tests remained significant (Fj1, Cu: $t = 3.59$*, Zn: $t = 3.47$*; Hm1, K: $t = 3.51$*). In these three cases, nutrient concentrations were higher in invaded plots. χ^2-tests revealed that increases in exchangeable mineral nutrient concentrations under invasive species were significantly more frequent than decreases (39 increases of 54 cases; $\chi^2 = 14.29$, $P < 0.001$). For Mn, all sites showed higher concentrations under the canopy of exotics. For K and Mg, increased concentrations were found in seven of eight sites. Figure 1 shows that when all sites were pooled, the ratio Invaded/Uninvaded (I/U) was greater than 1 (i.e. expected value under the null hypothesis that invaded and uninvaded soils have equal values) for all variables except pH, OM content and C/N ratio. The two-way ANOVA performed on pooled sites (Table 6) showed a significant invasion effect ($P < 0.05$) for K and Mn. On average, invaded plots had 32% higher K and 34% higher Mn concentrations compared to uninvaded controls. There was also a significant site effect for all variables except Cu. For 7 variables out of 15, there was a significant site∗invasion interaction, indicating that the impact of invasion differs according to site. The existence of significant differences in exchangeable mineral nutrients content between invaded and uninvaded plots was confirmed by the DA (Wilk's lambda $= 0.85$, $P < 0.02$; 65% of soil samples correctly classified). Despite the huge total variance of the whole data set, due to the wide range of habitats and native vegetation across sites, 15% of variance could thus be ascribed to the impact of invasion. The canonical discriminant root was mainly correlated with K content ($b = 0.89$; $P = 0.04$).

Aboveground biomass was always significantly higher in invaded plots compared to uninvaded plots (Table 7). *S. gigantea* and *F. japonica* were 3.5 and 4.2 times more productive than surrounding native vegetation, respectively. Nutrient concentration in the biomass was nearly always lower in the exotic plant compared to native vegetation (Table 7) (significant for Cu, K, P, Zn, N in Sg; Ca, Cu, P, Zn in Fj2 and Ca, Cu, K, Mg, P, N in Fj3). Aboveground nutrient stocks were significantly higher in invaded compared to uninvaded plots for all elements in all sites.

Discussion

Despite the increasing interest of the international scientific community for the impacts of exotic plant species on ecosystem properties (Ehrenfeld, 2003), very few studies have been published concerning the European subcontinent. To our knowledge, this study is the first to

Table 3. List of the most abundant species (ground cover >10%) and total number of species in the invaded and uninvaded plots

Site	Invaded area	Uninvaded area
Sg	*Solidago gigantea* (5)	*Agrostis stolonifera (3)* Leucanthemum vulgare *(2)* *Holcus lanatus* (2) *Cirsium arvense (2)* *Achillea millefolium* (2) *Pulicaria dysenterica* (2)
Total number of species	11	40
Ps	*Prunus serotina* (4) *Arrhenatherum elatius* (4) *Holcus lanatus* (2) *Agrostis sp*. (2)	*Arrhenatherum elatius* (4) *Agrostis* sp. (2)
Total number of species	12	17
Rr	*Rosa rugosa* (5)	Carex arenaria *(2)*
Total number of species	12	5
Fj1	*Fallopia japonica (5)*	*Rubus sp*.(3) *Juncus effusus* (2) *Deschampsia cespitosa* (2)
Total number of species	4	11
Fj2	*Fallopia japonica (5)*	*Arrhenatherum elatius (3)* *Cirsium arvense* (3) *Urtica dioica* (2) *Dactylis glomerata* (2)
Total number of species	1	9
Fj 3	*Fallopia japonica* (4) *Carex pendula* (2)	*Petasites hybridus* (5) *Chrysosplenium alternifolium* (2)
Total number of species	6	10
Hm1	*Heracleum mantegazzianum* (5) *Urtica dioica (*2)	*Urtica dioica* (3) *Petasites hybridus* (2) *Cirsium arvense* (2)
Total number of species	4	12
Hm2	*Heracleum mantegazzianum* (5)	*Urtica dioica (3)* *Rubus sp*. (3) *Petasites hybridus* (2)
Total number of species	14	7

Braun-Blanquet coefficients of abundance–dominance are given in brackets (means for six plots). Nomenclature follows Lambinon et al. (2004).

examine the impact of invasive species on soil in Europe (but see Plichta et al., 1997).

The observed impacts are to some extent idiosyncratic as revealed by the significant site∗invasion interaction for 7 of 15 parameters. Species-specific effects and site-specific effects may both explain this result. Contrasted impacts of exotics depending on site were observed with *Hieracium pilosella* L. for Ca, Mg and K (Scott et al., 2001), and *Bromus tectorum* L. for Ca, Fe, Mn and Cu (Belnap and Philips, 2001). This suggests that environmental factors (such as climate, soil conditions and/or topography), age of invasion and floristic composition of the invaded community may influence the response of soil to invasions (Ehrenfeld, 2003).

Table 4. Soil chemical properties in invaded (I) and uninvaded (U) plots (8 sites)

Site		pH H_2O	pH KCl	Ca†	Cu†	K†	Mg†	Mn†	P†	Zn†	H^+‡	Al^{3+}‡	CEC‡	Bs	OM	N	C/N	$CaCO_3$
Sg I	Mean	5.94	5.13	1386	0.24	97.9	126.0	30.77	4.63	4.83	0.01	0.18	8.40	97.8	3.60	0.15	11.80	0.00
	SD	0.44	0.45	207	0.05	22.9	17.4	5.32	1.36	0.43	0.00	0.08	0.91	1.1	1.09	0.03	1.68	0.00
U	Mean	6.48	5.65	1418	0.23	68.2	109.9	28.24	2.60	4.55	0.00	0.14	8.28	98.5	2.96	0.14	11.01	0.00
	SD	0.30	0.31	232	0.09	24.5	12.1	9.38	1.76	0.97	0.01	0.02	1.25	0.8	0.33	0.01	1.00	0.00
t-value		−2.49*	−2.29*	−0.25	0.25	2.16	1.86	0.58	2.24*	0.67	0.90	1.13	0.18	−1.40	1.37	1.28	0.99	
Ps I	Mean	5.05	4.08	840	0.13	122.0	127.1	34.12	3.89	5.08	0.06	0.35	5.96	92.5	3.87	0.16	12.09	0.00
	SD	0.29	0.39	172	0.03	12.9	28.9	3.02	0.76	2.11	0.05	0.32	0.72	7.6	0.48	0.02	0.62	0.00
U	Mean	4.66	3.66	590	0.15	108.2	97.6	31.20	4.72	5.28	0.10	1.00	5.23	75.2	3.62	0.15	12.21	0.00
	SD	0.21	0.24	163	0.05	12.1	24.1	1.60	1.34	0.78	0.09	0.59	0.46	11.7	0.45	0.02	0.63	0.00
t-value		2.51*	2.07	2.45*	−1.06	1.9	1.91	2.09	−1.33	−0.22	−1.01	−2.37*	1.95	2.97*	0.94	1.19	−0.33	
Rr I	Mean	7.34	7.02	nd	0.11	29.5	242.5	36.81	17.57	7.78	nd	nd	nd	nd	0.99	0.04	14.14	6.00
	SD	0.07	0.07		0.01	9.9	11.4	0.30	1.21	7.51					0.20	0.01	0.76	0.22
U	Mean	7.42	7.06	nd	0.10	39.8	237.4	36.77	17.58	4.91	nd	nd	nd	nd	0.82	0.02	17.46	5.71
	SD	0.08	0.08		0.01	9.0	11.8	0.78	0.44	1.96					0.32	0.01	5.24	0.24
t-value		−1.51	−0.86		1.15	−1.41	0.58	0.08	−0.01	0.63					0.89	2.65*	−1.29	1.67
Fj1 I	Mean	4.41	3.41	576	0.29	93.0	76.1	24.81	3.91	8.92	0.52	1.73	6.00	61.6	9.14	0.22	20.25	0.00
	SD	0.22	0.19	253	0.13	17.3	20.2	13.94	2.10	3.03	0.18	0.85	0.86	16.7	3.50	0.04	5.39	0.00
U	Mean	4.13	3.16	317	0.26	62.6	37.4	11.57	3.06	10.83	0.58	1.81	4.45	46.6	14.48	0.31	24.15	0.00
	SD	0.27	0.20	144	0.14	14.6	16.4	6.44	2.08	9.81	0.17	0.86	1.00	17.8	3.77	0.11	3.39	0.00
t-value		1.94	2.10	2.02	0.36	3.11*	3.42**	1.94	0.67	−0.46	−0.59	−0.14	2.77*	1.44	−2.44*	−1.84	−1.40	
Fj2 I	Mean	6.30	5.54	1387	0.20	257.7	92.8	10.24	29.85	21.46	0.01	0.15	8.52	97.7	8.17	0.28	14.49	0.00
	SD	0.61	0.69	438	0.09	120.3	13.8	2.52	21.76	5.03	0.02	0.14	2.09	2.5	1.61	0.05	0.84	0.00
U	Mean	6.82	6.20	1918	0.62	169.7	76.9	9.01	21.83	35.20	0.00	0.11	10.76	98.9	8.66	0.26	16.17	0.00
	SD	0.18	0.22	739	0.55	24.6	16.0	2.32	11.34	21.88	0.00	0.12	3.83	1.3	3.54	0.08	3.94	0.00
t-value		−1.97	−2.23*	−1.51	−1.81	1.76	1.84	0.88	0.80	−1.50	1.54	0.52	−1.26	−1.07	−0.31	0.47	−1.02	
Fj3 I	Mean	6.94	6.32	4560	0.34	170.1	275.1	24.44	16.60	24.21	nd	0.20	23.92	99.2	11.17	0.34	16.35	0.00
	SD	0.51	0.52	3678	0.08	51.7	148.7	14.47	4.45	5.97	0.00	0.00	18.12	0.9	2.33	0.04	2.12	0.00
U	Mean	7.19	6.54	3973	0.13	116.8	147.4	13.29	10.02	9.31	nd	nd	21.60	100.0	12.02	0.35	17.03	0.00
	SD	0.28	0.25	3015	0.11	119.3	114.3	11.08	8.75	8.65			14.95	0.0	1.96	0.04	2.12	0.00
t-value		−1.02	−0.94	0.26	3.60**	1.00	1.67	1.50	1.64	3.47**			0.21	−1.97	−0.68	−0.58	−0.55	

Hm1 I	Mean	7.46	6.77	nd	0.14	322.5	199.9	40.21	16.59	5.06	nd	nd	nd	nd	9.98	0.45	11.26	4.59
	SD	0.09	0.07		0.02	56.2	31.5	12.45	6.84	1.11					4.28	0.19	0.83	2.15
U	Mean	7.35	6.65	nd	0.13	187.1	181.8	28.58	16.46	4.09	nd	nd	nd	nd	11.31	0.52	10.89	4.97
	SD	0.18	0.19		0.02	93.7	24.9	9.59	6.35	0.73					3.29	0.14	0.94	2.67
t-value		1.52	1.61		0.85	3.51**	1.27	2.09	0.04	2.07					−0.69	−0.86	0.84	−0.31
Hm2 I	Mean	6.63	6.01	1634	0.26	109.9	144.1	15.99	9.49	10.76	0.00	0.17	13.85	98.4	7.72	0.25	15.63	0.00
	SD	0.20	0.23	261	0.29	14.0	28.1	4.73	2.76	2.80	0.00	0.02	10.62	0.7	1.79	0.04	1.24	0.00
U	Mean	6.87	6.11	1685	0.16	105.9	179.3	15.59	23.55	12.34	0.00	0.15	9.50	98.7	7.19	0.24	15.11	0.00
	SD	0.21	0.29	218	0.07	42.2	37.1	4.74	14.25	3.57	0.00	0.02	0.88	0.9	1.47	0.05	0.62	0.00
t-value		−1.97	−0.59	−0.32	0.69	0.22	−1.80	0.14	−2.39*	−0.83		1.11	0.80	−0.70	0.53	0.27	0.85	

Means and standard deviations (SD) for invaded (I) and uninvaded (U) plots. $n = 6$. Means are compared by t-tests. Values are in mg/kg (†) except for H^+, Al^{3+} and CEC (‡ meq/100 g). Organic matter (OM), N and $CaCO_3$ are in %. Sg = *Solidago gigantea*, Ps = *Prunus serotina*, Rr = *Rosa rugosa*, Fj = *Fallopia japonica*, Hm = *Heracleum mantegazzianum*. nd = not determined; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 5. Number of observations of increases vs. decreases in soil chemical properties under the canopy of exotics compared to adjacent native vegetation

	pH H_2O	pH KCl	Ca	Cu	K	Mg	Mn	P	Zn	H^+	Al^{3+}	CEC	Bs	OM	N	C/N	$CaCO_3$
Number of increases	3	3	3	6	7	7	8	5	4	2	3	5	2	4	5	4	1
Number of decreases	5	5	3	2	1	1	0	3	4	2	2	1	4	4	3	4	1
Number of significant increases	1	0	1	1	2	1	0	1	1	0	0	1	1	0	1	0	0
Number of significant decreases	1	2	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0

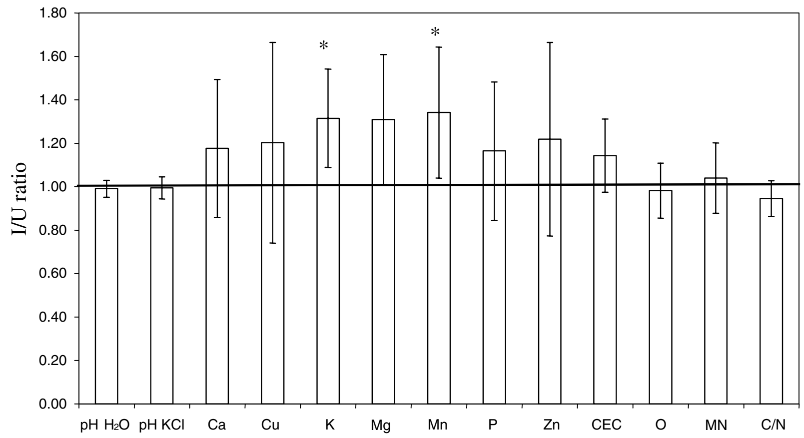

Figure 1. Ratio of mean value of invaded plots on mean value of uninvaded plots (I/U ratio) for pH, exchangeable nutrients (mg/kg except Al^{3+},H^{+}: meq/100 g), cation exchange capacity (CEC: meq/100 g), Organic matter (OM: %), N content (%) and C/N ratio (8 sites except for Ca and CEC (6 sites)). Whiskers are 95% confidence intervals. The horizontal line (I/U = 1) denotes equal value for invaded and uninvaded plots. Stars indicate significant invasion effect in the ANOVA with site (random) and invasion (fixed) as main factors ($P < 0.05$).

More surprisingly, however, we found a general trend of increased mineral nutrient concentrations in the topsoil under invasive species compared to adjacent native vegetation. This is a striking result considering that the studied species belong to different life forms and that they invade sites with contrasting vegetation cover and soil condition. Although the experimental design did not formally exclude the possibility of pre-existing differences, we believe that the most parsimonious explanation for the observed increase in exchangeable mineral nutrient content lies in the contrasting plant cover between invaded and uninvaded plots. The alternative hypothesis, i.e. pre-existing site variation in soil conditions with the exotic occupying specific microniches, seems unlikely. Most alien species in our sample occur in a wide range of soil conditions in Belgium (pH range for *F. japonica* = 4.4–7.3; pH range for *H. mantegazzianum* = 5.7–7.4; pH range for *S. gigantea* = 5.9–7.6) (pers. obs.). Therefore, it seems unlikely that the small variations in soil conditions observed locally between invaded and uninvaded areas are limiting the range of the invader. Moreover, in all sites, patches of exotic species are still extending.

Most studies examining impacts compare C and N fluxes and pools between invaded situations and native vegetation (Ehrenfeld et al., 2001; Kourtev et al., 1999, 2003; Scott et al., 2001) but other nutrients including phosphorus, metallic cations and trace elements have much more rarely been considered. In her recent review of 79 papers examining the effects of invasive plants on biogeochemical cycles, Ehrenfeld (2003) recorded only 11 studies examining metallic cations and phosphorus, without highlighting general patterns. Although our results were based on a relatively limited number of sites, the finding of increased availability of metallic cations fits in well with the enhanced availability and cycling rate of nitrogen often observed in invaded sites worldwide (Ehrenfeld, 2003). Taken together, these results may indicate that the most successful invasive species are those able to enhance topsoil mineral nutrient availability.

What could be the mechanisms of the observed impacts on soil? A first possibility is that alien invasive species enhance mineral nutrient turn over rates. Higher standing crop biomass, higher net primary productivity and faster growth rates have often been reported for invasive species compared to the native vegetation (Blank and Young, 2002; Ehrenfeld, 2003; Ehrenfeld et al., 2001). For some species, higher mineral nutrient concentrations in plant tissues may also explain accumulation of minerals

Table 6. Two-way ANOVA performed on soil chemical parameters

	pH H_2O	pH KCl	Ca	Cu	K	Mg	Mn	P	Zn	CEC	Bs	OM	N	C/N	$CaCO_3$
Site (random factor)	42.88 ***	49.54 ***	18.74 **	1.26	13.29 **	8.02 **	10.04 **	11.24 **	6.19 *	23.82 **	16.74 **	16.96 ***	39.55 ***	18.71 ***	694.2 ***
Invasion (fixed factor)	0.72	0.51	0.85	0.24	7.47 *	4.40	5.82 *	0.44	0.73	1.45	1.80	1.38	0.77	2.65	0.025
Site X Invasion	3.82 **	3.72 **	2.16	3.24 **	1.97	3.48 **	1.67	2.55 *	4.09 *	0.82	3.12 *	1.68	0.80	1.55	0.09

Invasion (i.e. invaded or uninvaded) was considered as a fixed factor, and site was considered as a random factor. *F*-ratio is based on Satterthwaite approximations (Sokal and Rohlf 1995). H^+ and Al^{3+} were not considered here, as they did not show enough valid cases. Analyses were performed for 8 sites (except for Ca, CEC and Bs, performed for the 6 non-carbonated sites).
$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

under the canopy of exotics (Blank and Young, 2002; Duda et al., 2003; McIntosh et al., 1995; Plichta et al., 1997; Scott et al., 2001). We measured aboveground primary productivity and plant mineral nutrient concentrations for two *F. japonica* sites and one *S. gigantea* site. We found 3.5–4.2-fold increase in productivity in invaded patches compared to adjacent uninvaded controls. In contrast, mineral nutrient concentrations in aboveground tissues (shoots and leaves pooled) were generally lower in plants of invaded patches. However, increased productivity was not compensated for by decreased concentrations in plant tissues, which resulted in much higher mineral nutrient stocks in standing biomass in invaded patches. Thus, for these two species, higher topsoil concentrations of nutrients can probably be ascribed to enhanced uptake rates, due to enhanced primary production in invasive species. High productivity alien invasive species may also root deeper compared to native vegetation and may thus contribute to the uplift of soil nutrients (Jobbagy and Jackson, 2004). Finally, other more specific processes may also be involved (Gordon, 1998), including increased organic matter mineralisation rates (Allison and Vitousek, 2004), increased mobilisation of nutrients through rhizosphere processes (Kourtev et al., 2002), and alteration of soil microbial communities (Kourtev et al., 2003).

A mechanistic explanation will definitely require a whole-site budget approach and detailed comparison of fluxes and pools of mineral nutrients in invaded plots and adjacent control vegetation. This work is currently in progress.

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Table 7. Biomass (Kg/m^2), nutrient concentrations in the biomass (mg/kg) and aboveground nutrient stock (g/m^2) in invaded (I) and uninvaded (U) plots (8 sites)

Biomass			Concentrations in plant tissue								Nutrient stocks in standing biomass							
Site			Ca	Cu	K	Mg	Mn	P	Zn	N	Ca	Cu	K	Mg	Mn	P	Zn	N
Sg I	Mean	0.89	7490	4.83	12164	1452	94.6	1357.9	33.84	0.64	6680	4.36	10880	1300	84.6	1211.2	30.17	5.79
	SD	0.10	768	0.75	1369	182	27.2	207.3	7.14	0.10	1082	1.07	2029	269	26.7	244.2	7.23	1.58
U	Mean	0.25	12621	8.44	15465	1700	102.2	2289.0	50.12	1.17	3226	2.29	4034	433	25.6	574.8	12.37	3.13
	SD	0.13	5797	1.97	1907	228	31.9	192.7	15.14	0.26	2008	1.55	2372	215	14.4	286.7	6.00	1.41
t-value		9.61***	−2.15	−4.18**	−3.44**	−2.08	−0.44	−8.06***	−2.38*	−4.59**	3.71**	2.69*	5.37***	6.17***	4.76***	4.14**	4.64***	2.91*
Fj2 I	Mean	2.39	11440	5.46	19023	1136	47.2	1620.1	62.89	1.11	26906	12.92	45368	2628	108.4	3901.3	146.30	26.41
	SD	0.71	1125	0.60	736	170	17.6	154.5	13.50	0.07	6774	3.72	13378	488	46.0	1312.8	38.59	7.74
U	Mean	0.56	16584	7.39	19044	1234	55.4	2352.2	128.79	1.46	9925	3.93	11931	631	25.3	1293.8	64.83	7.37
	SD	0.30	5431	1.65	6527	492	37.6	446.7	57.92	0.59	7123	1.66	10583	260	14.9	719.0	27.81	2.74
t-value		5.82***	−2.27*	−2.69*	−0.01	−0.46	−0.5	−3.8**	−2.71*	−1.45	4.23**	5.41***	4.80***	8.84***	4.21**	4.27**	4.19**	5.68***
Fj3 I	Mean	1.65	17279	7.84	18932	2289	18.8	2476.8	41.85	1.43	29119	13.15	29278	3747	26.9	3998.2	63.07	22.89
	SD	0.80	1480	1.03	3993	146	8.9	325.7	13.12	0.21	16699	7.44	9879	1768	11.3	1879.7	20.95	10.47
U	Mean	0.39	22363	13.59	45681	4136	16.2	4912.6	26.36	2.20	8984	5.25	17184	1650	6.6	1871.3	10.16	8.63
	SD	0.15	3447	1.35	9723	1132	3.9	662.9	1.78	0.02	4295	1.73	4444	804	3.7	526.3	3.10	3.22
t-value		3.78**	−3.32**	−8.29***	−6.23***	−3.96**	0.65	−8.08***	2.87*	−8.82***	2.86*	2.53*	2.73*	2.64*	4.19**	2.67*	6.12***	3.19**

Means and standard deviations (SD) for invaded (I) and uninvaded (U) plots. $n = 6$. Means are compared by *t*-tests.
*$P < 0.05$; ** $P < 0.01$; ***$P < 0.001$

References

Allison S D and Vitousek P M 2004 Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. Oecologia 141, 612–619.

Alpert P, Bone E and Holapfel C 2000 Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. 3, 52–66.

Belnap J and Philips SL 2001 Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecol. Appl. 11, 1261–1275.

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

Braun-Blanquet J 1972 Plant sociology: the study of plant communities (Fac simile of the edition of 1932, translated by Fuller G D and Conrad H S), Hafner Publishing Company, New York. 439 pp.

D'Antonio C M and Kark S 2002 Impacts and extent of biotic invasions in terrestrial ecosystems. Trends Ecol. Evol. 17, 202–204.

D'Antonio C M and Meyerson LA 2002 Exotic plant species as problems and solutions in ecological restoration: A synthesis. Restor. Ecol. 10, 703–713.

Duda J J, Freeman D C, Emlen J M, Belnap J, Kitchen S G, Zak J C, Sobek E, Tracy M and Montante J 2003 Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*. Biol. Fertil. Soils 38, 72–77.

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

Ehrenfeld J G, Kourtev P and Huang W 2001 Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecol. Appl. 11, 1287–1300.

Ehrenfeld J G and Scott N 2001 Invasive species and the soil: effects on organisms and ecosystem processes. Ecol. Appl. 11, 1259–1260.

EU Habitats Directive 1992/43/CEE Official Journal of European communities L206, 7.

Gordon D R 1998 Effects of the invasive, non-indigenous plant species on the processes: Lessons from Florida. Ecol. Appl. 8, 975–989.

Grotkopp E, Rejmánek M and Thomas Rost L 2002 Toward a causal explanation of plant invasiveness: Seedling growth and life history strategies of 29 Pine (*Pinus*) species. Am. Nat. 159, 396–419.

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

Kourtev P S, Ehrenfeld J G and Häggblom M 2003 Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. Soil Biol. Biochem. 35, 895–905.

Kourtev P S, Ehrenfeld J G and 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.

Kourtev P S, Huang W Z and Ehrenfeld J G 1999 Differences in earthworm densities and nitrogen dynamics in soil under exotic and native plant species. Biol. Invasions 1, 257–245.

Lambinon J, Delvosalle L and Duvigneaud J 2004 Nouvelle Flore de la Belgique, du Grand-Duché de Luxembourg, du nord de la France et des régions voisines (ptéridophytes et spermatophytes). 1170 pp. Jardin Botanique National de Belgique, Meise, Belgique.

Levine, J M, Vilà M, D'Antonio C M, Dukes J S, Grigulis K and Lavorel S 2003 Mechanisms underlying the impacts of exotic plant invasions. P. Roy. Soc. Lond. B 270, 775–781.

McIntosh P D, Loeseke M and Bechler K 1995 Soil changes under Mouse-ear Hawkweed (*Hieracium pilosella*). New Zeal. J. Ecol. 19, 29–34.

Muller S 2000 Les espèces végétales invasives en France: bilan des connaissances et propositions d'action. Rev. Ecol. (Terre Vie), Suppl. 7.

Plichta W, Kuczynska I and Rutkowski L 1997 The effect of American cherry (*Prunus serotina* Ehrh.) plantations on organic and humus horizons of cambic arenosols in a pine forest. Ekologia Polska 45, 385–394.

Pyšek P, Richardson D M, Rejmánek M, Webster G L, Williamson M and Kirschner J 2004 Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. Taxon 53, 131–143.

Rejmánek M and Richardson D M 1996 What attributes make some plant species more invasive? Ecology 77, 1655–1661.

Saintenoy-Simon J 2003 Les plantes exotiques naturalisées et les espèces invasives de Wallonie. Parcs et Réserves 58, 23–39.

Scott N A, Saggar S and McIntosh P D 2001 Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: Sustainability implications. Ecol. Appl. 11, 1311–1322.

Sokal R R and Rohlf F J 1995 Biometry. Freeman and co, New York.

StatSoft Inc. 2003 Statistica (Data analysis software) version 6. www.statsoft.com.

Verlaque R, Aboucaya A and Fridlender A 2002 Invasive alien flora of France: Ecology, life-forms and polyploidy. Bot. Helv. 112, 121–136.

Verloove F 2002 Ingeburgerde plantensoorten in Vlaanderen. Mededeling van het Instituut voor Natuurbehoud nr. 20, Brussels.

Walker L R and Smith S D 1996 Impacts of Invasive Plants on Community and Ecosystem Properties. *In* Assessment and Management of Plant Invasions. Eds. J O Luken and J W Thieret pp. 69–86. Springer-Verlag, New York.

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