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Distribution and functional traits of *Solidago gigantea* in a Swiss lakeshore wetland

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Abstract

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Alien plant species are of particular ecological concern when they invade native vegetation of high conservation value and alter its functioning. We mapped the area and cover of stands of invasive alien species in the lakeshore wetland "Grande Cariçaie" (CH) and examined whether the main invader, *Solidago gigantea* Ait., differs functionally from the resident vegetation. Seven alien species considered to be invasive in Switzerland occurred with a total area of 22.2 ha. The most frequent invaders were *S. gigantea* (60 stands) and *Robinia pseudoacacia* (42 stands, mostly in forest). Less than 1% of the non-forested wetland area was colonised by alien species, mostly *S. gigantea*. Dense stands of *S. gigantea* (>50% cover) occurred in mesotrophic, non-flooded vegetation, suggesting that its spread is limited by high water level rather than by low nutrient availability. *S. gigantea* appeared functionally similar to the invaded wetland vegetation: its shoot size, specific leaf area, and biomass N and P concentrations were similar to or lower than those of co-occurring native species. Total soil N and P concentrations under *S. gigantea* stands did not differ from those under non-invaded vegetation. Thus, the impact of invasive alien species on the non-forested wetlands of the Grande Cariçaie currently seems rather low but possible changes in soil processes as well as effects on other biota remain to be investigated.

Key words: Alien species, fens, foliar nutrient concentrations, invasive plants, nutrient availability, specific leaf area.

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Introduction

Invasive alien plants (invasive neophytes) can affect the invaded vegetation through competitive displacement of native species and by changing the resource availability, the disturbance regime, or ecological process rates (Mack and D'Antonio 1998; Parker et al. 1999; Richardson et al. 2000; Levine et al. 2003). Such effects of plant invasions are of particular concern for nature conservation when they affect vegetation types of high species diversity, those which are rare at regional or global scale, or those with a key function in ecosystem or landscape ecology (Higgins et al. 1999; Lockwood et al. 2001).

The impact of invasive neophytes on the invaded ecosystems is likely to increase with (i) increasing invaded area, (ii) increasing abundance of the invader within the invaded area, and (iii) increasing functional difference between the invader and the resident species (Parker et al. 1999; Mack et al. 2001). For example, in comparisons of invasive with non-invasive species, invasives often had a greater specific leaf area and higher nutrient concentrations in biomass (Smith and Knapp 2001; Craine and Lee 2003; Daehler 2003; Farnsworth and Meyerson 2003). These traits may cause invasive species to accelerate nutrient cycling and increase nutrient availability in soil (Ehrenfeld 2003). Invasive neophytes may also have specific properties causing them to interact differently with other plant species, animals or microbes than the resident species which they replace (Bais et al. 2003; Callaway et al. 2004a,b).

Wetlands are ecosystems of high conservation value that have been severely impacted by plant invasions world-wide (Zedler and Kercher 2004). Of the 33 world's most invasive plant species, 24% are wetland plants, which can form extensive monotypic stands and may dramatically alter the structure, biodiversity, hydrology and biogeochemistry of wetlands (Zedler and Kercher 2004). Research about plant invasions in wetlands has focused on the most invasible habitats, such as marshes, riversides or shallow waters, which receive regular influxes of water, nutrients, sediments and propagules. There is little information about plant invasions and their impact in fens or bogs, probably because these wetland types seem less vulnerable to invasions. However, fens and bogs are rich in slow-growing, threatened species, which might be displaced by invasive plants (Güsewell and Klötzli 1998; Tomassen et al. 2004). Monitoring the abundance of invasive species in these habitats is therefore particularly important to identify the need for control measures and design efficient strategies (Wadsworth et al. 2000).

About 350 neophytes are currently naturalised in Switzerland, of which 20 are troublesome invaders ("black list"), and further 20 potentially troublesome ("watch list"; www.cps-skew.ch/english/black_list.htm). Several species (e.g. *Solidago gigantea*, *Lonicera japonica*) are able to invade vegetation types of high conservation value, including wetlands, and to affect their diversity by displacing native species (Weber 2000). However, their invasiveness varies regionally; many are abundant only in some parts of the country or only in certain types of habitat (Walther 2003; www.cps-skew.ch/english/black_list.htm). Knowledge about their local distribution is still limited and needs to be completed by local field surveys.

In this study we first surveyed the occurrence of invasive neophytes in the largest lakeshore wetland of Switzerland to determine which species have invaded wetland vegetation of high conservation value, what area they have colonised, and how dominant they are. Since only *Solidago gigantea* Ait. proved to be abundant in the non-forested wetlands, the second part of the study focused on this species and examined

whether it differs functionally from the resident vegetation in a such a way that its invasion might lead to an increase in nutrient availability.

Materials and Methods

Study area

"La Grande Cariçaie" is a large wetland area (about 600 ha) on the southern shore of Lake Neuchâtel, an alkaline lake in western Switzerland (46°47'–47°00'N and 6°38'–7°04'E; 430 m a.s.l.). It is a young wetland system, which developed as a consequence of lowering the level of the lake by about 3 m in 1869 (Buttler et al. 1985). Soils are neutral to alkaline (pH 7–8.5) gleysols over sandy or clayey lake sediments (Buttler 1987); peat has only accumulated locally. Across most of the wetland, the water level fluctuates considerably, being at or above soil surface in winter but 20–100 cm below surface in summer (Buttler 1987). Since 1984, large parts of the "Grande Cariçaie" have been mown in a large-scale rotational scheme to slow down vegetation succession and afforestation (Güsewell and Le Nédic 2004). Since 2000, open water areas are also created deliberately at a larger scale through topsoil removal, and two sites are grazed (Gander et al. 2003).

Non-forested plant communities include wet grasslands (mesotrophic: *Molinion*, eutrophic: *Filipendulion*), wetland pioneer vegetation (*Nanocyperion*), sedge- or rush-dominated fen communities (*Caricion davallianae*, *Magnocaricion*, *Cladietum marisci*), reed stands (aquatic: *Phragmition*, terrestrial: *Phalaridion*) and open water (*Nymphaeion*) (Roulier 1983; Buttler and Gallandat 1990; Delarze et al. 1999). The area with non-forested wetland vegetation is separated from the higher-lying intensive farmland by a forested slope and a fringe of alluvial forest. Eutrophication from agriculture is therefore restricted to areas directly surrounding water inflow from the farmland. The vegetation types of greatest botanical conservation value based on their rarity in Switzerland and the occurrence of threatened species are the *Molinion*, *Nanocyperion* and *Caricion davallianae*.

Survey of invasive neophytes

Of the 20 black-listed invasive neophytes in Switzerland, seven were observed during previous field work in the Grande Cariçaie. The distribution of these seven species was mapped across the entire area in summer 2002 and 2003. Whenever the species were encountered, the position of the stand was located on 1:2000 aerial photographs; the area of the stand (m^2), and the cover of the alien species (Braun-Blanquet scale) were estimated visually. If there were several distinct patches or patches with contrasting cover, these were recorded separately provided that their size exceeded 2×2 m. The data were introduced in a Geographic Information System. We determined the number of individual stands for each species by defining a "stand" as the totality of all patches that were at most 50 m apart from each other (distance to the nearest patch). The map with patches was combined with a vegetation map established previously (C. Clerc, unpublished report), which distinguished 63 vegetation units (34 units of non-forested wetland vegetation, and 29 units of forest vegetation) as well as 18 types of anthropogenic or unvegetated sites. For the purpose of the present study, units were grouped into 14 main vegetation types (Table 1). The invaded area by species and vegetation type was calculated by summing up the area of the corresponding patches.

Tab. 1.   Occurrence of invasive neophytes in the "Grande Cariçaie": *Ambrosia artemisiifolia*, *Buddleja davidii*, *Impatiens glandulifera*, *Reynoutria japonica*, *Robinia pseudoacacia*, and *Solidago gigantea*. For each of the main vegetation types, the table gives the area (ha) colonised by each species and by the six invasive species together ("all"), the total area of the vegetation type, and the invaded area as % of total area (n.a. = data not available). The total area occupied by each species and the number of stands (patches or groups of patches at least 50 m apart from each other) are given at the bottom.

	Ambr. (ha)	*Buddl.* (ha)	*Impat.* (ha)	*Reyn.* (ha)	*Robin.* (ha)	*Solid.* (ha)	All (ha)	Total area (ha)	Invaded (%)
(a) Wetland vegetation (non-forested)									
Caricion davallianae						0.96	0.96	87.80	1.09
Molinion						0.24	0.24	15.30	1.54
Cladietum marisci						1.45	1.45	100.60	1.44
Nanocyperion						0.13	0.13	1.50	8.61
Magnocaricion			0.22	<0.01		1.42	1.64	180.10	0.91
Phragmition			0.01	<0.01	0.02	0.16	0.19	147.40	0.13
Phalaridion			0.01			0.51	0.52	26.70	1.93
Filipendulion						0.49	0.49	16.60	2.93
Nymphaeion						<0.01	<0.01	12.00	0.03
(b) Forest and non-wetland vegetation									
Natural forest		0.08	0.37		2.52	0.88	3.85	540.00	0.71
Tree plantation		<0.01			0.62	6.72	7.34	120.00	6.12
Forest clearing					<0.01	0.01	0.01	5.00	0.25
Ditch, river		<0.01	0.01		0.02	0.01	0.04	n.a.	n.a.
Ruderal	<0.01	0.03	0.52	0.03	2.60	2.12	5.31	n.a.	n.a.
Total area (ha)	<0.01	0.11	1.13	0.03	5.78	15.10	22.16	–	–
Number of stands	2	12	7	7	42	60	130	-	-

Unlike the other species, *Solidago gigantea* (nomenclature: Lauber and Wagner 1996) was not mapped along the railway between Yverdon and Yvonand because plants were dispersed over the entire distance instead of forming well-defined stands. *Solidago canadensis* was observed once on the aforementioned railway but not elsewhere and was therefore not included in the presentation of results. We cannot completely exclude that some stands of *S. gigantea* contained plants of *S. canadensis*, given the similarity of these species and the impossibility to check all plants in large stands during mapping.

Sampling of plant biomass and soil

Because *Solidago gigantea* was the only species to be abundant in wetland vegetation (Table 1), our analysis of plant traits was limited to this species. Between 16 and 30 August 2004 we randomly collected ten shoots from each of nine populations in various vegetation types within the Grande Cariçaie (Table 2). We also clipped 4–5 small plots (20×20 cm) of vegetation without *S. gigantea* at the same location; these subsamples were pooled. At three of the sites, several shoots of three native forbs typical of these habitats (*Lysimachia vulgaris*, *Mentha aquatica*, *Inula helvetica*) were sampled separately for a direct comparison of leaf traits with those of *S. gigantea*.

Tab. 2.　Leaf traits of (a) *Solidago gigantea* sampled in various vegetation types within the "Grande Cariçaie", and (b) native forbs co-occurring with *S. gigantea*. Leaf traits were determined on one leaf per shoot, sampled at 2/3 of its height: leaf dry mass in mg, dry matter as percentage of fresh mass, specific leaf area (one-sided area per g dry mass), and nutrient concentrations (mg N or P per g dry mass). Data are means ± *SD* of 10–30 leaves (10 per site), or of 1–3 sites for N and P concentrations and for native species (determined after pooling the leaves). No *SD* is given when figures are based on pooled leaf samples from 1–2 sites.

Vegetation type and number of sites (*n*)		Leaf mass (mg)	Dry matter content (%)	Specific leaf area (cm^2 g^{-1})	N conc. (mg g^{-1})	P conc. (mg g^{-1})
(a) *Solidago gigantea*						
Molinion	1	74.3 ± 11.2	33.6 ± 2.0	144.8 ± 15.7	21.7	0.9
Caricion davallianae	1	55.5 ± 12.8	33.2 ± 2.4	140.7 ± 08.2	17.8	1.1
Cladietum marisci	1	54.0 ± 13.4	32.9 ± 2.1	135.7 ± 21.4	19.5	0.9
Caricetum elatae	3	58.4 ± 17.5	35.3 ± 2.5	127.6 ± 15.7	12.9 ± 0.8	1.0 ± 0.2
Forest	3	49.5 ± 13.8	29.9 ± 4.0	182.1 ± 37.1	22.5 ± 4.0	1.3 ± 0.2
(b) Native species						
Inula helvetica[1]	1	n.d.[3]	31.8	163.4	22.7	1.1
Mentha aquatica[2]	2	n.d.[3]	23.1–26.6	148.0–169.6	13.3–13.8	1.2–1.2
Lysimachia vulgaris[2]	2	n.d.[3]	19.0–21.1	202.3–236.6	12.0–17.4	0.9–1.0

[1] *Molinion*, [2]*Caricetum elatae;* values for the two sites given separately, [3]not determined.

Soil was sampled at the six non-forested wetland sites. At each site, three cores (5 cm Ø, 10 cm deep) were taken under *S. gigantea* plants, and three in adjacent vegetation not yet colonised by *S. gigantea*. The three forested sites were not sampled because the large area and variable density of *S. gigantea* stands precluded the identification of appropriate non-invaded vegetation patches. Cores were kept in cooling boxes and processed on the next day.

Measurements

Two leaves were removed from each of the sampled *S. gigantea* shoots, one at 1/3 and the other at 2/3 of the height between the lowest leaf and the top of the culm ('low' and 'high' leaf, respectively). We determined the fresh mass of these leaves after at least 12 h storage between wet paper (for full hydration), their area (LI-3100 area meter, Li-Cor Inc., Lincoln, Nebraska, USA), their dry mass (after 24 h drying at 75 °C). The same measurements were done on 'high' leaves of the three native forb species. Data were used to calculate leaf dry matter content (dry mass/fresh mass) and specific leaf area (SLA, area/dry mass).

For nutrient analyses, the ten leaves per site were pooled (low and high leaves separately), ground, and digested in concentrated H_2SO_4 (1 h refluxing at 420 °C with a K_2SO_4-$CuSO_4$ Kjeltab). The total N and P concentrations in digests were analysed colorimetrically (Tecator FIA, Höganäs, SE).

The remainder of the *S. gigantea* shoots were dried at 75 °C to determine the mean shoot mass per site, ground, and analysed for N and P concentrations as described before. Samples of native vegetation were analysed in the same way.

Soil cores were cut at both ends to keep only the 1–6 cm layer; stones and coarse roots were removed. A subsample was extracted with 0.5 M $NaHCO_3$ followed by col-

orimetric analysis of phosphate-P (method of Watanabe and Olsen 1965, analysis on a Flowspek UV/VIS spectrophotometer, Basel, CH). No phosphate was detected in any of the extracts, suggesting orthophosphate concentrations below detection limit. The rest of the sample was weighed, dried at 80 °C and re-weighed to determine the water content. Dry samples were ground and analysed for total N and P concentrations as described before.

Means of leaf and soil variables were calculated for each of the nine sampled sites. Means and SD of leaf traits were also calculated by vegetation type. SLA was log-transformed to obtain a normal distribution. Leaf traits differed little between 'low' and 'high' leaves, except for 10–20% lower N and P concentrations in 'low' leaves. Only results for 'high' leaves are therefore reported here. Paired t-tests were used to compare nutrient concentrations in biomass and soil between *S. gigantea* and resident vegetation.

Results

Distribution of invasive neophytes

During the field surveys in 2002-03, 130 stands of invasive neophytes were recorded with a total area of 22.16 ha (Table 1). Of these, 5.62 ha were located in non-forested wetland vegetation, representing 0.96% of the wetland area.

Solidago gigantea was found at 60 separate locations and had invaded the largest area of all species (Table 1); it was also the only species to occur in non-forested wetland vegetation of particular value for species conservation (*Molinion, Nanocyperion* and *Caricion davallianae*). Only permanently flooded sites (*Nymphaeion, Phragmition*) were hardly colonised. In absolute terms, *S. gigantea* occupied the largest area in tree plantations, but relative to the size of each vegetation type, the *Nanocyperion* (wet pioneer vegetation) was invaded to the greatest extent (Table 1).

Robinia pseudoacacia was observed at 42 locations, but only four of them were located in the wetland area; all others occupied forested or ruderal sites. The four other species (*Ambrosia artemisiifolia, Buddleja davidii, Impatiens glandulifera, Reynoutria japonica*) were found only occasionally in the Grande Cariçaie; most stands were recorded outside the protected wetland area at places with anthropogenic disturbance (Table 1).

The cover of *S. gigantea* ranged from 0% to almost 100% (Fig. 1). Most stands in non-forested wetlands had a low cover (Fig. 1a), whereas a 25–50% cover was most frequent at forested or non-wetland sites (Fig. 1b). Within the wetland, the cover of *S. gigantea* was generally < 25% in the wetter vegetation types (*Phragmition, Magnocarion, Cladietum marisci, Nanocyperion*) but > 25% in the drier vegetation types (*Caricion davallianae, Molinion, Cladietum marisci*). *Robinia pseudoacacia* occupied 2 ha with < 25% cover, 1 ha with 25–50% cover, and 2.5 ha with > 50% cover. For *Impatiens glandulifera*, the corresponding areas were 0.7, 0.4 and 0.05 ha, respectively.

Functional traits of Solidago gigantea

Leaf traits of *S. gigantea* varied substantially among the nine stands, with leaf dry mass ranging from 38.5 to 74.3 mg, leaf dry matter content from 25.8% to 37.2%, and SLA from 126 to 217 cm^2 g^{-1} (Table 2). Compared with co-occurring native forbs, *S. gigantea* had a greater dry matter content, smaller SLA and similar nutrient concentrations (Table 2).
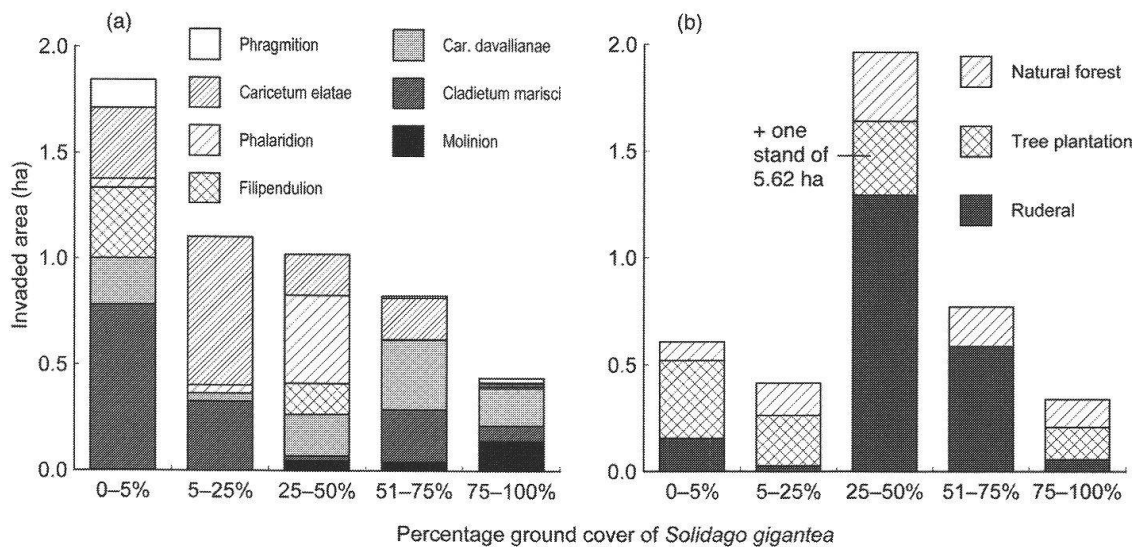
Fig. 1.   Area invaded by *Solidago gigantea* in relation to its cover (a) in wetland vegetation, (b) in forest and non-wetland vegetation, for all vegetation types with a total invaded area of > 0.1 ha.

Nutrient concentrations of whole shoots of *S. gigantea* (Fig. 2) were lower than those of individual leaves (on average 47 % lower for N and 24 % lower for P, $P < 0.001$ in paired t-tests) but well correlated with them ($r = 0.76$ for N and 0.91 for P, $P < 0.05$). The N concentration of *S. gigantea* was generally lower than that of the native vegetation (Fig. 2a, paired $t = 2.6$, $P < 0.05$), whereas there was no consistent difference for P (Fig. 2b, paired $t = 0.8$, $P = 0.45$). Only in the *Cladietum marisci* did the native species have clearly lower N and P concentrations than *S. gigantea*.

Total soil N and P concentrations within *S. gigantea* stands did not differ consistently from those of the non-invaded vegetation (paired t-tests, $P > 0.05$ for N and P), and differences at individual sites were always small (Fig. 3a,b).

Discussion

Our survey has shown that invasive neophytes are frequent in the Grande Cariçaie, since a total of 130 separate stands were recorded. Nevertheless, the non-forested wetland area has hardly been invaded until now. Less than 1 % of the wetland area is colonised by invasive neophytes, and these are mostly scattered within the matrix of native vegetation (< 25 % cover), except for a few dense stands of *S. gigantea*. Thus, the wetlands of the Grande Cariçaie have largely resisted plant invasions so far, in contrast with the high invasibility of wetlands world-wide (Zedler and Kercher 2004). One of the main factors promoting plant invasions in wetlands is flooding by surface water, which removes established vegetation and deposits fresh sediments (Minchinton 2002; Zedler and Kercher 2004). Most of the Grande Cariçaie is protected from flooding due to its topography and the water level regulation of Lake Neuchatel. In addition, soil disturbance by management and construction work are restricted to small areas. Stands of invasive neophytes occur mainly along the shoreline on sandy deposits or at forest margins, where shrub removal has disturbed the soil (C. Clerc, pers. obs.). It is possible that once neophytes are well established in these disturbed areas, they will also spread
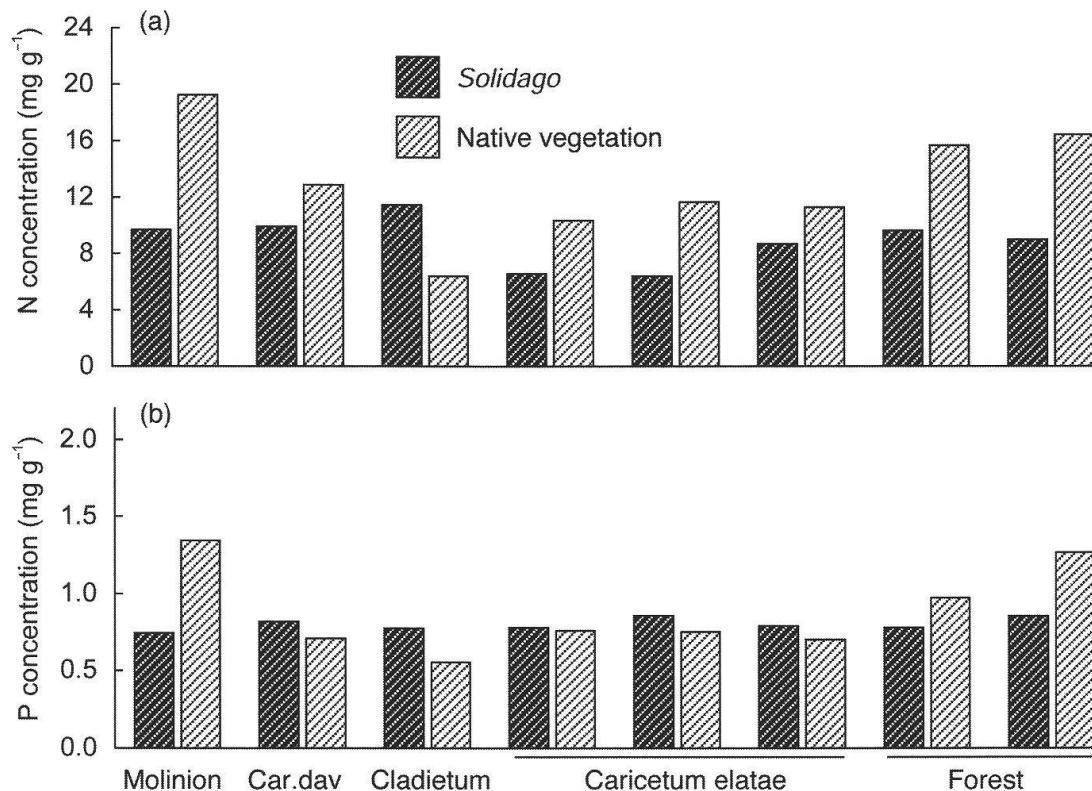
Fig. 2. Nutrient concentrations (a, nitrogen; b, phosphorus) in shoots of *Solidago gigantea* and native herbaceous species at sites with differing vegetation types. One pooled sample per site was analysed. One forest site is not included because other species were almost absent.

to a greater extent into undisturbed vegetation (Pyšek and Prach 1993). Our survey results from 2002–03 do therefore not imply that the Grande Cariçaie is unlikely to be severely invaded by neophytes in the future, and a continued monitoring will be essential.

Only *Solidago gigantea* has colonised the non-forested wetland area to a significant extent. The other species were far less frequent and largely confined to forested sites or around human constructions. For the woody species *R. pseudoacacia* and *B. davidii*, the non-forested wetlands are probably too wet. *I. glandulifera* and *R. japonica* also occur rarely in wetlands compared with other vegetation types of the Czech republic (Pyšek and Prach 1993). Flooding or low nutrient availability and competition from the established vegetation may prevent their spread. For *Reynoutria japonica*, which mostly spreads through vegetative fragments, opportunities for dispersal into the non-forested wetland may have been limited. The results of our survey confirm that *S. gigantea* has a greater ability to spread into natural habitats than any other alien species in Northern Switzerland (D. Jeanmonod, unpublished report).

The ability of *S. gigantea* to colonise the Grande Cariçaie appeared to be primarily limited by a high water level. The species hardly occurred in permanently flooded vegetation (Table 1) and mostly had a low cover in intermittently flooded vegetation (Fig. 1). This concurs with observations in wetlands near Zurich, north-eastern Switzerland,
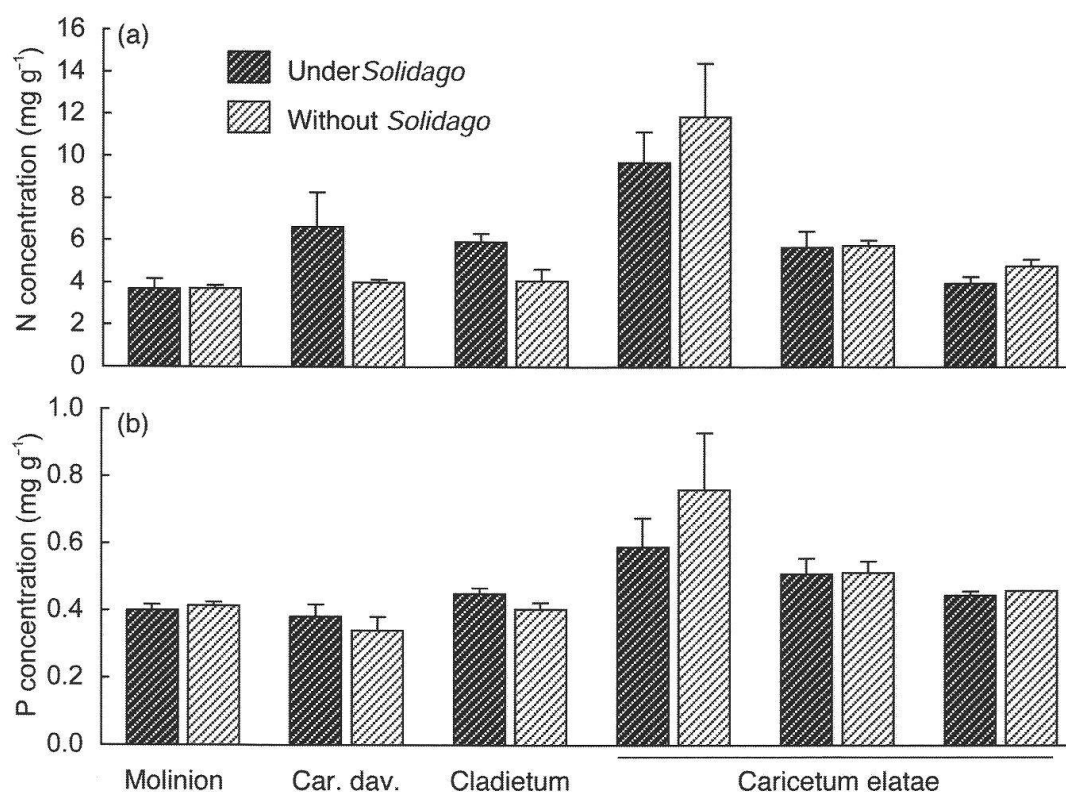
Fig. 3. Total nutrient concentrations (a, nitrogen; b, phosphorus) in soils of vegetation invaded by *Solidago gigantea* and adjacent vegetation without *Solidago* at sites with differing vegetation types. Forest sites are not included because their heterogeneity precluded the comparison of invaded and non-invaded areas. Data are means ± SE, $n = 3$.

where *S. gigantea* decreased at sites which had been flooded during an usually wet spring (A. Keel, pers. comm.). In a pot experiment, flooding (15 cm of water above sand surface during 72 days) did not reduce the biomass of *S. gigantea* more than that of 16 other wetland species (Kercher and Zedler 2004). However, the root airspace was lower in *S. gigantea* than in most other species, and its shoot:root ratio increased six-fold in the flooded pots (Kercher and Zedler 2004), which would reduce its ability to acquire and re-cycle nutrients and might lead to its exclusion under field conditions. On the landward side, a frequent occurrence of *S. gigantea* in forests and a tendency to invade tree plantations are also known from its native range in the USA (Kruse and Groninger 2004).

Low nutrient availability, unlike high water level, did not seem to be a major factor limiting the spread of *S. gigantea* in the Grande Cariçaie. The wetland vegetation types in which it reached the greatest cover were primarily nutrient-poor fens or wet meadows (*Cladietum marisci, Molinion, Caricion davallianae*). A different pattern might have been expected since *S. gigantea* is a tall, fast-growing, rhizomatous forb; these properties normally cause species to be most competitive at nutrient-rich sites but give them a disadvantage at nutrient-poor sites (Aerts 1999). The invasion pattern of *S. gigantea* in the Grande Cariçaie also contrasts with the frequent observation that the invasiveness of wetland plants depends more on resource availability and disturbance

than on the water level (Kercher and Zedler 2004; Lavergne and Molofsky 2004; Rickey and Anderson 2004).

Our measurements of leaf properties suggest that the ability of *S. gigantea* to invade mesotrophic wetland vegetation is related to low nutrient concentrations in biomass and a small SLA (high dry matter content). These traits were even lower in *S. gigantea* than in the co-occurring native forbs, suggesting a more conservative growth strategy (Grime et al. 1997; Grime 2001). *S. gigantea* seems to deviate from the tendency for invasive alien species to have nutrient-rich leaves with high SLA (Craine and Lee 2003; Daehler 2003). The same may hold for the congeneric *Solidago canadensis*, which had a lower N concentration and greater dry matter content than native species in a German old field (Schädler et al. 2003).

Nutrient concentrations and leaf structure are important for the effect of plants on nutrient availability in soil: nutrient-rich leaves with high SLA generally lead to litter that decomposes fast and releases nutrients rapidly (Cornelissen and Thompson 1997). These leaf properties generally correlate with those of roots (Craine and Lee 2003). As we found little difference in leaf traits between *S. gigantea* and resident species, we might expect *S. gigantea* to have little impact on nutrient availability in soil, which is consistent with the small data set collected here. However, *S. gigantea* forms an extensive, fast-growing and plastic rhizome and root system, which is decisive for its establishment and competitive ability (Jakobs 2004). If this is associated with large inputs of fresh organic matter into the soil through root exudations or turnover (van der Krift et al. 2001; van der Krift and Berendse 2002), there might be a stimulation of microbial activity, which might lead to faster nutrient cycling (Kourtev et al. 2002; Hahn 2003; Fontaine et al. 2004). Studies in Belgium have indeed revealed a greater activity of phosphatase in soils under *S. gigantea* (P. Meerts, pers. comm.).

Foliar nutrient concentrations and the SLA of *S. gigantea* were slightly lower in the Grande Cariçaie than in similar vegetation near Zurich (S. Güsewell and N. Zuberbühler, unpublished data). Large regional variation in life-history traits has been reported previously for this species. (Weber and Schmid 1998; Jakobs et al. 2004). While Weber and Schmid (1998) interpreted these differences as adaptations to local climate, Jakobs et al. (2004) found that climatic differences could only account for a fraction of total inter-population variation. They suggested the existence of ecotypes with contrasting invasion potential. In the present survey, the relatively "stress-tolerant" traits of *S. gigantea* in the Grande Cariçaie coincide with an (as yet) lower invasiveness than in the Zurich region, where the species has become far more dominant in wetlands (A. Gigon and E. Weber, unpublished report). Whether our results reflect a coincidence or a causal relationship between variation in functional traits and invasiveness cannot be decided here; similar studies for a greater number of regions would be required. If our results do hold more generally, then the most invasive populations of *S. gigantea* might also be those with the greatest *per-capita* impact on soil processes (Parker et al. 1999).

In conclusion, our survey has shown that the impact of invasive neophytes on the non-forested wetlands of the Grande Cariçaie is currently low according to invaded area (<1%) and moderate according to abundance within the invaded area (mostly <50% cover). However, invasive neophytes are present, and a regular monitoring of their stands is important, since alien species may suddenly start to exhibit an invasive behaviour (Pyšek and Prach 1993). Our results also suggest that the main invader, *S. gigantea*, is functionally similar to the resident vegetation and may therefore have little impact on ecosystem functioning. However, possible changes in soil processes as well as effects on other biota at the invaded sites remain to be investigated.

Résumé

Les plantes néophytes invasives représentent un problème écologique sérieux si elles envahissent des écosystèmes précieux pour la protection de la nature et si elles en changent le fonctionnement. Nous avons cartographié la surface et le recouvrement des néophytes invasifs dans la zone alluviale "Grande Cariçaie" (CH); pour l'espèce néophyte principale, *Solidago gigantea*, nous avons examiné si elle se distingue des espèces indigènes d'un point de vue fonctionnel. Sept espèces de néophytes considérées comme invasives en Suisse occupaient une surface totale de 22.2 ha. Les plus fréquentes étaient *Solidago gigantea* (60 stations) et *Robinia pseudoacacia* (42 stations, principalement en forêt). Moins de 1% des marais non-boisés étaient colonisés par des néophytes, principalement *S. gigantea*. La colonisation par *S. gigantea* semblait limitée davantage par un niveau d'eau élevé que par un manque de nutriments, vu que cette espèce avait son recouvrement maximal dans les types de végétation plus secs. *S. gigantea* apparaissait similaire aux espèces indigènes du point de vue de sa taille, structure des feuilles et concentrations d'azote et de phosphore dans sa biomasse. Les concentrations totales d'azote et de phosphore dans le sol sous *S. gigantea* ne différaient pas des concentrations sous la végétation non envahie. Nous concluons que l'impact des néophytes invasifs dans la Grande Cariçaie est encore faible, mais que les changements progressifs qui pourraient intervenir dans le sol ou les effets sur d'autres espèces animales ou végétales restent à étudier. Le développement des populations de néophytes invasifs devrait faire l'objet d'un suivi régulier.

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