REGULAR ARTICLE

Nitrogen uptake and utilisation as a competition factor between invasive *Duchesnea indica* and native *Fragaria vesca*

Johanna Littschwager · Marianne Lauerer ·
Evgenia Blagodatskaya · Yakov Kuzyakov

Abstract The Indian mock strawberry [*Duchesnea indica* (Andrews) Focke] is an invasive plant in several regions of central Europe and Germany. In order to explore its competitive ability, we compared it with the native woodland strawberry (*Fragaria vesca* L.) by growing it alone as well as in intra- or inter-specific competition in a pot experiment under greenhouse conditions. Nutrient solution was added several times at two nitrogen (N) levels. One addition involved ^{15}N labelling to determine whether the competition of both plant species depends on their ability to acquire N from soil. *Duchesnea* had a higher biomass production than *Fragaria* when grown in nutrient-rich soil, both in competition and as a solitary plant. Under N-poor conditions, root interference could change this superiority due to limited soil space. After 65 days of growth, total plant dry weight, total N content and ^{15}N content in the plant tissues were determined. The results show that the predominance of *Duchesnea* in biomass production was confirmed at high, but not at low N availability. The

assimilate partitioning strategy of *Duchesnea* differs from that of *Fragaria*: the former generally had a higher shoot-to-root ratio. The N content in shoots and roots was affected only by N addition but not by competition or species. *Duchesnea* allocated more N to the leaves, *Fragaria* to the roots. The amount of ^{15}N taken up was nearly equal for both species. In relation to root biomass, *Duchesnea* had a higher specific uptake rate at low N addition because of the higher root biomass in *Fragaria*. The roots of *Fragaria* and *Duchesnea* did not affect each other when grown together. We conclude that the invasive potential of *Duchesnea* is only poorly related to the N uptake rate or to better root competition for N. In N-rich environments, however, *Duchesnea* is highly competitive because of the preferred investment in shoot biomass. Therefore, environments with increased N deposition, i.e. from anthropogenic sources, could promote the invasive potential of *Duchesnea*.

Keywords N utilisation · *Duchesnea indica* ·
Fragaria vesca · ^{15}N uptake · Competition strategies ·
Invasive species

J. Littschwager (✉) · E. Blagodatskaya · Y. Kuzyakov
Department of Agroecosystem Research, BayCEER,
University of Bayreuth,
95440 Bayreuth, Germany
e-mail: johanna.littschwager@gmx.de

M. Lauerer
Ecological-Botanical Gardens, University of Bayreuth,
95440 Bayreuth, Germany

Introduction

The Indian mock strawberry [*Duchesnea indica* (Andrews) Focke] is a locally invasive plant in central Europe. Its spontaneous distribution in Germany,

Austria and Switzerland—although rarely at subnatural sites—shows a positive correlation with the average annual temperature (Liefländer and Lauerer 2007). Thus a warming climate could promote the range of *D. indica*. To measure its competitive ability, *Duchesnea* can be compared with the native woodland strawberry (*Fragaria vesca* L.), which has a similar growth strategy and biology. Both are perennial herbs belonging to the *Rosaceae* family, have red fleshy fruits, three-part dentate leaves and spread effectively via runners. Distinguishing features are the colour of the flowers and attributes of the fruits. *Fragaria* has white flowers and sweet, slightly hanging fruits, whereas *Duchesnea* has yellow flowers and tasteless fruits standing upright. The root system of both species consists of a main root with lateral branching roots. Additionally, *Fragaria* has adventitious roots above the main root of the mother plant. In contrast to *Duchesnea*, *Fragaria* exhibits additional tracheids in the vascular system (Albornoz et al. 2007). These differences in root anatomy may affect nutrient and water transport rates and thus determine competitive ability for belowground resources.

Previous studies on the competitive strength of *Fragaria* and *Duchesnea* closely examined aboveground parameters such as productivity and the photosynthetic properties under different competitive situations. Nepple (2003) showed that *Duchesnea* had twice as much aboveground biomass as *Fragaria* when grown for 16 weeks under field conditions. When grown in competition, the biomass in both species was reduced to less than 25% due to strong shoot competition. Overall, however, *Duchesnea* was a superior competitor under all the conditions tested.

In general, the intensity and importance of competition increases with the productivity of a habitat, and competition by aboveground plant organs is less important in N-poor versus N-rich soils (Grime 1977). In 1985, Tilman (cited in Craine 2005) stated that competition also plays an important role in less productive or unproductive sites, mainly because of nutrient limitations (Weiner et al. 1997). Also the chemical form of nutrients, e.g. nitrate versus ammonia, may affect competition between species, because the amount of transporters in root membranes for these two nitrogen forms could differ in the two species investigated (Kronzucker et al. 1997, 2003). Therefore, studying the underground competition of plants requires considering the reaction of the plants and their roots to varying nutrient conditions and the response to neighbouring roots.

In general, two different competition types are known: resource competition, i.e. for N in soil; and interference competition, when plants interact directly, e.g. two adjacent roots (Schenk 2006). Resource competition is an indirect competition between roots and takes place when the depletion zone of two roots overlaps (Fusseder and Kraus 1986). The plants do not 'recognise' that there is another competing root for water or nutrients. In this case, plants with root traits that allow nutrients to be acquired more effectively, e.g. low root diameter, high allocation rates to roots or high longevity, would benefit (Craine 2005). On the other hand, competitive strength is also influenced by the amount of nutrients taken up (Jungk 2001) and of organic compounds released (Kuzyakov 2002). The alteration of the environment by these processes is termed 'effect on resources' and contributes to the competition effect of a species (Goldberg 1990).

It has been argued that plants grown in belowground competition for nutrients allocate more assimilates to the roots than individually grown plants (Gersani et al. 2001). This is connected with the fact that limitation by nutrients lead to an increase in the portion of assimilates allocated below ground (Liljeroth et al. 1990; Kuzyakov et al. 2001). If all plants reacted in this way, then a 'tragedy of the commons' would occur: at the beginning, the individual plant has an advantage in building new roots to reach nutrients or water. After occupation of all spaces by several individuals, all plants will have fewer nutrients and a gainless investment in root growth (Zhang et al. 1999). Therefore, various plants have different competition strategies leading to a differentiation of realised niches.

Recent research also provides evidence for the second type of competition: roots can detect each other directly without changing the nutrient or water availability of the neighbouring plants ('interference competition', Callaway 2002). Two response patterns to other roots have to be considered, each based on active root-to-root communication such as non-toxic signals or allelochemical interactions: (1) the avoidance of densely rooted soil space, or (2) root proliferation in a rooted soil (Schenk et al. 1999). *Pseudororegneria spicata* decreased its root growth in contact with roots of *Agropyron desertorum* (Krannitz and Caldwell

1995). Moreover, Gersani et al. (2001) outlined results indicating that plants preferentially proliferate their roots in regions where there are fewer roots and more nutrients.

Maina et al. (2002) showed that accelerating root production in response to a neighbour starts long before the space in the pot is filled with roots, and that certain chemical signals activate that growth. *Cakile edentula* var. *lacustris* even distinguishes between stranger and kin roots: the plants allocated more carbon to fine root biomass, but when grown with their siblings they did not (Dudley and File 2007).

The fact that competitive ability is related to growth conditions (Grime 1977) calls for a closer examination of the strategy of *Duchesnea* and *Fragaria* grown at different nitrogen (N) levels. *Fragaria vesca* is relatively unspecific in its demands on soil fertility (Hegi 1906–1995), but grows most frequently in mesotrophic soils, whereas *Duchesnea* prefers eutrophic sites (Aeschimann et al. 2004). Nutrient-rich soils seem to benefit invasive plants because such plants are found mainly at fertile sites (Maskell et al. 2006). This could reflect either a better establishment of native plants in unfertile sites or more effective nutrient uptake by the invasive species. An efficient uptake rate and a large root surface help win the 'scramble competition'. Due to *Duchesnea*'s higher aboveground biomass and competitive strength (Nepple 2003), we suggest that it can utilise nitrogen from the soil more efficiently than *Fragaria*. Therefore, we tested the following hypotheses:

1) There is competition for N in soil between *Fragaria* and *Duchesnea*. This competition is reflected by the different root biomass of both species when grown in inter- and intra-specific competition.
2) *Duchesnea* builds more biomass than *Fragaria* at high N supply independently of competition.
3) *Duchesnea* takes up and utilises the offered N to build up biomass more effectively than *Fragaria* at high but not at low N supply.

Materials and methods

Competition between *Fragaria vesca* L. and *Duchesnea indica* (Andrews) Focke was investigated in a pot experiment. Daughter plants of similar size and biomass of both species were collected from a 5×5 m experimental field at the Ecological-Botanical Garden of the University of Bayreuth. For the experiment, both species were grown in pots at two N levels and in three competition situations, namely "no competition" (single), "intraspecific competition" (intra) and "interspecific competition" (inter). For the competition setup, four plants from each species (intraspecific) or two plants of the two species together (interspecific) were planted in pots with a volume of 310 cm^3 and a pot height of 9 cm. Single-grown plants were planted in a smaller pot having one-fourth of this volume (86 cm^3, pot height was 6 cm). The chosen pot size ensured that the roots would be able to fill the whole space and experience competition during the experiment. Each pot was filled with a 50:50 mixture of slightly loamy soil and quartz sand.

Plants were grown in a glasshouse from 30 April to 4 July 2008, when the mean temperature was 19°C (min. 5.6°C/max. 35°C). Three times a week, 5 or 20 ml nutrient solution was applied to the small and large pots, respectively. The nutrient solution was made up as a Hoagland solution (Taiz and Zeiger 2007), but had a four-fold concentration of all nutrients except N. The solution "high N" contained 4 mM $KHPO_4$, 42 mM KNO_3, 9 mM $Ca(NO_3)_2$, 8 mM $MgSO_4$, 0.648 mM Fe-EDTA, 0.184 mM H_3BO_3, 0.0364 mM $MnCl_2$, 0.00304 mM $ZnSO_4$, 0.00128 mM $CuSO_4$, 0.0004 mM H_2MoO_4. The "low N"-solution had the same nutrient composition but a lower N concentration [0.42 mM KNO_3 and 0.09 mM $Ca(NO_3)_2$] and additionally 8.91 mM $CaCl_2$ or $CaSO_4$ and 20.79 mM K_2SO_4 to hold the amount of potassium and phosphorus at the same level as in the high N solution. N was supplied as nitrate to ensure that all nitrogen was available and not adsorbed at the soil matrix. Nutrient addition started 3 weeks after planting.

To compensate for water losses by evapotranspiration, the pots were filled up with water to 70% water holding capacity after fertilising. All plants had the same access to light, and aboveground competition was excluded due to the relatively small plant size. Pot position in the greenhouse was randomised weekly.

To quantify N uptake, 33 days after planting, when maximal growth was assumed, nutrient solution labelled with ^{15}N was added to the pots. The solution contained 2.2% ^{15}N as NO_3^- (high N supply), or 21.2% ^{15}N as NO_3^- (low N supply) of the total NO_3^--N.

After 65 days of growth, the plants were harvested. Each plant was cut separately, separated into leaves, shoots, roots and stolons, and dried at 60°C in an oven for 3 days and subsequently weighed. Roots of the different plants were separated in a water bath. For nitrogen analysis, a sample of one plant ("without competition"), or a mixed sample of two per species ("interspecific competition") or four ("intraspecific competition") plants of each pot was ground to a powder. This was done separately for leaves, stems (including stolons) and roots. The relative abundance of ^{15}N and total N content in the plant material was analysed with a C-N analyser (CE Instruments, Milano, Italy) coupled via a ConFlo III (Finnigan MAT, Bremen, Germany) to an isotope ratio mass spectrometer Delta S (IRMS-a NA 1108, Finnigan MAT). The recovery of ^{15}N in plant biomass was 24% for the high-N and 51% for the low-N 28 days after adding ^{15}N-enriched nutrient solution. The remaining ^{15}N was assumed to be left in the soil, but the soil was not analysed for ^{15}N.

The ^{15}N uptake was calculated by:

$$^{15}N_{Uptake} = \frac{\left(^{15}N_{july} - {}^{15}N_{background}\right)}{A} \times \frac{N_{july}}{100}$$

$^{15}N_{background}$	$^{15}N/^{14}N$ atom-percent of a not labelled leaf
$^{15}N_{july}$	$^{15}N/^{14}N$ atom-percent, 25 days after applying ^{15}N-enriched nutrient solution
N_{july}	nitrogen content (mmol g dw^{-1}) 25 days after applying ^{15}N-enriched nutrient solution
A	enrichment factor (high N=6.14; low N=57.95)

Data were analysed statistically using STATISTICA (version 7.0, StatSoft, Tulsa, OK). To examine the effects of different treatments on biomass, a factorial ANOVA was used. An unequal n HSD test was conducted as post hoc test because of the unequal n in tested groups. Residuals were tested for normal distribution.
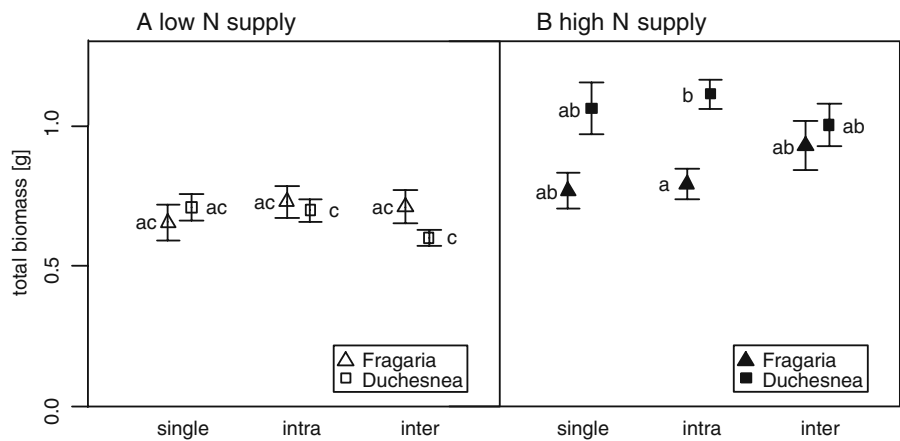
Results

Plant biomass production

All biomass parameters investigated in this experiment (dry weight of shoot, root and total biomass) were influenced strongly by nitrogen supply ($P< 0.005$) and species ($P<0.05$), but not by competition situation ($P>0.05$, Table 1). Under limiting N supply, both species had nearly the same total biomass (about 0.7 g; Fig. 1). Increasing N supply led to a significant ($P<0.005$, for plants in competition) increase in dry biomass in *Duchesnea* plants to about 1.1 g and a slight increase ($P>0.05$) in *Fragaria* plants (0.8–0.9 g depending on the competition). The dry shoot biomass also corresponded to this pattern (data not shown). Therefore, the reaction to N availability differed for the two species [Table 1, significant interaction n x spec ($P=0.002$)]. *Duchesnea* can increase its total biomass with higher nitrogen availability to a greater extent than *Fragaria*.

Root biomass of *Duchesnea* was independent of N availability, and nearly constant at about 0.2 g (Fig. 2), whereas root biomass of *Fragaria*, which was about the same as that of *Duchesnea* at high N supply (0.15–0.21 g, Fig. 2), increased significantly

Table 1 Differences between species (*Fragaria* and *Duchesnea*) and the effects of N supply and competition on total dry total plant biomass, root biomass, shoot/root (S/R) ratio, N content in total plant biomass and ^{15}N uptake (ANOVA)

	Total biomass		Root biomass		S/R-ratio$_{df}$		N$_{total\ plant}$ [%]		^{15}N uptake	
	F	P	F	P	F	P	F	P	F	P
Species effect (spec)	4.78*	0.030*	6.27*	0.013*	23.41*	0.000*	7.49*	0.008*	0.89	0.350
Competition effect (comp)	0.28	0.754	2.7	0.067	3.57	0.03	0.75	0.477	0.18	0.834
n x spec	10.22*	0.002*	7.64*	0.006*	2.35	0.127	0.18	0.673	0.70	0.407
n x comp	0.66	0.516	0.08	0.921	1.67	0.192	0.38	0.684	0.18	0.838
Spec x comp	1.79	0.171	1.16	0.316	1.99	0.140	2.61	0.082	0.82	0.443

*$P <0.05$

Fig. 1 Total dry biomass of *Fragaria* and *Duchesnea* plants grown for 65 days at low (**A**) and high (**B**) N supply under different levels of competition: *single* no competition, *intra* intraspecific competition, *inter* interspecific competition. Values are means ± standard errors ($n_{single}=6$, $n_{intra}=24$, $n_{inter}=12$). Different *lower case letters* denote significant differences among species and N treatments (post hoc, unequal n HSD test, $P<0.05$)
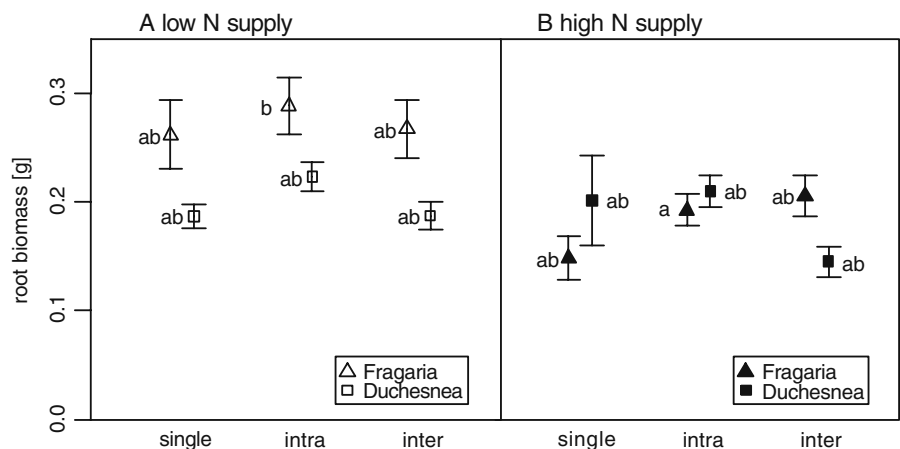
(for intraspecific competition, $P=0.002$) as N supply dropped (0.26–0.29 g).

The shoot-to-root ratio (S/R ratio) was—for both species and each competition treatment—higher at high N supply versus N limitation. The reason for this shift, however, depended on species: for *Fragaria* it was caused by greater root biomass when grown at low compared to high N (Fig. 2). In contrast, for *Duchesnea* it was due to greater shoot biomass in plants grown at high versus low N addition (data not shown). Nevertheless, *Duchesnea* always had a slightly higher S/R ratio than *Fragaria*, especially when both plants were grown without competition and at low N availability.
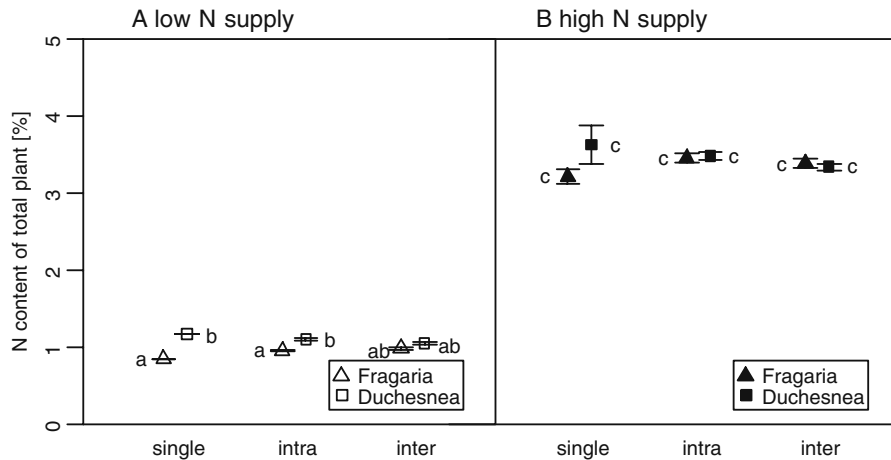
Nitrogen content in plant tissue

The N content in total plant biomass was affected only by N addition. The competition situation had no significant effect. A small but nevertheless significant ($P<0.005$) difference was detected between *Fragaria* and *Duchesnea* plants grown alone in a pot and in

Fig. 2 Root dry biomass per plant of *Fragaria* and *Duchesnea* grown at low N (**A**) and high N (**B**) supply under different levels of competition: *single* no competition, *intra* intraspecific competition, *inter* interspecific competition. Values are means ± standard errors ($n_{single}=6$, $n_{intra}=24$, $n_{inter}=12$). Different *lower case letters* denote significant differences among species and N treatments (post hoc, unequal n HSD test, $P<0.05$)

Fig. 3 Total plant N content of *Fragaria* and *Duchesnea* plants grown at low (**A**) and high (**B**) N supply under different levels of competition: *single* no competition, *intra* intraspecific competition, *inter* interspecific competition. Values are means ± standard errors (n_{single}=6, n_{intra}=24, n_{inter}=12). Different *lower case letters* denote significant differences among species and N treatments (post hoc, unequal *n* HSD test, $P<0.05$)
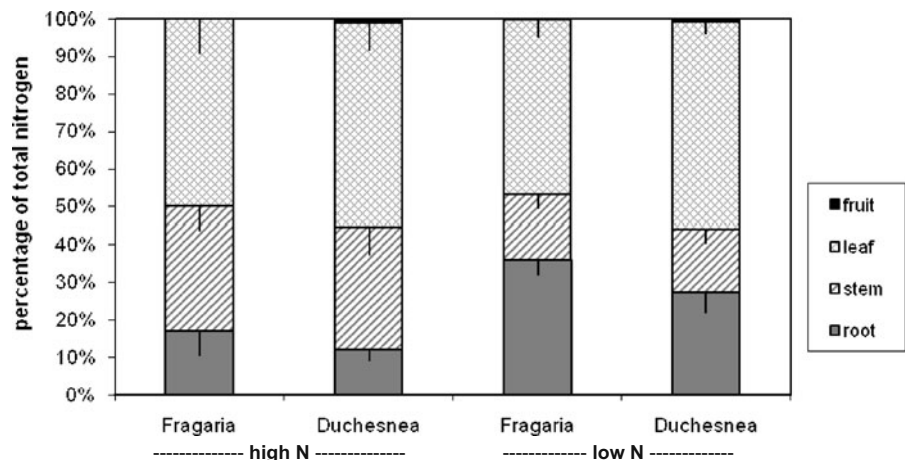
intraspecific competition at low N addition (Fig. 3, Table 1). In these cases *Duchesnea* had slightly more N.
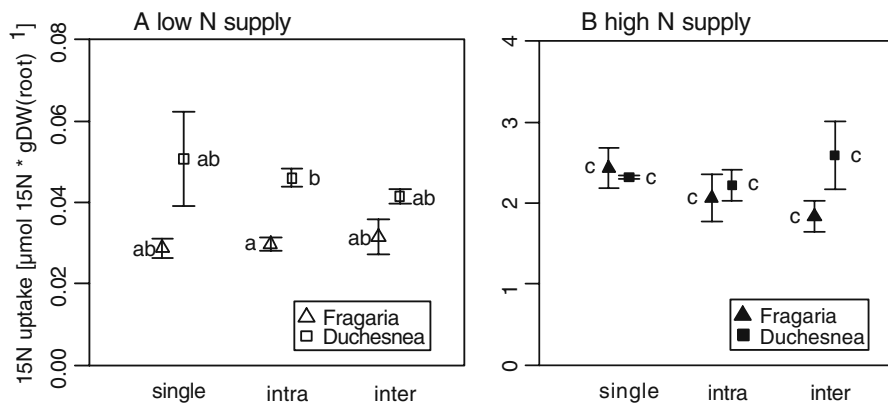
Under all investigated conditions, most N was located in the leaves. That was caused mainly by the much higher leaf biomass compared to roots, rather than by any difference in N content itself (Fig. 4). The N percentage (of the total plant) in the leaves was not correlated with N addition. *Duchesnea* leaves always had a slightly higher leaf N content than *Fragaria*. At low N supply, both species had a larger fraction of the particular total N in the root than in the shoot biomass. *Fragaria* allocated more N to the roots than *Duchesnea*.

Uptake of ^{15}N

The ^{15}N was added with nutrient solution at the time of maximal growth rate. Uptake was correlated with N addition ($P<0.005$, Fig. 5, Table 1): plants that had more available N incorporated more ^{15}N. The uptake rates under high N conditions were relatively equal in both plant species. At low N, however, *Duchesnea* acquired up to two times more ^{15}N than *Fragaria*. These significant differences were greatest between plants grown alone in a pot but were significant only in the case of intraspecific competition ($P=0.002$). *Duchesnea* showed no significant differences between the three competition situations. However, ^{15}N uptake

Fig. 4 Percentage of total N in different plant parts (leaf, shoot, root, fruit) of *Fragaria* and *Duchesnea* grown for 65 days at high and low N supply. Competition situations are not considered because their effect on the N distribution in the plants was not significant (ANOVA: $F_{2, 74}$=0.43, P=0.65). Values are means ± standard deviations (n=17)

Fig. 5 Uptake of ^{15}N [μmol ^{15}N g DW(root)$^{-1}$] of *Fragaria* and *Duchesnea* grown at low (**A**) and high (**B**) N supply and under different levels of competition: *single* no competition, *intra* intraspecific competition, *inter* interspecific competition. Uptake is calculated from the $^{15}N/^{14}N$ atom-% values of the total plant 28 days after ^{15}N application. Values are means ± standard errors ($n_{single/intra}$=2, n_{inter}=3). Note the different scales of the *y*-axes. Different *lower case letters* denote significant differences among species and N treatments (post hoc, unequal *n* HSD test, $P<0.05$)

increased slightly in the order "interspecific competition" < "intraspecific competition" < "single plant".

Discussion

Is there belowground competition for nitrogen between *Fragaria* and *Duchesnea*?

If competition between *Fragaria* and *Duchesnea* for N existed (hypothesis 1), it would be observable as (1) reduced roots or total biomass, (2) less N content in the plant biomass, or (3) reduced N uptake rate of the inferior plant in the presence of the other species.

Total biomass and root biomass of plants grown in interspecific and intraspecific competition did not decrease compared to solitary plants. Plants were affected neither by individuals of the same nor of the other species. Apparently, both species grown in competition could not influence—respectively only to the same strength—each other's N acquisition per unit of root biomass or their ability to build up a significantly higher aboveground biomass. Neither species was visibly affected by its neighbour, either in inter- or in intra-specific competition. These results contradict the findings of Gersani et al. (2001), who claimed that root biomass increases in competitive situations. In our experiment, N supply was probably sufficient for all plants, and production of additional roots was not required or all had the same nutrient deficit but do not invest in additional roots. Another

possible root reaction, namely reduced root growth due to the presence of neighbours (Maina et al. 2002), did not occur either. Our experiment therefore clearly shows that, for these two species, root growth rate is not restricted to competition but only to limited pot space or nitrogen availability. Because in our design, each plant—independently whether grown without competition or together with three neighbours (inter- or intra-specific competition)—had the same soil volume per individual plant and theoretically the same amount of nutrients available, we could separate nutrient and pot effects from competition effects. Naturally, the results may have differed if we had chosen another plant density in the competition pots. Our results that *Fragaria* roots are not affected by *Duchesnea* roots agreed with a root elongation experiment by Semchenko et al. (2007). Roots of *Fragaria vesca* grown in competition with *Glechoma hederacea* did not prefer a growth direction away from the neighbour roots. This implies that *Fragaria* or *Duchesnea* roots were not affected by nutrient depletion or any allelopathic reactions by other roots. Furthermore, the N content of the total plants and the ^{15}N uptake rate were not affected by competition.

The two species showed no 'effect on resources' (sensu Goldberg 1990) on the other species. They depleted the N for neighbour plants at the same rate as plants of the same species. The result of a previous competition experiment with *Fragaria* and *Duchesnea* at the Ecological-Botanical Garden of the University of Bayreuth showed certain competition effects. When

competing, both species showed only 25–30% of the total biomass of plants grown alone (Nepple 2003). The difference between these two investigations could be explained by the different growth conditions of the control plants. The separately grown plants in Nepple's (2003) open field experiment could—in contrast to our experiment—occupy unlimited soil space. Accordingly, the plants had more soil volume and more nutrients than plants grown in competition. This was avoided in our experimental design. Nonetheless, the small pot size could lead to limited growth. Biomass production is affected by pot size if all other factors, e.g. nutrient and water availability, are equal (McConnaughay and Bazzaz 1991).

The low N supply did not change the competitive behaviour of either plant. This supports Murphy and Dudley (2007), who found no interactions between root competition and nutrient levels and concluded that belowground competition does not depend on nutrient availability. In contrast, Weiner et al. (1997) claimed that root competition is more important in nutrient-poor soils.

Species-dependent biomass production

In the field experiment of Nepple (2003), *Duchesnea* always had nearly twice as much biomass as *Fragaria* even under competition conditions. This suggests that *Duchesnea* is able to build more biomass both at high N addition and under competition (hypothesis 2).

Our data support the findings of Nepple, i.e. that *Duchesnea* can build up more biomass than *Fragaria* if sufficient N is available. As the portion of biomass allocated to the leaf was larger at high N, more of the plant's total N was located in the leaves than at low N supply. Nevertheless, *Duchesnea* had a larger percentage of its N in the leaves, with *Fragaria* having a larger percentage in the roots. This higher leaf N might enable *Duchesnea* to promote photosynthesis (Schilling 2000). This suggestion was evident in the slightly deeper green of *Duchesnea* leaves compared to *Fragaria* leaves. In competition for light and space with other plants, the higher aboveground biomass could be an advantage for *Duchesnea* on N-rich soils. This is supported by the preferential occurrence of *Duchesnea* on relatively fertile soils, for example in Baden-Württemberg, SW-Germany (Breunig 2006). Increasing soil N contents due to anthropogenic N deposition might promote the competitive ability of *Duchesnea*.

At low N availability, *Duchesnea* lost the competitive advantage of higher shoot biomass. The differential loss between the two N levels, which is visible in the total biomass data of *Fragaria* and *Duchesnea*, can be attributed to *Fragaria*'s greater root growth at low N. *Duchesnea*'s root biomass was similar to that of *Fragaria* at high N. But while *Fragaria* developed more roots and allocated more N to these roots at lower N, *Duchesnea* did not. Therefore low soil N sustains the native *Fragaria*'s position and, in general, low N increased the competitive ability of the native relative to the invasive species (Kolb et al. 2002). N transport to the leaves (to increase aboveground competitive ability), as realised in *Duchesnea*, would be quite an effective mechanism leading to a competitive advantage, but only if sufficient N is available.

Nitrogen uptake

Although competition between the two species was not affected by N supply, all *Fragaria* and *Duchesnea* individuals showed the expected increase in biomass in response to nutrient availability. Plants at high N had higher biomass, higher N content in plant tissues and dark green leaves. We explain the higher aboveground biomass of *Duchesnea* by its ability to take up and utilise N more effectively than *Fragaria* at high and low N supply (hypothesis 3).

The N content of total plant biomass did not differ significantly between *Fragaria* and *Duchesnea*, although it was a little higher in the latter. Given that *Duchesnea* had less root mass to absorb N in the low N pots, it can take up nutrients more effectively than *Fragaria*. The N uptake per gram root dry weight was still twice as high as that of *Fragaria* at low N supply. The higher uptake actually implies a larger absorbing surface, e.g. more root hairs and/or finely branching roots, a smaller root diameter, higher carbon allocation rates to roots, or high longevity These are the common root traits profitable for plants (Craine 2005), which could enable *Duchesnea* to take up the same amount of N as *Fragaria* despite smaller root mass at low N supply. Thus, further studies should focus on the root anatomy of these two plant species. Adaptations of species-related root plasma transporters to the N source (Kronzucker et al. 1997, 2003) could also change the results if other N forms were offered. Thus, the presence of ammonium can

influence the uptake of nitrate and vice versa (Kamminga-van Wijk and Prins 1993). *Duchesnea* apparently lacks morphological root plasticity (root growth due to soil and plant conditions) but, for the uptake of the mobile nitrate ion, physiological plasticity (a higher uptake capacity or a higher ion affinity) is more important (Hodge 2004). Another reason for the equal shoot biomass despite the differing root biomass could be that the excess of roots does not help *Fragaria* to obtain more N, i.e. the new roots cannot reach other, new N sources any more effectively than the 'old' roots. The higher shoot-root-ratio of *Duchesnea* versus *Fragaria* could also indicate greater ability in acquiring and utilising nutrients. While having a higher S/R-ratio in the high N treatment, *Duchesnea*'s S/R-ratio was equal to that of *Fragaria* in the low N treatment. This reflected the lower shoot biomass of *Duchesnea* at low N. Thus, *Duchesnea* apparently needs fewer roots to build up a larger aboveground biomass. This promotes its competitiveness in high-N soils. Although the difference in total biomass between low and high N was somewhat larger for *Duchesnea*, it can accommodate having fewer roots at low N because the N content is similar to that of *Fragaria*.

Conclusions

The investigation of competition between native *Fragaria vesca* and invasive *Duchesnea indica* showed that neither species can impact the other directly (no effect of direct competition was detected). Nonetheless, *Duchesnea indica* apparently had an advantage based on its higher aboveground biomass in high-N soils. This advantage disappeared in low-N soil. We therefore conclude that the invasive form will grow preferentially on soils with high N supply and will benefit from increasing anthropogenic N deposition.

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