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Growth rates of rhizosphere microorganisms depend on competitive abilities of plants and N supply

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Abstract

Plant-microbial interactions under N-limiting conditions are governed by competitive abilities of plants for N. Our study aimed to examine how two plant species of strawberry, *Fragaria vesca* L. (native species) and *Duchesnea indica* (Andrews) Focke (an invasive plant in central Europe), growing in intra-specific and inter-specific competition alter the functions of rhizosphere microorganisms in dependence on N availability. By intra-specific competition at low N level, a 2.4-fold slower microbial-specific growth rate was observed under *D. indica* characterized by smaller root biomass and lower N content in roots compared with *F. vesca*. By inter-specific competition of both plants at low N level, microbial growth rates were similar to those for *D. indica* indicating that plants with stronger competitive abilities for N controls microbial community in the rhizosphere. Since a high N level smoothed the differences between plant species in root and microbial biomass as well as in microbial growth rates under both intra-specific and inter-specific competition, we conclude that competitive abilities of plant species were crucial for microbial growth in the rhizosphere only under N imitation.

Keywords: *Plant-microbial interactions, r- and K-strategies, N limitation, rhizosphere*

Introduction

Rhizosphere – one of the most important "hot spots" in soil – is characterized not only by accelerated turnover of microbial biomass and nutrients (Nannipieri et al. 2003) but also by strong intra- and inter-specific competition. Plant–microbial interactions are mainly governed by competition for available N sources, since N is one of the main growth-limiting nutrients in natural ecosystems (Vitousek & Howarth 1991). Functional structure and activity of microbial community in the rhizosphere are mediated by the quantity and quality of root exudates (Bolton et al. 1992; Grayston et al. 1998) which are plant specific. It is found that during a prolonged period, grassland plants are able to compete effectively with soil microorganisms for N (Harrison et al. 2008), but it is still unclear how plants with various competitive abilities alter the functions of rhizosphere microorganisms and competition for N. It is clearly shown by molecular approaches that plant species and even individual plants are responsible for the composition of rhizosphere microbial community (Hartmann et al. 2009). Since plants with a higher shoot-to-root ratio usually produce fewer amounts of root exudates, we hypothesized slower microbial growth rates in the rhizosphere of plants with smaller root biomass. We further hypothesized the greater effect of N availability on microbial growth in rhizosphere of plants with high competitive abilities, since strong N limitation can occur for microorganisms in the rhizosphere of such plants.

The aim of this study was to examine how plant species with different strategies affect the growth of rhizosphere microorganisms: (1) by intra-specific and inter-specific plants competition; and (2) as dependent on N availability.

Materials and methods

Two species of strawberry which have a similar growth strategy and biology but different

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competitive abilities for N: *Fragaria vesca* L. ("space capturing" native species) and *Duchesnea indica* (Andrews) Focke ("space occupation" species, an invasive plant in central Europe) were grown in microcosms with a volume of 310 cm^3 in a temperature-controlled greenhouse. Each microcosm was filled with a 50:50 mixture of slightly loamy soil and quartz sand to decrease N availability of the soil. Prior to potting, soil was passed through a 5 mm sieve and watered to field capacity. The chosen pot size ensured that the roots would be able to fill the whole space to get in competition during the 65 days of growth. A two-factorial experiment was established. The first factor was the plant species competition. Fifteen-day-old seedlings of each species were put in microcosms (1) as four plants of the same species – intra-specific competition, or (2) as 2 × 2 plants (2 *D. indica* × 2 *F. vesca*) – inter-specific competition. The second factor was N availability. For the "high N" treatment, 20 ml of solution with concentration 42 mM l^{-1} KNO_3 and 9 mM l^{-1} $Ca(NO_3)_2$ was added three times a week. For the "low N" treatment, the added amount of N was reduced by the factor of 100. Microcosms were set up to provide three replicates for each competition and each N treatment, yielding a total of 18 microcosms. Thirty-three days after planting, a stable isotope labeled ^{15}N nutrient solution of the same nutrient composition like above, but containing 2.2% $^{15}NO_3^-$ (high N solution) and 21.2% $^{15}NO_3^-$ (low N solution) of the total NO_3^- concentration of the nutrient solution. At the end of the experiment, the plants were cut, washed, separated in leaves, shoots, roots, and stolons, dried at 60°C in an oven for three days, weighted, and ground. The relative abundance of ^{15}N and total N content in the plant material was analyzed by C–N analyzer (CE Instruments, Milano, Italy) coupled with a ConFlo III (Finnigan MAT, Bremen, Germany) to an isotope ratio mass-spectrometer Delta S (IRMS-a NA 1108, Finnigan MAT).

Microbial biomass and the kinetic parameters of microbial growth in the rhizosphere were estimated by dynamics of CO_2 emission from the soil amended with glucose and nutrients (Blagodatsky et al. 2000). Ten grams (dry weight) of soil was amended with a powder-mixture containing glucose (10 mg g^{-1}), talcum (20 mg g^{-1}), and mineral salts: $(NH_4)_2SO_4$ – 1.9 mg g^{-1}, K_2HPO_4 – 2.25 mg g^{-1}, and $MgSO_4 \cdot 7H_2O$ – 3.8 mg g^{-1}, and the CO_2 production rate was measured hourly at 22°C using an automated infrared-gas analyzer system.

Soil microbial biomass-C was determined using the initial rate of substrate-induced respiration and recalculated according to the equation by Anderson and Domsch (1978):

$$\text{biomass} - \text{C}\ (\mu\text{g g}^{-1}\ \text{soil}) = (\mu l\ \ \text{CO}_2\ g^{-1}\, soil\ \ h^{-1}) \times 30 \qquad (1)$$

where 30 is the constant reflecting the microbial biomass-to-CO_2 production ratio that was obtained from the linear regression equation for a broad range of soils (Kaiser et al. 1992).

Specific growth rate (μ) of soil microorganisms was estimated by fitting the parameters of the equation:

$$\text{CO}_2(t) = A + B \times \exp(\mu \times t) \qquad (2)$$

to the measured CO_2 production rate ($CO_2[t]$) after glucose addition, where A is the initial respiration rate uncoupled from ATP production, B the initial rate of the growing fraction of total respiration coupled with ATP generation and cell growth, and t time (Blagodatsky et al. 2000).

Statistics

The experiment was conducted with three replicates for every treatment. Standard errors (SE) for plant characteristics and standard deviations (SD) for CO_2 dynamics, microbial biomass, and microbial-specific growth rates were calculated as a variability parameter. The significant effects of soil treatments were assessed by one-way ANOVA at $P < 0.05$.

Results

Plant species-specific competition

High levels of N availability caused mainly the increase in total plant biomass (Table I) while root mass was reduced in most of the treatments at high N (Table I). This resulted in a higher shoot-to-root ratio at high versus low N amendment for both plant species at intra- and inter-specific competition (Table I). By intra-specific competition, the N content in the roots was higher for *F. vesca* as compared with *D. indica* at both levels of N availability (Table I). Intra- or inter-specific competition did not affect the N distribution in the plants (data are not shown).

Low N availability. Under N-limiting conditions, the total biomass of both plant species was similar (Table I). Smaller root biomass of *D. indica* as compared with *F. vesca* (Table I) caused a higher shoot-to-root ratio for *D. indica* (Table I). *D. indica* was characterized by faster ^{15}N-uptake rate than *F. vesca* (Table I).

High N availability. As compared to *F. vesca*, *D. indica* had significantly higher total plant biomass by

Table I. Characteristics of plants *F. vesca* and *D. indica* grown for 65 days at low and high N supply under intra- and inter-specific competition.

	Intra-specific competition				Inter-specific competition			
	F. vesca		*D. indica*		*F. vesca*		*D. indica*	
Plant characteristics	Low N	High N	Low N	High N	Low N	High N	Low N	High N
Total plant mass, g	0.73 ± 0.05	0.79 ± 0.05	0.70 ± 0.04	1.11 ± 0.05	0.71 ± 0.06	0.93 ± 0.09	0.60 ± 0.03	1.0 ± 0.07
Root mass, g	0.29 ± 0.03	0.19 ± 0.01	0.22 ± 0.01	0.21 ± 0.01	0.27 ± 0.03	0.20 ± 0.02	0.19 ± 0.01	0.14 ± 0.02
Shoot-to-root ratio	1.7 ± 0.1	3.4 ± 0.2	2.2 ± 0.1	4.7 ± 0.3	1.8 ± 0.1	3.6 ± 0.3	2.3 ± 0.2	6.3 ± 0.8
N contribution to the roots, as % of total N	35.0 ± 1.5	18.0 ± 2.0	28.0 ± 2.0	12.0 ± 1.0	nc[a]	nc	nc	nc
^{15}N-uptake rate, nM g^{-1} day^{-1}	1.06 ± 0.06	73.6 ± 10.5	1.64 ± 0.08	79.3 ± 6.7	1.12 ± 0.15	65.4 ± 6.8	1.48 ± 0.06	92.5 ± 14.8

[a] nc – competition situations were not considered because they did not have an effect on the N distribution in the plants. Values are means ± standard errors.

intra-specific competition (Table I) while it had smaller root mass and faster N-uptake rate in inter-specific competition (Table I). The shoot-to-root ratio was always higher for *D. indica* versus *F. vesca* both in intra- and inter-specific competition (Table I).

Microbial competition

Microbial biomass. Under N-limiting conditions, microbial biomass in the rhizosphere of *F. vesca* was 13% lower than under *D. indica* (Figure 1). By inter-specific competition of both plants, microbial biomass was also significantly lower as compared with single species of *D. indica.* High levels of N smoothed these differences: microbial biomass under plants with intra- or inter-specific competition was nearly the same.

Microbial respiratory response and specific growth rates. Under N limitation, the microbial respiratory curves in the rhizosphere of *F. vesca* were steeper than under *D. indica* (Figure 2A). It means that microorganisms in the rhizosphere of *F. vesca* have higher growth rates. At high N availability, however, the patterns of respiratory response of rhizosphere microorganisms of both individual plant species were similar (Figure 2B). At N limitation, the specific microbial growth rates were 2.4-fold lower in rhizosphere of *D. indica* than of *F. vesca* (Figure 3). Microbial growth rates for the inter-specific

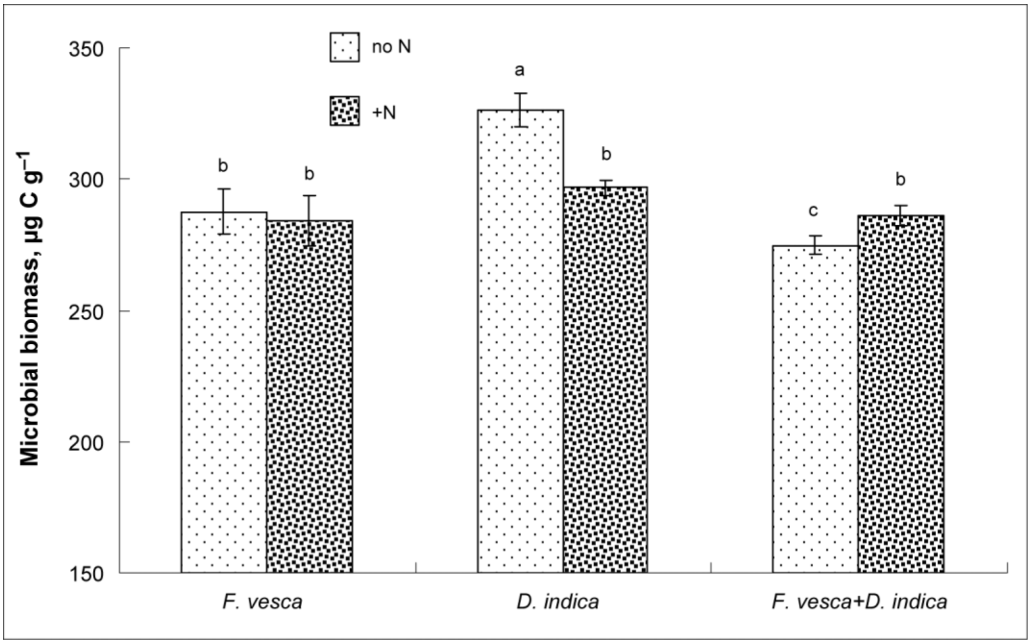

Figure 1. Microbial biomass in the rhizosphere of *F. vesca* and *D. indica* grown at low and high N supply under intra- and inter-specific competition. Bars represent standard deviations of means ($n = 3$). Values with the same letter are not significantly ($P < 0.05$) different.

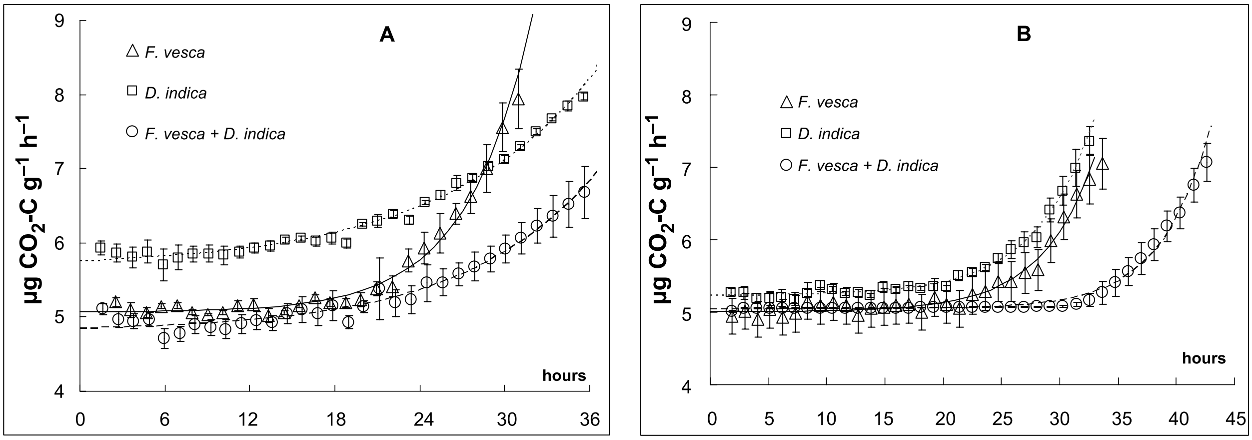

Figure 2. Kinetics of microbial respiration in the rhizosphere of *F. vesca* and *D. indica* growing under intra- and inter-specific competition at low (A) and at high (B) levels of nitrogen. Bars represent standard deviations of means ($n = 3$).

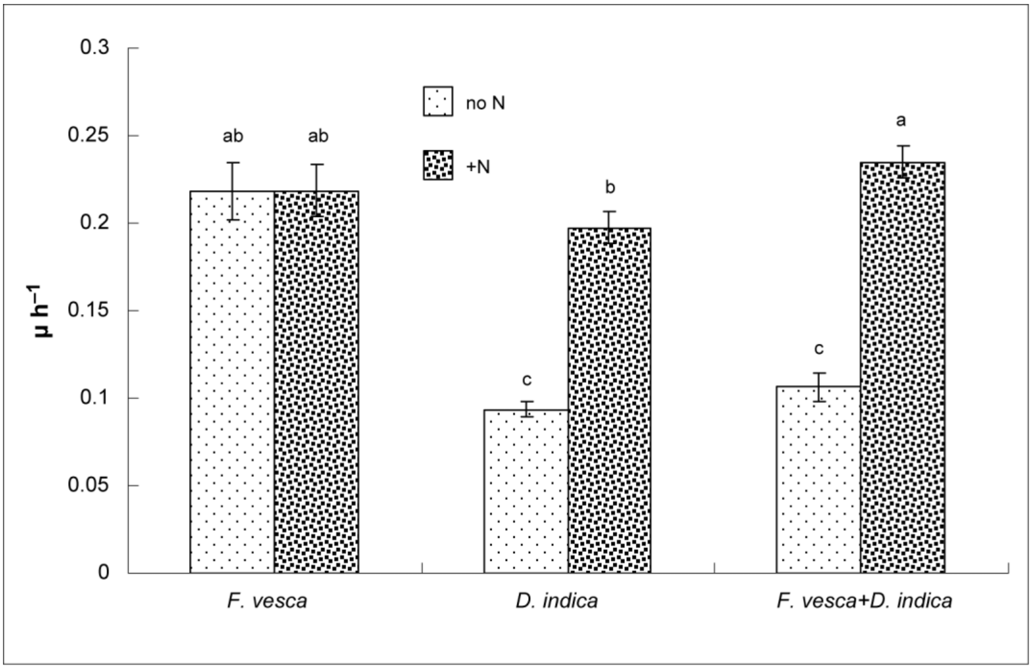

Figure 3. Microbial-specific growth rates (μ) in the rhizosphere of *F. vesca* and *D. indica* growing under intra- and inter-specific competition at low and at high nitrogen level. Bars represent standard deviations of means ($n = 3$). Values with the same letter are not significantly ($P < 0.05$) different.

competition of both plants were similar to those for *D. indica*. High N availability had no effect on microbial growth in the rhizosphere of *F. vesca* (Figure 3). However, specific growth rates of rhizosphere microorganisms of *D. indica* strongly increased at high as compared to low level of N amendment. Again, N fertilization eliminated all significant differences in microbial-specific growth rates for plants grown in intra- and inter-specific competition (Figure 3).

Discussion

Our study revealed faster N uptake, smaller root biomass, lower N content in roots, and greater shoot-to-root ratio for *D. indica* versus *F. vesca* (Littschwager et al. 2010). This allowed us to conclude that *D. indica* is a stronger competitor for N than *F. vesca*. At high N availability, the root biomass of both plants was similar while higher total plant biomass of *D. indica* than those of *F. vesca* was observed. Thus, in the absence of N limitation, *D. indica* benefited in the competition with *F. vesca* allocating more nutrients in shoot biomass. Such competition, however, did not affect microbial communities in rhizosphere of both plants because N was not limiting.

When N was limited, the total biomass of *D. indica* decreased sharply while root mass did not change significantly in comparison with the high level of N amendment. Contrary to that, N limitation did not alter total biomass of *F. vesca*, while a 1.5 increase in root mass was observed at low versus high N level (Table I). This may be indicative of the different species-specific mechanisms of plant-microbial interactions under N limitation. The competitive strategy of *D. indica* strengthened the N limitation in rhizosphere at low N causing the shift in functional structure of microbial community with domination of slow-growing microorganisms which are usually classified as K-strategists according to common ecological concepts (Andrews & Harris 1986; Blagodatskaya et al. 2007). So, our study revealed the intriguing situation when the retardation of microbial growth rates occurred in the rhizosphere of some plant species at low N availability. Since microorganisms are known to compete more effectively than plant roots for organic and inorganic N in soil (Hodge et al. 2000; Harrison et al. 2008; Xu et al. 2008), the retardation of microbial growth may indicate the microbial strategy benefiting under N-limiting conditions. Despite slow development, K-strategists are characterized by more efficient growth and by higher competitive abilities than r-strategists under nutrients limitation. Thus, the switch from r- to K-strategy can serve for rhizosphere microorganisms as the mechanism of adaptation to N limitation. Weaker fine root development of *D. indica* versus *F. vesca* at low N level caused the lack of root exudates, which are easily available for microorganisms. Slow-growing microorganisms with K-strategy were better adapted to N limitation in the rhizosphere of *D. indica*. The adaptation strategy of *F. vesca* to N limitation revealed itself as an increase in growth of fine roots. Better fine root proliferation corresponding to higher amounts of root exudates resulted in benefiting fast-growing microorganisms with r-strategy and thus in faster microbial turnover in the rhizosphere of *F. vesca* as compared with *D. indica*.

Our observations further confirmed the evidence that some plant species increase their root exudation under conditions of higher N competition (Lemaire & Millard 1999; Kuzyakov et al. 2001; Raynaud et al. 2008). Higher availability of root exudates favors the fast-growing microorganisms with an r-strategy (Blagodatskaya et al. 2009). This demonstrates the plant potential to modify microbial competition for N at the species level (Harrison et al. 2008) selecting for specific microbial communities by altering the quantity and quality of root exudates (Bardgett et al. 2003; Zak et al. 2003).

Since high N level smoothed the differences between plant species in root and microbial biomass as well as in microbial growth rates, we conclude that competitive abilities of plant species were responsible for microbial growth in rhizosphere only under N imitation. As it is common that fine root proliferation and root exudation decrease at high N level, N addition smoothed the differences in microbial growth independently on plant competitive abilities.

Conclusions

Our study revealed the linkage between growth strategies of rhizosphere microorganisms and different adaptation strategies of *F. vesca* and *D. indica* to N limitation:

(1) Root biomass of the plant with weak competitive abilities for N (*F. vesca*) increased under N limitation. This increase in root biomass and possible increase in the amount of root exudates coincided with no structural changes in microbial community in rhizosphere of *F. vesca*.
(2) Plants which are strong competitors for N (*D. indica*) did not change root mass under N limitation causing the deficit of N in the rhizosphere and altering the functional structure of rhizosphere microbial community. Benefiting of slow-growing microorganisms with K-strategy under N-limiting conditions was indicated by strong decrease in specific microbial growth rates in the rhizosphere of *D. indica*.
(3) By intra-specific competition under N limitation, the plant-microbial interactions were governed by plant competitive ability for N. This manifested as no change (*F. vesca*) or as a decrease (*D. indica)* in microbial growth rates and carbon turnover in the rhizosphere.
(4) By inter-specific competition at low N level, microbial growth in the rhizosphere was governed by plant with stronger competitive abilities for N. N addition smoothed the differences in growth strategies of rhizosphere microbial community independently on species-specific plant competitive abilities.

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