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REGULAR ARTICLE

Light affects competition for inorganic and organic nitrogen between maize and rhizosphere microorganisms

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Abstract Effects of light on the short term competition for organic and inorganic nitrogen between maize and rhizosphere microorganisms were investigated using a mixture of amino acid, ammonium and nitrate under controlled conditions. The amount and forms of N added in the three treatments was identical, but only one of the three N forms was labeled with ^{15}N. Glycine was additionally labeled with ^{14}C to prove its uptake by maize and incorporation into microbial biomass in an intact form. Maize out-competed microorganisms for $^{15}NO_3^-$ during the whole experiment under low and high light intensity. Microbial uptake of ^{15}N and ^{14}C was not directly influenced by the light intensity, but was indirectly related to the impact the light intensity had on the plant. More $^{15}NH_4^+$ was recovered in microbial biomass than in plants in the initial 4 h under the two light intensities, although more ^{15}N-glycine was incorporated into microbial biomass than in plants in the initial 4 h under low light intensity. Light had a significant effect on $^{15}NO_3^-$ uptake by maize, but no significant effects on the uptake of $^{15}NH_4^+$ or ^{15}N-glycine. High light intensity significantly increased plant uptake of $^{15}NO_3^-$ and glycine ^{14}C. Based on ^{14}C to ^{15}N recovery ratios of plants, intact glycine contributed at least 13% to glycine-derived nitrogen 4 h after

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tracer additions, but it contributed only 0.5% to total nitrogen uptake. These findings suggest that light intensity alters the competitive relationship between maize roots and rhizosphere microorganisms and that C4 cereals such as maize are able to access small amounts of intact glycine. We conclude that roots were stronger competitor than microorganisms for inorganic N, but microorganisms out competed plants during a short period for organic N, which was mineralized into inorganic N within a few hours of application to the soil and was thereafter available for root uptake.

Keywords Competition · Light · Inorganic nitrogen · Organic nitrogen · Soil microorganisms · Maize · ^{14}C · ^{15}N · Rhizosphere

Introduction

Nutrients, light and water availability are the most important factors controlling primary production in terrestrial ecosystems (Grime 1979; Tilman 1988; Vitousek and Howarth 1991; Olff et al. 1993; Aerts and Chapin 2000). In order to test the resource competition theory which uses a minimum concentration (R^*) of a limiting resource to predict the competitive outcome (Tilman 1982), attention has been paid to the competition for nutrients and light between plant species (De Montard et al. 1999; Schippers and Kropff 2001; Passarge et al. 2006, Miller et al. 2007).

A growing number of studies have shown that a variety of terrestrial plants have the capacity to take up intact organic N in the form of low molecular-weight substances (Melin and Nilsson 1953; Chapin et al. 1993; Kielland 1994; Schimel and Chapin 1996; Lipson and Monson 1998; Näsholm et al. 1998; Persson et al. 2003; Xu et al. 2004). It has been suggested that organic N serves as an important N source for plants in ecosystems with low inorganic N status (Chapin et al. 1993; Kielland 1994; Schimel and Chapin 1996; Henry and Jefferies 2003; Xu et al. 2006). Consequently, a large number of studies have focused on the comparison of inorganic and organic N acquisition by plants in a wide variety of terrestrial ecosystems. While some studies showed lower uptake rates of organic N than of inorganic N (Henry and Jefferies 2003), others demonstrated that many plants are able to take up organic N at similar rates or faster than inorganic N (Henry and Jefferies 2003; Cheng and Bledsoe 2004; Thornton and Robinson 2005; Weigelt et al. 2005). It has also been shown that inorganic and organic N uptake by plants is influenced by temperature (Thornton and Robinson 2005) and plant species (Weigelt et al. 2005; Miller et al. 2007). However, plants compete for N not only with other plants, but also with microorganisms in the rhizosphere (Kaye and Hart 1997). Hence, competition for inorganic and organic N between plants and soil microorganisms has been explored under both field and controlled conditions. Although it has been suggested that soil microorganisms compete well with plants for organic and inorganic N inputs (Bardgett et al. 2003; Cheng and Bledsoe 2004), some plant species showed a better capacity to acquire inorganic N (Jaeger et al. 1999) and organic N (Lipson and Monson 1998; Lipson et al. 1999) in the face of microbial competition.

As another important environmental factor, light has been suggested to mediate plant growth, e.g., Strengbom et al. (2004) have recently shown that light not nitrogen limits the growth of a grass species in boreal forests. Baligar et al. (2006) have reported that light intensity affects growth and nutrient uptake by legume cover crops. This implies that light affects the accumulation of organic matter and biomass via photosynthesis. Hence, light management has been considered as an effective approach in agroecosystems (Holt 1995). Light quantity and quality have an obvious role in plant biomass production however little is known about the effects on microbial competition for soil nutrients although inorganic N uptake by agricultural crops has been extensively studied (Mengel and Kirkby 1987; Haynes 1986; Loomis and Connor 1992). Due to the large quantities of inorganic N fertilizers that are applied to obtain high crop yields the importance of organic N may be insignificant for crops under conventional agriculture. Despite this, a growing body of evidence shows that some agricultural plant species are able to take up organic N in the form of amino acids under artificial conditions (Virtanen and Linkola 1946; Shobert and Komor 1987; Jones and Darrah 1994; Okamoto and Okada 2004), as well as under field conditions (Yamagata and Ae 1999; Matsumoto et al. 2000; Näsholm et al. 2000, 2001).

Maize (*Zea mays* L.) is the third most important crop globally, after wheat and rice (FAO 2000). Many studies have been conducted to improve the under-

standing of inorganic and organic N utilization by maize, e.g., it has been suggested that light regulates nitrate reductase in green leaves of maize (Beevers et al. 1965; Lillo 1994; Raghuram et al. 1999). Meanwhile, Meshram and Shende (1982) reported that *Azotobacter* inoculation enhances total N uptake by maize, while Schortemeyer et al. (1993) using hydroponics showed that mixed ammonium and nitrate nutrition is beneficial to maize growth. Moreover, it has been shown that maize can take up N from ^{15}N labeled biomass of *Paraserianthes facataria* (Chintu and Zaharah 2003). Okamoto and Okada (2004) showed that maize roots have a lower capacity to take up protein N than sorghum and rice. The literature suggests that maize has the capacity to take up nitrate, ammonium and organic N which is corroborated by the evidence that transporters for nitrate, ammonium and amino acids are present in maize roots (Miller and Cramer 2004). However, up to date little is known about the effects of light on the competition for inorganic and organic N between maize and rhizosphere microorganisms especially in an environment with high N status.

Therefore, the objectives of this study were to (1) determine if maize is able to access organic N in an inorganic N enriched environment, (2) compare organic and inorganic N uptake by maize, and (3) test if light affects the competition for organic and inorganic N between maize and soil microorganisms.

Materials and methods

Soil

Soil material was collected from the Ap horizon of a loamy Haplic Luvisol (long-term field experimental station Karlshof of Hohenheim University; 48°42′ 44.37″ N, 9°11′24.72″ E). The soil originated from loess, contained no $CaCO_3$, and had the following characteristics: pH 6.0, organic C 1.2%, total N 0.13%, clay 23%, silt 73%, and sand 4.4%. The soil was air-dried and sieved through a 2-mm screen before the experiment.

Experimental layout

Pots (10 cm in height, 5 cm in diameter) were filled with 50 g air-dried soil. Single maize (*Z. mays* L.) seedlings of similar size were planted into them two days after germination. The plants were grown in a growth chamber for 21 days, set to a 14 h daytime period, light intensity 800 µmol m^{-2} s^{-1}, with daytime and nighttime temperature of 27±1°C and 22±1°C. Soil moisture was maintained at 30% of soil dry weight by watering to weight daily. All treatments were supplied with 10 ml 0.2 mmol l^{-1} NH_4NO_3 solution per pot two weeks after planting, equal to 56 µg N g^{-1} soil. Three weeks after planting treatments were imposed, a mixture of glycine, NH_4^+, and NO_3^- $\left(1:1:1\ N-\text{glycine}/N-NH_4^+/N-NO_3^-\right)$ was injected into the soil, equal to 19 µg N g^{-1} soil. In each of the three treatments only one of the three N forms was labeled with ^{15}N (98.2% ^{15}N enrichment for $^{15}NO_3^-$, 98.4% enrichment for $^{15}NH_4^+$, and 95.0% enrichment for glycine). Uniformly labeled ^{14}C glycine was applied at 0.90 kBq per pot (equivalent to 0.90 kBq per plant) to allow determination of intact organic N uptake over the experimental period as ^{15}N-labeled amino acids cannot represent actual intact amino acid uptake over long-term periods. Plants which were not injected with a N tracer were supplied with equivalent amounts of water and were taken as controls. After fertilizer injection plants were immediately divided into two groups: one group was maintained under the same light conditions (high light intensity), the other group was subject to shading by reducing light levels to 10% of the incoming light (low light intensity). Therefore, a two factor design was construed: the first factor was N form with three treatments: ^{15}N in NO_3^-, NH_4^+ or glycine; and the second factor was light intensity with two levels, 800 and 80 µmol m^{-2} s^{-1}, during daytime. Three replicates were collected from each treatment and at each sampling time.

Sampling and analyses

Three individual pots from each treatment were randomly destructively sampled at 4, 24 and 48 h after tracer additions. The roots were carefully removed from the soil and quickly rinsed with water, then soaked in 0.5 mmol l^{-1} $CaCl_2$ solution for 30 mins, and again rinsed with distilled water. The roots and leaves were microwaved for 90 s, 600 W, and dried at 60°C for 48 h. Dried samples were weighed and ground to a fine powder using a ball mill (MM2, Fa Retsch).

^{15}N incorporation into microbial biomass was determined by chloroform fumigation (Brookes et al. 1985)–15 g fresh soil was fumigated with chloroform for 24 h and then immediately extracted with 60 ml 0.5 M K_2SO_4. An additional soil sample (15 g) was extracted without fumigation. This extract was used for determination of ammonium and nitrate concentration. Total dissolved N in extracts was converted to nitrate by a modified alkaline persulfate digestion method (Sollins et al. 1999). Nitrate concentrations and isotope ratios in extracts and persulfate digests were analysed by SpinMas system (Stange et al. 2007). In the SpinMas system nitrate in the aqueous samples (up to 10 ml) was reduced to NO with V(III) Cl_3 solution (Merck, Darmstadt, Germany) in acidic medium (HCl; Merck, Darmstadt, Germany) $\left(NO_3^- + 3V^{3+} + 4H^+ \rightarrow NO + 3V^{4+} + 2H_2O\right)$. The NO gas produced was transferred in a permanent He carrier stream (10 ml min^{-1}, Linde, Germany) from the vial via an open split to the inlet capillary of the quadrupole mass spectrometer (GAM 400, InProcess Instruments GmbH, Bremen, Germany). Water and CO_2 were removed by a cryo trap (−100°C). For nitric oxide the ion currents [*I*] at *m/z* 30 and 31 were measured allowing the calculation of the ^{15}N abundance of the NO_3^-. A correction was made for the presence of naturally abundant ^{17}O (0.037 at.%). Ammonium concentrations and isotope ratios were also quantified by SpinMas based on the chemical conversion of NH_4^+ to N_2 i.e. oxidation by NaOBr solution in alkaline medium (Stange et al. 2007). Gross N mineralization and nitrification rates were measured by ^{15}N pool dilution technique. Dissolved organic C (DOC) in extracts was measured by a Dimatoc automatic analyzer (Dimatec Essen, Germany).

For ^{14}C analyses, plant samples (50 mg) were combusted in an oxidizer (Model 307, Canberra Packard Ltd., USA). $^{14}CO_2$ was trapped in Carbo-Sorb E (Perkin Elmer Inc., USA) and scintillation cocktail (Permafluor E^+, Perkin Elmer Inc., USA). ^{14}C activities in these samples were then measured by liquid scintillation counting (Rackbeta, 1419 LKB, Wallac). Dry ground plant samples were weighed (2 mg) into tin cups for elemental N and ^{15}N analysis, which was performed by continuous-flow gas isotope ratio mass spectrometry (CF-IRMS). The CF-IRMS system consisted of an elemental analyser (EA 1110, CE Instruments, Milan, Italy), a ConFlo II interface (Finnigan MAT, Bremen, Germany) and a gas isotope ratio mass spectrometer (Delta^{PLUS}, Finnigan MAT).

Calculation and statistics

^{15}N calculations were based on atom percent excess (APE), calculated as the difference between ^{15}N treated and control plants. ^{15}N recovery in plants ($^{15}NR_{plant}$), as percentage of input, was calculated as the amount of ^{15}N taken up by plants divided by total ^{15}N added per pot. ^{15}N recovery in inorganic pools, as percentage of input, was calculated as the amount of ^{15}N recovered in the nitrate/ammonium pool divided by total ^{15}N added per pot. Because ^{15}N uptake is located in the roots, ^{15}N uptake rates were calculated by dividing total plant ^{15}N at time t by root dry weight in grams. *In situ* uptake rates of the three N forms were calculated as follows: Root NH_4^+/NO_3^- uptake was calculated dividing root $^{15}NH_4^+/^{15}NO_3^-$ uptake by at % ^{15}N in the NH_4^+/NO_3^- pool after 4 h in the NH_4^+/NO_3^- treatment, whereas root glycine uptake was estimated dividing root ^{15}N-glycine uptake by 95.0 at % ^{15}N and multiplying with ratio of ^{14}CR to ^{15}NR of plants. ^{15}N in microbial biomass ($^{15}NR_{MB}$) was calculated as the difference in ^{15}N mass between fumigated and non-fumigated soil samples, divided by total ^{15}N added per pot (Zogg et al. 2000). A K_{EN} factor (0.54) has been used to correct for the incomplete extraction of microbial N in a large number of studies, but the correction factor often varies dependent on the analysis method (Joergensen 1996). In this study the correction factor didn't alter the relationship between plants and soil microorganisms as well as microbial uptake of the three N species (Fig. 6), only changing the value of the microbial ^{15}N uptake. Furthermore, in short-term ^{15}N uptake experiments soluble ^{15}N and insoluble ^{15}N are in disequilibrium and the K_{EN} factor would therefore lead to overestimation of the microbial ^{15}N sink. We therefore did not apply the correction factor to correct microbial ^{15}N uptake. ^{14}C in plants ($^{14}CR_{plant}$) was calculated as the amount of ^{14}C taken up by plants divided by total ^{14}C added per pot. ^{14}C in microbial biomass ($^{14}CR_{MB}$) was calculated as the difference in ^{14}C between fumigated and non-fumigated soil samples, divided by total ^{14}C added per pot. ^{14}C recovery in dissolved organic matter (DOM, $^{14}CR_{DOM}$) was calculated as the ^{14}C amount recovered in extracts of unfumigated soil samples

divided by total added ^{14}C. Gross mineralization and nitrification rates were calculated based on the ^{15}N pool dilution approach using the equations developed by Kirkham and Bartholomew (1954).

Repeated measures analysis of variance was used to test for the effects of ^{15}N form added, light, time and their interactions on ^{15}N uptake by plants and by soil microorganisms. Two-way analysis of variance was used to test for the effects of light, time and light x time on ^{14}C uptake by plants. All results were considered significant at the $P<0.05$ level. Statistical calculations were run using a SPSS 11.5 statistical software package. SE of means are presented in the figures as a variability parameter.

Results

Plant biomass

Light intensity significantly affected total plant biomass 48 hours after imposing the light treatment ($P<0.01$, Fig. 1). Root to shoot ratios were not significantly influenced by light treatment and were on average about 0.43 (Fig. 1).

N turnover in the soil

Due to rapid N turnover in the soil, the variation between the replicates was high in both ammonium concentration (4.7±0.3 μg N g^{-1} soil d.w.) and ^{15}N abundance of NH_4^+. Therefore gross N mineralization rate using the pool dilution approach in the $^{15}NH_4^+$ labeled treatments yielded high standard errors. No statistical difference was observed between high and low light treatments and gross mineralization rates averaged 2.1±4.3 μg N g^{-1} soil d.w. day^{-1} (Fig. 2a). ^{15}N recovery in the NH_4^+ fraction decreased to <12% of tracer input after 4 h (Fig. 3). During the chase period, ^{15}N recovery in the ammonium pool in the $^{15}NO_3^-$ treatment was low while there was no significant difference for ^{15}N recovered in the ammonium pool in the ^{15}N-glycine and -ammonium treatments 24 h after tracer additions (Fig. 3 e,f). Fast turnover of the NO_3^- pool allowed an accurate calculation of gross nitrification rates in the soil using ^{15}N pool dilution techniques. It was shown that high light significantly enhanced gross nitrification rates. During the first 24 h period after tracer injection,

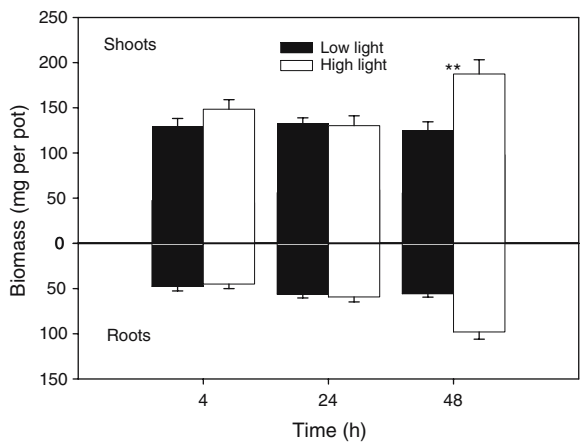


Fig. 1 Shoot and root biomass of maize seedlings under low and high light intensity. A mixture of three N forms was amended to each pot, where only one N form was labeled with ^{15}N at a time. *Asterisks* indicate significant differences of plant biomass under the two light conditions. Values are means (±SE) of three replicates

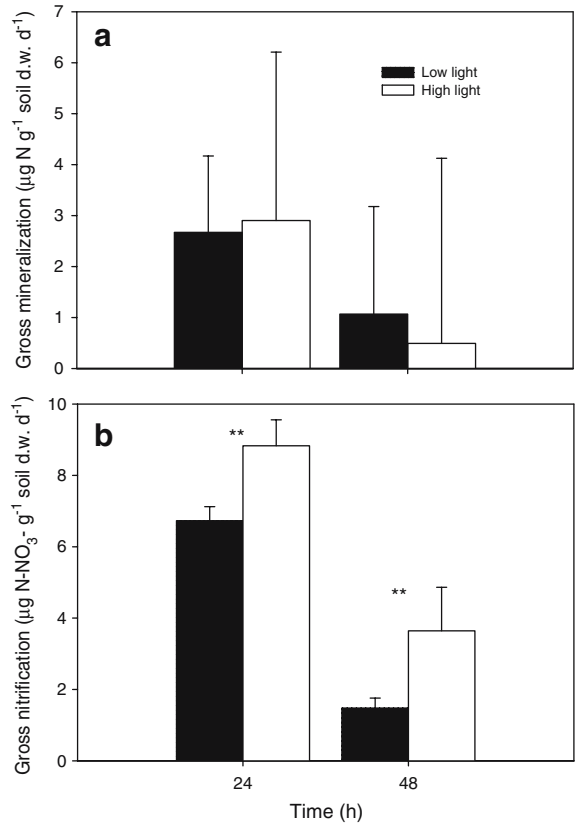
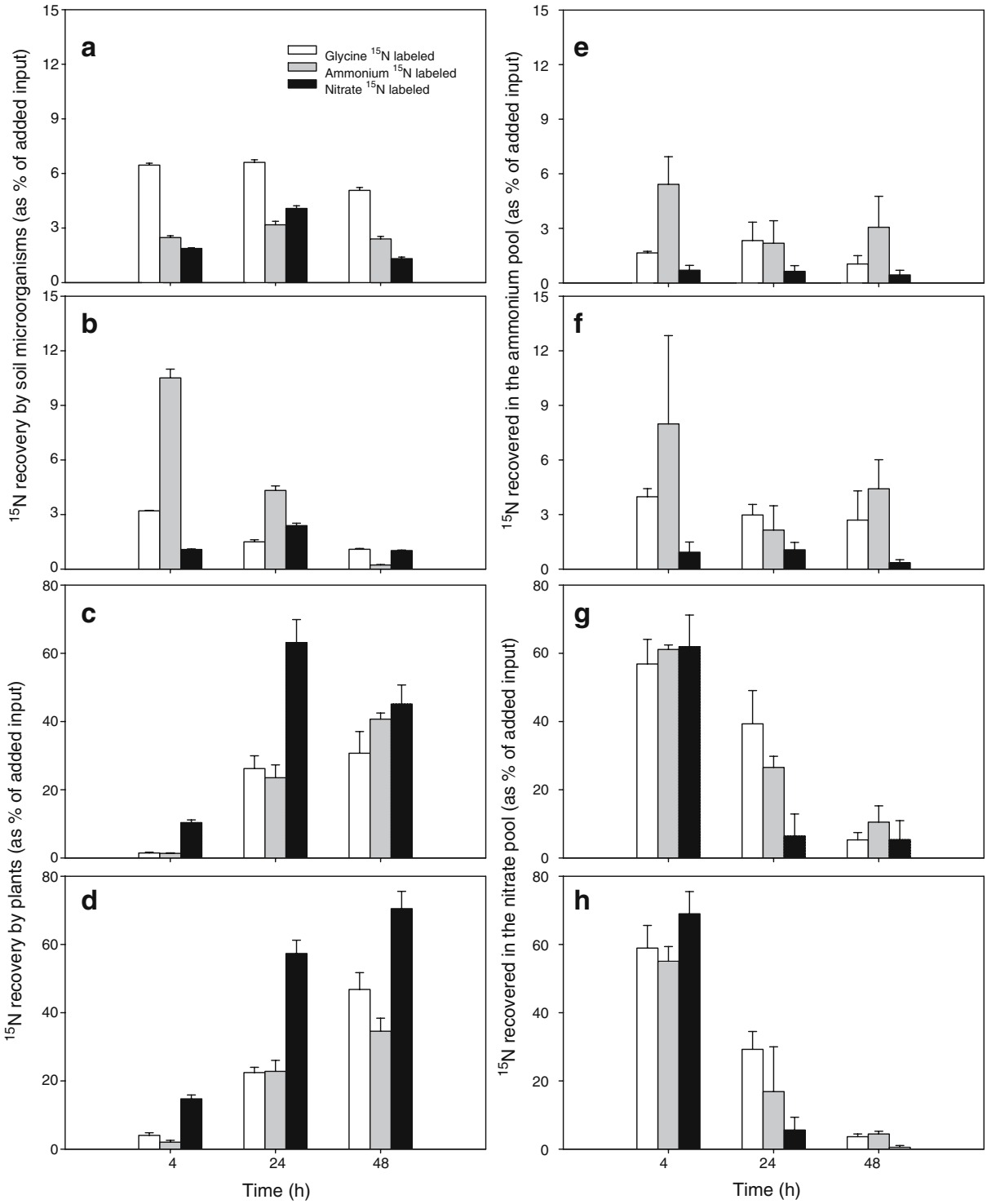


Fig. 2 Gross mineralization **a** and nitrification **b** rates under low and high light intensity. *Asterisks* indicate significant differences of gross mineralization/nitrification rates under the two light conditions. Values are means (±SE) of three replicates at each time



gross nitrification rate was 6.7±0.4 μg g^{-1} dry soil day^{-1} under low light intensity and 8.8±0.7 μg g^{-1} dry soil day^{-1} under high light. During the second 24 h, gross nitrification rates decreased strongly. They were 1.5±0.3 μg g^{-1} dry soil day^{-1} under low light and 3.6±1.2 μg g^{-1} dry soil day^{-1} under high light (Fig. 2). Fast turnover of glycine and ammonium and high nitrification rates led to high concentrations (9.6±

◀ **Fig. 3** Proportion of ^{15}N recovered by maize seedlings and soil microorganisms as well as inorganic N pools under different light intensities. **a** Soil microorganisms under low light intensity; **b** soil microorganisms under high light intensity; **c** plants under low light intensity; **d** plants under high light intensity; **e** soil ammonium pool under low light intensity, **f** soil ammonium pool under high light intensity, **g** soil nitrate pool under low light intensity, **h** soil nitrate pool under high light intensity. A mixture of three N forms was amended to each pot, where only one N form was labeled with ^{15}N at a time. Values are means (±SE) of three replicates. Note different *Y* scales for the different pools

0.6 μg N g^{-1} soil d.w.) and ^{15}N recoveries of NO_3^- in ^{15}N-glycine and $^{15}NH_4^+$ treatments, almost equal to the ^{15}N recoveries in NO_3^- of the $^{15}NO_3^-$ treatment (>50%; Fig. 3). ^{15}N recovery in the nitrate pool during the initial 4 h was not affected by N form and light level. With time less $^{15}NO_3^-$ was recovered (Fig. 3 g,h) due to rapid uptake for NO_3^- by plant roots.

^{15}N recovery and N uptake on a plant basis

Repeated measures analysis of variance indicated significant effects of ^{15}N form, light and time as well as their interactions on $^{15}NR_{plant}$ of maize seedlings (except N form × light) and $^{15}NR_{MB}$ of soil microorganisms ($P<0.05$, Table 1). Light therefore had a significant effect on ^{15}N uptake by maize seedlings and soil microorganisms (Fig. 3). Under low light intensity, microorganisms immobilized more ^{15}N from glycine than from NH_4^+ or NO_3^-, and ^{15}N acquisition by microorganisms was similar for NH_4^+ and NO_3^- (Fig. 3a). Microorganisms took up more ^{15}N from NH_4^+ than from either of the other N forms under high light intensity (except 48 h after tracer injection). $^{15}NR_{MB}$ for $^{15}NH_4^+$ decreased substantially from 10.5±0.5% at 4 h to 0.2±0.02% at 48 h. Uptake of ^{15}N-glycine by microorganisms showed a similar trend as for $^{15}NH_4^+$, $^{15}NR_{MB}$ of ^{15}N-glycine declining from 3.2±0.02% at 4 h to 1.1±0.05% at 48 h. In contrast, $^{15}NR_{MB}$ for $^{15}NO_3^-$ slightly increased from 4 h to 24 h after tracer addition and decreased thereafter (Fig. 3b). These results show that the maximal uptake of ^{15}N by soil microorganisms peaked within 4 h for amino acids and NH_4^+ and within 24 h for NO_3^-.

Under low light intensity, maize seedlings acquired three to four times more ^{15}N from NO_3^- than from either $^{15}NH_4^+$ or ^{15}N-glycine during the first 4 and 24 h. However, plants almost acquired an equivalent fraction of ^{15}N from the three N forms at 48 h after tracer addition (Fig. 3c). $^{15}NH_4^+$ uptake by plants substantially increased from 1.3±0.2% at 4 h to 40.7 ±1.8% at 48 h. Under low light, ^{15}N-glycine uptake by plants showed very similar values as ^{15}N uptake from NH_4^+ (Fig. 3c). Under high light, plants showed a substantial increase in $^{15}NR_{plant}$ with time for all three N forms (Fig. 3d). Maize seedlings took up much more $^{15}NO_3^-$ than either ^{15}N-glycine or $^{15}NH_4^+$ during the whole experimental period whereas ^{15}N-glycine and $^{15}NH_4^+$ uptake were similar under high light conditions.

Table 1 Results of repeated-measures ANOVA for the effects of ^{15}N form added, light, time and their interactions on ^{15}N uptake by plants and by soil microorganisms

Components	Sources of variation	*F* values	*P* values
Plants	^{15}N form	72.52	0.00
	Light	4.37	0.04
	Time	185.74	0.00
	^{15}N form x light	2.94	0.07
	^{15}N form x time	8.66	0.00
	Light x time	6.51	0.00
	^{15}N form x light x time	3.55	0.02
Microbial biomass	^{15}N form	285.36	0.00
	Light	135.05	0.00
	Time	352.08	0.00
	^{15}N form × light	578.31	0.00
	^{15}N form × time	147.15	0.00
	Light × time	207.77	0.00
	^{15}N form × light × time	159.48	0.00

Table 2 Results of repeated-measures ANOVA for the effects of light, time, and light × time on ^{14}C uptake by plants

Components	Sources of variation	*F* values	*P* values
Plants	Light	52.99	0.00
	Time	30.65	0.00
	Light × time	2.10	0.13
Microbial biomass	Light	0.15	0.70
	Time	3.88	0.03
	Light × time	0.92	0.41
Dissolved organic carbon	Light	1.15	0.29
	Time	27.84	0.00
	Light × time	1.88	0.17

^{14}C recovery in maize seedlings, microbial biomass and DOM

Repeated measures analysis of variance indicated significant effects of light and time on $^{14}CR_{plant}$ ($P<0.05$, Table 2). Time significantly affected $^{14}CR_{MB}$ and $^{14}CR_{DOM}$ while light and interactions of light x time had no significant effects on them (Table 2). In contrast, high light significantly enhanced ^{14}C uptake by maize seedlings (Fig. 4a). $^{14}CR_{plant}$ increased from 0.48±0.06% at 4 h to 0.91± 0.06% at 48 h under high light intensity. Uptake of glycine (measured as ^{14}C) under low light intensity reached a maximum after 24 h and was 30–50% less than under high light (Fig. 4a). $^{14}CR_{DOM}$ was much higher than $^{14}CR_{MB}$ at all times and in both light treatments. $^{14}CR_{MB}$ increased while $^{14}CR_{DOM}$ declined slightly with time (Fig. 4b,c).

^{14}CR to ^{15}NR ratio of plants and microbial biomass

Under low light, ^{14}CR to ^{15}NR ratios of microbial biomass were in the range of 0.34 and 0.53, with the lowest value at 48 h and the highest value at 24 h (Fig. 5a). The values between 24 and 48 hours were significantly different ($P<0.05$, Fig. 5a). By comparison, ^{14}CR to ^{15}NR ratios of microbial biomass increased with time from 0.60±0.13 at 4 h to 3.40± 0.14 at 48 h under high light (Fig. 5a). Under low light, ^{14}CR to ^{15}NR ratios of plants were 0.18±0.02 in the initial 4 h after tracer injection, which was nearly nine times higher than the values at 24 and 48 h. ^{14}CR to ^{15}NR ratios were similar for plants under high light and low light, except 24 h after tracer injection (Fig. 5a).

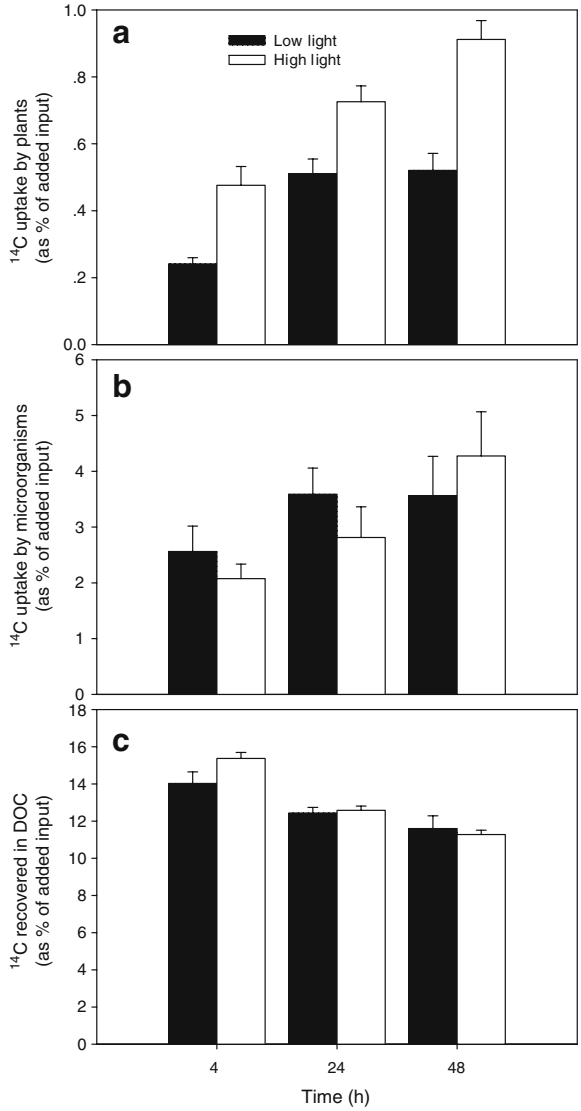


Fig. 4 Percent of added ^{14}C input recovered in **a** maize seedlings, **b** soil microorganisms and **c** dissolved organic carbon under low and high light intensity. Values are means (±SE) of nine replicates. Note different *Y* scales for plants, microorganisms and DOM

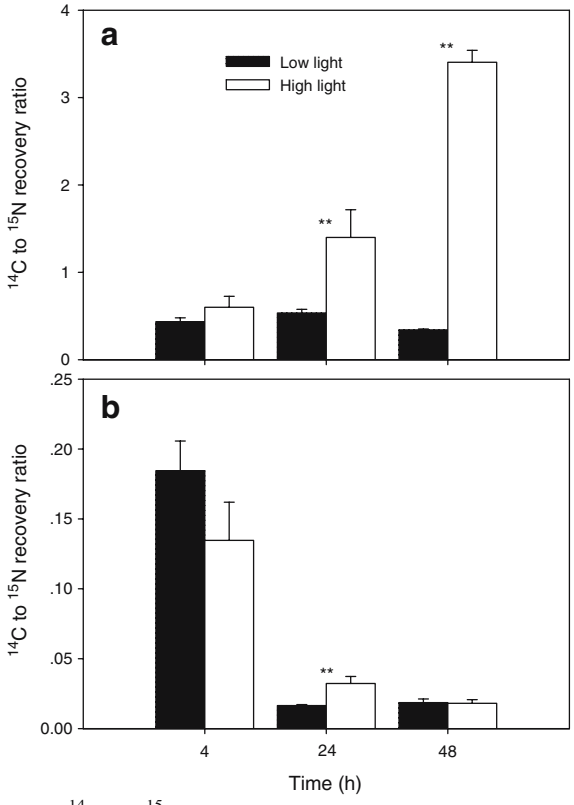


Fig. 5 ^{14}CR to ^{15}NR ratio of **a** microbial biomass and **b** maize plants. Values are means (±SE) of three replicates. Note different Y scales for microorganisms and plants. *Asterisks* indicate significant differences of ^{14}CR to ^{15}NR ratio of microbial biomass and maize plants between the two light conditions

Discussion

Competition for inorganic and organic N between soil microorganisms and plants

Numerous studies have shown that plant roots and rhizosphere microorganisms compete intensely for available N in the rhizosphere and that microorganisms are stronger competitors in the short-term (Jackson et al. 1989; Schimel et al. 1989; Zak et al. 1990; Schimel and Chapin 1996; Kaye and Hart 1997; Hodge et al. 1999; Owen and Jones 2001; Bardgett et al. 2003; Cheng and Bledsoe 2004). However, a few studies also showed contradictory results e.g. that some plant species were better able to acquire inorganic (Jaeger et al. 1999) or organic N (Lipson and Monson 1998) in the face of microbial competition. A possible explanation for this is that the competition for N between plants and soil microorganisms is strongly dependent on available N supplies in the soil, based on the hypothesis that only N in surplus of microbial growth is available for plants. In the current study we added inorganic N to the soil in the form of NH_4NO_3 at a rate of 56 μg N g^{-1} dry soil, resulting in high available N supplies for plant roots and rhizosphere microorganisms before tracer additions. This is confirmed by high mean NO_3^- concentration (9.6±0.6 μg N g^{-1} soil d.w.) during the trace period. Hence, it was not surprising that maize out-competed soil microorganisms for ^{15}N from NO_3^- both under low and high light intensities (Fig. 3c,d). Higher $^{15}NR_{plant}$ and greater ^{15}N acquisition by plants from $^{15}NO_3^-$ treatment can result from preferential NO_3^- uptake by maize or because the NO_3^- ion is more mobile in soil solutions (Jackson et al. 1989; Schimel et al. 1989; Owen and Jones 2001) therefore often serving as the most convenient N source for crop plants (Raven 2003). What's more, there exists a high affinity nitrate transport system in maize roots (Aslam et al. 1992; Glass and Siddiqi 1995) that confers a high capacity for root NO_3^- uptake.

Although a large amount of inorganic N was amended one week before tracer additions, plant uptake of ^{15}N-glycine during the initial 4 h (0.03 and 0.06 mg N g^{-1} root h^{-1} under low and high light, respectively, Fig. 6) was comparable to uptake rates published for other grass species (ca 0.03 to 1.35 mg N g^{-1} root h^{-1}, Raab et al. 1999; ca 0.01 to 0.12 mg N g^{-1} root h^{-1}, Xu et al. 2004). This clearly indicates that maize is able to access organic N even in an inorganic N enriched environment. ^{15}N-glycine uptake was very similar to $^{15}NH_4^+$ uptake by maize seedlings under the two light conditions. This might be explained by rapid decomposition of glycine by microorganisms to inorganic N (Kuzyakov and Demin 1998; Jones 1999; Jones and Kielland 2002; Nordin et al. 2004) and thereafter uptake of ^{15}N from glycine in the form of NH_4^+ or NO_3^- 4 h following tracer addition. In this study we didn't determine the rate of glycine turnover in the soil. However, nearly 60% of added ^{15}N from glycine appeared in the nitrate pool in the initial 4 h following tracer addition (Fig. 3 g,h). This clearly implies that rapid decomposition of glycine occurred in soils as observed by other studies (Kuzyakov and Demin 1998; Jones 1999), providing available $^{15}NH_4^+$ or $^{15}NO_3^-$ for plant uptake. As a result, the contribution of organic N to plants might be strongly overestimated by using

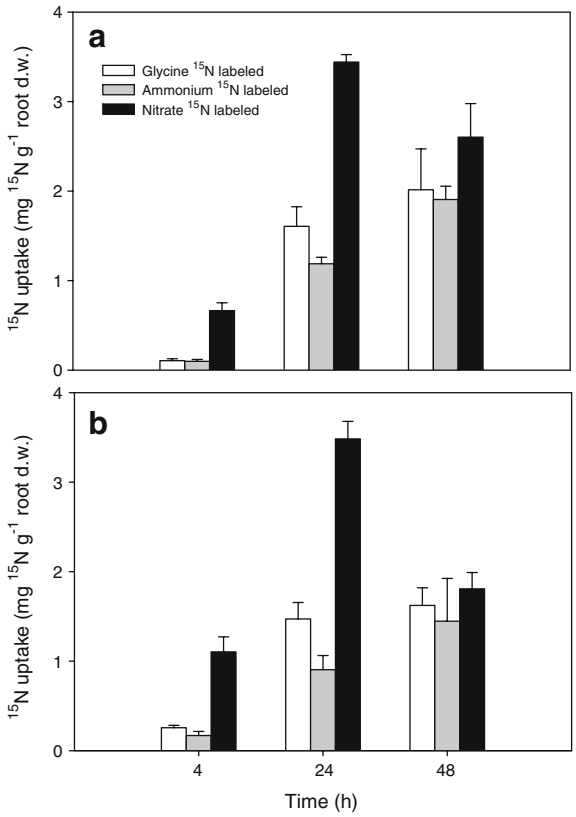


Fig. 6 Root ^{15}N uptake by maize seedlings under **a** low light intensity and **b** high light intensity. A mixture of three N forms was amended to each pot, where only one N form was labeled with ^{15}N at a time. Values are means (±SE) of three replicates

only ^{15}N-labelled amino acids without ^{14}C or ^{13}C tracer because of rapid mineralization of added amino acids.

The rapid mineralization of glycine and the rapid nitrification of ammonium (Fig. 3 g,h) hamper a similar interpretation of the measurements because 4 h after application of tracers all pools were highly enriched with ^{15}N. This implies that the competition for nitrate in this soil is more important than for glycine and ammonium and therefore the maize roots benefited from fast mineralization and nitrification compared to microorganisms.

Effects of light on the competition for inorganic and organic N between maize and rhizosphere microorganisms

Light had a significant effect on $^{15}NO_3^-$ uptake by maize seedlings ($P<0.01$, Table 1 and Fig. 6). This is corroborated by other studies showing that light is involved in the regulation of nitrate reductase gene expression in maize (Raghuram et al. 1999) and in the uptake of NO_3^- by plant roots (Miller and Cramer 2004). Light had no significant effect on ^{15}N uptake by maize from NH_4^+ or glycine pools (Fig. 6), whereas it significantly affected ^{14}C uptake by maize seedlings (Table 2 and Fig. 4). A possible explanation is that ^{15}N uptake derived from rapid decomposition of glycine conceals the uptake of intact glycine because plant roots compete directly for glycine in the first several hours following tracer additions and thereafter, after glycine depletion, plant roots acquire ^{15}N released from rhizosphere microorganisms as NH_4^+ (McFarland et al. 2002). Moreover, in this study plant roots might take up more ^{15}N from glycine as NO_3^- derived from the rapid decomposition of glycine and subsequent nitrification (Fig. 3 g,h).

Compared to the effect of light on inorganic and organic N uptake by plants, light cannot directly affect rhizosphere microorganisms. However, there is a difference in the uptake of ^{15}N from NH_4^+, NO_3^- and glycine by rhizosphere microorganisms between low and high light (Table 1). We here ascribe the difference to two major reasons. Firstly, under low light plants have lower transpiration and uptake rates and therefore rhizosphere microorganisms have more chance to take up N than under high light condition, e.g. more glycine was incorporated into microbial biomass under low light whereas this was reversed under high light. Besides, glycine is often considered as a relatively poor substrate for soil microorganisms (Lipson et al. 1999), though it contains two "C" atoms per molecule which can trigger microbial uptake of glycine (and ^{15}N) as a carbon source under low light. Secondly, under high light intensities plants release more C into the soil (Kuzyakov and Cheng 2001). Root exudates contain many amino acids and carbohydrates and are more appropriate for microorganisms than glycine (Yano et al. 1998; Lipson et al. 1999) which may facilitate the microbial acquisition of nutrients from soil (Jones et al. 2004). This might have been the case, since more ^{15}N from NH_4^+ was recovered in microbial biomass under high light, except 48 h after tracer addition (Fig. 3). The decrease of ^{15}N from NH_4^+ in microbial biomass might result from rapid microbial oxidation

of NH_4^+ i.e. nitrification and subsequent uptake by plants (Figs. 2, 3). In this study very high ^{15}NR from ^{15}N-glycine or $^{15}NH_4^+$ in the nitrate pool also indicates the occurrence of rapid N transformation processes in this experiment. In contrast, ^{15}N recovered by microbial biomass from NO_3^- decreased with time under high light (Fig. 3). This also can be ascribed to a stimulation of ^{15}N uptake by maize from NO_3^- pool by high light, thus reducing the microbial sink for ^{15}N from NO_3^-. A number of studies have shown that exudates released by roots in the form of a wide variety of organic compounds are most directly linked to photosynthesis (Meharg 1994; Uren 2001; Kuzyakov and Cheng 2001, 2004). These exudates are rapidly utilized by microorganisms in the rhizosphere and regulate rhizomicrobial activity (Anderson and Domsch 1985; Smith and Paul 1990; Kuzyakov and Cheng 2001). In the current study high light enhanced nitrification rates and thereby resulted in high NO_3^- concentrations in soil solution. This indicates that high light intensity might indirectly stimulate the activity of nitrobacteria by increasing the amount of root exudates.

In order to provide a better insight into the competition for inorganic and organic N between plants and soil microorganisms, we here calculated the ratios of ^{15}N uptake by plants to that by rhizosphere microorganisms (Fig. 7). These results clearly indicate that light strongly mediates the competition for inorganic and organic N between plants and rhizosphere microorganisms. Plant roots out-competed rhizosphere microorganisms for ^{15}N from NO_3^- under both light conditions over the whole experimental period (Fig. 7c). Although rhizosphere microorganisms out-competed plants for ammonium and glycine under low light during the initial 4 h, high light facilitated effective competition for glycine by plants (Fig. 7a). By comparison, high light enhanced the competition for NH_4^+ by rhizosphere microorganisms in the initial 24 h whereas it strongly stimulated the competition by plants during the later 24 h (Fig. 7b).

Contribution of organic and inorganic N to N acquisition by plants

In this study, application of dual-labeled (^{14}C, ^{15}N) glycine permitted a rough estimation of the minimal contribution of intact glycine molecules to glycine-derived ^{15}N acquisition by maize seedlings, based on ^{14}CR to ^{15}NR ratios of plants. Although ^{14}C uptake by maize indicates that light had a significant positive effect on organic N uptake, it had no significant effect on the contribution of intact glycine molecules to glycine-derived ^{15}N acquisition by maize (Fig. 4b). Based on ^{14}CR to ^{15}NR ratios of plants, intact glycine

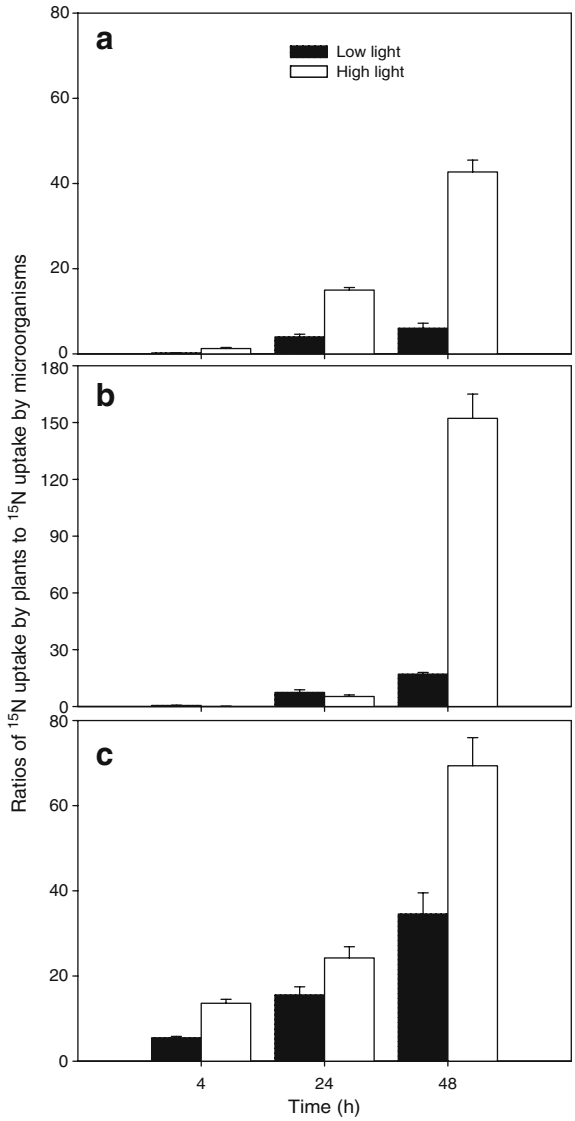


Fig. 7 Ratios of ^{15}N uptake by plants to that by soil microorganisms 4, 24 and 48 h after injecting ^{15}N labeled glycine **a**, ammonium **b** and nitrate **c**. A mixture of three N forms was amended to each pot, where only one N form was labeled with ^{15}N at a time. Values are means (±SE) of three replicates

molecules contributed at least 13% to the total N acquisition derived from glycine 4 h after tracer addition (Fig. 4b). This value was slightly lower compared to estimates for field grown wheat by Näsholm et al. (19–23%; 2001), using ^{13}C and ^{15}N labeled glycine. One day after tracer addition the contribution of intact glycine to glycine-derived ^{15}N uptake declined sharply (Fig. 4b). This is a result of ^{14}C release by respiration but also of continued ^{15}N uptake from inorganic N derived from rapid decomposition of glycine. Similar processes may have hindered the detection of intact dual-labeled glycine uptake in tundra plants 24 h after tracer addition (Schimel and Chapin 1996). Consequently, we should be cautious to draw conclusions when estimating organic N uptake by plants using ^{13}C or ^{14}C labeled amino acids over longer time scales. The most critical points to accurately estimate organic N uptake are the fraction of C isotopes taken up by plants that is subsequently lost via plant respiration and the fast turnover and breakdown of amino acids in soils (Jones 1999; Jones and Kielland 2002).

Uptake rates of glycine, ammonium and nitrate were estimated to be about 0.04±0.02, 2.62±2.33 and 4.28±1.20 mg g^{-1} root d.w. under high light conditions over 4 h. Under low light conditions they were estimated to be 0.02±0.01, 1.13±0.52 and 2.55±0.52 mg g^{-1} root d.w., respectively. Based on these uptake rates, the contribution of nitrate to the total N uptake was estimated to be 69% under low light and 62% under high light whereas it was 31% under low light and 38% under high light for ammonium. Although at least 13% of glycine-derived ^{15}N acquisition was due to uptake of intact glycine molecules, the contribution of organic N in the form of intact glycine to total N uptake was very small. It only contributed about 0.6% under low light and 0.5% under high light to total N uptake by maize. This calculation does not consider respiratory losses of the ^{14}C label taken up by plants, but implies that crop uptake of organic N is only of minor importance in agricultural soils amended with a large amount of inorganic fertilizer.

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