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ORIGINAL ARTICLE

Nitrogen nutrition of native and introduced forest tree species in N-limited ecosystems of the Qinling Mountains, China

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Abstract
Key Message Root N uptake capacity and soil C, N status indicate superior performance of a mixed forest stand with *Larix* and *Quercus* compared with the monocultures of *Picea* and *Larix* under N limitation condition.
Abstract Nitrogen availability and uptake capacity are key factors influencing forest growth and development in N-limited terrestrial ecosystems. With the aim to determine how species and forest management affect tree N nutrition, we conducted root N uptake experiments as well as soil N analyses at three forest stands with different native and introduced tree species (i.e. *Larix principis-rupprechtii* Mayr., *Quercus aliena* var. *acutiserrata* Maxim. ex Wenz. and *Picea wilsonii* Mast.) and two management approaches (i.e. monoculture versus mixed stand) in the Qinling Mountains of China. Across the native and introduced species studied, in general, investigated trees take up both, organic and inorganic N compounds, but prefer organic N (Gln- and Arg-) over inorganic NH_4^+–N. The introduced conifer species (*L. principis-ruprechtii*) showed higher root N acquisition capacities compared to a native conifer species (*P. wilsonii*) under N-limited conditions. Moreover, the mixed forest stand with *L. principis-ruprechtii* and *Q. alinea* var. *acutesserata* accumulated more nitrogen in soil pools and showed improved C and N retention capability through the whole soil profile as compared to the monocultures of *P. wilsonii* or *L. principis-ruprechtii*. Similar acquisition strategies were observed for specific N sources (i.e. organic versus inorganic) across all investigated tree species. Still the introduced species *Larix* exhibited a superior root N acquisition capacity and, therefore, may be a good candidate for afforestation programs in the studied region. The present results underpin the significance of forest management practices that achieve a mixed species structure with broadleaved tree species such as *Quercus* for restoration of soil C and N pools in order to stabilize forest ecosystems and to achieve sustainable forest development.

Keywords Root nitrogen uptake capacity · Soil microbial biomass · *Larix* · *Quercus* · *Picea* · Qinling Mountains

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Introduction

Nitrogen availability is one of the most important factors limiting growth and development of forests not exposed to significant anthropogenic N input (Rennenberg et al. 1998, 2009; Lovett et al. 2004; Chapman et al. 2006; Rennenberg

and Schmidt 2010; Rennenberg and Dannenmann 2015). In general, N can be taken up in inorganic and organic forms, which are both available for plants in the soil (Stoelken et al. 2010). However, in N-limited forests, preference for different N sources (e.g. inorganic versus organic sources) may differ among different tree species due to competition for N (Schimel and Bennett 2004; Rennenberg et al. 2009). Studies during the past decades investigating the competition for N have mainly focused on inorganic (i.e. ammonium, nitrate) N acquisition and only few studies determined organic N acquisition mainly in non-woody species (McKane et al. 2002; Miller et al. 2007; Robinson et al. 2010). In addition, most studies on the competition for N focused on the interaction of trees with other vegetation components. For example, inorganic N uptake capacity of slow-growing beech seedlings was significantly decreased when growing together with the fast-growing pioneer shrub *Rubus fruticosus* (Fotelli et al. 2002, 2005). Previous greenhouse studies investigated the short-term competition for N between European beech (*Fagus sylvatica* L.) and sycamore maple (*Acer pseudoplatanus* L.) seedlings. The results indicate that the two species use different strategies for N acquisition depending on environmental factors such as light availability and soil N availability (Simon et al. 2014). However, information from field studies about the interaction between the same or different tree species (Simon et al. 2010, 2014), the interaction of trees with soil microorganisms (Dannenmann et al. 2009; Simon et al. 2011), or the consequences of forest management (Fotelli et al. 2004; Gessler et al. 2005; Simon et al. 2011) on N acquisition are still scarce, especially for N-limited sites. Recent studies suggest that under N limitation, tree roots take up all N forms available in the soil (i.e. inorganic and organic), although sources of reduced N may be preferred even in N saturated soil with high nitrate availability (Rennenberg and Dannenmann 2015).

In China, Qinling Mountains represent the major catchment areas of the two largest river systems, the Yellow River and the Yangtze River. The quantity and continuity of water supply and the quality of the water depend to a large extent on the health of the forests in this mountain area. During the last century, the forests of the Qinling Mountains were repeatedly subjected to heavy logging and in some areas even to clear-cutting. As a consequence, soil erosion occurred and major nutrients, including nitrogen, essential for forest growth and development, were washed out even from deeper soil layers (Lal et al. 1989; Li 2004). To stop further forest destruction, restoration beyond natural regeneration of native species was achieved by planting *Larix principis-rupprechtii* Mayr. and *Larix kaempferi* (Lamb.) Carr. as non-endemic, introduced species into logged and clear-cut areas (Kang and Liu 2006). Whereas natural regeneration of native species led to rapid recovery of the forests, planted areas became too dense due to a lack of forest management resulting in low productivity (c.a. 60% of the average natural forest), high susceptibility to disturbances and strongly reduced regeneration capability (Wu et al. 2013). From this history of the Qinling Mountain forests, it can be assumed that soil N availability may be low as a consequence of disturbed ecosystem nitrogen cycling mediated by anthropogenic forest use. Therefore, the determination of N acquisition either at the species level (e.g. native *versus* introduced tree species) or in the context of forest management (e.g. monocultures *versus* mixed stands) in this area will contribute to understand how the N demand of the mature mountain forests is met on N-poor soils with low atmospheric N input (Rennenberg and Dannenmann 2015).

The aims of the present study were (1) to quantify root N uptake capacity for inorganic and organic N sources of native and introduced forest species; (2) to compare species-specific root N uptake capacity and plant available N sources in the soil within mixed plantation and monoculture stands.

Materials and methods

Site description and experimental design

This study was conducted at the Qinling National Forest Ecosystem Research Station on the south slope of the Qinling Mountains, Shaanxi Province, China. The Qinling Mountains constitute a dividing range that extents over 1500 km in Northwest China (Li et al. 2005; Liu et al. 2009). The area studied is situated at the northern border of a subtropical region with monsoon climate. Annual mean temperature amounts to 6–11 °C (below 2000 m a.s.l) or 1–6 °C (above 2000 m a.s.l), annual mean precipitation to 980 mm (Li et al. 2000; Dang et al. 2007). 60% of the precipitation falls during the period from July to September (Li et al. 2005). The abrupt and broken topography mainly consists of granite, gneiss, metamorphic sand stone and schist (Zhang and Liang 2012). The mean soil depth is 45–50 cm and the soil is classified as loam (Cheng et al. 2013). The details of soil physical and chemical characteristics in this area can be found in Zhang et al. (2012). The annual growth period of plants between 1300 and 2000 m a.s.l in this area amounts to 160 days from May to October (Li et al. 2005; Yang et al. 2014). The experiments were carried out at two forest sites (Supplementary Figure S1). The first site of ca. 33.30 ha contained a 50-year-old larch (*Larix principis-rupprechtii* Mayr.) monoculture stand on 33°28′01″, 108°29′26″NE, 2052 m a.s.l., and a 70-year-old spruce (*Picea wilsonii* Mast.) monoculture stand on 33°28′05″, 108°29′27″NE, 2048 m a.s.l.. These

two monoculture stands grew next to each other, but not in direct competition on a southern slope with a slope angle of 34°–39°. The second forest site (area of ca. 22.40 ha, 33°26′05″, 108°27′09″NE, 1604 m a.s.l.) contained a 50-year-old mixed larch (*Larix principis-rupprechtii* Mayr.) and oak (*Quercus aliena* var. *acutiserrata* Maxim. ex Wenz.) stand located on a south-eastern slope with a slope angle of 38°. At this mixed stand, *Larix principis-rupprechtii* was planted into natural regeneration of native *Quercus aliena* var. *acutiserrata*. Therefore, the two species grew in direct competition at this site. *Picea wilsonii* and *Quercus aliena* var. *acutiserrata* belong to the native vegetation of the Qinling Mountains, while *Larix principis-rupprechtii* constitutes an introduced species.

Experiments were conducted in early September 2012 before any visible signs of plant leaf senescence. Climate data of monoculture and mixed stands in 2012 are shown in Table 1. At each monoculture stand (i.e. *Larix* or *Picea*) or mixed stand (i.e. *Larix* mixed with *Quercus*) of the two forest sites (Supplementary Figure S1), three independent areas were chosen with 50×50 m^2 size each and within each area, seven independent mature trees of each species were selected and homogenously dispersed (distance between any two selected trees ≥17 m). In total, 21 mature trees per stand were selected for each species/forest stand. Roots up to 4 cm length of these trees were exposed to different inorganic (ammonium, nitrate) and organic (Gln, Arg) N source solutions. For each N source, twenty-one sets of roots per species were selected for ^{15}N uptake experiments. At the same time, soil samples were collected at each area.

Table 1 Mean daily air temperature and monthly precipitation of mixed and monoculture forest stands in 2012

Month	Mean daily air temperature/month (°C)		Monthly precipitation (mm)	
	Mixed stand	Monoculture stand	Mixed stand	Monoculture stand
January	0.38	−1.11	0	5.5
February	0.19	−1.32	4.2	12.8
March	3.59	1.98	42.1	45.3
April	8.07	6.75	21.2	33.2
May	12.81	10.26	40.9	43.5
June	16.23	14.25	180.5	198.3
July	19.18	16.54	257.4	277.2
August	18.28	15.86	212.1	222.5
September	14.92	13.35	44.3	47.3
October	8.54	6.56	56	64.1
November	4.34	2.89	15.4	20.1
December	−0.76	−3.1	0.2	3.7
mean	8.81	6.91	72.9	81.1

Root N uptake experiments

N uptake experiments were conducted using mycorrhizal fine roots (less than 2 mm in diameter) of mature spruce, larch and oak trees. For this purpose, the ^{15}N enrichment technique as described by Gessler et al. (1998) was applied. Mycorrhizal fine roots still attached to the trees were carefully dug out and rinsed with distilled water to remove adhering soil particles. Roots up to 4 cm length were carefully dipped into 4 mL of an artificial soil solution, and incubated for 2 h (between 10 am and 2 pm). pH and concentrations of inorganic anions and cations of the artificial soil solution were based on the soil solution at the research plot and were consistent with previous data reported from a forest site with low N availability (Gessler et al. 2005). As acquisition by roots is thought to significantly contribute to the fast turnover of particular amino acids in the soil, whereas other amino acids not taken up at the same extent accumulate in the soil solutions, amino acid composition of plant material is more suitable as an indicator of root acquired amino acids from the soil than soil solution itself. Therefore, in the present experiment, amino acids were added at concentrations previously reported for a N-limited forest site (Gessler et al. 2005), using Gln and Arg as surrogate for total soil solution amino acids. These amino acids were used, as they constitute the most abundant amino acids in the roots of the species studied. The artificial soil solution contained 100 µM KNO_3, 90 µM $CaCl_2{\cdot}2H_2O$, 70 µM $MgCl_2{\cdot}6H_2O$, 50 µM KCl, 24 µM $MnCl_2{\cdot}4H_2O$, 20 µM NaCl, 10 µM $AlCl_3$, 7 µM $FeSO_4{\cdot}7\ H_2O$, 6 µM K_2HPO_4, 1 µM NH_4Cl as well as glutamine and arginine (25 µM of each). N uptake experiments were conducted with one of the four N sources supplied as ^{15}N-labelled compound ($^{15}NH_4Cl$, $K^{15}NO_3$ or double labelled ^{15}N/^{13}C–Gln and ^{15}N/^{13}C–Arg, 99 atom %). Non-labelled solution was used as a control to account for natural abundance of ^{15}N or ^{13}C in the fine roots of the selected tree species. To prevent bacterial degradation of amino acids, 10 mg L^{-1} of ampicillin (ampicillin sodium salt, Sigma–Aldrich, Chemie GmbH, Steinheim, Germany), was added to all nutrient solutions. After 2 h incubation, submerged fine root tips and moistened upper parts (ca. 8–15 mm) were carefully cut off from the trees with scissors, washed in 0.5 mM $CaCl_2$ and distilled water, dried with cellulose paper and stored in plastic tubes. On the same day, fresh weight was determined and samples were placed into a drying oven at 60 °C for 2 days. Thereafter, dry weight of the samples was determined.

Total organic carbon, nitrogen concentrations and $\delta^{15}N$ abundance

Total carbon and nitrogen concentrations as well as ^{15}N abundance were determined in oven-dried (48 h, 60 °C), finely ground root material (0.1–1.0 mg aliquots) using an elemental analyser (NA 2500CE Instruments, Milan, Italy), coupled via a Conflo II interface to an isotope ratio mass spectrometer (Delta Plus, Thermo Finnigan MAT GmbH, Bremen, Germany). A working standard (glutamic acid) was calibrated against the primary standards of the U.S. Geological Survey 40 (USGS 40; glutamic acid $\delta^{13}C_{PDB} = -26.39‰$) and USGS 41 (glutamic acid $\delta^{13}C_{PDB} = 37.63‰$) for $\delta^{13}C$, and USGS 25 (ammonium sulphate, $\delta^{15}N_{Air} = -30.4‰$) and USGS 41 (glutamic acid $\delta^{15}N_{Air} = 47.600‰$) for $\delta^{15}N$ and analysed after every tenth sample to account for a potential instrument drift over time as described by Simon et al. (2011). Nitrogen uptake rates (nmol N g^{-1}fw h^{-1}) were calculated based on the incorporation of ^{15}N into root fresh weight according to the equation by Kreuzwieser et al. (2002). Net uptake rate $= (^{15}N_l - ^{15}N_n) \times N_{tot} \times dw \times 10^5)/(MW \times fw \times t)$, where $^{15}N_l$ and $^{15}N_n$ are the atom% of ^{15}N in labelled (N_l, labelled) and non-labelled (N_n, natural abundance) fine roots, respectively, N_{tot} is the total N percentage, MW is the molecular weight of ^{15}N and t represents the incubation time (2 h).

Soil analyses

Soil was sampled at three replicated sub-plots ($n = 3$) for each stand at the same time when root N uptake experiments were conducted. At each sub-plot, soil samples were taken at three different depths, i.e. 0–10, 10–25 and 25–50 cm by digging soil profiles of 0–80 cm. For each depth, three replicate samples were taken at each sub-plot and were mixed to one composite soil sample (0.5 kg). Soil samples were transported to the laboratories of IMK-IFU in Garmisch-Partenkirchen, Germany within 48 h after sampling for further analyses. To avoid internal soil nitrogen transformation, soil samples were stored in a cooling box with ice bags to keep air temperature below 4 °C during sampling and transport. Subsamples of 50 g of each composite soil sample were selected and air dried for the determination of soil organic carbon and total nitrogen (TN) concentration and the natural ^{15}N abundance of soil TN. The residual soil samples were immediately processed to determine soil extractable inorganic N (NH_4^+ and NO_3^-), dissolved organic N (DON) and microbial biomass C and N concentrations.

Soil TN, natural ^{15}N abundance of TN and SOC

Soil TN concentration, natural ^{15}N abundance of soil TN and SOC concentration of each soil sample were determined using a Costech Elemental Analyzer (Costech International S.p.A, Milan, Italy) coupled to an isotope ratio mass spectrometry (DeltaPlusXP, Thermo Fisher Scientific, Bremen, Germany) at the Center of Stable Isotopes of IMK-IFU, Garmisch-Partenkirchen, Germany. For correct determination of SOC, soil inorganic carbon compounds were removed prior to analyses by an acid washing procedure, if the soil pH was over seven (Harris et al. 2001). To avoid possible loss of soil organic carbon during the acid washing procedure, an acid fumigation method was applied for the analysis of SOC concentrations (Walthert et al. 2010).

Soil inorganic nitrogen, extractable DOC and DON concentrations

A 30 g subsample was taken from each sieved soil sample and extracted with 60 mL of 0.5 mol L^{-1} K_2SO_4 solution. For this purpose, the soil suspension was rigorously shaken for 1 h in a reciprocal shaker and thereafter filtered through Whatman No.1 filter paper (11 µm). The filtrates were passed through 0.45 µm syringe filters and two subsamples of 10 mL solution were immediately frozen until analysis. One subsample was sent to a commercial laboratory (Dr. Janssen, Gillersheim, Germany) for determining NH_4^+ and NO_3^- concentrations using the VDLUFA method C 221 based on colorimetric autoanalysis (Hoffmann 1991). The other subsample was measured for dissolved organic carbon (DOC) and extractable concentrations of total nitrogen (total chemically bound nitrogen, TNb) using a TOC analyser with a coupled TNb module (Dimatec Analysentechnik GmbH, Essen, Germany) as described by Dannenmann et al. (2006). Extractable DON was calculated by subtracting DIN (dissolved inorganic N, calculated as NH_4^+ concentrations + NO_3^- concentrations) from TNb.

Microbial biomass C and N measurement

Microbial biomass C and N were estimated using the chloroform fumigation–extraction (FE) method (Brooks et al. 1985; Vance et al. 1987; Tate et al. 1988) as described in detail by Dannenmann et al. (2006). After the removal of coarse organic material and stones, samples were divided into paired subsamples of 30 g each. One subsample was immediately extracted with 60 mL 0.5 M K_2SO_4 while the second subsample was fumigated under chloroform vapour for 24 h in a desiccator.

Subsequently, ten vacuum/release purge cycles ensured the complete removal of chloroform, and fumigated subsamples were extracted as described above. Extracts were filtered using a 0.45 µm syringe filter and immediately frozen until analysis for total organic carbon (TOC) and total chemically bound nitrogen (TNb). Total carbon (TC) and total inorganic carbon (TIC) were determined based on non-dispersive infrared photometric detection of evolving CO_2 after thermic and chemical oxidation of the samples. TOC was calculated as TC–TIC. In accordance with Brooks et al. (1985) and Vance et al. (1987), correction factors (i.e. 0.54 for microbial biomass N and 0.379 for microbial biomass C) were applied to account for the difference in total extractable N and TOC between paired untreated and fumigated subsamples for the estimation of microbial biomass C and N.

Statistical analyses

Data were statistically analysed by two different methods with similar results (Figs. 1, 2; Supplementary Tables S1–S2). In the first approach, data were firstly tested for normality (either Kolmogorov–Smirnov or Shapiro–Wilk test). Not normally distributed data were transformed using either log- or square-root transformation. Effects of two different tree species from either monoculture or mixed stand on root total N, C abundance and N uptake capacity were tested using paired *t*-tests (for each species, $n=21$). Effects of N sources per species on N uptake capacities were analysed using One-way analyses of variance (ANOVA) followed by Tukey's post hoc tests (for each N source per species: $n=21$). In the second approach, we performed the generalized linear mixed models (GLMM) to determine the independency of the three sampled areas from each stand and tree species-/N source-specific effects on root total N, C abundance and/or N uptake capacities (Gelman and Hill 2007; Bolker et al. 2009). We used the tree species and N sources as fixed parameters. The replicated trees were nested within species and/or N sources and used as random parameters to conduct the fitting process. The models were fitted assuming with a Poisson error distribution. The results from the statistical approach 2 showed insignificant interactions between the three sampled areas per forest stand (Supplementary Table S1). Therefore, we used the data of pooled replicated trees from each forest stand ($n=21$) for stepwise analysis. Additionally, stands and/or soil depth on soil properties were tested using One-way analyses of variance (ANOVA) on ranks (Tukey) (for each soil depth per stand: $n=3$). Differences were considered significant at $p\leq0.05$. Sigmaplot 12.5 (Systat Software GmbH, Erkrath, Germany) was employed for statistical analysis approach 1 and soil property analyses; Rv.3.3.2 (R Development Core Team 2016) was employed for approach 2 (Zuur et al. 2009). The statistical analysis approach 2 (GLMM) showed the same results of species-/N source-specific effects on the plant root C, N metabolite levels and/or N uptake capacities compared to approach 1 (Figs. 1, 2; Supplementary Table S2).

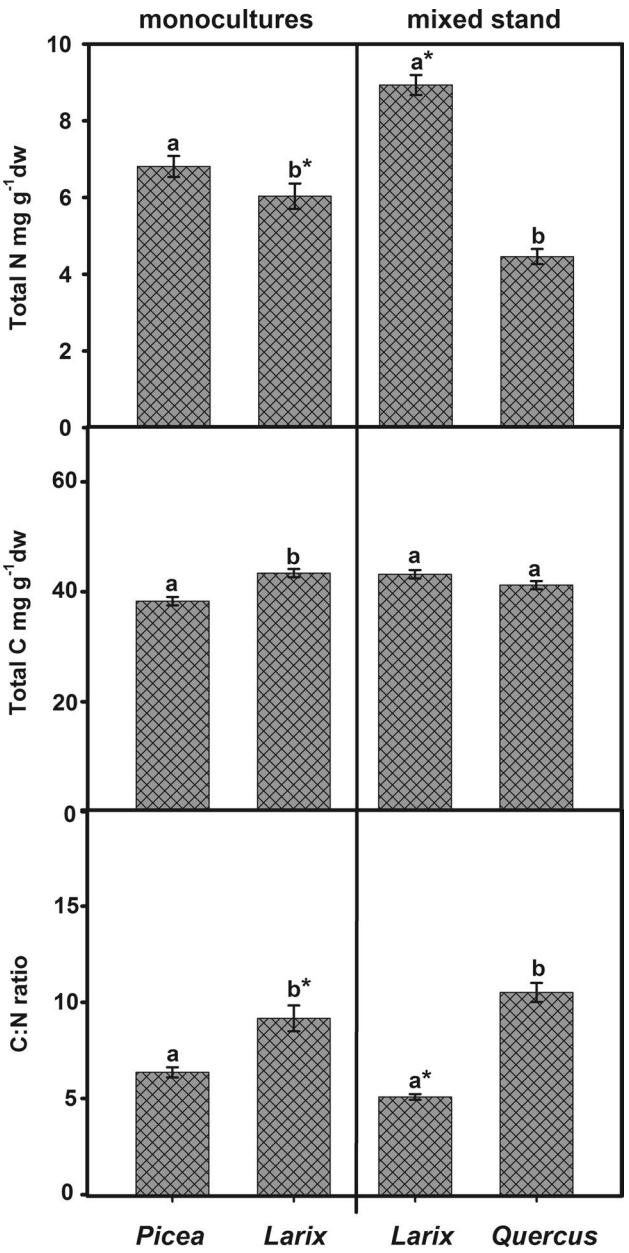

Fig. 1 Total N and C concentrations and C:N ratio of the roots of different tree species. *Vertical bar* charts show mean values ($n=21$) and standard errors *Different small letters* indicate significant difference between different tree species on the same stand and * indicate significant differences of *Larix* on different stands ($p\leq0.05$)

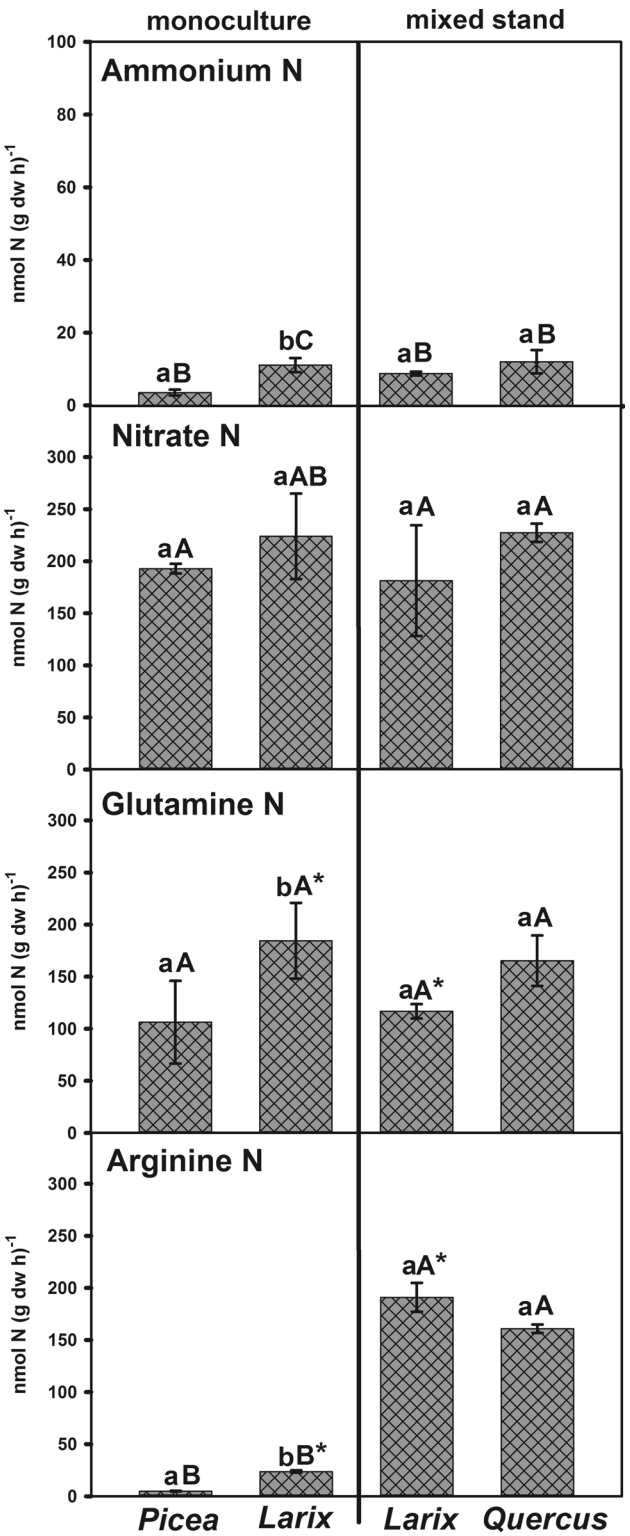

Fig. 2 N uptake capacity of the fine roots of different tree species for inorganic and organic N sources (nmol N g^{-1} dw h^{-1}). *Vertical bar* charts show mean values ($n=21$) and standard errors. *Different capital letters* indicate the significant difference between different N uptake compounds on the same tree species and *different small letters* indicate significant difference of each N uptake compound between different tree species on the same stand and * indicate significant differences of *Larix* on different stands ($p \leq 0.05$)

Results

Total N and C concentrations of the roots

Total N concentrations in the roots of the species studied were of similar magnitude, but exhibited significant differences between species in each monoculture and mixed stand ($p < 0.012$; Fig. 1). Root N concentrations were significantly higher in *Picea* compared to the *Larix* monoculture ($p = 0.011$; Fig. 1). Furthermore, root N concentrations were significantly higher in *Larix* roots of the mixed *Larix* + *Quercus* stand compared to the *Larix* monoculture ($p = 0.018$; Fig. 1) and lower root N concentrations were observed for *Quercus* compared with *Larix* in the mixed *Larix* + *Quercus* stand ($p = 0.003$; Fig. 1).

Patterns of root total C concentrations differed to those of total N concentrations and were significantly higher in *Larix* monoculture compared to *Picea* monoculture ($p = 0.048$; Fig. 1), whereas differences in root C concentrations between *Larix* and *Quercus* in the mixed *Larix* + *Quercus* stands were not observed. Root tissue C:N ratios of *Larix* monoculture were higher than *Picea* monoculture and root tissue C:N ratios of *Quercus* were higher than of *Larix* in the mixed *Larix* + *Quercus* stand.

Root N uptake capacities by different tree species

For the three species studied, uptake capacities for nitrate were similar and ranged between 180 and 230 nmol N g^{-1}dw h^{-1} (Fig. 2; Supplementary Figure S2). Uptake capacities of *Larix* in monoculture for ammonium and Gln were significantly higher compared to roots of the *Picea* monoculture stand and to *Larix* in the mixed *Larix* + *Quercus* stand ($p \leq 0.037$; Fig. 2; Supplementary Figure S2). Similarly, uptake capacity of *Larix* in monoculture for Arg was higher compared to *Picea* in monoculture ($p = 0.041$; Fig. 2; Supplementary Figure S2). Uptake capacities of ammonium were lower compared to nitrate and organic amino acids (i.e. Arg and Gln) ($p \leq 0.033$; Fig. 2). Moreover, similar patterns of amino acid C uptake compared to amino acid N uptake capacities in roots were observed across forest stands (Supplementary Figure S3).

Soil total N, organic carbon and microbial biomass C and N

Soil total N (TN) and soil organic C (SOC) concentrations were highest in upper soil levels in the *Larix* monoculture stand ($p < 0.01$; Fig. 3). In the monoculture stand of *Larix*, both parameters decreased with increasing soil depth. However, a significant decline with increasing soil depth was not observed in the *Picea* monoculture and the mixed *Larix* + *Quercus* stands (Fig. 3). Furthermore, there was no

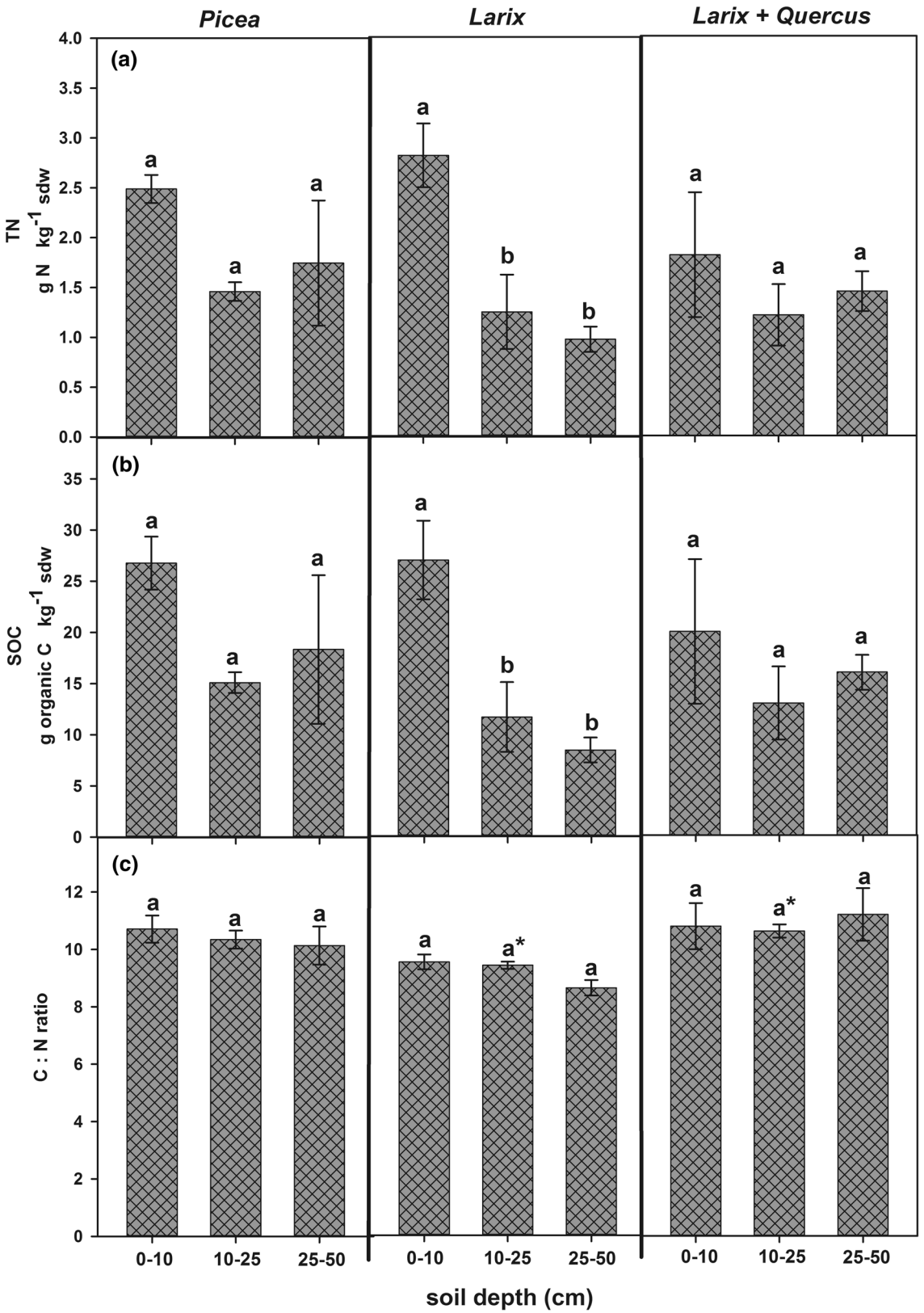

Fig. 3 Soil total N (TN), soil organic C (SOC) concentrations and C:N ratio status. *Vertical bar* charts show mean values ($n=3$) and standard errors. *Different small letters* indicate significant difference between different depths on the same stand, and * on different stands on the same depth ($p \leq 0.05$)

effect of soil depth on soil C:N ratio in the three monoculture and mixed stands (Fig. 3). At the soil depth level of 10–25 cm, the *Larix* monoculture stand showed a lower soil C:N ratio compared with the *Larix*+*Quercus* mixed stand ($p < 0.01$; Fig. 3).

Most of the plant available nitrogen in the soil was present in microbial biomass (MBN) (Fig. 4). While N concentrations of MBN were not significantly different between stands at the same soil depths, N concentrations in MBN decreased with increasing soil depth in all investigated stands ($p < 0.01$; Fig. 4). These decreases were less pronounced in soil from the *Larix*+*Quercus* stand compared to the monocultures (Fig. 4). Independent of soil depth, all other plant available N fractions were extremely low at all stands except for nitrate in the mixed *Larix*+*Quercus* stand ($\leq$5.3 mg N kg^{-1} sdw; Fig. 4). At this stand, nitrate in the upper soil layer was considerably higher compared to the soil of the monocultures, but decreased with increasing soil depth ($p < 0.033$; Fig. 4). Despite this decrease, nitrate was highest at the mixed *Larix*+*Quercus* stand irrespective of soil depth ($p < 0.017$; Fig. 4).

Also C in the soil was mostly present in microbial biomass (MBC) (Fig. 5). However, different to MBN, soil MBC did not decrease significantly with increasing soil depth down to 50 cm in the *Picea* monoculture and the mixed *Larix*+*Quercus* stand (Fig. 5). Only in the *Larix* monoculture stand, soil MBC was lower compared to the other stands at each soil depth and decreased with increasing soil depth ($p < 0.01$; Fig. 5). Similar low DOC concentrations of the soil were observed for all stands independent from soil depth ($\leq$45 mg C kg^{-1} sdw; Fig. 5).

Discussion

Comparison of root N concentration and N uptake capacity

Root N concentrations of the investigated tree species of the Qinling mountains are relatively low (mean: <8.7 mg g^{-1} dw) compared to other tree species (i.e. ca. 12.6 mg g^{-1} dw in the fine roots of *Fagus sylvatica*; ca. 17.3 mg g^{-1} dw in the fine roots of *Acer pseudoplatanus*; ca. 21.4 mg g^{-1} dw in the fine roots of *Acer saccharum* and *Fraxinus americana*) in N-limited temperate forest ecosystems and in experiments with N-limited soil under controlled conditions (e.g. Pregitzer et al. 1997; Dannenmann et al. 2009; Simon et al. 2010, 2011, 2014). These low root N concentrations are consistent with the results on N acquisition from the soil.

Net uptake rates of inorganic and organic compounds of the investigated tree species in the Qinling Mountains were considerably lower than observed for other temperate forest ecosystems with the same approach (uptake rates for $^{15}NH_4^+$-N: ca. 3.4 vs 3010.2 nmol g^{-1}fw h^{-1}; for $^{15}NO_3$–N: ca. 80.8 vs 8010.4 nmol g^{-1}fw h^{-1} and for Gln–^{15}N: ca. 61.5 vs 13750.2 nmol g^{-1}fw h^{-1} in *Fagus sylvatica* as reported by Gessler et al. (1998); Simon et al. (2011); Fig. 2; Supplementary Figure S2) suggesting site differences of N uptake capacity. Moreover, this study shows a lower NH_4^+ uptake capacity of the roots of all species compared to nitrate and organic N uptake capacity (Fig. 2). Similar results were obtained for a number of tree species, both conifers and deciduous trees (e.g. uptake rates of ca. 30,000 nmol g^{-1}fw h^{-1} for $^{15}NH_4^+$–N, <8000 nmol g^{-1}fw h^{-1} for $^{15}NO_3$–N and 13,800 nmol g^{-1}fw h^{-1} for Gln–^{15}N in *Fagus sylvatica*; ca. 24.8 nmol g^{-1}fw h^{-1} for $^{15}NH_4^+$–N, <110.3 nmol g^{-1}fw h^{-1} for Arg– and Gln–^{15}N in *Pinus sylvestris*) (Fig. 2; Supplementary Figure S2; Dannenmann et al. 2009; Simon et al. 2010, 2011, 2013, 2014; Schulz et al. 2011). However, ammonium concentration in the artificial soil solution was relatively low and higher net uptake rates may develop, if higher amounts of ammonium are available (Gessler et al. 1998; Stoelken et al. 2010). Ammonium and organic N uptake capacities (i.e. Arg- and Gln-N) were significantly higher in *Larix* compared to *Picea* monocultures indicating differences in inorganic and organic N acquisition capacity between the two native and introduced tree species investigated, particularly because all species were in the exponential stage of growth (Habib et al. 1989). It appeared that the root system of the introduced conifer species (*Larix*) had a superior N acquisition strategy compared to the native conifer species (*Picea*) in adaption to the limited N availability.

Comparing the introduced species *Larix* in monoculture and mixed stand, the N acquisition strategy appeared to shift depending on the presence of *Quercus*. In monoculture, Gln-N uptake capacity was higher, whereas Arg-N uptake capacity was lower compared to the mixed stand (Supplementary Figure S2). Former studies of two beech forest sites on calcareous soil in southern Germany differing in elevation by ca. 350 m did not show significant differences in N uptake capacity (Simon and Rennenberg, unpublished results). The mean daily air temperature between the two forest sites differed ca. 1.6 °C in the month of harvest (Table 1). According to the dependency of N uptake rates on temperature as reported by Gessler et al. (2005), a decrease (−) in N uptake capacity of ca. 18.6% from the lower (warmer) to the higher (colder) study site would be expected. However, the present results show an increase (+) for $^{15}NH_4^+$-N of (+) 26.8%, for $^{15}NO_3$–N of (+) 23.5% and for Gln-^{15}N of (+) 57.9%. For Arg–^{15}N a decrease was observed, but with (−) 87.6%, this decrease was much higher as expected from the temperature dependency of uptake capacity. Therefore, the differences in N uptake capacity between the monoculture and the mixed

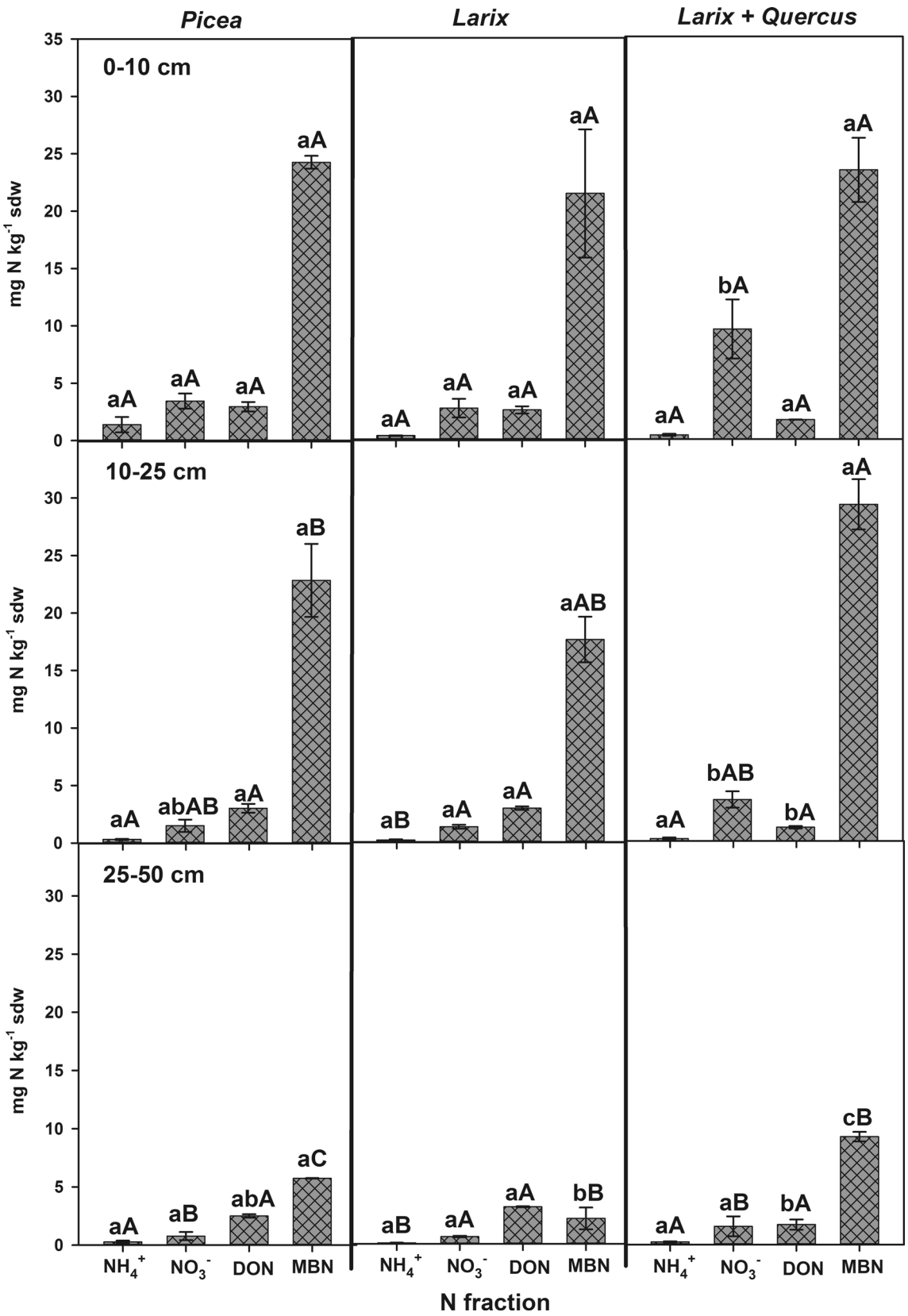

Fig. 4 Plant available N in different soil fractions. *Vertical bar* charts show mean values ($n=3$) and standard errors. *Different small letters* indicate significant differences between different stands on the same soil depth, and *different capital letters* between different soil depths of the same stand ($p \leq 0.05$)

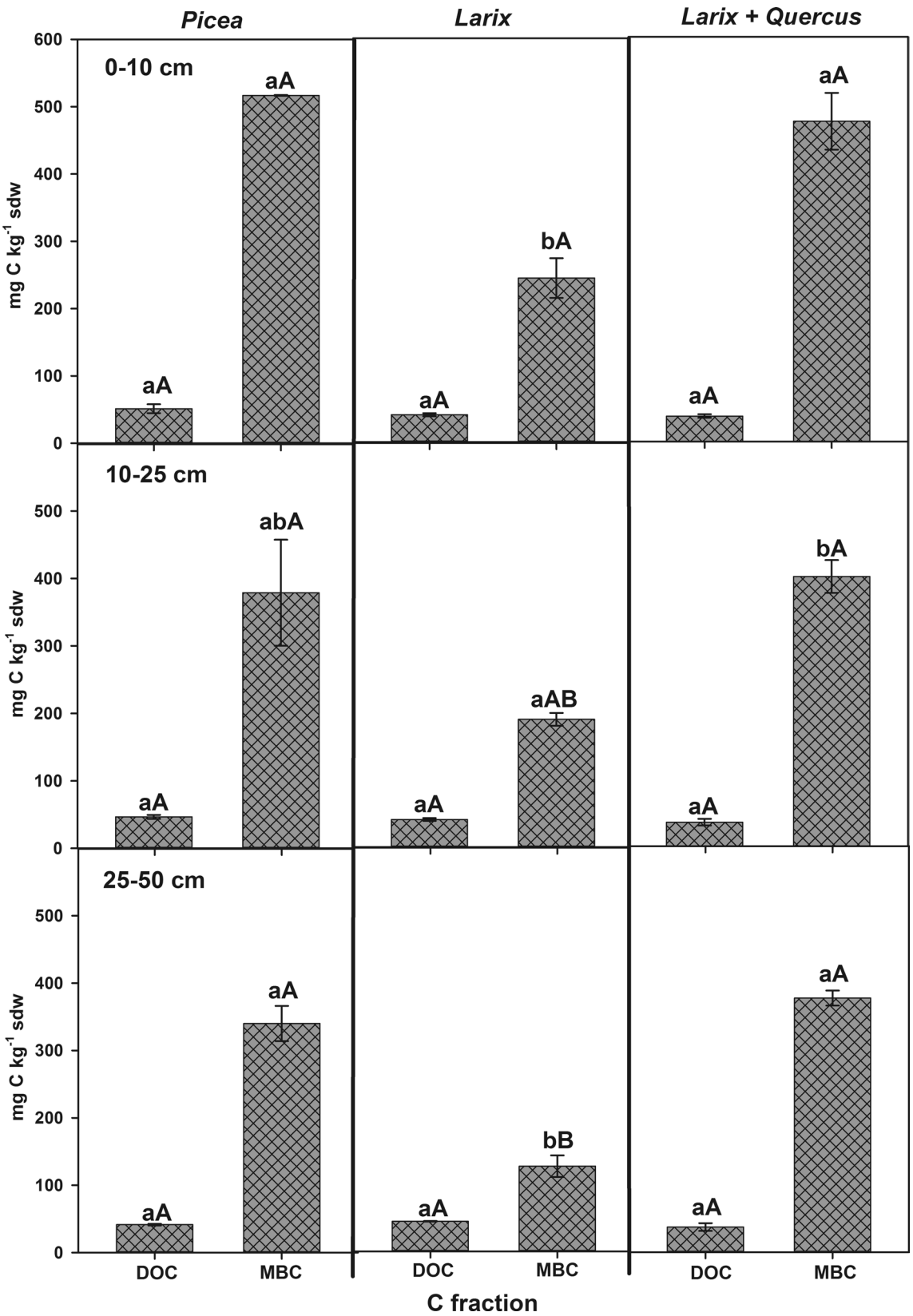

Fig. 5 Dissolved organic carbon (DOC) and microbial biomass carbon (MBC) in different soil fractions. *Vertical bar* charts show mean values ($n = 3$) and standard errors. *Different small letters* indicate significant differences between different stands on the same soil depth, and *different capital letters* between different soil depths of the same stand ($p \leq 0.05$)

culture stands cannot be explained by differences in elevation. They are likely caused by the presence of a competitor in the mixed stand that may have altered the N acquisition strategy, as previously observed for the competition between beech and maple seedlings (Simon et al. 2010, 2014).

The availability of N sources in the soil solution varies by orders of magnitude within sites, between sites and over short periods of time. Thus, matching concentrations are impossible to achieve in uptake experiments. Furthermore, former study showed that using equal concentrations of N sources will neglect the interaction of different N sources in N uptake rates (e.g. Stoelken et al. 2010). In addition, it is a matter of current debate to which extent N abundances in the soil solution reflect N abundances at the site of N uptake by the roots. Therefore, the approach used in the present study is a compromise between these constraints and the current knowledge of N sources in the soil of ecosystems with low N availability (Gessler et al. 2005). This information was the basis for the different N concentrations used in the present root uptake experiment. Thus, the data presented in the present study can only be used for comparison of processes, not for the absolute quantification of N fluxes at the tree, ecosystem or landscape levels.

Influences of tree species on soil available N and C

The present results show that, for the Qinling Mountain forests, either soil NH_4^+ (<2.0 mg N kg^{-1}) or NO_3^- (<4.0 mg N kg^{-1}) concentrations (Fig. 4) were lower than for other Chinese forest sites (Li et al. 2001; Yang et al. 2010; Zhang et al. 2013). For example, Zhang et al. (2013) determined soil NH_4^+ and NO_3^- of multiple forest types across Northern (8 sites) to Southern China (17 sites) and reported two times lower soil NH_4^+ concentrations for Northern forest soils (0.5 to 31.9 mg N kg^{-1}, mean: 12.2 mg N kg^{-1}) than for Southern forest soils (2.1 to 93.2 mg N kg^{-1}, mean: 22.4 mg N kg^{-1}). In turn, soil NO_3^- concentrations were higher in Northern forest soils (mean: 24.3 mg N kg^{-1}) than in Southern forest soils (mean: 5.8 mg N kg^{-1}). Zhang et al. (2013) assumed that a higher loss of NO_3^- by leaching due to the larger precipitation in Southern China as compared to Northern China is a main driver for the differences in soil NH_4^+ and NO_3^- concentrations among northern and southern forest sites. This assumption could also explain the findings in the present study, because the climate conditions of low temperature (mean: 6–11 ◦C) and high precipitation (mean: 980 mm $year^{-1}$) at the experimental sites likely result in a relatively slow soil N transformation, but a high N loss by leaching. Thus, the present observations of soil N status indicate N limitation of the soil at forest sites in the Qinling Mountain region of China. Moreover, a similar trend was also found for root N concentrations, i.e. lower root N concentrations in the Qinling Mountain compared to tree species from other N-limited temperate ecosystems. Together, our findings suggest a severe reduction in N availability in the Qinling Mountain region compared with other N-limited forest ecosystems as also reported by Chang et al. (1995) and Bradley et al. (2000).

Moreover across different soil depths, the mixed stands of *Larix* and *Quercus* seemed to accumulate more plant available N through the whole soil profile as compared to the pure *Larix* stand (Fig. 4). In general, soil N stores in deeper soil layers tend to be lower than in upper soil horizons. Moreover, except for the *Picea* stand, soil C storage in the surface soil layer (0–10 cm) was all higher than for deeper soil layers, indicating that the top soil layers may sequester more organic carbon in soils due to a positive feedback effect of plant litter decomposition (e.g. Chen et al. 2002). Nevertheless, we found more carbon accumulated in the soil layer of 10–25 cm in the *Picea* stand and the mixed stand of *Larix* and *Quercus*, indicating species-specific differences in soil C sequestration between different stands.

The present study was not specifically designed to address the mechanisms of soil C and N distribution, but several potential mechanisms could explain the observed patterns. Leaching of DOC and mineral N compounds from the forest floor is a pathway for C and N to enter deeper soil horizons (Froberg et al. 2006). However, significant differences in DOC and MBC, and in the concentration of plant available N compounds (NH_4^+, NO_3^-, DON and MBN) of different mineral soil layers were not found for different stands (Figs. 4, 5). Thus, hydrological transport (e.g. leaching) was probably not the most important factor for the differences in C and N distribution in mineral soil horizons at the different stands. Therefore, the differences of soil C and N along the different soil layers may be a consequence of differences in root distribution between different species (e.g. Yang et al. 2009). In this context, root litter may contribute an amount of organic C to the soil C pool that equals that in foliar litter fall as reported by several *in situ* root growth and incubation (i.e. free mixing of plant residues into soil or litter bag experiments) studies (Rasse et al. 2005). It can therefore be expected that the roots of different species contributed differently to soil C and N storage in particular mineral soil layers. In the present study, soil C and N storage in the 0–50 cm soil profile was still comparable across the three forest stands (Fig. 3).

Plant litter quality and quantity of different species contribute to the size and quality of soil N pools (e.g. Giardina et al. 2001). For example, Neirynck et al. (2000) found that soil N pools of a maple forest were much higher compared to a nearby beech forest, indicating that maple litter has a relatively faster decomposition rate compared to beech

litter and more N compounds from maple litter decomposition were incorporated into soil N pools. In addition to different litter decomposition rates, tree species also have specific capacities in the uptake of soil available C and N compounds, which in turn can also influence soil C and N pools in forest soil (Vesterdal et al. 2008). Thus, the low C/N ratios in the soil observed in the present study can also be a consequence of low quality plant litter of the investigated species (e.g. Yang et al. 2009; Manzoni et al. 2010). Nevertheless, the relatively low microbial biomass N concentrations (e.g. ca. ≤8.0 vs ca. 40 mg N kg^{-1} sdw in soils of Northeast China as reported by Yang et al. (2010); Fig. 4) in our study may suggest an enhancement of N immobilization by soil microbes (Mooshammer et al. 2014).

Conclusions

The present results demonstrate that the roots of the native and introduced species studied are capable to take up both, organic and inorganic N sources, but prefer organic (Gln- and Arg-) over inorganic NH_4^+-N, as previously reported for other tree species in the field (Dannenmann et al. 2009; Simon et al. 2011) and under controlled conditions (Stoelken et al. 2010). The roots of the introduced species (*Larix*) showed a superior N acquisition strategy compared to the native *Picea* species in adaption to N-limited conditions. Moreover, native and introduced species did not show different influences on soil properties, whereas mixed plantation of species seems to improve soil C and N retention capabilities. This result cannot be explained by the difference in elevation of the study site because of only small differences in precipitation and temperature. Our results suggest that the introduced conifer species (*Larix*) could be considered as a suitable candidate for future afforestation programs and indicate that a mixed forest structure of conifers with broadleaved tree species such as *Quercus* could be beneficial to restore soil fertility of degraded forests (Pandey et al. 2007; Wang et al. 2008). However, in the present study stands with a mixture of only two tree species were analysed. Thus, future studies should consider more complex mixtures of dominant tree species including introduced species at a set of similar sites (a) to enhance knowledge of candidate tree species for selection in afforestation programs, (b) to elucidate the significance of mixed stand structure for forest management approaches in this region in more detail, and (c) to design concepts to stabilize the forest ecosystems for sustainable development.

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Author Contributions BH, MH Zh, JS, SX Zh and HR designed the experimental setup, BH, MH Zh, SB, XP Liu, LH, HCh, SX Zh and JS implemented it in the field, BH, MH Zh, MD, SB, SA and JS analysed the root and soil samples in the laboratory and drafted the paper. BH, MH Zh, BB, KBB and HR have contributed significantly to the data analysis, discussing the results, writing and reading of the paper.

Compliance with Ethical Standards

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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