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MARSCHNER REVIEW

Nitrogen nutrition of beech forests in a changing climate: importance of plant-soil-microbe water, carbon, and nitrogen interactions

Judy Simon · Michael Dannenmann · Rodica Pena · Arthur Gessler · Heinz Rennenberg

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Abstract

Background For 15+ years, a beech (*Fagus sylvatica* L.) dominated forest on calcareous soil was studied on two opposing slopes with contrasting microclimate in Tuttlingen, Swabian Alb, Germany. The cool-humid NE aspect of these slopes represents the majority of beech forests under current climate, the warmer and drier SW aspect represents beech forests under future climate conditions. The field studies were supplemented by investigations under controlled conditions.

Scope The research program aimed to provide a comprehensive understanding of plant-soil-microbe water, carbon and nitrogen feedbacks in a changing climate and a holistic view of the sensitivity of beech to climate change.

Conclusions The results of comparative and experimental studies underpin the high vulnerability of adult beech and its natural regeneration on calcareous soil to both direct climate change effects on plant physiology and indirect effects mediated by soil biogeochemical cycles. Mechanisms contributing to this vulnerability at the ecosystem and organismic level indicate a high significance of competitive interactions of beech with other vegetation components and soil microbial communities. Obvious forest management practices such as selective felling did not necessarily counteract negative effects of climate change.

Keywords Climate extremes · Competition · Forest management strategies · Girdling · Rhizodeposition and mycorrhiza · Thinning

Introduction

Together with a significant increase in atmospheric surface temperature, global climate change has already caused considerable changes in precipitation amount, intensity and geographic as well as seasonal patterns with comparable or stronger alterations to be expected in the future (IPCC 2007, 2013). In Central Europe, a decrease of summer precipitation by 9–41% is projected

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J. Simon (✉)
Ecology, Department of Biology, University of Konstanz,
Universitätsstrasse 10, 78457 Konstanz, Germany
e-mail: judy.simon@uni-konstanz.de

M. Dannenmann
Institute of Meteorology and Climate Research – Atmospheric Environmental Research, Karlsruhe Institute of Technology,
Kreuzeckbahnstrasse 19, 82467 Garmisch-Partenkirchen,
Germany

R. Pena
Forest Botany and Tree Physiology, Georg-August Universität
Göttingen, Büsgenweg 2, 37077 Göttingen, Germany

A. Gessler
Swiss Federal Research Institute WSL, Zürcherstrasse 111,
8903 Birmensdorf, Switzerland

H. Rennenberg
Chair of Tree Physiology, Institute of Forest Sciences,
Albert-Ludwigs-University Freiburg, Georges-Köhler-Allee 53/
54, 79110 Freiburg, Germany

until 2070 (Frei 2004), as well as an increase in frequency and intensity of extreme events, such as local heavy rain and flooding or exceptionally hot and dry summers (Coumou et al. 2013; Feldmann et al. 2013; Wagner et al. 2013). Such climate extremes already occurred, e.g. in 2003 and 2015 (Ciais et al. 2005; Deutscher Wetterdienst 2015) and might provide a hint at the future situation. In forest ecosystems, these environmental changes resulted in direct negative effects of changes in precipitation and temperature on water relations and carbon (C) assimilation of trees (Leuschner et al. 2001; Ciais et al. 2005; Rennenberg et al. 2006; Nahm et al. 2007) increasing the risk of tree mortality by hydraulic failure and C starvation (e.g. McDowell et al. 2008). Drought and heat can also have indirect negative impact on tree functioning and survival mediated by their effects on mineral nutrition and ecosystem nutrient cycling (Rennenberg et al. 2006, 2009; Nahm et al. 2007; Dannenmann et al. 2016; Gessler et al. 2016). Together, these direct and indirect effects of global climate change are projected to cause forest productivity to decline in future (IPCC 2007, 2013), particularly for European beech (e.g. Weemstra et al. 2013; Zimmermann et al. 2015; Levesque et al. 2016). A meta-analyses by Charru et al. (2017) including data over a period of 25 years suggests that rapid changes in climate can affect forest growth strongly, and already today for species of the Mediterranean, whereas species in colder habitats showed moderate to no responses, indicating the importance of environmental conditions when conducting studies.

European beech (*Fagus sylvatica* L.), the potential natural vegetation and the most abundant broad-leaved tree species in Central Europe (Ellenberg and Leuschner 2014), is particularly affected by these environmental changes. The distribution of beech is limited on the one hand by excess soil moisture in riparian floodplain forests, on the other hand by drought in southern Europe (Ellenberg and Leuschner 2014) indicating the high sensitivity of this tree species to both, high and low water availability. Already today, the geographic distribution of beech is changing towards adequate water supply, either to higher elevation or to Northern Europe (Kramer et al. 2010). At its southern – drier – distribution limit, beech is in the process of being replaced by more drought-tolerant oak species (Falk and Hempelmann 2013; Hanewinkel et al. 2013; Rasztovits et al. 2014). Still, there are also reports indicating that beech trees can be reasonably resistant and resilient towards drought (e.g. Tegel et al. 2014; Hentschel et al. 2016).

Although many studies have investigated the consequences of climate change on single players in forest ecosystems, e.g. focusing on tree morphological and/or physiological responses or potential changes in soil microbial processes and ecosystem N cycling, only little is known how the different players in forests interact. Thus, an interdisciplinary research program was set up in the late 1990ies investigating the mechanisms responsible for the direct and indirect consequences of climate change on beech forest ecosystems in Central Europe. The program focused on water relations and ecosystem nitrogen (N) cycling at a mature beech forest site with significant natural regeneration on calcareous soil in Tuttlingen, Germany. Field investigations were supplemented by studies with beech seedlings under controlled conditions in greenhouse environments. Beech on calcareous soil was chosen, because it represents more than 30% of the potential beech forest area in Europe and is characterized by a high sensitivity to drought because of the relatively low water and nutrient availability (Tarp et al. 2000; Dannenmann et al. 2016). N availability at the field site is very low due to shallow soils and low atmospheric N deposition (<10 kg N ha^{-1} year^{-1}), thereby providing ideal conditions to study the significance of N in ecosystem water, C, and N feedbacks. The present review summarizes the results of the studies performed in the context of this program over almost two decades. Within this program, four main research questions were addressed: (1) What are the drivers of competition for N between different players (i.e. plants vs. soil microbes, plants vs. plants in N-limited forest ecosystems? (2) How does climate change (i.e. drought, enhanced temperature) affect the competition for N and its underlying mechanisms? (3) How is N linked to C at the tree and ecosystem scale in the view of climate change? (4) Can thinning as a forest management strategy increase the resistance and resilience of beech stands in a changing climate?

Research approaches

To gain insight into the drivers of competition for N between the different players in a beech forest on N-limited soil (aim 1), soil N pools and processes of N turnover and cycling were characterized and quantified simultaneously with plant processes (e.g. Dannenmann et al. 2009, 2016; Rennenberg and Dannenmann 2015).

Mechanisms involved in the competition between beech seedlings and the soil microbial community were studied in an aeroponic root fumigation system and in microcosms in the greenhouse (Simon et al. 2009, 2013; Dong et al. 2015). Using ^{15}N–labeled leaf litter (Guo et al. 2013a) its fate was studied in beech natural regeneration, mycorrhizal association, and soil. Further greenhouse studies addressed the competition for N between beech and maple, a tree species co-occurring with beech on calcareous soil (Simon et al. 2010, 2014; Li et al. 2015), and the consequences of sequential removal of components of the understorey vegetation on N nutrition of beech natural regeneration were studied (Simon et al. 2011). The consequences of climate change (i.e. drought, enhanced temperature) on the competition for N and its underlying mechanisms (aim 2) were studied primarily in the field using a "space for time study" approach (e.g. Blois et al. 2013). In this study, ecophysiological and growth parameters of adult beech trees and their natural regeneration, soil microbial, biochemical as well as meteorological parameters were compared between the relatively cold and humid NE aspect, and the relatively warm and dry SW aspect of the Tuttlingen research site (Gessler et al. 2001, 2005; Fotelli et al. 2002a, 2003, 2004; Grayston and Rennenberg 2006; Nahm et al. 2006; Holst et al. 2010; Bilela et al. 2012). These studies included the application of inorganic ^{15}N label (Fotelli et al. 2004), current and retrospective analyses as well as modeling of water relations and growth of adult beech trees (Gessler et al. 2001; Keitel et al. 2003; Holst et al. 2010; Offermann et al. 2011; Hentschel et al. 2016). To further elucidate the consequences of a warm and dry climate on ecosystem N cycling, soil monoliths containing beech natural regeneration were transferred from the NE to the SW slope and subjected to water deprivation using a roof construction (Bimüller et al. 2014; Dannenmann et al. 2016). At the field site, distribution of N in different components of understorey vegetation and natural regeneration was compared between the NE and SW slopes (Fotelli et al. 2003). Under controlled conditions, competition for water and N between beech seedlings and an early successional woody species (Fotelli et al. 2001, 2002b, 2005) was studied in the greenhouse. In addition, the significance of mycorrhizal association for drought-N interactions in beech seedlings was investigated in the greenhouse (Pena et al. 2013a; Leberecht et al. 2015). Furthermore, a mesocosm study was conducted to analyze the consequences of water deprivation on the distribution of N from ^{15}N–labelled leaf and root litter between beech seedlings and microbial biomass (Guo et al. 2013b). Consequences of drought-mediated reduction in carbohydrate allocation to the roots (aim 3) were studied at the NE aspect of the field site by girdling adult beech trees, analyzing microbial and plant N relations as well as mycorrhizal biodiversity and bacterial abundance (Dannenmann et al. 2009; Pena et al. 2010) and were complemented by ^{13}C pulse labelling studies under controlled conditions (Ruehr et al. 2009; Winkler et al. 2010; Hommel et al. 2016). To elucidate the consequences to thinning as a strategy of forest management (aim 4), plots located on the two slopes were subjected to selective felling at two different intensities (Fotelli et al. 2002a, 2004; Gessler et al. 2005; Grayston and Rennenberg 2006; Nahm et al. 2006; Dannenmann et al. 2006, 2007a, b, 2008).

Site characteristics

The Tuttlingen beech forest research site is located in southern Germany, approx. 100 km south-south-west from Stuttgart at 8°40′E 48°00′N. The site is part of the low mountain range of the Swabian Jura at 740–760 m a.s.l. with a mean annual air temperature of 6.6 °C, recorded at a climate station of the Deutscher Wetterdienst in Tuttlingen, approx. 5 km from the experimental sites (Gessler et al. 2001). Average annual precipitation amounts to 856 mm with monthly maxima in June and July. During the growing season (May to October) mean air temperature is 11.5 °C and mean precipitation is 410 mm (Gessler et al. 2001). Potential evaporation could exceed precipitation in July and August (Gessler et al. 2001; Fotelli et al. 2002a).

The experimental areas are located on two opposing slopes – less than 1000 m apart – of a single narrow valley (Gessler et al. 2005). One slope represents a north-east (NE), the other a south-west (SW) aspect. Precipitation does not vary significantly between these aspects across the valley (Gessler et al. 2004; Nahm et al. 2006). On both slopes, the soil is a *Terra fusca – Rendzina* or a *Rendzic Leptosol* – according to the International Union of Soil Sciences Working Group WRB (WRB 2007) – derived from limestone (White Jura beta and gamma series) (Bimüller et al. 2013). Soil pH (H_2O) is c. 5.7 in the organic surface layer and 7.6 at 60 cm soil depth; soil profiles are shallow with an average depth of the topsoil of less than 20 cm before dominated by parent rock, interspersed with pockets of organic matter and mineral soil (Bimüller et al. 2013). At the SW aspect, the soil is particularly rocky containing, on a volumetric basis, more than 40% rocks and stones of more than 63 mm diameter in the topsoil (top 20 cm) increasing to c. 80% below 50 cm soil depth (Nahm et al. 2006). At the NE aspect, the topsoil up to 20 cm contains c. 15% rocks and stones, increasing to approx. 30% below 50 cm (Nahm et al. 2006). Both slopes are moderately steep with 58–100% inclination at the NE and 36–58% at the SW aspect (Gessler et al. 2001; Fotelli et al. 2002a).

The difference in aspect (NE versus SW) results in a difference in radiation interception at the canopy level. Maximum daily radiation above the canopy at the NE aspect amounts to 79% and 47% of the radiation available at the SW aspect in July and October, respectively (Gessler et al. 2001). At the forest floor, radiation does not vary significantly between the two slopes. Retrospective analyses of meteorological data, growth and water status of adult beech trees and beech seedlings indicate that vegetation on the SW slope permanently experiences lower water availability and higher air temperatures than vegetation on the NE slope (Gessler et al. 2001). As a consequence, the understorey vegetation differs between the two slopes and has been classified as *Hordelymo-Fagetum* on the NE and as *Carici-Fagetum* at the SW aspect (Gessler et al. 2001, 2005; Fotelli et al. 2002a, 2004; Keitel et al. 2003).

At both slopes, adult European beech (*Fagus sylvatica* L.) developed from natural regeneration after a complete clear-cutting in the 1920–1930s with no further interference (Paul 1998) and constitutes the dominant tree species contributing more than 90% to the total basal area of the adult trees (Nahm et al. 2006). The average age of adult beech trees was 70–80 years at the beginning of the research program in the late 1990ies (Nahm et al. 2006). Both sites are characterized by natural regeneration of beech. Genetic analyses by microsatellite and isozyme markers showed that the natural regeneration of the populations on both slopes and adult trees at the NE aspect were genetically closer than the adult trees on the SW aspect (Bilela et al. 2012). Apparently, natural selection and potential adaptation at the SW aspect account for genetic changes and different genetic structures of the adult populations on the two opposing slopes. Thus, differences in growth and functioning of the understorey should be mainly attributed to phenotypic acclimation, whereas differences in the adult trees might be at least partially attributed to microevolutionary processes due to local adaptation and environmental filtering. Still, differences among beech ecotypes in their response towards drought are small compared to the general species-specific drought effects (e.g. Arend et al. 2016). Thus, the general conclusions on drought responses of beech drawn here will be not affected by genetic differentiation. Fine roots of adult beech trees and natural regeneration were c. 97% mycorrhizal and *Coenococcum geophilum* was the most abundant fungal species (Pena et al. 2010, 2013b).

At each slope, the experimental design consisted of two blocks. In each block, two silvicultural thinning treatments plus an untreated control were established with approx. 0.53 ha each. Basal area of the trees (BA) of the untreated control plots differed between the slopes and amounted to 27 m^2 ha^{-1} at the NE and 20 m^2 ha^{-1} at the SW aspect (Nahm et al. 2006). At both slopes, two thinning treatments reduced BA to 15 m^{-1} ha^{-1} and 10 m^{-1} ha^{-1}, respectively (Nahm et al. 2006). Thinning reduced the leaf area index (LAI) in the first year from 5.16 to 3.15 (BA 15 m^{-1} ha^{-1}) and 1.68 (BA 10 m^{-1} ha^{-1}), respectively, on the NE slope and from 5.12 to 3.24 (BA 15 m^{-1} ha^{-1}) and 2.12 (BA 10 m^{-1} ha^{-1}), respectively, on the SW slope (Nahm et al. 2006). Due to the thinning treatments, radiation at the forest floor increased, but to a higher extent at the SW than at the NE aspect. As a consequence, the thinned plots experienced consistently higher daily mean temperature of surface air and soil compared to the untreated control plots (Holst et al. 2004). One year after thinning, vegetation density of other than beech natural regeneration increased in the understorey by approx. 25% on the NE and approx. 8% in the SW aspect (Gessler et al. 2001; Fotelli et al. 2002a, 2003; Keitel et al. 2003).

Ecosystem functioning at present climate - Drivers of competition for N between different players

Soil N pools and processes of N turnover and cycling

Soil N pools

In terrestrial forest ecosystems not receiving chronic and excessive atmospheric N deposition, N availability (Wang and Houlton 2009; De Vries et al. 2013; Zaehle 2013) besides water supply (Rosegrant et al. 2009; Strzepek and Boehlert 2010; Mekonnen and Hoekstra

2014) is considered the main limiting factor for plant growth and development, as well as for C sequestration and storage on large spatial scales. In particular, the widespread beech forests growing on marginal calcareous soil (i.e. usually Rendzic Leptosols) have a relatively high N demand of c. 100 kg N ha^{-1} $year^{-1}$ (Rennenberg and Dannenmann 2015) raising questions towards the bioavailability of N in Rendzic Leptosol soils. In these forests, the N demand is met almost exclusively by internal sources (Rennenberg and Dannenmann 2015) – such as the degradation of plant litter as well as decaying microbial biomass.

Generally, these soils store large amounts of N due to their high content of organic matter despite their shallow profile. For example, the entire soil profile of the Tuttlingen experimental beech forest stores 5659 ± 1036 kg N ha^{-1} in soil organic N stocks (Rennenberg and Dannenmann 2015). However, these N stocks consist of polymeric organic N compounds largely bound to the clay fraction (Bimüller et al. 2014) and, thus, are unavailable for plant uptake, in contrast to dissolved monomeric organic N (DON) (Näsholm et al. 2009) and inorganic N (DIN) forms. Based on soil extractions using 1 M KCl, the soil ammonium and nitrate stocks in the Tuttlingen soil were only 3.2 ± 0.5 and 1.3 ± 0.6 kg N ha^{-1}, respectively, (Rennenberg and Dannenmann 2015). Such soil extractions might not accurately represent inorganic N availability for plants in particular with regard to NH_4^+-N because fractions bound to the soil matrix might be included. On the other hand, part of the NH_4^+-N extracted from cation exchange sites might be plant-available due to mobilization through exchange processes in the rhizosphere. NH_4^+ concentrations in soil solution collected with suction cups never exceeded the detection limit of 0.1 mmol m^{-3}, whereas NO_3^- concentrations ranged from 0 to 500 mmol NO_3^- with the highest values found under canopy gaps (Gessler et al. 2005). Hence, NH_4^+-N from percolation water in macropores might rarely be available for root acquisition. In natural or semi-natural intact plant-soil systems such as the Tuttlingen research site, this might also be related to the very tight coupling of microbial ammonification and NH_4^+ consumption via both heterotrophic microbial immobilization and autotrophic nitrification, strongly reducing the mean residence time of NH_4^+ in soil to few hours or days (Dannenmann et al. 2006). In conclusion, nitrate is very likely the dominant mineral N form available for plant N uptake from Rendzic Leptosol at the Tuttlingen field site, which is consistent with the general tendency of plants growing in calcareous soil to prefer nitrate over ammonium (e.g. Marschner 1995).

Information on DON availability (incl. monomeric substances such as amino acids and amino sugars) in the soil at the Tuttlingen forest is available only for soil extractions with 0.5 M K_2SO_4 and for a restricted number of sampling dates (Dannenmann et al. 2009; Simon et al. 2011). Based on these data, DON stocks were estimated to be 11.5 ± 3.8 kg N ha^{-1}, thus exceeding DIN stocks by a factor of 2.5. However, DON availability in mobile soil solution might be smaller than that estimated from soil extracts. The production of DON by depolymerization is considered as the bottleneck of the soil N cycle with tightly coupled gross microbial production and consumption (Schimel and Bennett 2004), exceeding plant N uptake by orders of magnitude (Rennenberg and Dannenmann 2015; Dannenmann et al. 2016), thus limiting N uptake by plants. Overall, N availability for trees in Rendzic Leptosols is low despite the large N stocks stored in soil organic matter.

Considering that the annual N demand of beech forests is relatively high (Rennenberg and Dannenmann 2015), but N deposition and soil N availability at the Tuttlingen forest site are relatively low, two mechanisms might explain this discrepancy: (1) The balance of gross microbial production and consumption both by microbes and trees affects the labile N pools in soils (which represent steady state concentrations), thus, not necessarily indicating the real N availability. Instead, a detailed quantification of gross process rates and competitive partitioning in the plant-soil microbe system is required, which is provided in the next chapters. (2) Trees are highly efficient in N resorption and remobilization from leaves etc. which might reduce N losses via litter (no data available).

N turnover and cycling

Despite the low labile bioavailable N concentrations in the soil (see "Soil N pools" section), the Tuttlingen Rendzic Leptosol shows large and tightly coupled gross N mineralization-immobilization turnover rates of c. five times that of tree N requirement. Overall, N mineralization of 550 ± 110 kg N ha^{-1} $year^{-1}$ is followed by ammonium partitioning to heterotrophic immobilization by free living soil microorganisms (c. 2/3) and autotrophic nitrification (c. 1/3), with only 8 kg N ha^{-1} $year^{-1}$

taken up by the beech stand (Rennenberg and Dannenmann 2015). Gross nitrate production is 242 kg N ha^{-1} year^{-1} with 91 kg nitrate-N taken up by the stand, 143 kg nitrate-N immobilized into microbial biomass and 6 kg nitrate-N undergoing denitrification with associated N_2O and N_2 gaseous emissions (Rennenberg and Dannenmann 2015). Denitrification roughly equals atmospheric N input and is completely dominated by N_2 losses with only insignificant emission of the greenhouse gas N_2O (Rennenberg and Dannenmann 2015). This is likely due to high N_2O reductase activity in these soils, favored by high pH values, and thus converting N_2O to N_2 in the terminal step of denitrification (Dannenmann et al. 2008). This pH effect on denitrification N gas product ratios has also been found for other ecosystems (Bakken et al. 2012; Butterbach-Bahl et al. 2013). In the Tuttlingen forest soil, fungi are predominantly responsible for the production of N_2O, whereas N_2O is mainly reduced by bacteria to N_2 in the terminal step of denitrification (Blagodatskaya et al. 2010). The contribution of mycorrhiza is estimated to be 7.5 kg N ha^{-1}, i.e. about 10% of total soil microbial biomass (Rennenberg and Dannenmann 2015), assuming an EM external mycelium biomass of 30 g m^{-2} (Hendricks et al. 2016) with 2.5% N content (R. Pena, pers. comm.). N leaching was not recorded in this stands situated on steep slopes with complex karst hydrology. Only for the N-saturated Höglwald spruce forest in Southern Germany, comparable information on annual gross N turnover is available (Kreutzer et al. 2009). In comparison, the beech forest in Tuttlingen with comparably low N availability shows lower annual gross nitrification, lower N_2O emissions and higher N_2:N_2O emission ratios. Furthermore, the large stocks of microbial biomass N (121 kg N ha^{-1}) indicate a very high activity in this shallow soil (Rennenberg and Dannenmann 2015).

A three-year *in situ* ^{15}N tracing study using ^{15}N–enriched beech leaf litter revealed that – despite a significant release of >50 kg N ha^{-1} year^{-1} – N sources from the previous year's leaf litter play only a minor role for N nutrition of beech (Guo et al. 2013b). In a microcosm experiment under controlled conditions using ^{15}N labelled root and/or ^{15}N labelled leaf litter, N derived from root litter was preferred over that derived from leaves by both beech and soil microorganisms (Guo et al. 2013a). In situ ^{15}N tracing released from labeled leaf litter also revealed a comparable rapid incorporation into the clay fraction in mineral soil mediated through microbial immobilization indicating the important role of microbial biomass in stabilization of litter-derived N in organo-mineral associations (Bimüller et al. 2013). These findings contradict the general view of ecosystem-internal N cycling, which is based on the assumption that N release from the previous year's leaf decomposition is important for the provision of bioavailable N to plants (e.g. Cotrufo et al. 2000). In contrast, the results from the Tuttlingen forest site suggest that beech relies more on N sources originating from root rather than leaf litter turnover, as well as microbial release of N sources not originating from litter turnover of the previous three years, but from sources such as older soil organic matter, atmospheric N input, or biological N fixation (BNF). The latter was quantified by incubating intact beech seedling-soil systems in an $^{15}N_2$-enriched atmosphere in the laboratory, which revealed a small BNF rate of c. 1 kg N ha^{-1} year^{-1} (Tejedor et al., unpublished results) confirming earlier estimates of BNF by free living microorganisms in temperate forests (Cleveland et al. 1999).

Overall, microbial mineralization-immobilization turnover largely dominates internal N cycling (Bimüller et al. 2013) as compared to plant-mediated pathways in the Tuttlingen beech forests. Furthermore, the ecosystem is characterized by effective closure of the N cycle, i.e. by removal of reactive N from the biosphere and reduction into harmless N_2. Thus, the Tuttlingen forest ecosystem represents a closed N cycle characterized by competitive N partitioning between beech and microbial N retention pathways without accumulation of inorganic N, despite very high N mineralization rates and also large gross nitrification.

Competition for N

Plants vs. soil microbes

Under low N availability, the demand for DIN and DON of plants with their associated mycorrhizal fungal symbionts as well as free living soil microorganisms results in competition for these resources (Kuzyakov and Xu 2013). Indeed, in a girdling experiment microbial N turnover and N pools and the competing plant N acquisition processes and N pools were negatively correlated suggesting strong competition for N between free living soil microorganisms and adult beech with the associated mycorrhizal fungal symbionts (Dannenmann et al. 2009; Fig. 1). In addition, the abundance of the

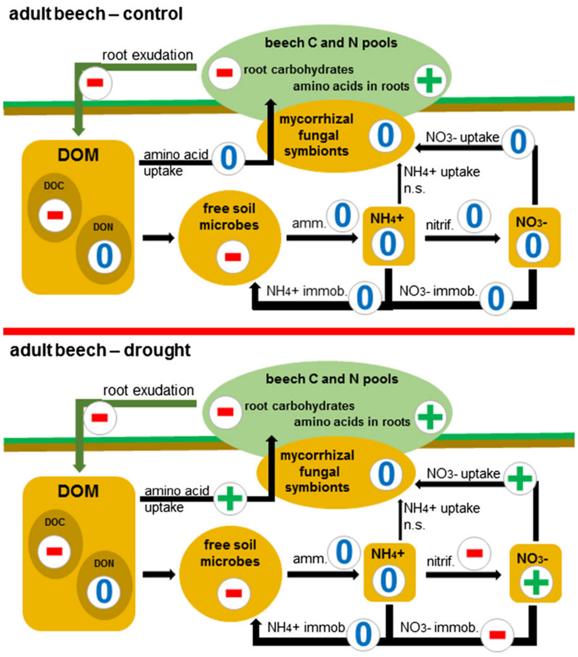

Fig. 1 Effects of girdling on adult beech – mycorrhiza – soil microbe – interactions. Consequences of drought-mediated reduction in carbohydrate allocation to the roots were studied by girdling adult beech trees, analyzing microbial and plant N relations as well as mycorrhizal biodiversity and bacterial abundance. Here, the significant differences between girdled compared to intact trees are shown ($p \leq 0.050$) under with sufficient (= control, top) and reduced water supply (bottom). Girdling represents a proxy of reduced water availability and its effects on C allocation to the roots. DOM = dissolved organic matter; DOC = dissolved organic C; DON = dissolved organic N; amm. = ammonification; nitrif. = nitrification; NH_4^+ immob. = NH_4^+ immobilization; NO_3^- immob. = NO_3^- immobilization; n.s. = not significant. Based on data from Dannenmann et al. (2009) and Pena et al. (2010)

dominant mycorrhizal fungus *Cenococcum geophilum* was negatively correlated to soil microbial biomass, but positively correlated to glutamine-N uptake of beech trees (Dannenmann et al. 2009; see also "Consequences of climate on soil processes" section). Furthermore, soil microbial N processes did not change over the seasonal course in response to removal of vegetation components; thus indicating that competition for N between soil microorganisms and beech trees was not avoided over the entire vegetation period regardless of tree age (Simon et al. 2011).

This competition for N between plants and soil microbes is indirectly influenced by the production of nitric oxide (NO) during auto- or heterotrophic nitrification using ammonium or organic N, or during denitrification (Robertson and Groffman 2005; Simon et al. 2013). Both, the microbial production of NO as well as tree N acquisition strongly depend on soil N availability (Dong et al. 2015). In comparison with N-limited forests in Northern and Central Europe, N saturated forests produce more NO (Butterbach-Bahl et al. 1997; Davidson and Kingerlee 1997) due to higher availability of inorganic N as a substrate for nitrifying and denitrifying bacteria (Kitzler et al. 2006). Overall, rhizospheric NO acts as a signaling substance that affects N uptake and N nutrition of trees regardless of species (e.g. deciduous or coniferous) and/or age (e.g. seedlings, mature trees) in the field and under controlled conditions (Simon et al. 2009, 2013; Dong et al. 2015, 2016; see Table 1). However, the extent of this influence strongly depends on tree species, soil N availability, rhizospheric CO_2 concentration, available N sources (Dong et al. 2015), and other environmental factors that are yet not fully understood (Dong et al. 2016; Table 1).

Mycorrhiza – competition or facilitation?

Unlike many free-living soil microbes, EM fungi are directly maintained by plant fixed C, and might facilitate plant N acquisition under nutrient poor conditions (Read and Perez-Moreno 2003; Helmisaari et al. 2009). EM fungi encapsulate each root tip by a mycelial mantle with hyphae that extend into the soil building up large networks (Simard et al. 2012). This maximizes the foraging capacities and nutrient acquisition (Pena 2016) by increased surface area and specific root lengths (Högberg 1989; van der Heijden and Kuyper 2003; Felten et al. 2009; Pena et al. 2013a). Additionally, EM fungi aid beech trees in N acquisition from organic sources (Dannenmann et al. 2009; Pena et al. 2013b; Leberecht et al. 2016). However, the general positive output of the EM association in terms of beech N nutrition might be questioned. A comparison between EM beech seedlings, colonized by native (Tuttlingen) fungal assemblages, and non-mycorrhizal beech trees grown on ^{15}N–ammonium as the sole N source indicated a negative influence of EM association on plant N uptake and a high N accumulation in EM root tips (Pena et al. 2013a) suggesting competitive interactions between plant and EM fungi. Another experimental approach showed the accumulation of NH_4^+-N in EM fungal colonized root tips and NO_3^--N in the plant (Leberecht et al. 2016) indicating competition avoidance between EM fungi and plants by complementary utilization of resources.

Table 1 Effects of climate change-related drivers on net N uptake capacity of woody species observed in different studies at the Tuttlingen field site and corresponding greenhouse studies. The artificial soil solution contained inorganic and organic N sources and was modelled based on the composition determined in the soil solution at the low-N field site. The same composition was used for all experiments, thus allowing direct comparison

Driver	Species	Competitor	Study type	Effects	References
[NO]	European beech	n.a.	indoor	NH_4^+ / Gln-N uptake increased with higher [NO] with low N supply	Simon et al. 2009
				NH_4^+ uptake increased with higher [NO] with low N supply	Dong et al. 2015
	Scots pine	n.a.	indoor	N uptake reduced with lower [NO] with low N supply	Simon et al. 2013
				Gln-N uptake increased with lower [NO] with high N supply	
				N uptake increased with higher [NO] with high N supply	
[CO_2]	European beech	n.a.	indoor	with low N supply:	Dong et al. 2015
				Arg-N uptake increased with lower [CO_2]	
				NH_4^+ uptake increased with higher [CO_2]	
				with high N supply:	
				Arg-N uptake reduced with higher [CO_2]	
N availability	Scots pine	n.a.	indoor	increased N uptake with rising N supply	Simon et al. 2013
	European beech	n.a.	indoor	increased N uptake with rising N supply	Dong et al. 2015
			field	increased N uptake with rising N supply	Dong et al. 2016
	Norway spruce	n.a.	field	increased N uptake with rising N supply	Dong et al. 2016
	European beech	Sycamore maple	indoor	increased Arg-N uptake only with comp at high N	Li et al. 2015
	Sycamore maple	European beech	indoor	reduced inorgN uptake only with comp at high N	Li et al. 2015
Light availability	European beech	Sycamore maple	indoor	orgN uptake reduced with high light, but not shade	Simon et al. 2014
	Sycamore maple	European beech	indoor	no change in inorg/orgN uptake	Simon et al. 2014
Season	European beech	seedlings vs. adults	field	spring: seedlings > adults	Simon et al. 2011
				autumn: adults > seedlings	

Similar to other EMs, the response of beech to EM nutrient uptake might vary along a mutualism-antagonism continuum (Johnson et al. 1997; Jones and Smith 2004; De Mazancourt et al. 2005). In beech, the EM influence on N uptake has been shown to depend on the form and size of soil available N sources (Näsholm et al. 2013; Hasselquist et al. 2016), environmental factors (i.e. drought, Pena and Polle 2014; Leberecht et al. 2015), and EM fungal community richness and composition. Beech NUE and short-term N uptake from glutamine increased with EM fungal species richness (Leberecht et al. 2016). The abilities to access different N pools in the soil and the functional response to environmental alteration differ among EM fungal taxa (Pena et al. 2013b; Pena and Polle 2014; Valtanen et al. 2014). At the Tuttlingen forest site, about 97% of beech root tips are colonized by EM fungi forming large communities of 80–90 taxa (Pena et al. 2010) that might be advantageous in ecosystems with limiting N availability. Beech trees take up amino acids, either directly from the soil (Stoelken et al. 2010) or indirectly via the mycorrhizal fungal interface. However, for mature beech trees in natural environments where all root tips form EMs, the main route of organic N acquisition involves the fungal uptake and the subsequent transfer to the tree. Moreover, the uptake capacities for amino acids are higher in fungal mycelium than in non-mycorrhizal roots (Bledsoe et al. 1989; Javelle et al. 1999) and in mycorrhizal compared to non-mycorrhizal roots (Boukcim and Plassard 2003) indicating that the amino acid uptake of plants via EM fungi is more opportune than the direct uptake from the soil which might also be an advantage in plant-plant competition for N (see also chapter "Soil N pools" section, "Plants vs. plants" section). Although it is difficult to fully appreciate the role of EM symbiosis on beech N nutrition under field conditions, a positive EM influence for this aspect should be granted (see also chapter "Plants and mycorrhiza – competition or facilitation?" section).

Plants vs. plants

Particularly in forest ecosystems with N limitation, competition for N between different vegetation components, such as woody and herbaceous species and/or different woody species is intensified (Schenk 2006). Plants might have developed one or more mechanisms to cope with this competition for N by avoidance (Schimel and Bennett 2004; Hodge and Fitter 2013). Avoidance might by accomplished by (1) inhibition of root access to resources via exudation of allelochemicals (e.g. reviews by Schenk 2006; Trinder et al. 2013), (2) positive interaction with mycorrhiza and/or N_2-fixing bacteria (e.g. Lankau et al. 2011; Hodge and Fitter 2013), (3) spatial niche differentiation (e.g. different rooting depths; e.g. Berendse 1981; Schenk et al. 1999; von Felten et al. 2012), (4) temporal (seasonal) complementary of N acquisition (e.g. Hodge et al. 1999; Hodge and Fitter 2013), and (5) preferences for different N sources (e.g. inorganic vs. organic N) (e.g. Näsholm et al. 2009; Hodge and Fitter 2013). We investigated the interactions between mycorrhizal plants focussing on inorganic and organic N acquisition strategies and N metabolism in the field and in controlled environments in the greenhouse using stable isotope approaches.

Organic N sources play an important role in tree N nutrition with and without the support of mycorrhiza (e.g. Read and Perez-Moreno 2003; Näsholm et al. 2009; Gärdenäs et al. 2011). Studies in the field and under controlled conditions showed that trees generally prefer organic over inorganic N sources regardless of age (Simon et al. 2011) and species (Simon et al. 2010; Dong et al. 2016; Li et al. 2016a). This pattern was also found with shifts in environmental conditions, e.g. light availability (Simon et al. 2014), as well as in competition with other plant species (Simon et al. 2010, 2013; Dong et al. 2016; Li et al. 2016a; see Table 1). However, this preference also depends on soil N availability (Stoelken et al. 2010; Simon et al. 2013; Li et al. 2015; see Table 1). Comparing N acquisition strategies of different species and age classes when subjected to either low or high N soil availability showed that with increasing soil N the preference for specific N forms strongly depends on the investigated species. For example, a study using Scots pine seedlings found that N acquisition patterns might change with differences in N availability and result in a higher uptake by the seedlings of usually non-favored N sources, such as nitrate (Simon et al. 2013).

Using a removal approach, we studied the interactions between adult beech trees and their natural regeneration for an entire growing season focussing on the influence of different vegetation components on beech seedlings and mature beech trees. We removed either only beech natural regeneration, only other understorey species, or both (Simon et al. 2011). There was no intraspecific competition for N between adult beech and beech seedlings, but rather seasonal avoidance regardless of N source: In spring, most N was acquired by beech seedlings, whereas in autumn, mature beech took up most of the N (Simon et al. 2011, see Table 1). This strategy is based on various genetic and/or micro-environmental differences that occur at different developmental stages, such as a lower storage capacity of internal N pools for seedlings (Cavender-Bares and Bazzaz 2000; Millard and Grelet 2010) or higher light availability prior to leaf development of adult beech (Fotelli et al. 2004). During summer, soil N was preferentially taken up by herbaceous species likely because of their increased N demand for flowering and reproduction processes. The N acquired by herbaceous species is released again into the ecosystem during senescence in autumn (Fotelli et al. 2004; Simon et al. 2011). Avoidance of competition for N by spatial niche complementarity can be excluded for this field site, because of a lack of root zonation due to the marginal depth of the soil (Simon et al. 2011). The study by Fotelli et al. (2004) also showed that high N acquisition in spring is a general strategy of woody seedlings at the field site (e.g. maple), not just of beech.

Assuming that competition for N between plants might thus be most relevant during woody seedling establishment, we set up a series of greenhouse experiments with beech seedlings and its – at the field site co-occurring – woody competitor at this developmental stage, i.e. sycamore maple. Short-term competition for N resulted in an increased inorganic, but not organic N uptake of maple seedlings at the cost of beech seedlings when grown in direct competition (Simon et al. 2010). Differences in N uptake strategies of the two species might be due to the contrasting growth strategies (Simon et al. 2010). At the seedling stage, sycamore maple grows faster (Ellenberg 1996), and might thus have an advantage over beech. This advantage, however, strongly depends on environmental conditions. With decreased light availability (i.e. representing the light conditions in the forest understorey), the disadvantage of reduced organic N uptake by beech seedlings compared to ambient light conditions (representing the light conditions in a forest canopy gap) was no longer apparent (Simon et al. 2014; Table 1). When competing, both species showed increased levels of soluble protein in the roots suggesting adaptation to competition with de novo protein synthesis (Simon et al. 2010, 2014). In beech, this increase was found despite a decrease in total N concentration indicating a compensation of reduced N uptake by reduced incorporation of N into structural components (Simon et al. 2010).

The responses to competition by both species also depended on the length of competition. In a medium-term (i.e. 10 months from November to July) experiment, different preferences of N sources of the two species became apparent (Li et al. 2015). Beech seedlings preferred organic N in competition with sycamore maple, whereas sycamore maple preferred inorganic N but with an impaired uptake when growing with beech (Li et al. 2015). Thus, the short-term advantage sycamore maple might have over beech seedlings does not persist over time, providing an explanation why sycamore maple is found at the field site only at the seedling stage and only in areas with relatively low canopy cover (i.e. at forest edges or in gaps). Overall, our results on plant-plant interactions support the stress gradient hypothesis (Bertness and Callaway 1994; Maestre et al. 2009) that predicts that the frequency of facilitative and competitive interactions varies inversely across abiotic stress gradients, with facilitation being more common in conditions of high abiotic stress (e.g. nutrient limitation). In our studies, we also found rather avoidance of competition by different mechanisms, such as increased N uptake at different times during the season or preference for different N sources.

In several experiments in the greenhouse and in the field, we studied the effects of climate-change related drivers on N acquisition of woody species (see Table 1 for details). We found that inorganic and organic N acquisition depends on abiotic factors, such as rhizospheric concentration of NO (Simon et al. 2009, 2013; Dong et al. 2015) and CO_2 (Dong et al. 2015), but also the availability of light (Simon et al. 2014). The main influence, however, appears to be N availability in the soil (Simon et al. 2013; Dong et al. 2015, 2016; Li et al. 2015). Under given environmental conditions, N acquisition also strongly varies between species.

C and N interplay

Sink or source – C allocation within the tree and into the rhizosphere

Uptake and assimilation of N are important energy demanding processes in tree roots (Bloom et al. 1989, 1992; Pfautsch et al. 2009) that are mainly fuelled by the availability of recent assimilates transported belowground (Högberg et al. 2001; Bhupinderpal-Singh et al. 2003). Thus, there is reason to assume that recent assimilate supply strongly controls actual N uptake (Gessler et al. 2016). Moreover, N metabolism is closely coupled to C metabolism via the demand for C skeletons during N assimilation; indeed up to 55% of the assimilated C can be committed to N assimilation and metabolism (Huppe and Turpin 1994). Newly assimilated C is transported to belowground tissues via the phloem from the C source to the C sink (van Bel 2003). If plant growth and C allocation were, however, mainly sink controlled as recently proposed (Palacio et al. 2014; Hagedorn et al. 2016), this would have strong implications for C-N interactions in trees going beyond the classical view of C (i.e. energy) supply driving N acquisition. Changes in N availability to the roots might then rather alter their C sink strength and, as a consequence, shift C allocation from the leaves to the roots. In this respect, increased competition for N with microbes at low soil N supply as seen at our forest sites, and thus reduced N availability in and reduced growth of the roots, will decrease root sink strength for C and, as a consequence C assimilate allocation to the roots. This might, in turn, lead to reduced C transfer to mycorrhizal fungi and rhizodeposition, and finally to reduced microbial activity. Therefore, a feedback loop might exist allowing trees to modulate microbial activity when competition for N increases (see "C and competition for N – roots and free-living soil microbes" section).

Compared to non-mycorrhizal plants, EM plants have higher root exudation rates (Johansson et al. 2009). EM fungi directly contribute to the passive loss of exudates because they typically maximize the number of root tips, and root surface area (Pena et al. 2013a), and stimulate photosynthesis, which is closely coupled with rhizodeposition (Kuzyakov and Cheng 2001; Kaiser et al. 2015). However, EM fungi, as primary utilizers of the belowground transported photoassimilates, and mediators of tree N uptake might also play an active role in the regulation of rhizodeposition, especially when plants compete for N with free soil microbes (Dannenmann et al. 2009). Although the mechanisms underlying the active regulation of rhizodeposition in response to soil N availability remain unclear, Kaiser et al. (2015) showed that an additional N source in the soil hyphal compartment stimulated the amount of plant C allocated to that compartment, and consequently C exudation, showing the role of mycorrhizal fungi in rhizodeposition regulation. In summary, there is evidence that the interplay between C and N metabolism within the tree and modified by the mycorrhizal symbiosis ("Trading C for N – Mycorrhizal associations and the mycorrhizosphere" section) can play a role in controlling C availability in the rhizosphere, and thus modulate the competition between roots and free-living soil microbes ("C and competition for N – roots and free-living soil microbes" section).

Trading C for N – Mycorrhizal associations and the mycorrhizosphere

EM symbiosis with plants is based on the exchange of nutrients, amongst them N, against plant carbohydrates (Simard et al. 2003). The symbiosis influences tree C balance by source enhancing photosynthesis, and by sink as an intermediary of N uptake, due to their extensive biomass built up in the soil to forage for N (Smith and Read 2008). C investment per unit N uptake was higher in EM- than non-mycorrhizal beech trees (Druebert et al. 2009; Pena et al. 2013a). However, there is no clear evidence of compensatory N uptake for C allocation in EM beech root tips (Valtanen et al. 2014; Leberecht et al. 2015). A meta-analysis indicated that plant C investment in fungal partners is controlled by soil N availability, but unrelated to the amounts of N transferred to the host (Corrêa et al. 2008). Under N-limiting conditions, EM fungi might cheat the tree by N immobilization in their biomass at the expense of N transfer (Näsholm et al. 2013; Hasselquist et al. 2016) (but see "Sink or source – C allocation within the tree and into the rhizosphere" section). The adult beech trees increase the competitive strength of EM fungi for N uptake relative to the free-living soil microorganisms by inducing a significant decline in C exudation into the soil (Dannenmann et al. 2009), but a control of beech on N transfer from the fungal interface by C availability modulation remains unknown.

EM fungal N acquisition and transfer to plants involve an energy cost, thus, fungal performances might depend mainly on plant C availability. This was found for some fungal species (e.g. *Tuber rufum*), while others (e.g. *Cenococcum geophilum*, *Tuber* sp.) were less affected by C limitation (Pena and Polle 2014). However, in beech seedlings, C supply was positively correlated with EM fungal colonization and species richness (Druebert et al. 2009; Leberecht et al. 2016). Furthermore, acknowledging the high functional diversity of EM fungal communities for N uptake (Pena et al.

2013b; Pena and Polle 2014), a low rate of C assimilation might induce a high susceptibility to N limitation in juvenile beech in temperate forests.

In summary, beech trees seem to invest significant amounts of C resources in their microbial symbiosis. Competitive strength of EM is increased compared to free living microorganisms. C limitation seems to affect mycorrhizal abundance, especially in juvenile beech, thus negatively affecting N availability.

C and competition for N – roots and free-living soil microbes

Tree girdling (Fig. 1), understorey removal (see "Plants vs. soil microbes" section) and isotope labelling approaches were used as tools to disentangle plant-soil-microbe C transfer and C/N interactions at the Tuttlingen forest site as well as in complementary experiments under controlled conditions. Tree girdling decreased the availability of dissolved organic carbon (DOC) in the soil and consequently heterotrophic microbial N immobilization and microbial biomass, while at the same time the abundance of *Cenococcum geophilum,* the dominant mycorrhizal fungus remained unaffected and amino acid-N and NO_3^-N uptake of adult beech increased (Dannenmann et al. 2009). Hence, the girdling-induced decline of rhizodeposition of labile C compounds shifted the competitive balance in favor of adult beech and its associated fungal symbionts at the expense of heterotrophic N turnover by free living microorganisms in the soil (Dannenmann et al. 2009). Thus, this in situ girdling experiment revealed that adult beech trees could "starve out" competition for N with free living soil microorganisms in periods of environmental stress via down-regulation of rhizodeposition of labile C compounds. This contrasts the strong dependence of energy demanding processes in the roots on the belowground transport of new assimilates (Högberg et al. 2001), and consequently the impairment of plant nutrient uptake by reduced accumulation of assimilates (c.f. Kreuzwieser and Gessler 2010) as well as the stimulation of N uptake by glucose addition (Winkler et al. 2010). The results from the Tuttlingen forest site indicate, however, that not only physiological but also synecological aspects as well as species interactions should be considered when estimating ecosystem C-N relationships. It remains to be tested whether this control of beech over microbial activity only occurs with a strongly changed or manipulated C source strength (e.g. girdling), or whether N limitation could also lead to lower C transfer to the roots via reduced sink and/or source activity (see "Sink or source – C allocation within the tree and into the rhizosphere" section), and in turn to lower rhizodeposition rates of C.

Generally, labile carbohydrates are important regulators of the plant-microbial N balance which was confirmed in microcosm experiments under controlled conditions using beech seedlings in girdling and glucose addition treatments (Winkler et al. 2010). However, a girdling-induced suppression of the biomass of free living soil microorganisms was not observed despite C limitation in the investigated beech-soil system (Winkler et al. 2010). A possible explanation could be that root density and thus the amounts of exudates supplied by the seedlings were low, therefore not showing any effects in response to girdling. Consequently, only adult beech trees but not beech seedlings might be able to gain control in the competition for N via a reduction in rhizodeposition. This assumption is supported by an in situ understorey removal experiment showing the generally minor role of beech seedlings and other understorey vegetation for soil N turnover (Simon et al. 2011): In this manipulative field experiment, removal of neither (1) beech natural regeneration, (2) other understorey vegetation, nor (3) all understorey vegetation, had an effect on soil gross rates of ammonification, nitrification, microbial NH_4^+ and NO_3^- immobilization over the course of the entire growing season (Simon et al. 2011). Furthermore, there was no removal effect on concentrations of dissolved organic and inorganic N, DOC, and levels of microbial biomass C and N (Simon et al. 2011). Overall, the combination of field girdling and understorey removal experiments with laboratory studies under controlled conditions showed that microbial activity in the soil is largely controlled by exudation of carbohydrates by the roots of old-growth beech trees at the Tuttlingen field site and that this control is mediated by C-N interactions.

Main drivers in the plant-mycorrhiza-soil system

Summarizing the interactions between plants, mycorrhiza and/or free-living soil microbes at the N-limited forest ecosystem at the Tuttlingen field site, our data show that competition for N between adult beech and beech seedlings is avoided by "good parenting", i.e. seasonal differences in N acquisition strategies (Simon et al. 2011). Adding another woody species competitor (i.e. maple) into the equation, competition for N is also avoided even at the crucial phase during seedling establishment, namely by preference for different N sources (i.e. organic N for beech, inorganic N for maple; Simon et al. 2014; Li et al. 2015). In this phase, light conditions play an important role, as potential competitors of beech seedlings have no advantage in the competition for N under low light conditions in the understorey (Simon et al. 2014). Beech N acquisition is further facilitated by EM fungi, thus potentially providing an advantage over non-EM species, although this infers a C cost by the plant to trade for N. Again, utilisation of different N sources (Leberecht et al. 2015) ensures the avoidance of potential competition for N, now between beech and EM fungi. However, when N availability is low, EM fungi might "cheat" beech. Although free living soil microbes dominate ecosystem internal N cycling, potential competition for N can be regulated by beech. In times of need, adult beech trees can most probably control the activity of free-living soil microbes via reduction of rhizodeposition. Overall, these interactions are strongly driven by the availability and pool size of different N forms.

Ecosystem functioning in future climate

Consequences of climate on soil processes

The major environmental drivers of the complex network of N turnover in the plant-soil system include temperature and water availability; thus, any shifts in climate might directly affect forest N cycling. However, understanding these climate change effects at the ecosystem or landscape level is complicated because of the inherent complexity of the involved N cycle processes and the spatio-temporal interactions of climate change effects with microbial and plant community responses and landscape-scale nutrient flows (Rennenberg et al. 2009; Butterbach-Bahl and Dannenmann 2012; Butterbach-Bahl et al. 2013). More specifically, a holistic understanding of climate change effects on ecosystem N biogeochemistry and plant-microbial interactions should be based on both process studies including ^{15}N isotope labelling approaches and molecular studies on the functioning and diversity of the soil microbial community, thereby also considering spatial variability from rhizosphere to landscape level (e.g. Butterbach-Bahl et al. 2013; van Groeningen et al. 2015), which still remains a challenge. Furthermore, the combined effects of climate change factors such as changes in temperature and water availability as well as elevated atmospheric CO_2 levels are rather synergistic or antagonistic than additive (e.g. Larsen et al. 2011). Therefore, studying the consequences of only single climate change factors might result in misleading responses. While direct physiological plant responses to climate change have become clearer in recent years (e.g. McDowell et al. 2008, 2011), our understanding of climate change impacts on soil N cycling and plant-microbial interactions still suffers from methodological shortcomings, because it is largely based on studies that use (1) net rather than gross rates of N turnover, (2) largely ignore plant-microbial interactions, and/or (3) provide only limited spatio-temporal resolution.

Increased frequency and duration of drought periods in a changing climate might generally reduce ammonification and nitrification rates, and thus could result in nutritional limitations of trees in a changing climate, on top of direct adverse effects of reduced water availability on plant physiology (Rennenberg et al. 2009). This might be true indeed for tree seedlings that suffer from reduced N substrate availability when soil moisture quickly drops below the optimal levels for nitrification activity during drought periods as found in the study by Dannenmann et al. (2016) in intact beech-soil-microbe systems. On the other hand, adult beech trees can actively lower microbial competition under drought stress via reduced C rhizodeposition (Dannenmann et al. 2009, see "Plants vs. soil microbes" section, "C and competition for N – roots and free-living soil microbes" section for details), whereas, beech seedlings might not have such options (Winkler et al. 2010, see "C and competition for N – roots and free-living soil microbes" section). In agreement with this hypothesis, genetic differentiation between the populations from the two aspects at the Tuttlingen field site using nuclear microsatellites and isozyme markers (Bilela et al. 2012) showed that beech natural regeneration from the SW aspect was genetically closer to both natural regeneration and adult trees of the NE aspect rather than the mature trees from the SW aspect (Bilela et al. 2012, see also "Site characteristics" section).

The sensitivity of beech seedlings to N limitations in a changing climate were confirmed in a recent space-for-time climate change experiment (see Fig. 2) in which intact beech-seedling-soil-microbe systems were translocated within the Tuttlingen research site from a

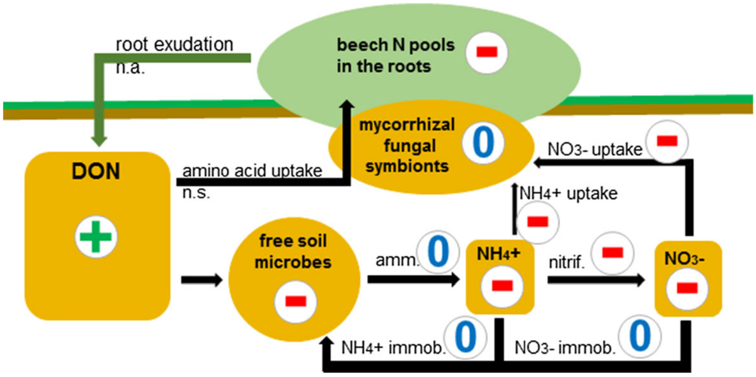

Fig. 2 N turnover rates and N pool sizes at present and future climate. Gross N turnover rates and N pool sizes are based on a space-for-time climate change experiment (Dannenmann et al. 2016): Intact beech-seedling-soil-microbe systems were translocated within the Tuttlingen research site from a slope with N exposure (featuring a cool-moist model climate representing present climate conditions) to S exposure (featuring the warm-dry microclimate with summer drought periods projected for Central Europe in the mid of the twenty-first century). In this experiment, homogenous triple isotope labeling allowed the simultaneous quantification of all major N turnover processes in intact beech-seedling-soil-microbe systems as affected by exposure to projected climate change conditions. Comparing present to future conditions, + = increase; − = decrease; 0 = no significant change. N.s. = no significant uptake; n.a. = no data available

slope with NE exposure (featuring a cool-moist model climate representing present climate conditions of many beech forests in Central Europe) to SW exposure (featuring the warm-dry microclimate with summer drought periods projected for Central Europe in the mid of the twenty-first century) (Bimüller et al. 2013; Dannenmann et al. 2016). In this experiment, homogenous triple isotope labeling allowed the simultaneous quantification of all major N turnover processes in intact beech-seedling-soil-microbe systems as affected by exposure to projected climate change conditions. NO_3^- was the sole significant N source for beech seedlings in the presence of strong microbial competition for amino acids and NH_4^+ (Dannenmann et al. 2016). Simulated climate change altered soil moisture levels from optimal conditions for nitrification to much lower levels, which caused a strong and persistent reduction of the community of ammonia oxidizing bacteria (Gschwendtner et al. 2015; Dannenmann et al. 2016) in the soil. This triggered a chain of effects with about five-fold reduced gross nitrification rates and NO_3^- concentrations in the soil, and also a similar decline of NO_3^- uptake by beech seedlings that was not compensated for by other N sources (Dannenmann et al. 2016). Thus, after one year under simulated future climate conditions, beech seedlings already had reduced biomass, N content and N metabolite levels suggesting a severely reduced competitive strength (Dannenmann et al. 2016). Consequently, in addition to the direct effects of drought on tree physiology, the strong dependence of beech seedlings on nitrification and NO_3^- appears to represent their "Achilles' heel" in a changing climate.

In the "space for time" approach, the different locations might not be totally comparable concerning geology and soil; however, with our approach to assess two slopes in close distance to each other, the effects of such potentially confounding factors have been kept as small as possible. The shallower soil and thus lower soil water availability at the SW aspect might intensify the climatic differences between the two slopes. This is, however, a rather desirable effect as reduced water availability due to drought periods are likely to occur more frequently in future. As already stated, environmental filtering and local adaptation influence the genetic structure of the adult population on the SW slope, which might – to a small extent – affect the reaction of the ecosystem towards the environment. Still, this shift in the genetic structure will most likely occur also over time, with changing environmental conditions at a given site, and thus is most likely part of the stand development under future climate conditions. Generally, understanding these mechanisms provides pointers for mitigation measures ranging from N fertilization, reduction of stand density or mixing beech stands with deep-rooting trees such as oak and white fir, which might facilitate hydraulic lift of deeper water resources with associated water efflux from roots (Caldwell et al. 1998), thereby benefitting beech (del Rio et al. 2014).

A further ^{15}N labeling study of intact beech-seedling-soil systems in the Tuttlingen experimental beech forest revealed another undesired consequence of prolonged summer droughts in a changing climate (Bimüller et al. 2014). In this space-for-time climate change experiment, $^{15}NH_4^+$ and $^{15}NO_3^-$ isotope labels were traced into extractable organic, mineral and microbial N pools as well as into soil organic matter pools separated by physical fractionation. Drought-induced deceleration of microbial mineralization-immobilization turnover reduced the long-term stabilization of N via reduced transfer to stabilization in organo-mineral associations (Bimüller et al. 2014). This coincided with an increasing importance of the labile light fraction. Consequently, increased occurrence of summer droughts in a changing climate could impair N stabilization and increase the risk of leaching losses after extreme rainfall events (Bimüller et al. 2014).

Overall, there is a strong connection between the direct consequences of altered water availability in a changing climate on soil and plant processes with regard to N. For example, in an experiment under controlled conditions, simulating C limitation belowground via girdling, drought resulted in c. 30% increased ammonium and amino acid concentrations in the roots of beech seedlings and c. 65% higher soil NH_4^+ concentration which was likely due to a lower consumption of NH_4^+ by free-living soil microbes (Winkler et al. 2010). Apparently, climate changes also affect the strong link between soil microbial activity and plant N nutrition most likely via plant C allocation (see "C and N interplay" section).

Consequences of climate on plant processes

Trading C for N

Drought decreases photosynthesis, thus, limitation of new photoassimilates can occur under drought; one major impact of long-lasting droughts on plant performance is summarized as C starvation (McDowell and Sevanto 2010). C starvation refers to the situation, when the C demand for maintenance of cellular and defensive metabolism is not met because of low carbohydrate supply from photosynthesis and storage (McDowell et al. 2008). Moreover, drought (Ruehr et al. 2009) as well as heat combined with drought (von Rein et al. 2016) reduce the transfer of recent assimilates from the leaves to belowground tissues and soil microorganisms. Reduced and retarded assimilate transport to belowground tissues was observed in beech seedlings exposed to intensive drought in a greenhouse experiment (Ruehr et al. 2009) leading to a 33% reduction of the contribution of recently (2–6 d previously) assimilated C to soil CO_2 efflux mainly attributed to root and rhizosphere respiration. A comparable reduction upon drought was observed for the contribution of new assimilates to the fine root C pool. At the same time, mean residence time of ^{13}C labelled sugars in leaves increased. In contrast, beech seedlings allocated more new assimilates to the roots under moderate drought compared to non-limited water supply conditions (Hommel et al. 2016). These results show that physiological responses of trees do not necessarily linearly follow the intensity of environmental drivers. Under moderate drought, the C demand of mycorrhizal roots might be increased due to higher need for repair, maintenance and growth. Under severe drought, however, root functioning might be largely impaired leading to a low demand for new assimilates (Hagedorn et al. 2016) and, additionally, the supply with new assimilates by photosynthesis might also be strongly reduced (Ruehr et al. 2009). A microcosm experiment under controlled conditions studied the transfer of new assimilates from beech forest understorey vegetation to the soil microbial community (von Rein et al. 2016): The authors showed that shifts in the composition of the microbial community in response to heat and drought resulted from the dynamics of the plant-soil-microbial system and reduced C transfer rather than directly from the abiotic influence on soil microorganisms. Drought and heat thus caused a reduction of rhizodeposition and C transfer to soil microorganisms similar to girdling ("C and competition for N – roots and free-living soil microbes" section). Consequently, we need to assume that climate change has a comparable effect on the competition between plants and microorganisms, favoring the plant side.

A drought-induced reduction of belowground C transport had different effects on plant N uptake depending on N source (Winkler et al. 2010). Whereas glutamine-N uptake was 2-fold lower in response to drought, inorganic uptake was not affected suggesting that part of the C and energy demand under drought is not met by organic N sources but rather by reserves. In contrast, adding C to the system lead to an increase in plant nitrate uptake (Winkler et al. 2010). Similarly, in an indoor experiment, drought lead to a significantly reduced ^{15}N recovery from litter by beech seedlings regardless of litter type (Guo et al. 2013b). These results indicate that drought can decrease transfer of new assimilates belowground and also affect rhizodeposition which plays a major role in the regulation of the N balance between soil microbes and plants (see also "Sink or source – C allocation within the tree and into the rhizosphere" section).

Plant – plant competition for N

The influence of drought, either as a single effect or in combination with increased temperature, on the competition between beech seedlings and the early successional species blackberry was studied in greenhouse experiments (Fotelli et al. 2001, 2002b, 2005). In three watering regimes (i.e. high, intermediate, none), beech was grown with and without blackberry (Fotelli et al. 2001, 2002b): Regardless of water availability, inorganic ^{15}N acquisition of beech seedlings was impaired in the presence of blackberry which in turn had higher N uptake rates (Fotelli et al. 2002b). Reduced water availability in competition had negative effects on water status and N uptake of beech, whereas blackberry could profit from the impaired resource use of beech by taking up more N under drought (Fotelli et al. 2001). The combination of competition with blackberry and drought resulted in a decrease of ^{15}N allocated to beech roots, and lead to protein degradation in leaves to provide increased levels of amino acid that served as osmoprotectants (Fotelli et al. 2002b). As moderate drought already negatively affected beech biomass, experiments that included increased air temperature under two light regimes with moderate drought were conducted (Fotelli et al. 2005). Depending on the light conditions, the competitive disadvantage of beech reversed: When increased temperature was accompanied by low irradiance, biomass, root-to-shoot ratio, N uptake and assimilation rates of blackberry were lower compared with beech, either grown alone or with blackberry. By contrast, when elevated temperature and high irradiance were combined, the root-to-shoot ratio and specific N uptake rates of blackberry were substantially increased, while N acquisition of beech was impaired (Fotelli et al. 2005). Under lower temperature, with either full light or shade, the presence of blackberry had no significant effects on beech, for almost all tested parameters (Fotelli et al. 2005). These results are similar to those found for the competition for N between beech and fast-growing sycamore maple (Simon et al. 2014) suggesting that the growth strategy (fast-growing vs. slow-growing) applied by the species might be important and early successional species have an advantage under high light conditions only.

A field study at the Tuttlingen site on the competition for N between seedlings of beech and sycamore maple looked at the consequences of enhanced temperature and reduced water availability between two slopes of the study site (Li et al., unpublished results). In the understorey of the relatively cool-moist NE slope, beech seedlings showed generally higher organic and inorganic N uptake capacity over the entire vegetation period (Li et al., unpublished results) consistent with a previous experiment under controlled conditions that compared N acquisition strategies of beech and two maple species co-occurring at the Tuttlingen field site (Li et al. 2016a). However, beech and sycamore maple seedlings established at the relatively warm-dry SW slope no longer showed significant differences in N uptake capacities suggesting that the competitive advantage of beech natural regeneration in N acquisition at current climate conditions might disappear in a changing climate. More specifically, nitrate and glutamine-N uptake capacity were reduced in beech, whereas it was increased in sycamore maple (Li et al. 2016a; unpublished results). Overall, interacting effects between abiotic and biotic factors, particularly during drought periods in summer, influence beech establishment and, thus, might have consequences for future forest development in view of climate change (Fotelli et al. 2001; see also "Consequences of climate on soil processes" section).

Plant-plant competition cannot only be influenced directly by environmental factors, such as drought, on plant physiological processes, but also indirectly, for example via changes in the soil microbial community. For example, soil microbes control plant available N because of their role in soil mineralization processes, high competitive abilities for N uptake (e.g. Hodge et al. 2000; Schimel and Bennett 2004; Kuzyakov and Xu 2013) and as a potential reservoir for plant nutrients (Rennenberg and Dannenmann 2015), thus changes in their activity in response to reduced water availability for example, might also affect plant-plant interactions. On the other hand, plants can also influence soil microbial N cycling via rhizodeposition and also via litter quality (e.g. Kaye and Hart 1997; Schimel and Bennett 2004; Kuzyakov and Xu 2013). Overall, the mechanisms underlying plant-plant competition in the rhizosphere are very complex and still not very well understood.

Plants and mycorrhiza – competition or facilitation?

During drought, beech seedlings benefitted more from EM symbiosis for N acquisition than non-stressed seedlings (Pena et al. 2013a). EM increased inorganic N uptake (Alvarez et al. 2009), although, photosynthetic rates and belowground C allocation decline under drought (Hagedorn et al. 2016) which might negatively affect EM fungal activity. However, with additional C limitation in the drought treatment (i.e. a shade treatment to reduce photosynthetic capacity), EM fungi were less efficient in N uptake (Pena et al. 2013a). These results suggest that plant C supply controls to a large extent the performances of EM fungi in N uptake (Näsholm et al. 2013). Short-term EM fungal efficiency could also be the result of an enhanced competitive strength for N uptake of beech and its associated fungi at the expense of free soil microorganisms induced by drought-declined rhizodeposition (Brunner et al. 2015). Leberecht et al. (2015) cultivated beech seedlings originating from the NW and SE slopes at the Tuttlingen field site and colonized the seedlings with site origin specific EM fungal assemblages. Although no differences in $^{15}NH_4^+$ uptake between non-mycorrhizal root tips from both slopes were observed, ^{15}N uptake was higher in the EM root tips of seedlings from the drier SW aspect compared to the mesic NE aspect origin (Leberecht et al. 2015). These results indicate the significant role the EM fungal community plays with regard to beech N nutrition and the adaptation of beech to environmental constraints (Bever et al. 2010).

EM fungal efficiency for N uptake and its variation with environmental stressors depends on fungal identity. For example, in comparison with other taxa, *Tuber rufum* and *Cenococcum geophilum* show more efficient N uptake with drought than sufficient water supply (Pena and Polle 2014), and *Tomentella badia* had better access to leaf litter-derived N (Pena et al. 2013b). In a girdling experiment, EM species richness decreased by about 50%, however maintaining the most abundant taxa, which were able to keep an unaltered beech N acquisition (Dannenmann et al. 2009; Pena et al. 2010). Overall, under stressful conditions beech maintains rich EM communities including also numerous rare EM species that might enlarge functional diversity of beech EMs facilitating tree N nutrition and adaptation to environmental changes (Dannenmann et al. 2009; Pena et al. 2010; Pretzsch et al. 2014).

Consequences of climate for players and interactions

The consequences of a changing climate, or more specifically increased temperature in combination with reduced water availability might be severe for forest ecosystems. More frequent periods of summer drought might impair the microbial production of inorganic N as well as its re-stabilization in the soil, thereby rising potential losses of N due to leaching at rewetting (Bimüller et al. 2014). Because plant N uptake is directly linked to N availability in soil water (Gessler et al. 2005), the competition for N would increase resulting in lower N acquisition by beech in favor of other woody species (Fotelli et al. 2001). Although, the availability of light does make a difference in the beech – maple (Simon et al. 2014) or beech – blackberry interaction (Fotelli et al. 2005), with beech winning the competition for N under understory low light conditions, this advantage might no longer exist under future climate conditions (Rennenberg et al. 2004; Li et al., unpublished results). EM fungi might support beech, whereas soil microorganisms might increase the competition for N in beech forest ecosystems. However, the N partitioning between plants and soil microbes is controlled to a large extent by the mechanism of C rhizodeposition. Plant C supply regulates the facilitative effect of EM fungi on plant N uptake, which apparently is a key factor with regard to beech N nutrition in times of environmental stress. Adult beech might also actively decrease microbial competition for N under drought by a reduction in C rhizodeposition, which results in microbial dieback and in turn, higher soil N availability and uptake by beech (Dannenmann et al. 2009). Overall, C and N balance in beech forest systems are closely linked which might intensify the potential negative outcomes of key environmental drivers.

Forest management strategies to adapt to climate change

Consequences of thinning on soil processes

Forest management measures such as artificial gap formation can cause undesired impacts on soil N cycling of beech forests including soil NO_3^- accumulation and gaseous N losses (e.g. Bauhus and Barthel 1995; Bauhus and Bartsch 1995; Brumme 1995; Bauhus et al. 2004). In the Tuttlingen experimental beech forest, the effects of heavy thinning, i.e. the even reduction of the stand density by about 2/3, on C and N turnover in the plant-soil-microbe system was monitored for more than ten years (see Fig. 3). This approach turned out to be key to a holistic understanding of thinning effects on soil N turnover mediated by C/N interactions with strong variation over time. Studies included both short- (1–2 years), medium- (4–6 years) and long-term (>10 years) effects at NE exposure (Fig. 3), while at SW exposure only medium-term and long-term effects were investigated.

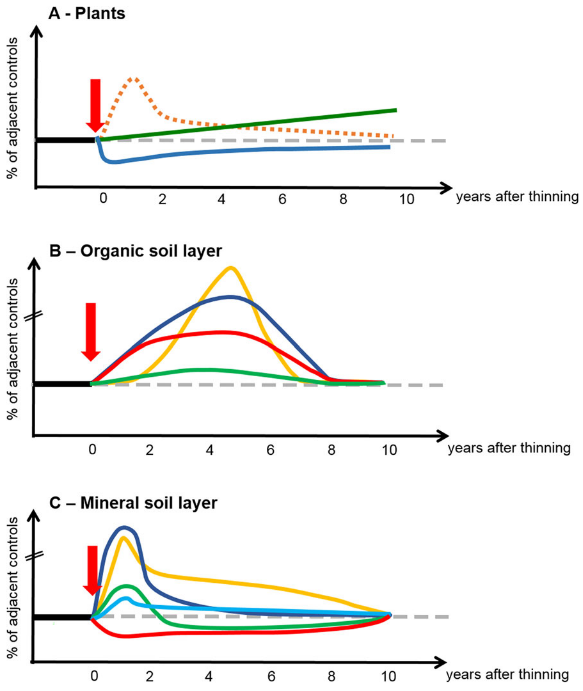

Fig. 3 Scheme of effects of thinning for plants, organic and mineral soil layer. The consequences of forest management were investigated in response to selective felling. Shown is a schematic of the dynamics of the relative effect sizes and directions compared to unmanaged controls (indicated by black line before thinning, grey dotted line after thinning). Red arrow = thinning event. Based on data from Fotelli et al. (2004, plant N uptake), Holst et al. (2004, understorey vegetation), Dannenmann et al. (2006, 2007a, b, soil). Data for inorganic N uptake is available only for one year; thus, the dashed line indicates the predicted N uptake based on soil N availability (following nitrate concentration in the mineral soil) as a key driver of N uptake (Li et al. 2015). A - Plants: dark green – understorey vegetation; light brown – inorganic N uptake; blue – N and C sink in plants, competition for N (plants vs. soil microbes). B – organic soil layer: yellow – nitrate concentration; blue – gross nitrification; red – net N_2O production; light green – gross ammonification, microbial biomass N. C – mineral soil layer: yellow – nitrate concentration; light blue – microbial biomass N; light green – gross ammonification; dark blue – gross nitrification; red – relative microbial N retention

The first and immediate thinning effect was microclimatic: a persistent increase in soil temperature and moisture (Dannenmann et al. 2006, 2007b). Although autotrophic root respiration should have declined after tree felling, soil respiration (i.e. the sum of root and microbial respiration) almost doubled in the first months after thinning (Dannenmann et al. 2007b) as a result of a large soil C mineralization flush due to the changes in microclimate and substrate availability after tree felling. This was largely attributed to heterotrophic microbial respiration. Similarly, gross N mineralization and gross nitrification as well as soil ammonium and nitrate concentrations strongly increased in the first year after thinning (Dannenmann et al. 2006), likely due to reduced competition for DON and NH_4^+ of the stand. These clear effects of forest management on soil microbial N cycling, however, were not solely triggered by the altered microclimate and reduced N competition of the stand. They were also mediated by C/N interactions, i.e. a narrowing soil C/N ratio as the result of significant C loss from soil and lower C input due to the reduction in stand biomass (Dannenmann et al. 2006, 2007b). As a consequence of this C shortage, heterotrophic microbial NH_4^+ immobilization decreased, thus leaving more NH_4^+ for autotrophic nitrification (Dannenmann et al. 2006, 2007a; Butterbach-Bahl and Dannenmann 2012).

Consequently, after an initial microbial uptake of the DIN and DON surplus in the soil, microbial N retention was less important in the first two years after thinning (Dannenmann et al. 2006, 2007a), thus transiently opening the largely closed N cycle by increased soil N_2O emissions (Dannenmann et al. 2007b). These thinning-induced N_2O emissions from the soil, however, were comparably small due to the high microbial activity in the N_2O-reducing, terminal step of denitrification (Dannenmann et al. 2008; Butterbach-Bahl et al. 2013). With the warm-dry microclimate at SW exposure, thinning effects on soil N cycling were weakened by the higher C/N ratios, promoting a more effective heterotrophic microbial N retention in the system, thus preventing N losses and inorganic N accumulation (Dannenmann et al. 2006, 2007b).

These plant-soil-microbe C-N interactions triggered by thinning were observed in the first two years after tree felling. After three years, however, intense growth of understorey vegetation reduced the initial effects of thinning due to competition for water and nutrients, shading and increased C input into soil, diminishing the initial thinning effects over time (Dannenmann et al. 2006, 2007a, b). Consequently, after ten years and more, no thinning effects were observed on soil C and N stocks, irrespective of climate (NE vs. SW aspect; Tejedor et al. 2017). Furthermore, the δ^{15}N signature in total soil N as an indicator of total soil N cycling did not differ between control and thinned plots, suggesting that thinning effects on soil N cycling were short- to mid-term rather than long-term effects. In conclusion, thinning, however, not only affected soil process but also the remaining trees and understorey vegetation in the forest.

Consequences of thinning on plant processes

In general, thinning is assumed to be beneficial for the remaining trees as indicated by enhanced radial growth as a result of increased availability of light, water, and nutrients (Aussenac 2000). While the growth increase is mainly attributed to the alleviation of aboveground competition, the increase in light interception and thus higher photosynthesis rates (Medhurst and Beadle 2005), under dry conditions the effect of increasing water availability per tree prevails (Giuggiola et al. 2015). For Scots pine, these authors showed that the increase in stomatal conductance far outweighed the increase in assimilation, implying that growth release of the trees in the thinned forests was primarily driven by enhanced water supply. In contrast to these results, δ^{13}C in the phloem of adult beech trees – as a short-time measure of stomatal conductance (Keitel et al. 2003) – increased in the thinned plots on the dry-warm SW aspect of the field site Tuttlingen (but not on the NE slope) during drought periods to values of up to ±20 ‰ indicating stomatal closure (Gessler et al. 2001; Keitel et al. 2003). These finding are in line with calculations of canopy stomatal conductance from sapflow measurements in the thinned and unthinned stands (see Keitel et al. 2003). Both independent methods indicate very low stomatal conductance and thus drought stress during times of reduced water availability on the SW thinned plots at least in the first two years after thinning The sap flow measurements also revealed that stand transpiration of the beech overstorey decreased on both slopes as a result from thinning. Still, on the SW slope the remaining trees did not benefit from the reduced water loss via beech transpiration. In contrast to other studies, our results indicate that under unfavourable climatic conditions, thinning might reduce soil water availability for the overstorey most likely due to increased soil evaporation or transpiration of particular species of the forest understorey (Gessler et al. 2004).

The reduced stomatal conductance upon thinning at the SW aspect did, however, not lead to growth depression but to an increase in radial stem growth similar to the NE site (Diaconu et al. 2016). Under the warm and dry conditions at the SW aspect, the increase in nutrient availability together with the increased light availability for the remaining trees after felling might have led to an increase in photosynthesis and consequently growth. A reduction of interspecific competition for N upon thinning leads to higher N allocation to the foliage (Briggs et al. 2000), and consequently to higher photosynthetic capacity (Li et al. 2016b). The increase in leaf soluble N contents after thinning points to such mechanisms also on the SW slope of the Tuttlingen study site (Nahm et al. 2006). Still, different from the NE aspect, the increase in radial growth under the warm and dry conditions on the SW exposed site lead to an increase in wood density and thus smaller vessels (Diaconu et al. 2016). Higher wood density can reduce the cavitation risk even though other factors such as leaf size and leaf to sapwood area are also important to determine cavitation resistance (e.g. Markensteijn et al. 2011). Still, this stem structural trait might be seen as an acclimation to the low water availability at the SW aspect and might also be partially a result of selection and adaptation processes of the adult trees.

Thinning increased stomatal conductance and, consequently, transpiration of beech seedlings at the cool, moist NE aspect indicating a release in the competition for water, but did not affect the seedlings at the SW exposed site (Fotelli et al. 2003). Inorganic ^{15}N uptake of beech seedlings increased upon thinning at the NE slope approx. 5-fold and coincided with a significant biomass accumulation compared to the control treatment (Fotelli et al. 2004; see Fig. 3). In contrast, at the SW aspect, thinning decreased N uptake and growth of the beech seedlings (Fotelli et al. 2004; Gessler et al. 2004). Thus, the SW and the NE aspect generally differed in response to thinning (Gessler et al. 2004): At the cold-moist NE aspect thinning improved the growth conditions for young and adult beech trees leading to higher water availability, water use and biomass accumulation. At the dry-warm SW aspect, however, the situation was more complex: Water use of the adult trees was impaired but growth increased most likely due to higher N availability (see above) and higher photosynthetic capacity. For seedlings, not only water availability but also N uptake and biomass accumulation was strongly impaired at the SW aspect. Overall, this suggests that seedlings strongly suffered from the adverse growth conditions at the SW aspect (c.f. Cavender-Bares and Bazzaz 2000) and that the increase in N availability upon thinning was mainly exploited by adult rather than young trees. Further responses of plant-plant competition to thinning have not been investigated; however, this should be considered in future studies.

Conclusions and perspectives

Beech forests at many Central European sites constitute the potential natural vegetation. In the studies at the Tuttlingen field site and in experiments under controlled conditions, we provide suggestions for strategies that account for the successful occupation by beech even of resource-limited sites. At the ecosystem level, N nutrition of beech trees was characterized by avoidance of competition with preferential acquisition of N by adult beech, its natural regeneration, and the herbaceous understorey in autumn, spring, and summer, respectively (Simon et al. 2011). Another avoidance strategy is the preference for different N forms between different woody species (Li et al. 2015). The high preference of beech for organic N constitutes a competitive advantage to both beech and other vegetation components. Highly efficient N cycling at the ecosystem level is achieved in beech forests by efficient N retention through tightly coupled microbial mineralization-immobilization turnover (Rennenberg and Dannenmann 2015). Even if beech trees take up significantly less bioavailable N compared to free living soil microorganisms at the process level, trees profit from the longer residence time of N in plant compared to microbial biomass. In contrast, microbial biomass N is released into plant-microbe competition processes multiple times during a single growing season, resulting in retarded availability of recycled nutrients for beech. On the other hand, high N resorption efficiency from leaves before shedding is a strategy to cover a high fraction of the annual N supply of trees growing at low N availability in the soil (Coté et al. 2002; Sun et al. 2016). Apparently, the combination of this strategy at the organism level with highly efficient competition for N and ecosystem N cycling allows the successful occupation of low N calcareous soils by beech forests. In the understorey, potential tree competitors are suppressed also by the low light environment generated by adult beech trees and the adaptation of beech natural regeneration to this low light environment (Simon et al. 2014). Active downregulation of microbial competition for N by reduced rhizodeposition contributes to the nutritional flexibility of beech and its dominating performance at the ecosystem level when carbohydrate allocation to the roots is reduced by environmental constraints such as drought (Dannenmann et al. 2009). The capability of ectomycorrhizal fungi to maintain full occupation of the roots, but allow for changes in ectomycorrhizal fungi biodiversity (Pena et al. 2010) appears to be an important strategy to even improve N acquisition under these conditions (Dannenmann et al. 2009). The fast recovery of ecosystem N cycling upon disturbances such as tree felling further contributes to the superior performance of beech forests in Central Europe.

However, studies at the Tuttlingen field site show the vulnerability of beech forests on calcareous soil to direct and indirect consequences of climate change. Beech trees at the SW aspect have lower growth and impaired water relations as indicated by lower stomatal conductance and increased $\delta^{13}C$ values compared to beech trees at the NE aspect. This might not only be a consequence of differences in microclimate between the opposing slopes but also due to the shallower soil at the SW aspect compared to the NE aspect. As a biogeochemical feedback of impaired water relations, N nutrition of beech trees is negatively affected. This is evident from reduced abundance of the nitrifier community and reduced gross rates of nitrification and nitrate availability in the soil observed in plant-soil mesocosms transferred from the NE to the SW aspect (Dannenmann et al. 2016) as well as reduced N acquisition from leaf and root litter in labeling experiments under controlled conditions (Guo et al. 2013a). In addition, impaired water relations constitute a strong disadvantage for beech trees compared to fast-growing competing species in the understorey such as *Rubus fructicosus* (Fotelli et al. 2002b).

Considering the direct and indirect responses of beech to the predicted climate changes, management measures might maintain a sustainable development of these forests. Selective thinning had positive consequences for seedlings growing at the NE slope (i.e. current climate), but negative consequences for seedlings growing at the SW slope (i.e. future climate). At the Tuttlingen field sites, thinning did not result in a clearly improved water status of the trees under a warmer and drier climate, as indicated by the water potential of the trees (Gessler et al. 2001). Particularly at the SW aspect, radiation modified the effect of thinning on water availability, thereby mediating a stronger reduction of stomatal conductance of beech trees on the thinned compared to the untreated plots (Keitel et al. 2003) indicating that thinning might even reduce soil water availability in forests, especially in the upper soil layer, during periods of drought. Therefore, thinning cannot unambiguously be recommended as a general practice to counteract the negative effects of climate change. While in other studies at dry sites thinning is recommended to release drought stress for the remaining trees (see Giuggiola et al. 2015), our results indicate that also the effects on total water balance and water availability for both the under- and overstorey need to be taken into account.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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