



Species-specific effects of temperate trees on greenhouse gas exchange of forest soil are diminished by drought



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ABSTRACT

Tree species identity and root-associated microbes are assumed to play an important role in the global terrestrial fluxes of the key biogenic greenhouse gases (GHG; CO₂, CH₄, N₂O), but the specific processes driving this influence and the importance against abiotic impacts are poorly understood. To what extent changes in the species composition of temperate forests and increases in the frequency and duration of summer droughts in the course of global climate change will alter GHG emissions remains unclear. We analyzed the effect of tree species identity and mycorrhizal association type vs. soil drought on GHG fluxes by conducting a greenhouse experiment with four important deciduous tree species which form either ectomycorrhizal or arbuscular mycorrhizal associations. We combined soil gas flux measurements with analyses of leaf gas fluxes, potential fine root respiration, fine root growth and turnover, and N turnover in soil microsites. Our experiment tests the hypotheses that (1) GHG emissions differ between tree species and mycorrhizal association type mainly due to differences in root activity and root-induced processes, and (2) soil drought decreases the amount of GHG exchange from different tree species to a different extent. We found a two times higher global warming potential (GWP) from soil gas exchange in European ash than in the other three tree species (1.9 vs. 0.8–1.0 g CO₂-eq kg⁻¹ h⁻¹) mainly due to much higher root mass-specific CO₂ emission rates (495 vs. 210–236 mg C kg⁻¹ h⁻¹). Apart from the influence of species differences in fine root productivity, we show a stronger increase in CO₂ emission rates per portion of white roots in ash which may indicate a higher metabolic activity of unsuberized fine roots in this tree species. Ectomycorrhizal tree species differed from arbuscular mycorrhizal tree species by a two times greater increase in CO₂ emissions per fine root production. The N₂O emissions per root mass were up to five times higher in beech than in the other species, caused either by higher nitrate production in the rhizosphere or by lower nitrate consumption. Soil porosity drove the amount of methane uptake, while biotic influences were subordinate. Soil drought generally exerted an important control on GHG fluxes: low water-filled pore space decreased the GWP from soil emissions by only 9% in sycamore, but by 40% (European beech) to 68% (European ash) in the other tree species and largely diminished any tree species differences. This suggests that tree species identity may substantially alter the GWP of temperate forests through rhizosphere processes, but this influence on GHG exchange is diminished by soil drought.

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1. Introduction

During the past 150 years, the atmospheric concentration of the key biogenic greenhouse gases (GHG) has increased beyond any previous level and mitigation of the consequences of this increase for atmospheric warming becomes increasingly important. It is well established that temperate deciduous forest soils play an important role for GHG balances (Schulze et al., 2010). Increasing interest is recently paid to the quantity and drivers of the key GHG fluxes (CO₂, N₂O and CH₄) from forest soils (Luyssaert et al., 2010).

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Beside the known effects of abiotic variables on GHG exchange, the influences of biotic factors such as tree species identity, mycorrhizal symbiosis, and the activity of rhizosphere microbes on soil processes have received increased attention during the past decades (Binkley and Menyailo, 2005). However, the consequences of variation in biotic factors on GHG fluxes and source–sink relations are still poorly understood (Hanson et al., 2000; Matamala et al., 2003; Paterson et al., 2007; Vargas and Allen, 2008). Recent studies reported significant tree species effects on GHG fluxes from temperate deciduous forest soils (Borken and Beese, 2006; Degelmann et al., 2009; Vesterdal et al., 2012). The impact of tree species on GHG fluxes has been explained by an alteration of the physical and chemical properties of the soil as a consequence of species-specific characteristics of stemflow, throughfall (Hagen-Thorn et al., 2004), leaf litter input (Erickson et al., 2002; Guckland et al., 2009, 2010; Van Haren et al., 2010), root activity (Zechmeister-Boltenstern et al., 2005), and a change in the microbial community composition in the rhizosphere (Menyailo et al., 2009). In most cases, tree species-related effects on CH₄ uptake or N₂O release have been thought to be caused by the input of leaf litter and its specific properties (Hagen-Thorn et al., 2004; Papen et al., 2005; Chapman et al., 2006; Vesterdal et al., 2012), despite the knowledge that roots have a large influence on the C and N cycling in the soil (Brady and Weil, 2002; Gregory, 2006). Studies on the effects of leaf litter quality and throughfall on soil C and N cycling (e.g. Nordén, 1994; Smith and Bradford, 2003; Knorr et al., 2005; Hobbie et al., 2006; Hansen et al., 2009) typically do not consider possible root litter effects.

The activity of fine roots is altering their direct surrounding, i.e. the rhizosphere, through root respiration, the release of rhizodeposits, water and nutrient uptake, and physical compaction (Rovira, 1965; Hinsinger et al., 2005; Cheng and Gershenson, 2007). Hence, important biochemical and physical properties such as soil moisture, pH, the redox potential, base saturation, O₂ and CO₂ concentrations, and the labile C and N content in the rhizosphere are substantially different from those of bulk soil (Gregory and Hinsinger, 1999). However, most ecosystem GHG models estimating the forest sink strength for atmospheric CO₂ and the source function for N₂O include little if any representation of root-derived C fluxes and rhizosphere processes, despite the influence of fine root decay and root exudation on microbial activity and nutrient turnover in the rhizosphere (priming effects) and the disproportionate consequences for the ecosystem (Pregitzer et al., 2007; Kuzyakov, 2010).

The effects of roots on their direct surrounding soil may closely be linked to plant physiological processes such as leaf photosynthetic activity, water flux through the plant as well as nutrient uptake (Ekblad and Högberg, 2001; Kuzyakov, 2002; Cramer et al., 2009; Carminati et al., 2010). Until now, the link between plant physiology and morphology with GHG exchange from forest soil, however, has received little attention.

For a better understanding of the relationship of plant physiological processes and growth to GHG fluxes from forest soil, experimental investigations of tree species-specific effects on belowground biogeochemical processes are urgently needed. In earlier studies, we observed a pronounced difference in the effect of beech and ash saplings on the GHG sink and source strengths of temperate forest soil (Fender et al., 2013a, 2013b). However, we could not link these species effects with differences in plant growth rate or other functional attributes. The current study focuses on the importance of (i) leaf and root gas exchange, plant morphology, biomass, and productivity for GHG gas exchange with the atmosphere and (ii) species identity and mycorrhizal association type for the global warming potential (GWP) of temperate forest soils and how these relationships change with drought. In a climate chamber

experiment, we simulated an early summer drought and measured the fluxes of three GHGs (CO₂, N₂O, and CH₄) from natural forest soil planted with four important European tree species with different mycorrhizal associations: two arbuscular mycorrhizal (AM) (*Acer pseudoplatanus* L. and *Fraxinus excelsior* L.) tree species and two ectomycorrhizal (ECM) (*Tilia cordata* Mill. and *Fagus sylvatica* L.) species. Among these tree species, *F. excelsior* and *F. sylvatica* are highly drought sensitive, while *A. pseudoplatanus* and *T. cordata* are only little to hardly drought sensitive (Ellenberg and Leuschner, 2010). We hypothesized that (1) the exchange of CO₂, N₂O and CH₄ between soil and atmosphere is more influenced by the trees' root system morphology and productivity than by aboveground morphology and physiological activity, (2) GHG exchange differs between different tree species and mycorrhizal associations, and (3) soil drought leads to a reduction in the GWP of forest soils but the degree of reduction is different among different tree species.

2. Material and methods

2.1. Study site and sample collection

Tree saplings and soil for this study were collected from a mature broad-leaved mixed forest stand in Billingshausen Gorge, southern Lower Saxony, Germany (51°34' N 9°58' E, about 310 m a.s.l.). This forest stand is dominated by European beech (*F. sylvatica* L.) growing in association with other broadleaf tree species (i.e., *A. pseudoplatanus* L., *Ulmus glabra* Hud., *F. excelsior* L., *T. cordata* Mill.). The tree assemblage represents a community in the transition between a Hordelymo-Fagetum and a *Lunario redivivae*–*Aceretum pseudoplatani* community. The site is located on a nutrient-rich Cambisol-Phaeozem (IUSS-ISRIC-FAO, 2006) of silty texture developed from a Triassic limestone (Lower Muschelkalk) substrate covered by loess. The climate is sub-oceanic with a sub-continental element characterized by humid summers and cool winters. Mean annual precipitation is 630 mm and mean annual temperature is 9.0 °C.

In October 2012, we selected each 16 tree saplings (lime: 12) of four different tree species: two AM (sycamore maple and European ash) and two ECM (European beech and small-leaved lime) species. The selected individuals were similar in tree height (about 45 cm), root length (about 18 cm), and crown dimensions. Saplings were excavated and adherent soil material was carefully removed from the roots. Saplings were stored in plastic bags to minimize transpiration, kept cool, and transported to the greenhouse immediately. Close to the sapling sampling site, soil from the upper 10 cm of the mineral soil was collected after the 1–3 cm-thick vermimull had been removed, was sieved (<2 mm) and homogenized. Mineral soil from this soil depth contains in native forests the majority of the fine root biomass total of all investigated tree species (34–47% in the profile to 40 cm; cf. Meinen et al., 2009); while the lower soil layers contain exponentially less. The soil had a pH (KCl) of 4.9 and a base saturation of 98.5%.

2.2. Experimental set-up

A fully randomized two-factorial experiment with tree species and soil moisture as independent factors was established: each two saplings of the same tree species were planted together into one plant container of c. 5 L volume ('rhizobox'; cf. Hajek et al., 2014) filled with 4.7 kg of freshly sieved soil (equivalent to 4.0 kg dry soil). Each rhizobox had two transparent Plexiglas windows (420 mm × 300 mm, w × h) on two opposite sides, which were covered with removable black PE panels to prevent light penetration. The windows were held together by a 40 mm wide plastic

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