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Implications of structural diversity for seasonal and annual carbon dioxide fluxes in two temperate deciduous forests

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ABSTRACT

The effects of structural diversity on the carbon dioxide exchange (CO_2) of forests has become an important area of research for improving the predictability of future CO_2 budgets. We report the results of a paired eddy covariance tower study with 11 years of data on two forest sites of similar mean stand age, near-identical site conditions, and dominated by beech trees (*Fagus sylvatica*), but with a very different stand structure (incl. age, diameter distribution, stocks of dead wood and species composition) because of different management regimes. Here we address the question of how management and related structural diversity may affect CO_2 fluxes, and tested the hypothesis that more structurally diverse stands are less sensitive to variations in abiotic and biotic drivers. Higher annual net ecosystem productivity (NEP) was observed in the managed, even-aged, and homogenous forest (585 ± 57.8 g C m^{-2} yr^{-1}), than in the unmanaged, uneven-aged, and structurally diverse forest (487 ± 144 g C m^{-2} yr^{-1}). About two-third of the difference in NEP between the sites was contributed by a higher annual gross primary productivity (GPP, 1627 ± 164 vs 1558 ± 118 g C m^{-2} yr^{-1}) and one-third by a lower annual ecosystem respiration (Reco, 1042 ± 60 vs 1071 ± 96 g C m^{-2} yr^{-1}) in the homogenous forest. Spring (April – May) and summer (June – July) were the two main seasons contributing to the overall annual differences between the sites, also, the sensitivities of seasonal NEP and GPP to environmental variables were stronger in the homogenous forest during those periods. Inter-annual variation of NEP was higher in the homogenous forest (coefficient of variation (CV) = 25%) compared to the heterogeneous forest (CV = 12%). At annual time scale, the higher variability of NEP in the homogenous forest is attributed to biotic factors such as fruit production and a time-dependent growth trend, outweighing differences in environmental sensitivities.

1. Introduction

The carbon uptake of forests is affected by changes in both abiotic and biotic factors (Chen et al., 2015; Ciais et al., 2005). The former includes temperature, radiation, water and nutrient availability, and their intra and inter-annual variability. Biotic factors include plant functional traits such as nutrient status, structure, phenology, etc., that govern photosynthesis and respiration process (Jensen et al., 2017) as well as inter- and intra-specific competition. Identifying and understanding the factors that contribute to the variability in net carbon dioxide (CO_2) uptake, i.e. net ecosystem productivity (NEP), between forest ecosystems and the atmosphere is crucial for understanding how forests will respond to and affect future climate (Baldocchi et al., 2001; IGBP Terrestrial Carbon Working Group, 1998; Luo et al., 2015) as well as for answering questions relevant to forest management and ecology.

Many eddy covariance (EC) flux studies (e.g. Barr et al., 2007; Dragoni et al., 2011; Hui et al., 2003; Humphreys and Lafleur, 2011; Jensen et al., 2017; Kitamura et al., 2012; Richardson et al., 2009; Shao et al., 2016, 2015; Wu et al., 2013; Yuan et al., 2009) have attributed the inter-annual variability (IAV) of NEP variously to climatic variables, to phenological changes induced by climatic variables and to biotic changes, with Richardson et al. (2009) contending that, on an annual scale, variation in NEP is more strongly dominated by changes in biotic factors than by climate. To date, most studies have focused on understanding effects of climate and biotic changes on CO_2 fluxes at single sites (Granier et al., 2008; Pilegaard et al., 2011; Wilkinson et al., 2012) or across contrasting ecosystem types (Baldocchi and Xu, 2005; Chu et al., 2016; Jensen et al., 2017; Ma et al., 2007; Novick et al., 2015; Pereira et al., 2007; Shao et al., 2014, 2015, 2016; Wu et al., 2012). Other studies have used multiple sites from across global and regional

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networks to understand the variability of CO_2 fluxes from different plant functional types and/or climatic zones (Beer et al., 2010; Chen et al., 2015; Law et al., 2002; Musavi et al., 2017). Such studies have been beneficial for understanding the underlying causes of variability in CO_2 uptake, but because flux stations are not closely located, there are typically very large differences in the environmental conditions between sites, making it challenging to disentangle the effects of abiotic vs biotic factors. The short period of time analysed is also a limitation found in some studies (Anthoni et al., 2004; Hommeltenberg et al., 2014; Jensen et al., 2017). Only a few have investigated how structure and management scheme affect CO_2 fluxes (Herbst et al., 2015; Musavi et al., 2017) even though it is reasonable to suppose that these are important drivers of CO_2 fluxes and that they may interact with climate and biotic variables (Luyssaert, 2014).

Here we present a case study that, in contrast, focuses on two forest sites that a) are characterized by similar site conditions, b) have a similar mean age, and c) are both dominated by beech trees (*Fagus sylvatica*) but differ in management regime and structure. We thus tackle the question of how management and related structural diversity may affect CO_2 fluxes, and directly test the hypothesis that more structurally diverse stands are less sensitive to variations in abiotic and biotic drivers. This study builds on the work of Herbst et al. (2015), which was done at the same sites and showed their difference in carbon uptake and water use.

We seek to identify the major drivers of seasonal and inter-annual variability of net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (Reco) of a structurally-diverse and a structurally-homogeneous temperate broadleaf forest. We test two hypotheses:

1) The annual NEP and GPP of the homogeneous forest is more sensitive to variation in climate variables compared to the heterogeneous forest. A study utilizing tree rings has shown that productivity of diverse temperate beech forests exhibited higher temporal stability than monoculture forests mainly due to lower inter-annual variation as well as due to overyielding because of asynchronous behaviour of different tree species and their interactions (Jucker et al., 2014). Grossiord et al. (2014) observed higher water availability in mixed temperate beech forests than in single species forests during drought, which they speculate as result of niche partitioning and/or facilitation processes among the interacting species.
2) NEP and GPP of the homogeneous forest is more sensitive to intrinsic species-determined characteristics such as fruit production. Synchronous fruit production, also known as masting, is a sink for plant resources that may compete with vegetative growth (Obeso, 2002) and a negative correlation between fruit production and radial stem increment has been observed (Dittmar et al., 2003; Selås et al., 2002). Herbst et al. (2015) reported higher fruit production in the homogenous forest and here we will also quantify the effect of fruit production on annual NEP and GPP.

2. Materials and methods

2.1. Site description

Data were obtained from two forest sites, Hainich (DE-Hai) and Leinefelde (DE-Lnf), located in central Germany (Fig. 1). The two sites are ca. 30 km apart both at an altitude of 450 mean above sea level. Soil at both sites is composed of Triassic limestone covered with variable Pleistocene loess deposits. The climate is suboceanic-submontane with a long-term annual mean air temperature of ca. 8 °C. General site characteristics are given in Table 1. The phenology of both sites is similar, with the dormant season lasting typically from November to March and growing season lasting from April to October.

Hainich: The Hainich site (DE-Hai) is an unmanaged forest with a heterogeneous structure, located in the central part of the Hainich National Park. Site details can be found in Anthoni et al. (2004) and Knohl et al. (2003). Until the end of the 19th century, it was managed as a coppice-with-standards system and was subjected to selective cutting until 1965. From 1965–1997, the area was used as a military training base and a large part of the forest was left untouched, with only single and very valuable trees being cut. The forest has never been clear felled and, as a result, it exhibits characteristics of an unmanaged, old-growth forest with highly diverse horizontal and vertical structure,

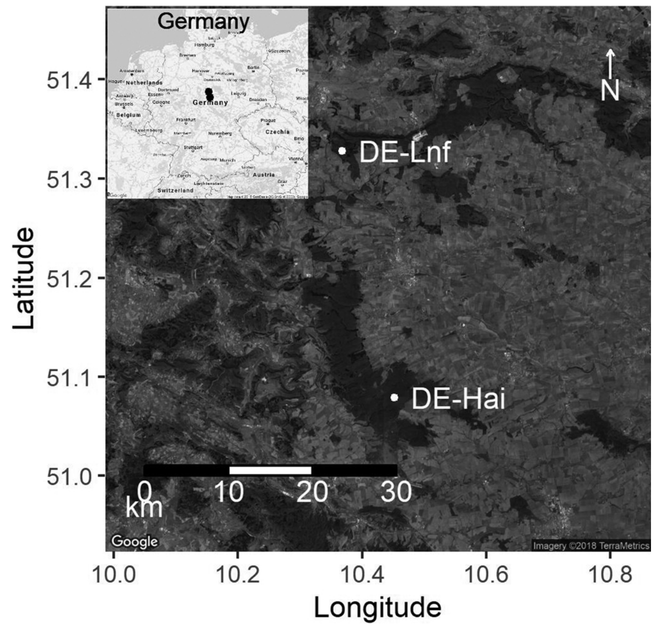

Fig. 1. Map showing the location of the two study sites in the central Germany. Darker patches are forests and white dots show the positions of the eddy covariance flux towers at each site. Map of Germany in inset is not to scale.

Table 1
Instrumentation and stand characteristics for the research sites.

	Hainich (DE-Hai)	Leinefelde (DE-Lnf)
Characteristics		
Latitude	51°04'45,36"N	51°19'41,58"N
Longitude	10°27'07,20"E	10°22'04,08"E
Altitude [m]	440	450
Soil	Pleistocene loess deposits with dominance of Cambisols	Pleistocene loess deposits with dominance of Luvisols
Instrumentation		
EC measuring height [m]	44	44
Displacement height [m]	22	22
Sonic anemometer	Gill Sonic Model R3	Gill Sonic Model R3
Infra-red gas analyser (IRGA)	Li6262	Li6262
Stand characteristics		
Primary species	*Fagus sylvatica* L. (64%)., *Fraxinus excelsior* L. (28%), *Acer pseudoplatanus* L (7%). and other species	*Fagus sylvatica* L. (single *Quercus petraea*)
Biomass [t C ha^{-1}]	212	237
Plant density [trees ha^{-1}]	334	224
Canopy height [m]	35	35
LAI [$m^2\,m^{-2}$]	5.1	4.2
Age (years)	Maximum up to 265, biomass weighted average = 140	130 ± 8