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Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits

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ABSTRACT

There is an ongoing debate about how European beech might be affected by a future drier climate. While numerous studies have examined the effects of soil drought on beech growth and development, studies investigating the effects of elevated atmospheric water vapour pressure deficit (VPD) are lacking. By increasing VPD in climate and open-top chamber experiments, with moisture in the rooting medium near optimum, we tested the hypothesis that increased VPD negatively affects the growth and development of European beech saplings. In the climate chambers, a reduction in relative air humidity by 40% resulted in a 68% reduction in productivity. Similarly, in the open-top chamber experiment conducted on the forest floor, biomass declined by 30% when relative air humidity was 15% lower. The reduction in biomass was mainly a consequence of a dramatically reduced leaf growth of beech in the elevated VPD treatments. Our results show that growth and development of beech saplings strongly depend not only on soil moisture but also on the prevailing VPD level. We conclude that the vapour pressure deficit is a widely ignored factor which influences the growth and vitality, and possibly also the distribution of European beech. Future forest management schemes under an altered climate should take this factor into account.

1. Introduction

Drought is a key factor limiting tree growth not only in arid but often also in humid climates (Gower et al., 1992; Becker et al., 1994). When soil water is depleted, a number of tree functions are inhibited. The ability of trees to function under drought stress depends on various physiological and morphological traits, among the most important one are the capacity of the roots to guarantee water uptake in drying soils, and the ability to continue leaf growth during drought (Kozlowski and Pallardy, 1997; Saxe et al., 1998). The maintenance of leaf area is crucial for tree vitality because light interception, carbon assimilation and transpiration are closely linked to canopy surface area.

With respect to its natural abundance, European beech (*Fagus sylvatica* L.) is the most important broad-leaved tree species in Central and Western Europe. Prior to human intervention, this species dominated forests on moderately dry to moist soils and, only in drier environments, it was displaced by more drought-tolerant species such as *Quercus petraea* (Mattuschka) Liebl. or *Q. pubescens* Willd. The drought sensitivity is assumed to be a key factor limiting the range of beech in Southern and Southeastern Europe (Horvat et al., 1974; Aranda et al., 1996; Backes and Leuschner, 2000).

In climate chamber and garden experiments, and also in transect studies, it has been found that water shortage reduces beech canopy conductance (Granier et al., 2000; Gessler et al., 2004; Schipka et al., 2005), photosynthetic activity (Terborg, 1998), leaf water potential (Tognetti et al., 1995; Backes and Leuschner, 2000), diameter increment (Becker et al., 1994; Schipka et al., 2005), and height growth (Braun and Flückiger, 1987; Frech, 2006). Nearly all of these studies focused on the effect of limited soil moisture while the consequences of elevated water vapour saturation deficits of the air (VPD) were not investigated. This is surprising because VPD has been found to have a significant and often large influence on plant growth and development of crop and horticultural plants (e.g., Ford and Thorne, 1974; Hoffman et al., 1971; Hoffman and Jobes, 1978; Tibbitts, 1979; Grange and Hand, 1987; Gisleröd and Mortensen, 1990; Marsden et al., 1996; Mortensen and Gisleröd, 2000; Roberts and Zwiazek, 2001; Leuschner, 2002; Codarin et al., 2006).

In the light of climate change, it has been suggested that the growth and competitive ability of beech will strongly be affected by a longer duration and higher frequency of summer droughts (Gessler et al., 2001, 2007; Fotelli et al., 2003). Beech seedlings and saplings have been found to be particularly sensitive to soil drought (Bolte and Roloff, 1993; Löf and Welander, 2000; Kölling

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et al., 2005). Decreases in summer rainfall and increases in temperature should also rise VPD, a factor that may increase the drought exposure of beech saplings and mature trees. While several studies have reported on negative effects of depleted soil moisture for growth and development of beech saplings (e.g., Madsen and Larsen, 1997; Fotelli et al., 2001; Czajkowski et al., 2006; Meier and Leuschner, 2008), no study has investigated the effects of elevated VPD levels for growth and vitality of beech so far. This weakens any predictions of how European beech will respond to a drier and warmer climate in the coming decades.

This study examines the effects of different VPD levels on the physiology and productivity of beech saplings. Defined VPD levels in the sapling environment were achieved by manipulating atmospheric moisture both in a climate chamber experiment and a field experiment on the forest floor. We used a recently developed open-top chamber technique for manipulating humidity in the natural environment of beech saplings on the forest floor. We tested the hypothesis that elevated VPD negatively affects productivity and thus represents a stress factor for beech saplings. From experiments conducted with herbaceous plants, we expected that elevated VPD would decrease biomass production and leaf expansion of beech saplings in a similar manner as soil drought does.

2. Material and methods

2.1. Plant material

Seeds of *F. sylvatica* L. were collected in autumn 2004 in the woodlands of the surroundings of Göttingen (Lower Saxony, Central Germany). The seeds were placed in moist sand and kept at a constant temperature of 5 °C. After 4 weeks, the seeds were transferred to a glasshouse with a constant temperature of 20 °C. After germination, the seedlings were grown for about 10 weeks in moist sand at quantum flux densities of 200 μmol photons m^{-2} s^{-1} (20 °C, VPD = 500–800 Pa). When the saplings were about 70 days old, they were transferred either to the climate chambers (duration of experiment: April 11 to July 13, 2005) or to the open-top chambers in the field (August 5, 2005 to August 9, 2006). At the beginning of the experiments, the plants had an average dry weight of 2.3 ± 0.05 g, a shoot length of 10.4 ± 0.3 cm, an average root length of 14.1 ± 0.2 cm and the average number of leaves was 2.4 ± 1.2 (mean number of leaf buds: 2.7 ± 0.4; mean total leaf area per plant: 18 cm^2).

2.2. Climate chamber experiment

The climate chamber experiment was undertaken from April to July 2005. To guarantee a non-limiting soil moisture and nutrient supply regime the saplings were cultivated in hydroponic culture in pots that contained 1500 cm^3 of a nutrient solution (one sapling per pot). Complete 0.2× Shive solutions (Baumeister and Ernst, 1978) were added once a week to prevent any nutrient limitation during the experiment. Every 2 or 3 days, the pH of the solution was adjusted to a value of 4.5. The ionic concentration of the solution was ca. 4 mosmol L^{-1} which relates to a water potential of −0.009 MPa. To avoid oxygen limitation, compressed air was bubbled through small perforated tubes into the solutions; the air pressure remained low in order to minimize water turbulence in the direct root environment.

The beech saplings were grown for a period of 3 months in the climate chambers (BBC, Brown Boveri-York, Hamburg, Germany) at constant vapour pressure deficits of 350 (treatment A), 930 (B) and 1400 Pa (C) in the 14-h light phase, and of 250, 712 and 1068 Pa in the 10-h dark phase. These VPD values relate to relative air humidities of 85%, 60% and 40% in the treatments A, B and C, respectively. The air temperature during the light phase was 20 (±1) °C, and 15 (±1) °C during the dark phase. Thermo-hygrographs were used to control air humidity in each chamber. Fluora lamps (Osram Inc.) provided a constant quantum flux density of 142 (±10) μmol m^{-2} s^{-1} during the light phase in order to simulate realistic below-canopy light regimes (Table 1). Earlier measurements with quantum sensors on the forest floor of Central German beech forests reported a quantum flux density of 100–200 μmol photons m^{-2} s^{-1} before leaf flushing of beech, and of 10–15 μmol m^{-2} s^{-1} after leaf development.

Table 1
Environmental parameters during the climate chamber experiment, and the open-top chamber experiment conducted on the forest floor

	Climate chambers			Open-top chambers		
	A	B	C	a	b	c
VPD [Pa]	350	930	1400	410	582	815
Relative humidity [%]	85	60	40	76	69	55
Air temperature [°C]	20	20	20	13	14	14
PAR [μmol m^{-2} s^{-1}]		142			150[a]	
Soil water regime		Hydroponic culture			Soil water content near field capacity	
Nutrient supply		Nutrient solution			Natural forest soil	

Given are daytime means of the different climate chamber treatments (A, B, C), and of the forest floor environment: a = outside the open-top chambers (herbaceous layer near the chambers), b = ambient humidity (inside the chambers, control), c = reduced humidity (inside the chambers).
[a] Mean value according to Eggert (1985) and Ehrhardt (1988).

2.3. Open-top chamber experiment

For simulating a drier climate on the forest floor with elevated VPD but with otherwise unchanged environmental conditions, we designed an open-top chamber system that allowed to manipulate air humidity on the forest floor *in situ*. The system consisted of eight circular open-top chambers and was in its principal design similar to those open-top chamber systems that are used for CO_2-manipulation experiments in grasslands (e.g., Hättenschwiler and Körner, 2000; Hollister and Webber, 2000). The open-top chambers were established for 1 year (August 2005 to August 2006) on the forest floor of the Göttinger Wald beech forest east of Göttingen (51°32′N, 10°03′E). The research site is situated at an altitude of 430 m a.s.l. in a 100- to 130-year-old beech forest. The climate has a sub-oceanic to sub-continental character with a mean annual precipitation of 720 mm and annual mean temperature of 7.9 °C. The bedrock is Triassic limestone which gave rise of mull humus soils (mostly of the type Orthic Rendzina). The actual and natural forest community of the study area is the Hordelymo-Fagetum beech forest with a species-rich herb layer including spring geophytes and shade-tolerant summer herbs and grasses.

The open-top chambers were made of 2-mm thick UV-transmissive plexiglass with a diameter of 65 cm and a height of 60 cm. The eight chambers were positioned randomly on the forest floor. Four of the chambers were treated with ambient air (control) and four with air of reduced water vapour content. In order to produce a steady air flow through the chambers, one large radial fan was installed for the four chambers of each treatment. The air flow was adjusted in all eight chambers to a mean of 0.5 m s^{-1} and was continuously controlled. This procedure guaranteed a complete turnover of the air inside the chambers every 30 s. For decreasing air humidity, two absorption air driers (Resuscorb, DST Seibu Giken, Sweden) were used to reach a constant reduction of air humidity by 15 percentage points in the dry-air chambers relative to the control chambers. Plastic pipes with access to the