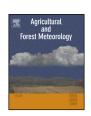
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Meteorological forcing of day-to-day stem radius variations of beech is highly synchronic on opposing aspects of a valley



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ABSTRACT

Projected changes in climate highlight the need for a better understanding of the effects of forest meteorological factors on the growth of Central European forests. In this study, we used automatic point dendrometers to investigate day-to-day stem radius variations of 24 European beech trees (Fagus sylvatica L.) in relation to daily forest meteorological conditions. Study trees were located at opposing north-east (NE) and south-west (SW) exposed slopes of a valley in southwestern Germany, and monitored over a six-year period (2001-2006). Seasonal courses of day-to-day stem radius variation (SRV) were analyzed in hierarchical mixed models based on first-order derivatives of cumulative Weibull functions. Responses of SRV to weather conditions were found to be remarkably synchronic within and between the NE and SW aspect. This latter finding suggests that trees at both slopes may have adapted to prevailing environmental conditions. Further, responses were found to be mostly linear within the range of forest meteorological conditions encountered in this study. Highly distinct effects of forest meteorological fluctuations were observed when daily lags were considered. The daily parameters mean air temperature at lag1 (=one day lag), maximum air temperature and soil water content at lag1 were found to explain 59% of the variance in day-to-day stem radius variations. We discuss the complex responses of SRV to lagged and currentday weather variables in relation to stem hydraulics and growth, varying time scales of tree physiological processes, and pre-conditioning of tree water status.

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1. Introduction

Central European forests may be impacted by climate change, which will have consequences for the provision of forest goods and services like wood production, carbon sequestration and biodiversity (Spathelf et al., 2013). Forests will likely face both changes in extreme climatic conditions, such as more frequent and severe summer droughts, as well as less obvious gradual changes (changes in mean values). To formulate adaptive forest management strategies that can cope with the projected changes in climate (Christensen et al., 2007), a thorough understanding of the climatic forcing of tree growth is needed for a variety of tree species and sites. Currently, this understanding mostly relies on analyses of inter-annual growth variability (e.g., Becker, 1989; Cook and

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Johnson, 1989; Dittmar and Elling, 1999; Lebourgeois et al., 2005).

In such classical dendrochronological studies, climate-growth relationships are commonly analyzed by relating annual ring width to monthly climate variables. But, as climate events are often punctual in natural environments while cambial activity is continuous and takes place at time scales ranging from days to weeks (Deslauriers et al., 2011), an apparent mismatch in time domain, i.e., months versus days to weeks, poses the problem of what monthly climate data actually represent for the growth trees.

Studies on seasonal growth dynamics of trees further illustrate that tree-ring width alone may capture only limited information on climatic forcing of tree growth, as comparable growth levels can be achieved through very different seasonal growth patterns (e.g., Duchesne et al., 2012; van der Maaten, 2013). Hence, classical dendrochronological studies may not be able to completely elucidate climatic forcing of tree growth, which is needed to assess the impacts of contemporary changes in climate, i.e., in mean climate and seasonal patterns (Christensen et al., 2007). In this respect, it is notable that changes in climate seasonality were discussed as a possible causing factor of a phenomenon called "divergence problem", which refers to a recently observed weakening in mean

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air temperature responses in tree-ring chronologies from previously air temperature-limited northern sites (D'Arrigo et al., 2008). Besides, complex non-linear or threshold responses of tree growth to climate have been suggested to explain the observed divergence as well (D'Arrigo et al., 2004; Vaganov et al., 1999).

To gain more insight in environmental conditions driving tree growth at a higher temporal and spatial resolution, high-resolution dendrometer data are increasingly analyzed (e.g., Biondi and Hartsough, 2010; Deslauriers et al., 2003; Giovannelli et al., 2007; Köcher et al., 2012). Dendrometers continuously monitor variations in stem size without invasive sampling of the cambium, and record a signal that is composed of irreversible tree growth as well as reversible rhythms of water storage depletion and replenishment, reflecting courses of xylem water potential (Deslauriers et al., 2003; Herzog et al., 1995; Kozlowski and Winget, 1964; Panterne et al., 1998; Tardif et al., 2001). Dendrometer studies have focused on tree water status and physiology (e.g., Betsch et al., 2011; Cocozza et al., 2012; Daudet et al., 2005; Steppe et al., 2006; Zweifel and Häsler, 2000), which are the primary signals obtained from highfrequency monitoring of stem diameter variations. Dendrometers proved to be very efficient in relating stem diameter variations to the sap flow and water status of trees (Zweifel and Häsler, 2001). Growth signals, on the other hand, often have a lesser magnitude and need to be extracted from the high-resolution changes in stem radius. However, various studies showed that dendrometer measurements are useful in analyzing intra-annual growth or wood properties as well (e.g., Bouriaud et al., 2005; Drew et al., 2009; van der Maaten et al., 2012). A majority of dendrometer studies analyzed relationships between stem size variations and forest meteorological variables at short time scales (Deslauriers et al., 2003; Downes et al., 1999; Drew et al., 2011; Duchesne and Houle, 2011; Pietarinen et al., 1982). These analyses are often characterized by a limited number of study trees and (or) a short observation period, hampering the development of models that are able to accurately capture stem radius variations under contrasting weather conditions.

In this study, we analyzed day-to-day stem radius variation of 24 European beech trees over a six-year period from 2001 till 2006 based on half-hourly records. Rather than analyzing seasonal growth dynamics or modeling radial growth of beech, the main objective of this paper is to identify driving forest meteorological factors for daily stem radius variations over the study period, and, in addition, to reveal how established relationships differ in dependence of aspect (opposing slopes of a valley). Further, we aimed to explore the linearity of day-to-day stem radius variations in response to meteorological variables and tested the existence of short-term lagged effects.

2. Material and methods

2.1. Site description

This study was conducted in two permanent plots situated not more than 750 m apart at opposite exposed slopes (north-east: NE, south-west: SW; inclination: 23–30°) of a narrow valley. The study area is located in southwestern Germany within the low mountain range Swabian Alb (altitude: 740–760 m a.s.l., latitude: 48°00′ N, longitude: 8°50′ E), around 100 km south-southwest of Stuttgart. Mean annual air temperature over the climate period 1977–2006 is about 7.4°C and mean annual precipitation sums up to 925 mm (source: 1 km × 1 km gridded climate surface of German Weather Service, WebWerdis, 2011). Over the growing period April–August, mean air temperature and precipitation sum are 12.8°C and 449 mm, respectively. Rainfall does not vary significantly across the valley (Geßler et al., 2001).

The canopy vegetation is dominated by 80–90 year old European beech on both aspects. Mean stand height, diameter at breast height (DBH) and basal area are greater at NE compared to the SW. According to a forest inventory in 2001 (Hauser, 2003), mean stand height amounted to 26.5 and 21.1 m, DBH to 25.6 and 21.5 cm, and basal area to 25.6 and 21.0 m 2 ha $^{-1}$ on NE and SW, respectively.

Soils are classified as Terra Fusca-Rendzinas (Chromo-Calcic Cambisol (FAO)) derived from limestone and are shallow (<20 cm) before becoming dominated by bedrock (Geßler et al., 2005; Hildebrand et al., 1998). Especially the SW aspect is rocky, with higher radiation interception at the canopy level, resulting in permanently higher air and soil temperature and lower water availability compared to NE (Mayer et al., 2002).

2.2. Dendrometer monitoring

Stem radius variations of 24 dominant or co-dominant European beech trees were monitored over a six-year period (2001–2006) using automatic point dendrometers. Twelve trees per aspect were equipped with dendrometers that consist of a stainless steel body with a linear displacement transducer (Trans-Tek Inc., Connecticut, USA), positioned perpendicularly to the stem (see also Hauser, 2003). Dendrometers were installed at 1.40 m and at NW-exposed sides of the trees to prevent direct solar irradiation on the measurement devices and to avoid disturbing effects of reaction wood formation. Stem radius variations were measured as an electric signal at 30-s intervals and averaged to half-hour values by dataloggers. Each dendrometer was individually calibrated to convert the recorded millivolt signals to a metric scale (1 mV \approx 0.001 mm).

Dendrometer measurements were regularly read out and checked for erroneous measurements using a remote connection. Hence, instrument failures could be quickly detected and solved. However, in spite of the frequent checks, temporary interruptions in dendrometer series were inevitable.

2.3. Forest meteorological data

Over the study period, extensive forest meteorological data was collected at both aspects using an experimental set-up described in detail by Mayer et al. (2002) and Holst et al. (2004, 2005). In our analyses, we used daily forest meteorological data from two on-plot meteorological walk-up towers (1.5 times stand height) on above-canopy air temperature (minimum, mean and maximum), solar radiation, precipitation, and vapor pressure deficit (VPD; i.e., the difference between saturated and actual vapor pressure). In addition, we considered soil water content (SWC) data of the uppermost soil layer, which was continuously monitored using time domain reflectometry (TDR). Per aspect, two probes with needle lengths of 30 cm (CS615, Campbell Scientific, Logan, USA) were buried vertically into the soil. Averages and ranges for each of these forest meteorological variables are reported in Table 1 for the NE aspect. For detailed analyses on microclimatic differences at SW, as addressed in Section 2.1, we refer to papers by Mayer et al. (2002) and Holst et al. (2004, 2005).

2.4. Data analysis

As dendrometers record both irreversible tree growth and reversible hydrological swelling and shrinking, several studies separated daily stem size variations into distinct phases of contraction, expansion and stem radius increment to extract information on xylem development (Deslauriers et al., 2003; Downes et al., 1999; Herzog et al., 1995). Such stem cycle approaches require complex algorithms to disentangle cyclic phases and phase durations (see Deslauriers et al., 2011). However, as time series produced from stem cycle approaches are highly correlated with daily approaches

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