



Drought sensitivity and stem growth variation of nine alien and native tree species on a productive forest site in Germany

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ABSTRACT

Many non-native tree species have been introduced to Europe to improve forest productivity. It is assumed that some of these species are better able than native species to mitigate negative effects of climate change. A high growth-related tolerance to climatic extremes is essential to qualify a tree species' suitability for cultivation and must be quantified before initiating adaptation measures. This study investigated basal area and volume increment (BAI and VI) data at various stem height positions to evaluate inter-annual growth variation (mean sensitivity) and drought tolerance of seven alien tree species (*Acer rubrum* L., *Betula maximowicziana* Regel, *Castanea sativa* Mill., *Cryptomeria japonica* D. Don, *Metasequoia glyptostroboides* Hu et Cheng, *Thuja plicata* Donn and *Tsuga heterophylla* Sarg.) which are considered stress tolerant, and two native species (*Fagus sylvatica* L., *Picea abies* H. Karst.) in the Arboretum Burgholz in West Germany. We found that mean sensitivity and response to drought (*resistance*, *recovery*, *resilience*) were related; i.e., sensitive species exhibited greater drought response than less sensitive species. In the drought years 2003, 2006 and 2010/2011, VI of the highly sensitive species *C. japonica* and *P. abies* and rather moderate sensitive *A. rubrum* decreased most strongly (36%), while less sensitive *C. sativa* and *T. heterophylla* were the most resistant tree species (25% decrease). *B. maximowicziana*, *F. sylvatica*, *M. glyptostroboides* and *T. plicata* were moderately sensitive to drought events (growth depression by 29%). *Recovery* after drought showed mainly a reverse response pattern; species with lower *resistance* recovered faster, but this trade-off was not uniform among species. Across drought events, we observed high variation in the response of individual trees and between different tree species. This finding indicates that species' drought sensitivity depends strongly on the drought's onset, duration and frequency. Along tree stems, mean sensitivity and response to drought in 2003 decreased species-specifically from lower to upper stem section height. Thus, quantifying drought sensitivity based solely on breast height measures may result in biased estimates of production declines.

1. Introduction

Increases in temperature and climate variability (IPCC, 2013) are associated with increases in the future frequency, magnitude and duration of extreme weather events in Europe (Beniston et al., 2007; Smith, 2011). These climatic extremes, i.e. storms, heat waves and severe drought periods (Dai, 2011) have become important drivers of long-term forest ecosystem dynamics (Bréda et al., 2006; Pretzsch et al., 2013). They may modify pathogen and pest regimes and increase the vulnerability of trees to altered site conditions (Bolte et al., 2009). Declines in forest productivity (Ciais et al., 2005) and higher tree mortality (Allen et al., 2010; Carnicer et al., 2011) entail hazards to

cultivation of a number of economically relevant native tree species. As a result, adaptive forest management may be obliged to consider exotic tree species and the establishment of mixed forests to reduce risk (Jandl et al., 2015; Neuner et al., 2015). In this context, exotic tree species that seem to be adapted to the expected environmental conditions due to their wide natural and climatological ranges are of special importance (Bolte et al., 2009; Kölling et al., 2009). Properties such as drought tolerance or adaptability to extreme weather conditions in general are of special interest (Choat et al., 2012; Niinemets and Valladares, 2006).

To counteract climatic stress, tree species have developed various anatomical and physiological strategies (George et al., 2015); for example, leaf area control (Le Dantec et al., 2000), stomatal regulation of

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transpiration (McDowell et al., 2008), or biomass allocation to below-ground plant compartments (Delucia et al., 2000; Schall et al., 2012). A tree's drought sensitivity depends in particular on the limitations of its vascular wooden tissue's hydraulic architecture (xylem; Tyree and Ewers, 1991). Cavitation-induced emboli inhibit xylem conductivity and reduce water transport potentials from lower parts of the tree to the sites of photosynthesis (Choat et al., 2012). While direct assessment of embolism resistance is challenging (George et al., 2015), tree growth performance, typically captured by retrospective tree ring analyses, can be used as an indicator of drought susceptibility with less effort. Annual ring formation is coupled with tree water availability and carbon allocation for cambial activity (Hinckley et al., 1979; Zweifel et al., 2006). The growth response to climatic stress conditions can be assessed by tolerance components such as *resistance* (R_s), *recovery* (R_c), and *resilience* (R_l) according to Lloret et al. (2011). These attributes quantify changes in growth patterns during and after climatic disturbances and indicate the capacity of a tree (i) to withstand disturbances, (ii) to recover after drought, and (iii) to regain pre-disturbance growth performance (Lloret et al., 2011). *Resistance*, *resilience*, and *recovery* of major European tree species have been investigated in numerous studies (e.g. George et al., 2015; Knutzen et al., 2017; Zang et al., 2011, 2014). Further investigations have dealt with the effects of tree age and size (Lloret et al., 2011; Zang et al., 2012), competition status and species composition (Carnwath et al., 2016; Merlin et al., 2015; Metz et al., 2016; Pretzsch et al., 2013), thinning and changes in stand density (e.g. Kohler et al., 2010; Sohn et al., 2013) and interactions of growth responses with site, tree, and stand characteristics (Rais et al., 2014; for an overview see Ammer, 2017). However, to date few investigations have taken into account the drought sensitivity of alternative, alien tree species (Eilmann and Rigling, 2012) that are potentially well adapted to changing climate conditions.

Growth measurements at breast height (diameter = DBH and basal area = BA) are conventionally applied in forest research as useful predictors for approximation of tree dimension, biomass production and stand density. Several allometric models use DBH as the key variable to predict tree volume, stem form or diameter at an arbitrary stem location (Kublin et al., 2013). The majority of dendrochronological studies have been based on increment core sampling at breast height (Chhin et al., 2010), taking advantage of relatively long time series (Schweingruber et al., 1990). The underlying assumption is that increment measurements at breast height do not bias whole stem growth patterns or responses to external factors (Latte et al., 2016; Sohn et al., 2012). Hence, growth measures at breast height or stem base (Chhin and Wang, 2005) and volume increment (Corona et al., 1995; Hogg et al., 2005) have shown comparable climate-growth relationships. However, increment changes in upper stem sections were found to be less sensitive to drought (for trees of lower altitude; < 430 m a.s.l.) when compared with diameter increment at breast height (Bouriaud et al., 2005; van der Maaten-Theunissen and Bouriaud, 2012). Increasing climate sensitivity with tree height (Kerhoulas and Kane, 2012; Latte et al., 2016), higher growth recovery for topmost heights after drought stress (Sohn et al., 2012), and inconsistencies in the responses of lower and upper stem segments to temperature and climate moisture have been reported (Chhin et al., 2010). Due to allometric discrepancies, model-based growth projections acquired by breast height measures (e.g. Bauwe et al., 2016; Fernandez-de-Una et al., 2015; Williams et al., 2012) may therefore over- or under-estimate drought tolerance. Validation of height- and volume-related growth responses is needed to better assess tree species' suitability in terms of climatic stress tolerance and productivity.

Here we analysed the growth sensitivity of two native tree species and seven alien tree species introduced to Europe, and the growth response of trees to drought at various tree heights in order to capture intra-tree variability. The aims of this study were to (1) quantify and characterize tree species-specific inter-annual growth variability, to (2) determine *resistance* during, and *recovery* and *resilience* after heat and

drought, and to (3) examine species-specific growth variation at various stem height positions.

2. Material and methods

2.1. Species selection and study site

The following tree species not native to Europe were selected: *Acer rubrum* L., *Betula maximowicziana* REGEL, *Castanea sativa* MILL., *Cryptomeria japonica* D. DON, *Metasequoia glyptostroboides* HU ET CHENG, *Thuja plicata* DONN and *Tsuga heterophylla* (RAF.) SARG. Besides economic criteria (high growth rates, low management risks), all referred species are characterized by a wide range of climatic amplitudes (e.g. Burns and Honkala, 1990; Praciak, 2013; Roloff et al., 2011; SRC NRW, 1986; Walters and Yawney, 1990). Two of the economically most important European native tree species (*Fagus sylvatica* L. and *Picea abies* H. KARST.), one representing a deciduous and the other a coniferous tree species, were included as reference species. In the following, species will be denoted by genus only (for example *Thuja plicata* = *Thuja*).

In order to evaluate species growth performance under comparable site conditions, a uniform forest district was chosen. Stands of the tree species mentioned above are located in the Arboretum Burgholz near Wuppertal in North Rhine-Westphalia (West Germany). This Arboretum is characterized by a podzolic Cambisol with poor to moderate nutrient supply, a silty loam soil texture, good soil water supply and a mor humus layer (Wald und Holz NRW, 2013). In addition to similar soil and climatic conditions, all stands were evenly aged (34–58 years) and had undergone the same silvicultural treatment (thinning from above). However, some of the stands were mixed (but dominated by the target species and selected since no alternative monocultures for these rare species exist nearby exist) while others were monospecific (see Table A.1 for details). For the period 1960–2014, annual temperature was 9.8 °C and annual total precipitation sum was 1131 mm. The values for the vegetation period (May–September) were 15.5 °C with 468 mm (DWD, 2015).

2.2. Tree sampling, preparation and analysis of stem disks

Six to ten vital and dominant or co-dominant (according to Kraft, 1884) individuals per tree species were selected for stem analysis. Cross-sectional disks were cut along the main stem of the felled target trees at 0.5 m, 1.3 m and subsequently every 2 m to the top (29.3 m for the highest trees, Fig. 1). The dried stem disks were planed, polished with progressively fine grit sandpaper, and scanned at 1200 dpi resolution (A3 scanner 2400 S, Mustek). To minimize eccentric growth effects, tree ring width was measured along four radii at the main cardinal direction using the semiautomatic image analysis software LignoVision™ (version 1.38e, Rinntech e. K., Heidelberg, Germany) with a precision of 0.01 mm (Rinn, 2006). The obtained radial series were post-edited using the TSAP software (TSAP-Win professional version 4.68e Rinntech e. K., Heidelberg, Germany) to verify the synchronicity within each tree and species. After visual crossdating according to the list method (Yamaguchi, 1991) the series were statistically crossdated in a stepwise procedure using averaged reference series according to the "leave-one-out principle" (Bunn, 2010). In the first step we examined the radial series within a stem disk (comparison of radial directions). We then tested the synchronicity within a tree (comparison of height sections). Finally, we checked the simultaneity among the trees using the mean series at 1.3 m stem height (comparison of individuals). The synchronicities were verified using the statistical parameters *Gleichläufigkeit* (Eckstein and Bauch, 1969), *Gleichläufigkeit*-Significance (Rinn, 2005) and *t*-value (Baillie and Pilcher, 1973). A total of 75 trees and 903 stem disks met these criteria and were included in further analyses (Table A.2).

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