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Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe

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ABSTRACT

Climate change projections indicate drier conditions and an increase in the frequency and duration of extreme drought events in the coming decades in Central Europe. However, it is not clear which tree species will be able to cope with drier climatic conditions and higher year-to-year climatic variability. We analyzed tree-growth responses of five co-occurring conifer species to past climatic variations and severe droughts across a wide climatic gradient in Central Europe, covering four distinct biogeographic regions: the northern Swiss Alps, the Swiss Plateau, the foothills of the Jura Mountains and the dry Central Alps. We studied three native tree species (*Larix decidua* Mill, *Picea abies* (L.) Karst. and *Pinus sylvestris* L.) and two non-native species (*Pinus nigra* Arn. and *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Tree-ring width was measured for 770 trees from 14 sites and species-specific site chronologies were established. Response-function analysis, Principal Component Analysis (PCA), linear regressions and Superposed Epoch Analysis were used to assess the species-specific growth sensitivity to climate and severe drought along the gradient. Irrespective of the species and site conditions, high temperatures and low precipitation amounts in summer and autumn of the year prior growth significantly reduced tree growth. When evaporative demand, precipitation and soil water holding capacity were considered together, low water availability in current summer strongly reduced growth. Overall, the growth-climate relationships of the species were not or only slightly related to the site water balance per se. However, when all species-specific growth response coefficients were introduced into a PCA, a clear separation of the populations of the Central Alps (driest sites) became apparent. At these sites, soil water deficits in previous autumn and current spring strongly reduced radial growth, whereas at moist and wet sites on the Swiss Plateau, in the Jura Mountains and northern Alps summer drought impeded growth. Along the gradient, the native *P. abies*, *L. decidua* and *P. sylvestris* were the most sensitive species to drought, implying that their long-term performance and survival on nowadays dry sites can be compromised under a drier climate in Central Europe.

1. Introduction

Consequences of global warming and reduced water availability on forest ecosystems are already visible worldwide (Allen et al., 2010). In Europe, prolonged water deficits and severe droughts have caused increasing rates of tree mortality, severe forest decline and vegetation shifts on dry sites and at the edge of species distribution ranges (Galiano et al., 2010; Rigling et al., 2013). These phenomena will likely increase in magnitude in the coming years with the anticipated higher year-to-year climatic variability and long-term increase in aridity (Christensen et al., 2007), challenging forest management practices and compromising the provision of forest ecosystem goods and services (Elkin et al., 2013). Since anticipated drier climatic conditions may differ in magnitude between sites, priority should be given to understanding the sensitivity of tree species to drought along wide ecological gradients. This is becoming particularly critical as there is growing evidence of drought-induced growth declines at the range margins of species distribution (Andreu-Hayles et al., 2011; Lévesque et al., 2014), but also in the center of the species' ranges (Carnicer et al., 2011). At the same time, the search for alternative tree species that are drought tolerant, but also able to produce a sufficient amount of high

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quality timber becomes essential for the elaboration of future adaptive forest management strategies (cf. Eilmann et al., 2013; Temperli et al., 2012).

Dendrochronological studies using tree-ring width are valuable to retrospectively analyze tree performance to past climatic conditions including droughts, as radial growth has a lower allocation priority in the short term than root and foliage formation (Kozlowski and Pallardy, 2002), making tree-ring width highly sensitive to climate variations (Fritts, 1976). By investigating tree growth responses to past climatic conditions and extreme drought events, the present sensitivity to climate of co-occurring tree species can be determined, and inferences can be drawn regarding their future performance. Tree response to drought depends on many environmental and site-related factors such as precipitation, temperature, topography and soil characteristics (Pasho et al., 2012; Weber et al., 2013). In regions with heterogeneous relief, topographic conditions and soil characteristics strongly influence and modulate tree-growth response to drought. Growth is most sensitive to drought at sites with low water holding capacity (Rigling et al., 2002; Weber et al., 2007) and on south and southwest aspects (Fekedulegn et al., 2003) where water deficits are exacerbated. Although drought sensitivity of tree species can vary markedly in space due to different ecological and climatic conditions, dendroecological analyses have rarely been conducted at large scales. Instead, they usually focus on a single or a few sites along a small ecological gradient. This is particularly true for Central Europe where the drought tolerance of co-occurring species has rarely been compared along wide ecological gradients (e.g. Zang, 2011). However, such analyses are highly relevant since recent findings indicate that co-occurring species with different life history strategies and contrasting responses to annual climate variability may reduce species-specific sensitivity to drought and enhance forest resilience to climate change (Drobyshev et al., 2013; Lebourgeois et al., 2013).

In this study, we analyzed tree-growth responses of five co-occurring conifer species to climatic variations (temperature, precipitation), soil moisture and to severe drought events across a wide climatic gradient in Central Europe. We studied three species that are native to Central Europe (*Larix decidua* Mill, *Picea abies* (L.) Karst. and *Pinus sylvestris* L.) and two non-native species (*Pinus nigra* Arn. and *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). *L. decidua* is a deciduous, pioneer and shade-intolerant species of mid to high altitudes, able to tolerate a high thermal amplitude (Ellenberg, 2009), but known to be somewhat sensitive to summer water deficits (Lévesque et al., 2013; Schuster and Oberhuber, 2013). *P. abies* is an intermediately shade-tolerant species, which is widely distributed across the Alps but has also been planted widely outside its natural range in Central Europe for economic reasons (Klimo et al., 2000). This species is quite sensitive to summer drought (Lebourgeois et al., 2010; Lévesque et al., 2013) and highly susceptible to bark beetle attacks during dry and hot summers (Wermelinger, 2004). *P. sylvestris* and *P. nigra* are light-demanding pioneer species, *P. sylvestris* being more drought sensitive (Lebourgeois et al., 2012; Martin-Benito et al., 2013). *P. sylvestris* occurs in a wide range of habitats from Spain to Siberia, and at elevations from sea level to 2600 m a.s.l. (Matías and Jump, 2012). *P. nigra* is native to the Mediterranean and Vienna basins, where summer droughts are frequent, and has been planted in Central Europe for ca. 130 years (Bürgi and Diez, 1986). This species is considered as a potential substitute for *P. sylvestris* under a drier climate in Central Europe (Thiel et al., 2012). *P. menziesii* (var. *menziesii*) is an intermediately shade-tolerant species native to western North America and was introduced to Europe in the mid 19th century. It is fast growing, produces high quality timber and is considered as a potential alternative to the more drought sensitive *P. abies* in Central Europe (Jansen et al., 2013).

The main objective of this study was to assess the growth sensitivity of five co-occurring conifers to climatic variability and severe droughts along a wide climatic gradient, with the goal of making inference about possible species responses to future increases in aridity in Central Europe. Specifically, the research questions were (1) How does tree growth response to temperature, precipitation and drought vary along a site moisture gradient? and (2) Do co-occurring species differ in their drought sensitivity along the gradient?

2. Materials and methods

2.1. Study area and sites

The study area is located in Switzerland and northern Italy and includes four distinct biogeographic regions: the northern Swiss Alps, the Swiss Plateau, the foothills of the Jura Mountains and the dry Central Alps (Table 1, Fig. 1). The order of the geographical regions corresponds to an ecological gradient of decreasing annual precipitation and increasing occurrence of summer drought. Within the study area, we selected 14 sites that met three criteria: (1) presence of at least one non-native species: *P. menziesii* or *P. nigra*, (2) co-occurrence of at least three of the five studied species, i.e., *P. abies*, *L. decidua*, *P. sylvestris*, *P. menziesii* and *P. nigra*, (3) even-aged stand with the presence of trees being at least 70 years old. Accordingly, 770 trees were sampled for dendroecological analysis (Table 2, Table S1). At each site, a soil profile was dug to determine soil type and soil properties. The physical and chemical properties of each soil horizon were recorded up to a depth of 1 m. The available water holding capacity of the soil between 0 and 100 cm depth was estimated using data on soil texture (content of sand, silt and clay), bulk density, content of coarse fragments (>2 mm) and depth of each of the recorded soil horizons according to AG Bodenkunde (1982).

2.2. Dendrochronological methods

At each site, between 11 and 15 healthy dominant or co-dominant trees per species were sampled by taking two increment cores per tree at ca. 50 cm height. Cores were mounted on wood supports and their surfaces were prepared using a core microtome (Gärtner and Nievergelt, 2010). Cambial age at sampling height was determined by estimating the number of missing rings between the first complete ring on the core and the pith according to the geometric method of Duncan (1989). The sampled trees were between 72 and 158 years old at coring height. Ring width was measured to the nearest 0.01 mm with a stereo microscope connected to a LINTAB digital positioning table and the software TSAP (Rinntech, Heidelberg, Germany). Individual tree-ring series were visually crossdated and verified statistically using COFECHA (Holmes, 1983). Cores that could not be correctly crossdated were removed from further analyses. For each tree, measurements from the two cores were averaged. Individual tree-ring width series were detrended to retain the high-to-mid frequency variability of growth using a 32 years cubic smoothing spline with a 50% frequency response using the package *dplR* (Bunn, 2008) within the R software (R Core Team, 2013). Individual standardized series were averaged per site using a biweight robust mean and standard chronologies were produced. To assess the signal strength of each chronology, inter-series correlations and expressed population signals were calculated (Wigley et al., 1984). The first order serial autocorrelation, which measures the influence of previous year's conditions on ring formation, and mean sensitivity, which quantifies the year-to-year variability in the width of consecutive tree rings (Fritts, 1976), were also calculated from the raw chronologies.