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Summer droughts limit tree growth across 10 temperate species on a productive forest site



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ABSTRACT

Studies on climate impacts on tree annual growth are mainly restricted to marginal sites. To date, the climate effects on annual growth of trees in favorable environments remain therefore unclear despite the importance of these sites in terms of forest productivity. Because species respond differently to climate, comparing a multitude of species further enhances our knowledge on climate impacts on tree growth and forest productivity.

We present a first study that reveals to what extent radial growth is limited by climate and the groundwater table across 10 temperate tree species growing on a uniform, productive soil (i.e. high nutrient and water contents) in the Netherlands. We ranked our study species according to their shade tolerance, which is associated with species' resource requirements and growth rates, and examined their annual growth using tree-ring analysis. This allowed us to investigate how these species with diverse ecological backgrounds differ in their growth response to precipitation, temperature, irradiance, potential evapotranspiration (PET), and the groundwater table, when growing under similar and favorable site conditions.

Nine out of 10 species had strikingly similar radial growth rates (on average 3.9–4.8 mm yr⁻¹), which contradicts the widely established trade-off between shade tolerance and growth. *Populus trichocarpa*, the least shade-tolerant of our species, however grew much faster (on average 6.8 mm yr⁻¹). Trees of all species reduced their growth significantly during dry summers, driven by low rainfall and high PET. Yet, the magnitude of their growth responses to climate conditions and especially the groundwater table differed across species. Receding groundwater tables significantly and strongly reduced radial growth of the shade-intolerant species, but not of the shade-tolerant species. The climate impacts on growth were not associated with variation in shade tolerance across our species.

Our study demonstrates that even on a productive forest site, summer droughts reduced radial growth across a multitude of common tree species, whereas lower groundwater tables only affected the shade-intolerant species significantly. Thus, the productivity of forests in favorable environments may be seriously affected when summers in north western Europe become hotter and drier as predicted by climate models.

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1. Introduction

Climate models predict higher yearly mean temperatures and a change in precipitation patterns leading to wetter winters and drier, hotter summers in northwestern Europe (Alcamo et al., 2007; Lindner et al., 2010). These forecasts imply that temperate forests will encounter increased water supply in spring, but more frequent and intense droughts in summer (Broadmeadow et al., 2005; Scharnweber et al., 2011) with possibly detrimental effects on tree growth (Bolte et al., 2009; Allen et al., 2010). Tree growth

depends on several interrelated climate variables. High evaporative pull from the atmosphere for example, associated with high air temperature and irradiance can hamper growth when water supply does not meet atmospheric demand (Bréda et al., 2006). Under these conditions, stomatal closure reduces tree water loss but also carbon uptake which limits growth (Bréda et al., 2006; McDowell et al., 2008). At the same time, the effects of temperature on tree growth depend on water availability: temperature can enhance growth (Lindner et al., 2010), but only if water is sufficiently available (Bolte et al., 2009).

Previous dendrochronological studies assessed climate impacts on radial growth, but mainly under extreme site conditions (e.g. Van der Werf et al., 2007; Eilmann et al., 2009; Helama et al., 2009; Mérian and Lebourgeois, 2011; Scharnweber et al., 2011),

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or at the limits of a species' natural distribution (e.g. Andreu et al., 2007; Eilmann et al., 2011), where growth-limiting factors are more manifest. These studies are often restricted to a single or a few species (e.g. one to five species in the references given above). So far, it is uncertain if and to what extent trees growing in productive temperate forests with favorable water-holding capacities also suffer from the predicted water deficits and temperature rise, and whether this varies across species. This knowledge is nonetheless essential to predict the productivity of forests, especially because wood production of different species is even more important on productive than on marginal sites. Furthermore, assessing the climate impacts across a large species set could contribute to selecting appropriate species for these economically relevant forests.

In order to expand our insights into climate effects on tree growth beyond marginal sites and few species, this study compares annual growth rates and responses to climatic variation across 10 temperate, deciduous tree species under productive and uniform soil conditions. These beneficial conditions include a calcareous clay soil with high water-holding capacities, high moisture and nutrient contents (Cornelissen et al., 2012), and shallow groundwater tables (Bijlsma and Verkaik, 2008). In order to compare our study species from an ecological background, we have ranked them based on a shade tolerance index (Niinemets and Valladares, 2006). The shade tolerance of a species is largely associated with its plant strategy (Grime, 1974) where shade-intolerant species typically acquire resources rapidly in order to maintain high growth rates under resource-rich conditions. More shade-tolerant species generally take up resources at a slower pace and retain them longer. This enhances tolerance to and occurrence in resource-poor environments, but at the expense of growth rate (Grime, 1974; Aerts and Chapin, 2000; Reich et al., 2003; Díaz et al., 2004).

From this species classification, we first test whether more shade-intolerant species indeed grow faster than more shade-tolerant species on this water- and nutrient-rich soil. Secondly, we hypothesize that shade-intolerant species respond more strongly to climate conditions and to the depth of the groundwater table than shade-tolerant species and that their growth is more limited by low water availability, as they exploit their resources faster. We expect that such growth limitations are strongest in summer when water supply is insufficient to meet the high evaporative demand associated with high temperature and irradiance. We expect less severe water limitations for growth in spring because lower temperatures reduce evaporative water demand and more water will be available from winter rainfall (Dittmar et al., 2003).

To test our hypotheses, we selected an experimental forest setting in the Netherlands that hosts a variety of temperate tree species growing under uniform climate and soil conditions, where the soil is characterized by high nutrient and soil moisture levels compared to other forests in northwestern Europe (Cornelissen et al., 2012). This study site provides a unique opportunity to compare growth rates and responses to climate among dominant, mostly 35–40-year old trees from 10 different tree species (Table 1) in monospecific stands on a homogeneous, favorable soil. We tested the impacts of spring and summer precipitation, temperature, potential evapotranspiration (PET), irradiance, and groundwater depth on tree growth using tree-ring analyses.

2. Methods

2.1. Study site

Field work was conducted at an experimental forest setting in the Hollandse Hout, in the centre of the Netherlands (52°28'N, 5°26'E). The area was reclaimed from the sea in the 1960s and is sit-

uated at approximately 4 m below sea level. It is characterized by a temperate marine climate with mild winters and summers (Fig. 1) and an annual precipitation of approximately 800 mm (KNMI, 2009). The Hollandse Hout forest comprises approximately 900 ha and was established in the late 1960s and the 1970s, with a variety of deciduous and coniferous species planted in monospecific stands. Its marine clay soil is calcareous and nutrient-rich (see Appendix 1 for soil characteristics; Kemmers et al., 2000; Cornelissen et al., 2012) and has a uniform texture across the forest (Alterra, n.d.). Groundwater tables are highly controlled by the regional water board to prevent flooding (P. Ponsteen, personal communication), and range from 1.6 to 1.2 m below the surface averaged over 17 years of available groundwater data (TNO-NITG, 2011).

To test growth responses to climate, climate data were retrieved from the De Bilt weather station of the Royal Dutch Meteorological Institute (Klein Tank et al., 2002) at approximately 50 km from the study site. They include daily precipitation (mm), temperature (°C), potential evapotranspiration (PET; mm) and irradiance (J cm^{-2}) records. PET was calculated according to Makkink's method which integrates temperature and irradiance (Klein Tank et al., 2002). Groundwater depth data (cm below ground level) were available from the Dutch Organization for Applied Scientific Research (TNO-NITG, 2011), and were retrieved from one station located in the centre of the forest, where they were recorded twice per month. The groundwater data covered only a short time span (17 years, 1981–1997), with data missing for 23 months that were replaced by data from a nearby station that correlated highly ($r = 0.94$). Climate and groundwater data were grouped into two seasons: spring (1 March – 31 May) and summer (1 June – 31 August), and we calculated seasonal sums (for precipitation and PET) or averages (for temperature, irradiance and groundwater depth).

In this system, spring precipitation and spring groundwater depth were correlated such that high rainfall coincides with shallow groundwater tables (Fig. 2a, $r = 0.54$, $P < 0.05$, $N = 17$). In summer however, precipitation and groundwater were not significantly correlated (Fig. 2c, $r = 0.10$, $P = 0.70$, $N = 17$). Precipitation had no significant impact on the summer groundwater table after a one, three and six month time lag either (not shown). Precipitation correlated negatively with irradiance in spring ($r = -0.47$, $P < 0.01$) and in summer ($r = -0.54$, $P < 0.001$), and with PET in summer ($r = -0.43$, $P < 0.01$). Temperature increases evaporative demand in spring (Fig. 2b, $r = 0.32$, $P < 0.05$, $N = 40$) and summer (Fig. 2d, $r = 0.87$, $P < 0.001$, $N = 40$). Irradiance (not shown) correlated with PET in summer ($r = 0.97$, $P < 0.001$, $N = 40$), and to a lesser degree in spring ($r = 0.44$, $P < 0.01$, $N = 40$), as well as with temperature in both summer ($r = 0.82$, $P < 0.001$, $N = 40$) and spring ($r = 0.44$, $P < 0.01$, $N = 40$).

2.2. Study species and sampling

We collected increment cores of 10 mostly even-aged (35–40 year old) individuals for each of 10 deciduous tree species: *Acer pseudoplatanus* L. (sycamore maple), *Alnus glutinosa* L. Gaertn. (black alder), *Betula pendula* Roth. (silver birch), *Fagus sylvatica* L. (European beech), *Fraxinus excelsior* L. (European ash), *Populus trichocarpa* (black cottonwood), *Prunus avium* L. (wild cherry), *Quercus robur* L. (pedunculate oak), *Salix alba* L. (white willow), *Tilia cordata* Mill. (small-leaved lime) (Table 1). Some *P. avium* and *S. alba* trees sampled, were however younger, i.e. 20–30 years from the year of establishment.

Two dominant trees were sampled from each of five monospecific stands per species to ensure that our study trees were fully light-exposed and to minimize the effects of competition by other trees on growth. The stands were evenly distributed across the forest to guarantee sufficient replicates. Two increment cores per tree were extracted at breast height, and diameter (DBH) was mea-

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