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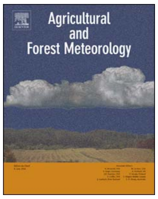

Projecting tree-growth responses into future climate: A study case from a Danish-wide common garden

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ABSTRACT

Assessing growth responses to climate variations from common garden experiments is vital to identify a species portfolio matching future climate. In the present study we make use of a 50 years old common garden experiment spanning six sites with different soil types across Denmark to (i) analyse climate-growth responses and resilience to drought and (ii) model future growth predictions for six non-native conifers and two native broadleaved tree species. Species-specific response-functions and Superposed Epoch Analysis of drought events are used to assess differences in sensitivity to drought.

The results show that the growth of all species, except for *Quercus robur* L., are significantly ($P < 0.05$) and negatively correlated with summer drought from June-August in at least one of the sites, whereby *Larix kaempferi* (Lamb.) Carr, *Abies grandis* (Dougl.) Lindl., *Picea sitchensis* (Bong.) Carr., and *Picea abies* (L.) Karst. are the less resilient. Negative effects of previous warm autumn or late summer were found for *P. abies*, *A. grandis*, *Abies alba* Mill. and *Pseudotsuga menziesii* (Mirb.) Franco. Moreover, independently of the site conditions, our model projections of growth responses under future climate prediction (RCP4.5 emission scenario) forecast that growth of *L. kaempferi*, *A. grandis*, *P. abies* and *Fagus sylvatica* L. will be reduced by up to 10–16% by 2100. Minor changes in growth responses are expected for *P. sitchensis*, *A. alba* and *P. menziesii*, while *Q. robur* will increase by 12%.

This study demonstrates how such projections based on old common garden experiments could be used as inputs to today's forest management decisions.

1. Introduction

Today's composition and structure of European forests are often the results of management decisions taken decades or even centuries ago. These decisions were based on the assessment of the growth behaviour of the tree species at the given site and by an assessment of future needs. However, due to uncertainties related to expected shift in climate, today's forest management decisions are additionally challenged by the fact that future forest ecosystems might soon be exposed to unprecedented environmental conditions (Kirilenko and Sedjo, 2007). Current scenarios of climate change are predicting important modifications in both temperature and precipitation regimes in many regions, with in particular the intensification of extreme events and disturbances (Dai, 2013; Field et al., 2014). In Denmark for example, depending on the greenhouse gases concentration scenarios, it is expected that by the year 2100 the temperature will increase between 1 and 4 °C (Kjellström et al., 2011; Olesen et al., 2014) with an increased risk of more frequent and longer drought spells in summer (Olesen et al., 2014).

Climatic changes will profoundly affect the interactions between trees and their physical and biological environments, with important implications for tree growth and mortality (Anderegg et al., 2015). Indeed, widespread episodes of mortality have already been observed all over the globe, either directly linked to climate events (e.g. Allen et al., 2010) or indirectly through modifications of the relationships with pests and diseases (Gaylord et al., 2013; Jactel et al., 2012). Drought is one of the main constraints on forest productivity especially at soils with low water holding capacity (Weber et al., 2007). Drought events trigger abrupt growth decline (Orwig and Abrams, 1997) and mortality (McDowell et al., 2011), which may have important consequences for the structure and functions of Earth's forest ecosystems (Lindner et al., 2014). Drought episodes, defined as episodes of severe

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climatic water deficit, have been reported to reduce growth and induce incomplete recovery for 1–4 years after the event, with pervasive legacy effect most prevalent in dry ecosystems (Anderegg et al., 2015).

For appropriate species selection and management of future forest resources a deeper insight into tree growth and mortality responses is needed (Sass-Klaassen et al., 2016). To survive under rapid climate changes, a high degree of phenotypic plasticity and a high adaptive potential of species are required. For example, previous studies have reported that *Quercus* spp and *Abies alba* Mill. are more competitive than *Fagus sylvatica* L., while *Picea abies* (L.) Karst. is more sensitive than *A. alba* and *F. sylvatica* under dry and warm summers (Bolte et al., 2010; Leuschner et al., 2001a; Mette et al., 2013; Zang et al., 2014). It is thus expected that *P. abies* will shift northward and be replaced by more drought tolerant species at low elevations in central Europe (e.g. *Quecus* spp and *Pseudotsuga menziesii* (Mirb.) Franco) (Hanewinkel et al., 2013). Forest managers are requiring more and more indications on how growth and survival of different tree species will develop in a changing climate in order to compose an optimal species portfolio and guarantee forests are preserved to meet future generation needs (Forest Europe et al., 2015). However, this is a challenging task, since the mechanisms of responses are complex, diverse, and may differ between species. Often they do not only depend on the magnitude and frequency of the climatic factors, but also on the genetic characteristics, life stage, and life history of trees (Reichstein et al., 2013). More data on the genetic and environmental sources of variability in response to climatic events are thus necessary to address this challenge and to provide better prediction about where and how different tree species will survive and perform under future climates.

An important contribution towards a better understanding of how climate and other environmental factors can affect growth and survival of different trees species or provenances is offered by the common garden experiments. Old common garden experiments represent an important source of information, since they often combine information about the genetic background of the planted trees and provide a long history of how trees responded to the environmental conditions occurring at the site. Through the use of dendrochronological approaches, these settings represent an opportunity to evaluate how different tree species have responded to climate variations and extreme climatic events. Depending on the location of the experiments, this can be achieved even outside the natural range of the species.

In this study we use a nationwide Danish common garden experiment established in 1964 and 1965 that included several native and non-native tree species in order to assess how growth responded to climate conditions and extremes events across sites and species. Specifically, (i) we identified which climatic factor mostly affected the growth of several species at different field trials; (ii) we assessed species differences in growth resilience to drought; (iii) and used obtained results to project growth into future climate scenarios.

2. Materials and methods

2.1. The common garden experiment

This study is based on a nationwide Danish common garden experiment (Fig. 1) established between autumn 1964 and spring 1965. The common garden was established by the *Danish Forest Experiment Station*, now part of the University of Copenhagen, with the aim of assessing the growth potential for high quality wood production in Denmark (Holmsgaard and Bang, 1977). The whole common garden includes 13 field trials with a total of 10 conifer and 2 broadleaved species, both native and non-native to Denmark. Each species is represented by the same Danish landrace or provenance at all sites (Holmsgaard and Bang 1977). Field trials are composed by 0.17–0.31 ha monospecific plots randomly located within each trial. The trees were planted at an age of two to four years and with a spacing of 1.3 × 1.3 m for conifers and 1.3 × 0.65 m for broadleaved species. The plots were thinned regularly in order to favour the higher quality candidates and limit competition between trees. The applied thinning regimes were from below, but over time it included also co-dominant and dominant trees. Thinning activities started at the time when the canopy of the plots closed (year 1974–1982 depending on site and species) and were subsequently made every four years according to the management practices of the owners of the field trials and with few exceptions in case of windfall.

2.2. Site selection and collection of wood material

For this study, we selected six field trials to cover the range of common Danish site and climatic conditions (Table 1) and to share the same species (Fig. 1). The soils at the six trial sites were classified as Luvisols, Arenosols and Podsols, some with seasonally shallow groundwater. Soil texture classes vary from coarse sand to sandy loam with subsoil clay percentages ranging from 2% (1013) to 23% (1011) (Callesen, 2003), representing water holding capacities from relatively dry to moist (Table 1). The climate at the trial sites is characterized by the typical Danish temperate climate with mild winters and cool summers. According to the Climate Research Unit grid data (CRU TS v.3.22; Harris et al., 2014), the mean annual temperature of the trial sites from 1961 to 2012 ranged between 7.7 and 8.5 °C, while precipitation was fairly well distributed with an annual sum ranging between 572 and 855 mm yr^{-1} (Table 1).

Each selected field trial included six non-native conifer and two native broadleaved species, namely *P. abies*, *Picea sitchensis* (Bong.) Carr., *A. alba*, *Abies grandis* (Dougl.) Lindl., *P. menziesii*, *Larix kaempferi* (Lamb.) Carr., *Quercus robur* L. and *F. sylvatica*. Stem discs were collected from 6 individuals per species plot and site, with the exception of *P. sitchensis* (at site 1014 and 1013) and *P. menziesii* (at site 1009), for a total of 268 stem discs. Stem discs were collected at stem breast height (1.3 m) during a thinning aimed at reducing competition performed in winter 2012. The diameter at breast height (DBH) of the sampled trees was similar or slightly smaller than DBH of all the standing trees in 2012 and thus represents the growth of co-dominant trees (Table 2).

2.3. Tree-ring width measurements and ring chronology

The selected stem discs were oven-dried to avoid decay and then polished with sandpaper. A flatbed distortion-free scanner (Epson, Expression 11000XL) was used to collect digital images of the disc surfaces. The widths of the annual growth rings of four to five radii per disc were measured on the digital image using the WinDendro software (Regent Instruments Canada Inc., 2012). Each individual time-series (radius) was visually cross-dated, and dating was verified using the COFECHA software (Holmes, 1983). Individual time series were then detrended using a 10-year cubic smoothing spline to only preserve high-frequency climatic information (Cook and Peters, 1981). Site and species chronologies were built using a biweight robust mean of the detrended tree-ring width indexes (Cook and Kairiukstis, 1990). The strength of the common signal among radii was quantified as the mean inter-trees correlation (Rbar) and the expressed population signal (EPS) from the detrended chronologies (Wigley et al., 1984). All calculations were performed with the “dplR” package within the R environment (Bunn, 2008).

2.4. Growth responses to climate

For each site and species, growth-climate relationships were assessed with bootstrapped principal component regression (PCR) analyses (Biondi and Waikul, 2004) using the growth chronologies as dependent variables and the monthly climate data as independent variables. Bootstrapped correlation coefficients were calculated with the R package *bootRes* (Zang and Biondi, 2013) including climate variables from June of the previous year to September of the current