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Divergent regeneration responses of two closely related tree species to direct abiotic and indirect biotic effects of climate change

M.M. Carón [a,*], P. De Frenne [a], J. Brunet [b], O. Chabrerie [c], S.A.O. Cousins [d], G. Decocq [c], M. Diekmann [e], B.J. Graae [f], T. Heinken [g], A. Kolb [e], J. Lenoir [c], T. Naaf [h], J. Plue [d], F. Selvi [i], M. Wulf [h,j], K. Verheyen [a]

[a] *Forest & Nature Lab, Ghent University, Gontrode-Melle, Belgium*
[b] *Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Alnarp, Sweden*
[c] *Jules Verne University of Picardie, UR Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN, FRE 3498 CNRS-UPJV), 1 rue des Louvels, F-80037 Amiens Cedex 1, France*
[d] *Department of Physical Geography and Quaternary Geology, Stockholm University, Stockholm, Sweden*
[e] *Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Bremen, Germany*
[f] *Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway*
[g] *Biodiversity and Systematic Botany, Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany*
[h] *Institute of Land Use Systems, Leibniz-Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany*
[i] *Department of Agrifood Production and Environmental Sciences, Section of Soil and Plant Sciences University of Florence, Firenze, Italy*
[j] *Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany*

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ABSTRACT

Changing temperature and precipitation can strongly influence plant reproduction. However, also biotic interactions might indirectly affect the reproduction and recruitment success of plants in the context of climate change. Information about the interactive effects of changes in abiotic and biotic factors is essential, but still largely lacking, to better understand the potential effects of a changing climate on plant populations. Here we analyze the regeneration from seeds of *Acer platanoides* and *Acer pseudoplatanus*, two currently secondary forest tree species from seven regions along a 2200 km-wide latitudinal gradient in Europe. We assessed the germination, seedling survival and growth during two years in a common garden experiment where temperature, precipitation and competition with the understory vegetation were manipulated. *A. platanoides* was more sensitive to changes in biotic conditions while *A. pseudoplatanus* was affected by both abiotic and biotic changes. In general, competition reduced (in *A. platanoides*) and warming enhanced (in *A. pseudoplatanus*) germination and survival, respectively. Reduced competition strongly increased the growth of *A. platanoides* seedlings. Seedling responses were independent of the conditions experienced by the mother tree during seed production and maturation. Our results indicate that, due to the negative effects of competition on the regeneration of *A. platanoides*, it is likely that under stronger competition (projected under future climatic conditions) this species will be negatively affected in terms of germination, survival and seedling biomass. Climate-change experiments including both abiotic and biotic factors constitute a key step forward to better understand the response of tree species' regeneration to climate change.

1. Introduction

Climate has a strong influence on plant reproduction (Walck et al., 2011). First, the prevalent climatic conditions experienced by the mother tree may influence seed size, quality, germination and seedlings performance (Carón et al., 2014a; De Frenne et al., 2011b; González-Rodríguez et al., 2011). Second, early establishment and seedlings' growth are also highly dependent on the seed bed conditions such as temperature and precipitation (e.g. Fay and Schultz, 2009; Milbau et al., 2009). Temperature affects plants biochemical and physiological processes such as photosynthesis, respiration, and transpiration (Carón et al., 2014b; Chmura et al., 2011; Wan et al., 2004), while precipitation is an important factor for the mobilization of soil nutrients and for plant growth (e.g. Scharnweber et al., 2011; Dreesen et al., 2012). Additionally, interspecific and intraspecific plant–plant interactions might affect the reproduction and recruitment success of plants (Adler and HilleRisLambers, 2008; George and Bazzaz, 2014). Seedlings are more susceptible to the interaction with dominant plants than more established plants. Positive impacts of such interactions on

* Corresponding author at: Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle, Belgium. Tel.: +32 (0)9 264 90 36.
E-mail address: MariaMercedes.Caron@UGent.be (M.M. Carón).

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the recruitment stage (i.e. germination), but negative for survival, have been identified (Callaway and Walker, 1997). These impacts were often linked to abiotic factors. Positive interactions can be caused by a higher soil moisture under plant canopies, whereas negative interactions may involve competition for water in deeper soil layers (Adler and HilleRisLambers, 2008).

In the context of climate change, information about the effects of temperature (De Frenne et al., 2011a; Hedhly et al., 2008) and precipitation changes (Abrams, 1990; Scharnweber et al., 2011) on plant communities has been rapidly built up in recent years. Unfortunately, there is less knowledge about the effects of interacting climate-change factors (but see Garten et al., 2009; Bai et al., 2010; Dreesen et al., 2012). Moreover, reliable information about the joint effect of changes in abiotic and biotic factors is essential to better understand the potential impact of a changing environment on plants populations (Adler and HilleRisLambers, 2008; HilleRisLambers et al., 2013).

It is known that the effects of individual environmental factors (e.g. temperature, precipitation and soil conditions) on tree populations can differ from the effects observed when these factors are jointly manipulated. For instance, in one experiment conducted by Paradis et al. (2014) with *Betula glandulosa* seedlings, it was proven that seedlings exposed to nutrient addition had greater phosphorus concentrations in their leaves. However, when nutrient addition was combined with enhanced precipitation, phosphorus availability declined while this did not affect seedling biomass (Paradis et al., 2014). Furthermore, changes in abiotic conditions (levels of soil moisture and light) altered biotic interactions between *Quercus macrocarpa* and *Quercus ellipsoidalis* seedlings and the surrounding vegetation. Drought enhanced competition intensity and reduced seedling establishment success, while increased soil water content decreased competition for water with herbaceous vegetation (Davis et al., 1998).

Due to the variability of results obtained under contrasting environmental conditions, the impacts of interacting abiotic and biotic factors in the context of climate change are still difficult to predict (HilleRisLambers et al., 2013). Given the important link between the structure and composition of the understory and tree regeneration due its influence on microhabitat conditions, and interactions such as competition and facilitation (George and Bazzaz, 2014). It is essential to consider direct (abiotic) and indirect (biotic) effects of climate change when studying trees' regeneration. Yet, a relatively small number of climate change experiments jointly manipulated abiotic and biotic factors (but see Davis et al., 1998; Paradis et al., 2014). Nevertheless, it was shown that warming enhanced survival, drought decreased germination and reduced growth with a differential allocation of resources in favor of belowground biomass (Dreesen et al., 2012; Scharnweber et al., 2011). While biotic interactions such as reduced competition generally enhanced early establishment and increased growth (Davis et al., 1998).

The impacts of different aspects of climate change on plants populations can be studied with the use of several techniques that allow to analyze different aspects of plants' life cycle. Experimental warming techniques include the use of facilities such as infrared heaters (Dreesen et al., 2012), soil heating cables (Carón et al., 2014b) and open top chambers (OTCs) (De Frenne et al., 2011a; Klady et al., 2011). Precipitation can be manipulated using controlled watering (Carón et al., 2014b; Fay and Schultz, 2009) or by installing rainout shelters (Grime, 2000; Heisler-White et al., 2008). Through the use of climatic gradients, e.g. those across elevations or latitudes, the effects of several environmental characteristics such as temperature, precipitation, soil conditions, etc. (De Frenne et al., 2013; Koch et al., 1995) on plants can be examined. However, the combination of techniques is an important step forward because that allows to illuminate different aspects of the impacts of climate change that are not easily analyzed through the use of only one technique. The impacts of climate change on seed production of long-living species, such as trees, can easily be studied along latitudinal gradients (Carón et al., 2014a), while seedling establishment, growth and mortality are frequently studied through experimental warming and precipitation manipulation (De Frenne et al., 2011a; Dreesen et al., 2012).

Here we analyze the regeneration from seeds of *Acer platanoides* and *Acer pseudoplatanus* from seven regions along a 2200 km-wide latitudinal gradient in Europe. The species are two currently secondary forest tree species that can, potentially, change their performance and distribution in European forests under climate change (Hanewinkel et al., 2013; Zimmermann et al., 2013). It is expected that currently dominant species such as European beech, spruce and pine will decrease their fitness and abundance and secondary forest tree species will gain relevance (Hanewinkel et al., 2013; Kramer et al., 2010).

However, due the current relatively limited economic importance of *A. platanoides* and *A. pseudoplatanus*, insufficient information is available on their expected responses to climate change. Based on the current knowledge of the ecology of these species it can be expected that both species will show different responses to the environmental changes induced by climate change. For example, the higher susceptibility of *A. pseudoplatanus* to drought will likely make this species more susceptible to summer drought than *A. platanoides*. Regarding regeneration, one can expect that the recruitment phase of both species will not be equally impacted. For instance, seeds of *A. platanoides* require more days of cold stratification than *A. pseudoplatanus* for successful dormancy break. Therefore, despite that probably the dormancy break of both species will be impacted by warming due to the projected reduction of the amount of chilling days in winter, it is likely that the impact will be larger in *A. platanoides*. Additionally, *A. platanoides* shows an inhibition of germination at temperatures above 10–15 °C, but can germinate after a second chilling period (Jensen, 2001), while *A. pseudoplatanus* shows very good germination at temperatures up to 25 °C (Jinks et al., 2006). Hence, it is likely that *A. platanoides* will be more impacted by warming than *A. pseudoplatanus.* This dissimilar behavior underlines the relevance of studying the response to climate change of closely related species, avoiding improper conclusions at the genus level.

Here, we assessed the germination, seedling survival and growth over two growing seasons *of A. platanoides* and *A. pseudoplatanus* sampled along a latitudinal gradient in a common garden experiment that included full factorial temperature, precipitation and competition treatments.

We specifically addressed the following questions (i) is there an effect of the temperature experienced by the mother tree during seed production on seed germination and seedling performance?, (ii) do experimental warming, reduced precipitation and interspecific competition impact germination, seedling survival and growth?, (iii) do temperature, precipitation and competition interact in affecting germination, seedling survival and growth? We hypothesized that seed germination and seedling survival will show a latitudinal pattern in relationship with the temperature experienced by the mother tree during seed production. It is expected that seedlings resulting from seeds produced under warmer conditions can better cope with warming than seedlings resulting from seeds produced under colder conditions. Additionally, we expect that competition and reduced precipitation will reduce seed germination, seedling survival and growth, while warming will produce the opposite effect.

2. Materials and methods

2.1. Study region and populations

In 2011, seeds of *A. platanoides* and *A. pseudoplatanus* were collected in seven regions located along a latitudinal gradient in Europe from Arezzo, Italy to Trondheim, Norway (Fig. 1). The seed