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Impacts of warming and changes in precipitation frequency on the regeneration of two *Acer* species

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A B S T R A C T

Climate projections indicate that temperatures will increase by up to 4.5 °C in Europe by the end of this century, and that more extreme rainfall events and longer intervening dry periods will take place. Climate change will likely affect all phases of the life cycle of plants, but plant reproduction has been suggested to be especially sensitive. Here, using a combination of approaches (soil heaters and different provenances along a latitudinal gradient), we analyzed the regeneration from seeds of *Acer platanoides* and *A. pseudoplatanus*, two tree species considered, from a management point of view, of secondary relevance. We studied germination, seedling survival and growth in a full-factorial experiment including warming and changes in watering frequency. Both species responded to warming, watering frequency and seed provenance, with stronger (negative) effects of warming and provenance than of watering frequency. In general, the central provenances performed better than the northernmost and southernmost provenances. We also detected interactive effects between warming, watering frequency and/or seed provenance. Based on these results, both species are expected to show dissimilar responses to the changes in the studied climatic factors, but also the impacts of climate change on the different phases of plant regeneration may differ in direction and magnitude. In general increases in the precipitation, frequency will stimulate germination while warming will reduce survival and growth. Moreover, the frequent divergent responses of seedlings along the latitudinal gradient suggest that climate change will likely have heterogeneous impacts across Europe, with stronger impacts in the northern and southern parts of the species' distribution ranges.

1. Introduction

Depending on the concentration-driven scenario considered (suite of greenhouse gases, aerosols and chemically active gases), a future increase of the average annual temperature between 0.6 °C and 4.5 °C is expected in Europe by the end of this century (IPCC, 2013). The projections predict that the winter mean temperature will rise more in Northern Europe than in Central Europe and the Mediterranean area while the summer warming will likely be more intense in the Mediterranean area and Central Europe than in Northern Europe (Christensen et al., 2013). Extreme events of warming are also expected; the length, frequency, and/or intensity of warm periods are expected to increase (IPCC, 2013). As a consequence of global warming, the water cycle is also expected to change non-uniformly. Precipitation frequencies will be likely modified, with more extreme rainfall events and longer dry intervals (Chaoyang et al., 2012; IPCC, 2012, 2013). However, not only

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the changes in individual factors will be important in the future. The interaction between different climatic factors can produce different impacts on terrestrial ecosystems compared to the effects of individual factors; for example, the combination of drought, extreme heat and/or low humidity will clearly have stronger impacts than any factor alone (IPCC, 2012, 2013). Additionally, changes in climatic factors can induce changes in other abiotic environmental factors. For instance, soil moisture is the result of a combination of different abiotic factors such as precipitation, temperature, air humidity, soil texture and organic matter content (Wang, 2005; Chaoyang et al., 2012; Schneider et al., 2014).

Even though the changes in climatic drivers and other related abiotic aspects are expected to be larger at the end of the century, the effects of current global warming are already visible in several ecosystems (Hedhly et al., 2008; Van Mantgem et al., 2009) and affect the ecology of many species, including their geographical distribution, phenology, biotic interactions and extinction risks (for a review see Peñuelas et al., 2013). Temperature has been shown to influence seed production (Walck et al., 2011; Carón et al., 2014a), germination, establishment (Lewis et al., 1999; Jensen, 2001) and growth of plants (Rapp et al., 2012). Rainfall amount or soil moisture content may affect plant distributions (North et al., 2005), seed germination (Fay & Schultz, 2009,b; Carón et al., 2014a,b), growth (Fay and Schultz, 2009; Dreesen et al., 2012), phenology (Seghieri et al., 2009), and mortality (Anderegg et al., 2013). However, changes of different climatic factors have not received the same level of attention. For instance, the impacts of changes in precipitation frequency are rarely assessed (but see e.g. Fay et al., 2003; Chaoyang et al., 2012; Schneider et al., 2014). Precipitation frequency may change separately from rainfall totals when the total amount of rainfall over a certain period remains constant, but the number of rainfall events decreases and the precipitation amount in each rainfall event increases. Some of the few available studies on plants have shown that reduced rainfall frequencies can increase productivity, decrease root-to-shoot ratios or affect leaf senescence in grassland species (Fay et al., 2003, 2002; Schneider et al., 2014). Yet, more research is urgently needed to better understand the effect of changes in precipitation frequency on other plant growth parameters, functional groups, and ecosystems (Schneider et al., 2014).

Even though climate change will likely affect all plant life cycle phases, plant reproduction has been suggested to be especially sensitive (Hedhly et al., 2008; Walck et al., 2011). In many cases, warming has been shown to positively influence seed germination (Milbau et al., 2009; McCarragher et al., 2011) or to enhance seedling survival and growth (Piper et al., 2013). In contrast, reduced soil moisture contents tend to negatively affect seed germination and seedling survival and growth (Fay and Schultz, 2009; Shevtsova et al., 2009). Information about the impacts of climate change on regeneration from seeds is essential for tree species because it is the most common natural way through which forests regenerate around the globe. In practice, the majority of tree species used for afforestation or reforestation in Europe are grown from seeds (Den Ouden et al., 2010). Throughout Europe, young trees that are used for reforestation and afforestation generally come from a pool of recommended and/or autochthonous provenances (cf. the EU Directive 1999/105/EC on the marketing of forest reproductive material). However, only very limited information is available on how these recommended provenances will perform under future climatic conditions.

Here, we analyze the effects of warming and changed watering frequency on regeneration from seeds of two important, currently secondary tree species in forest management, namely *A. platanoides* and *A. pseudoplatanus*. Both species might become more abundant in the context of climate change due to the projected compositional change in European forests as a consequence of the decline in fitness and abundance of currently primary species such as *Picea abies* and *Fagus sylvatica* (Hanewinkel et al., 2012). We analyze the impacts of warming and changes in precipitation frequency (as simulated by various watering intervals) on germination and early establishment of these two *Acer* species from different European provenances. A variety of techniques are available to study the effects of climate change on plant species including soil heating cables, open top chambers, growth chambers, and natural climatic gradients such as those across latitudes or elevations (Carón et al., 2015; De Frenne et al., 2013; Deines et al., 2007; Dunnett and Grime, 1999). The technique selected in each case depends on several factors including the life cycle phase that is being investigated. Here, we combine the use of soil heating mats (Carón et al., 2014a) with seed collection along a latitudinal gradient (Fukami and Wardle, 2005; De Frenne et al., 2013). The combination of various techniques constitutes an interesting step further, relative to the use of only one technique because it allows to illuminate the impacts of climate change on different aspects of plant populations such as different phases of plant reproduction (De Frenne et al., 2013).

We specifically address (i) How do warming and changes in watering frequency affect seed germination, seedling survival and growth? (ii) Is there an interacting effect of warming and watering frequency on tree species' regeneration? (iii) Is there a variation in the seed and seedlings response to changes in temperature and watering frequency according to the provenance of the seeds? We hypothesize that the seeds and seedlings from mother trees from southern provenances will be able to better cope with interactive warming and less frequent watering than the seeds and seedlings from mother trees growing under colder and wetter northerly conditions. Additionally, we expect that warming will enhance seedling survival and growth and that more frequent watering will stimulate germination.

2. Material and methods

2.1. Study species

Acer platanoides L. and *A. pseudoplatanus* L. are two secondary forest tree species that currently cover ≤3% of the total forest cover in Europe in pure stands (Spiecker et al., 2009). However, both species are likely to become more abundant and important due to a climate change-driven decrease in fitness and abundance of currently primary forest tree species (Hanewinkel et al., 2012).

Both species have a relative wide distribution in Europe and similar soil requirements. Both species can grow on loamy and clayey soils as long as these are rich in nutrients. Additionally, the study species show phenological and morphological similarities: They flower in April, are insect pollinated, and the wind-dispersed seeds ripen in September–October (Forest Ecology & Forest Management Group, 2005).

Acer pseudoplatanus is naturally distributed across western, central and southern Europe (Forest Ecology & Forest Management Group, 2005). This species has moderate site requirements (Krabel and Wolf, 2013) is medium shade tolerant and medium drought tolerant. This species has a wide ecological amplitude and high reproductive capacity (Krabel and Wolf, 2013). Its wide ecological amplitude and high reproductive capacity explain the potential expansion to some European areas such as Sweden and Norway (Weidema and Buchwald, 2010; Krabel and Wolf, 2013).

A. platanoides is a native species in northern and central Europe, in the Kaukasus and Turkey (Forest Ecology & Forest Management Group, 2005). This species is considered more shade tolerant than *A. pseudoplatanus.* Some authors indicate that *A. platanoides* and *A. pseudoplatanus* are similarly drought tolerant (Forest Ecology & Forest Management Group, 2005), while others consider *A. platanoides* more drought tolerant than *A. pseudoplatanus* (Hemery