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

ARTICLE INFO

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.

© 2015 Elsevier B.V. All rights reserved.

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).

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

collection included both native (located in the natural distribution range of the species) and non-native (located outside the natural distribution range of the species) populations (Appendix A Table A1). In each region, one landscape window of 40×40 km^2 was selected. In each window, three forest patches (with similar canopy cover of ca. 85–95% and mesotrophic soil) and one seed-bearing healthy mother tree per forest patch were selected. Seeds were collected using permeable nets (Amiens, France; Brussels, Belgium; Templin, Germany and Lund, Sweden) or picked directly from the forest floor immediately after seed dispersal (Arezzo, Italy; Stockholm, Sweden and Trondheim, Norway) (Appendix A Table A1).

Climatic data from weather stations close to the sampling point (<50 km apart) available through the European Climate assessment and Dataset project (Klein Tank et al., 2002) and Centro Funzionale della Regione Toscana and Archivio CFS – Ufficio Territoriale per la Biodiversità di Pratovecchio were used to calculate the growing degree hours (GHD) experienced by the mother tree during the mean reproductive period, between flowering and seed maturation (1st of April until 30th of September 2011). The growing degree hours (GDH) were selected for the analysis because of the established relationships with plant development (e.g. Diekmann, 1996) and were calculated with a base temperature of 5 °C following Graae et al. (2012). For both species, the GDH values were subsequently standardized per location, by dividing site-specific values by the overall mean across the gradient (Graae et al., 2009). The correlation coefficient between GDH and latitude was $r = -0.75$ ($n = 42$, $p < 0.001$), while the correlation between the average temperature between April and September and the average annual temperature (period 1992–2011) was $r = 0.81$ ($n = 9$, $p < 0.01$). Finally, the correlation between the average single-seed mass (without dispersal structures) calculated from 30 seeds per mother tree and the GDH experienced by the mother tree during seed production, was 0.73 ($n = 9$ provenances, $P = 0.03$) and 0.37 ($n = 9$, $P = 0.32$) for *A. platanoides* and *A. pseudoplatanus*, respectively.

2.2. Experimental design

A full factorial experiment, with seeds from seven provenances along a latitudinal gradient and additional manipulation of temperature, precipitation and competition with natural understory vegetation, was installed in the experimental area of the Aelmoeseneie forest in Gontrode – Belgium (50°58′N 3°49′E and 11–21 m a.s.l.). The mean annual precipitation in the area is 726 mm, evenly distributed throughout the year, while the mean annual temperature is 9.5 °C, with a mean monthly minimum and maximum temperature of 2.5 °C and 16.8 °C, respectively (average for the period 1981–2010) (Royal Meteorological Institute of Belgium). The experimental area is located in a mixed deciduous forest dominated by ash (*Fraxinus excelsior*) and pedunculate oak (*Quercus robur*) with sycamore maple (*A. pseudoplatanus*) in a lower proportion. The mean basal area of the study site is 34.09 m^2 ha^{-1}, the humus type is in general acidic mull, the topsoil pH (0–5 cm) varies between 3.04 and 3.87 (Vanhellemont et al., 2014) and the recorded soil moisture content between September and May in the forest was of 17% (De Frenne et al., 2010). The forest understory is composed mainly of *Anemone nemorosa*, co-occurring with *Lamiastrum galeobdolon*, *Oxalis acetosella*, *Polygonatum multiflorum*, *Hedera helix* (De Frenne et al., 2010).

To simulate warming, 20 hexagonal open-top chambers (OTCs) were randomly located in a ca. 0.5 ha zone. The OTCs are small plexiglas greenhouses with inclined walls to passively heat a small plot of vegetation (De Frenne et al., 2010; Dermody et al., 2007; Wan et al., 2004). The OTCs were 60 cm high, covering a total surface of 1.15 m^2. Additionally, 20 hexagonal control plots (same area as the open top chambers) were randomly located within the same experimental area. During the experiment (October 2011 – July 2013), the mean temperature recorded in the control plots was 12.12 °C, 11.35 °C and 11.04 °C at 20 cm above the soil surface, at the soil surface below the litter layer and 5 cm below the soil surface, respectively. The temperature recorded at the same position inside the OTCs was 12.81 °C, 12.34 °C, and 14.31 °C. Therefore, the heating inside the OTCs amounted to 0.69 °C in the air at 20 cm height, 0.99 °C at the soil surface below the litter layer and no less than 3.27 °C at 5 cm below the soil surface. The minimum average temperature recorded in winter 5 cm below the soil surface were 9.78 °C and 6.28 °C in the open top chambers and control plots, respectively (difference of 3.50 °C). The average minimum temperature recorded in winter 5 cm below the soil surface were 8.95 °C and 4.48 °C in the open top chambers and control plots, respectively (difference of 4.47 °C). Finally, the temperature at the soil level and 20 cm above the soil surface were 1.88 °C and 2.03 °C higher in control plots than inside the OTCs, respectively. All values are averages of two Type T miniature thermocouples (TC Direct, Nederweert, NL) placed in plots with and without OTCs.

Next, removable transparent plastic rainout shelters (0.84 m^2) were installed above half of the open top chambers and half of the control plots approximately 1.5 m above ground. The rainout shelters were removed and re-installed every two weeks to reduce the direct natural precipitation by approximately 50%. However, due to the effect of wind and other factors such as the systematic removal of the shelters every two weeks independently of the precipitation pattern, the effective reduction of the precipitation was of 18% (14%, 25% and 16% for the years 2011, 2012, 2013 respectively). The precipitation was measured by using bucket rain gauges with a funnel diameter of 14 cm and collected every two to three weeks depending on the period of the year. The amount of precipitation collected during the experimental period in the plots without rainout shelters was 136.17 mm, 510.92 mm and 296.39 mm (average of eight collectors), while in the plots with rainout shelters the precipitation was 117.18, 384.11 and 249.05 mm (average of eight collectors) in October–December 2011, January–December 2012 and January–July 2013, respectively. The amount of precipitation recorded in an open-field weather station close to the forest at *ca.* 1 km distance was

Fig. 1. Location of the sampled *A. pseudoplatanus* and *A. platanoides* populations along the latitudinal gradient from Italy to Norway.

209.4, 976.5 and 452.3 mm during the same period in 2011, 2012 and 2013, respectively (i.e. *ca.* 40% reduction in the forest due to canopy interception, comparable with the results obtained by Staelens et al., 2006).

Finally, for the competition treatments, the natural vegetation, that normally cover between 75% and 90% of the soil, was systematically removed in spring and summer by clipping away all other plants (100% of the understory vegetation) to a height of 1–2 cm above the soil surface in half of the open top chambers and half of the control plots. The combination of treatments allowed a full factorial design with 5 replications of each combination of treatments (temperature ∗ precipitation ∗ competition).

In the center of each experimental plot (combination of temperature, precipitation and competition treatments) 7–9 plastic rings (12 cm diameter) were placed approximately 5 cm in the soil leaving one centimeter above the forest floor for easy identification of the sown individuals (the variable number of rings was due to the installation of rain collectors in some of the plots to quantify the direct precipitation). In each ring, 20 seeds from each mother tree were randomly sown in November 2011, making sure that only one mother tree per provenance per species was sowed in each experimental plot

Fig. 2. Scheme of the experimental setup.

(Fig. 2), (i.e. 2 species × 7 provenances × 3 mother trees), which made a total of 6720 seeds distributed in 312 tubes.

Between March and June 2012 (first growing season), the germination rate was recorded (maximum number of germinated seeds). In June 2012, the seedlings were randomly weeded and only a maximum of four seedlings per ring remained to avoid excessive competition between seedlings. The random weeding of four seedlings was done to avoid favor the best prepared seedlings in the face of climate change allowing analyze the response of all the seedlings that can be produced by the seeds collected from the mother trees. In late August of the same year, the number of surviving seedlings (i.e., early survival), the number of leaves and the height reached by the seedlings were recorded. In July 2013 (the second growing season) the number of surviving seedlings (i.e., interannual survival), the number of leaves and the height of the seedlings were recorded. Next, each individual seedling was carefully collected and the belowground and aboveground plant parts were separated, dried at 60 °C during 24 h and weighed.

2.3. Data analysis

For each species separately, mixed-effects models using the *glmer* and *lmer* functions, lme4 and nlme libraries in R version 3.0.0 (R Core Team, 2013) were applied. These models combine fixed and random components into a single model (Zuur et al., 2009). For the binomial data (germination rate, early survival and interannual survival), count data (number of leaves at the end of the first and second growing season) and continuous data (height at the end of the first and second growing season, total biomass and root:shoot ratio) we used binomial, Poisson and Gaussian errors structures, respectively. To fulfil the requirements of normality and homoscedasticity (graphically tested), the aboveground, belowground and total biomass were log-transformed prior to the analyses.

The temperature (OTCs vs. control plots), precipitation (with and without rainout shelter) and competition treatments (natural competition vs. reduced natural competition) as well as the standardized growing degree hours (GDH) experienced by the mother tree between the 1st of April and 30th of September were used as fixed effects. We found no significant effects of the status of the mother
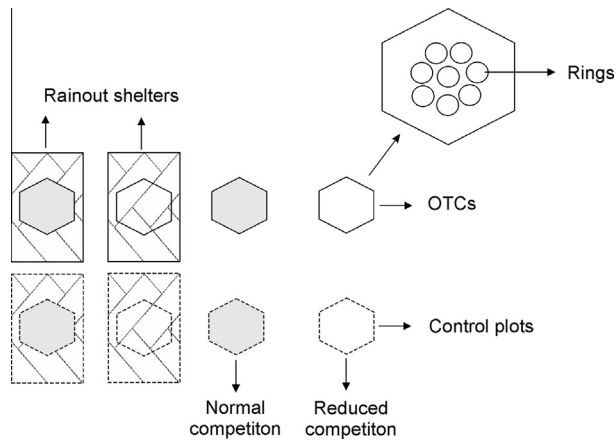
Table 1
Effects of the GDH, temperature, precipitation and competition on establishment and growth variables of *A. platanoides* and *A. pseudoplatanus* over two growing seasons.

Variables	Acer platanoides		Acer pseudoplatanus	
	Predictor	Chi square	Predictor	Chi square
Establishment variables				
Germination rate	Reduced competition	↑3.70*		n.s.
Early survival	Reduced competition	↑12.41***	Warming	↑3.69*
			Reduced competition	↑7.74**
Inter annual survival	Reduced competition	↑6.04*	Warming	↑15.51***
Growth first year (2012)				
Number of leaves		n.s.		n.s.
Height	Reduced precipitation	↑5.72*	Reduced precipitation	↑5.27*
			Reduced competition	↓10.08**
	Reduced precipitation ∗ Reduced competition	↑5.23*	Reduced precipitation ∗ Reduced competition	↑10.95***
			Warming ∗ Reduced competition	↓7.03**
Growth second year (2013)				
Number of leaves	GDH mother tree	↓5.03*		n.s.
Height	Reduced precipitation	↑6.79**	Reduced competition	↓6.27*
	Reduced precipitation ∗ Reduced competition	↑4.77*	Reduced precipitation ∗ Reduced competition	↑7.14**
Total biomass	Reduced competition	↑3.70*		n.s.
Aboveground biomass		n.s.		n.s.
Belowground biomass	Reduced competition	↑5.12*	Reduced precipitation	↑4.44*
Root: shoot ratio	Reduced precipitation	↓6.11*		n.s.
	Reduced competition	↑5.62*		

Values are X^2-values and significances from likelihood ratio tests of mixed-effect models. The direction of the effect is indicated by arrows: ↑ and ↓ correspond to an increase or decrease of the variables analyzed, respectively (n.s.: $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

tree (native vs. non-native) on the germination, survival and growth of the seedlings (except for the height of *A. platanoides* in both growing seasons; results not shown). For the model selection of each species, we followed the modeling framework recommended by Zuur et al. (2009) for nested data. We started by defining the optimal variance structure of the random component from the "beyond optimal model" containing all fixed effects and the possible two ways interaction terms. The random structure selection was based on the Akaike's Information Criterion (AIC) comparing models with different random structures, including mother tree, region and plot number; considering nested (i.e. mother tree nested in country) and not nested structures, and selecting the model with the lower AIC value. For the continuous data the resulting random structure included the mother tree nested in region and the plot number, while for the binomial and count data, only plot number was used as random-effect. Afterwards the full model was fitted (all fixed effects and possible interactions): for *A. platanoides* the full model was based on the standardized growing degree hours experienced by the mother tree during seed production (GDH), the individual factors and all the possible two way interactions between temperature, precipitation and competition treatments. For *A. pseudoplatanus* the full model was the same as for *A. platanoides* but without the interaction between temperature and competition due the null interannual survival of seedlings recorded under this combination of treatments. For each variable analyzed, first the full model was fitted and model simplification was achieved by dropping first the less significant interactions and then the less significant variables at each step based on likelihood ratio tests (Zuur et al., 2009).

3. Results

3.1. Establishment variables

The study species responded differently to the temperature, precipitation and competition treatments. Establishment (germination, early survival and interannual survival) of *A. platanoides* was affected most by competition, while the main factor affecting the seedling establishment of *A. pseudoplatanus* was warming (Table 1). The tested interactions were not significant.

The germination of *A. platanoides* was negatively affected by competition; the germination in plots where the natural vegetation was eliminated was 35% higher than in plots with natural competition, while the germination rate of *A. pseudoplatanus* was independent of all the treatments applied (Table 1 and Fig. 3A).

For both species, competition reduced the survival at the end of the first growing season (Table 1). The early survival was 17% and 44% higher in plots where the vegetation was periodically eliminated in *A. platanoides* and *A. pseudoplatanus* seedlings, respectively (Fig. 3B and Appendix B Table 1B). Additionally, the early survival of *A. pseudoplatanus* increased under warmer conditions. Under this treatment, the early survival was 27% higher than in un-warmed plots (Fig. 3B). Still in *A. pseudoplatanus*, the temperature also increased the interannual survival of seedlings, being 91% higher in warmed plots than in un-warmed plots (Fig. 3C). Conversely, the interannual survival of *A. platanoides* was 30% higher in plots without natural competition than in plots with competition (Fig. 3C and Appendix B Table B1).

The growing degree hours (GDH) experienced by the mother tree did not influence seed germination and seedling survival (Table 1). Additionally, the treatments applied did not unidirectionally affect germination along the latitudinal gradient (Fig. 4).

3.2. Growth during the first growing season

For both species, the number of leaves developed by the seedlings during the first growing season was independent on
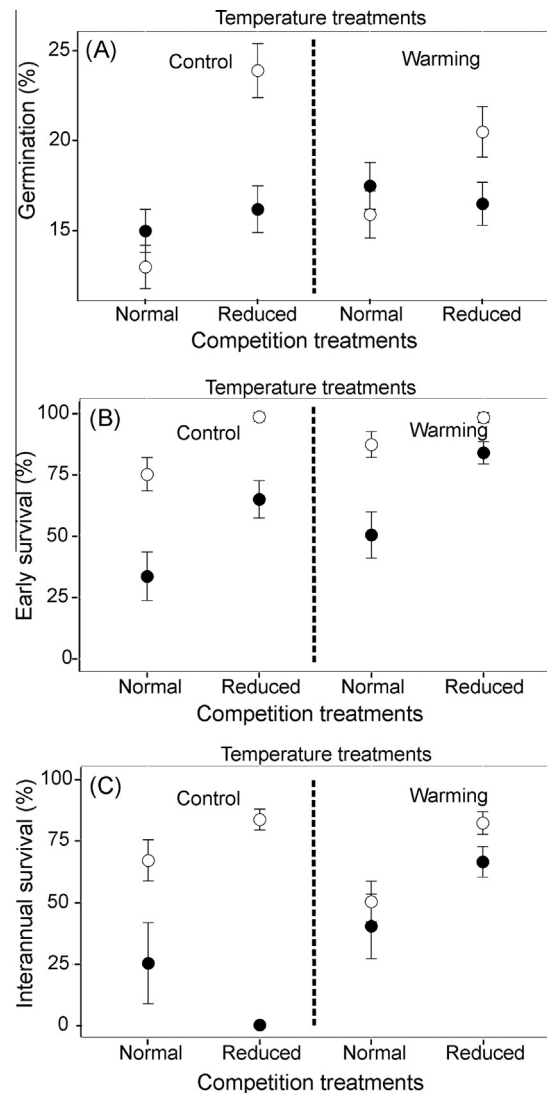

Fig. 3. Germination (A), early survival (B) and interannual survival (C) as a function of the joint manipulation of temperature and competition. Open circles denote *A. platanoides* and closed circles represent *A. pseudoplatanus*. Error bars indicate standard error.

treatments applied and the growing degree hours (GDH) experienced by the mother tree during seed production.

The height reached by the seedlings of both species during the first growing season was positively affected by reduced precipitation: *A. platanoides* and *A. pseudoplatanus* seedlings were 12% and 10% taller when growing under reduced precipitation than under full precipitation (Table 1, Fig. 5, Appendix B Table B2 and Table B3). Additionally, competition positively affected seedling height: *A. pseudoplatanus*' seedlings were 22% shorter under reduced competition than under full competition (Table 1 and Fig. 5 and Appendix B Table B3). Still, in *A. pseudoplatanus* warming intensified the effects of competition on seedling height: the seedlings growing under warmer conditions and competing with the surrounding vegetation were 25% larger than the seedlings growing in un-warmed and competition-free plots (Table 1 and Appendix B Table B3). Finally, for both species, reduced precipitation increased the positive effect of natural competition on seedling height (Fig. 5).

3.3. Growth during the second growing season

At the end of the second growing season, only the number of leaves of *A. platanoides* seedlings was negatively affected by the
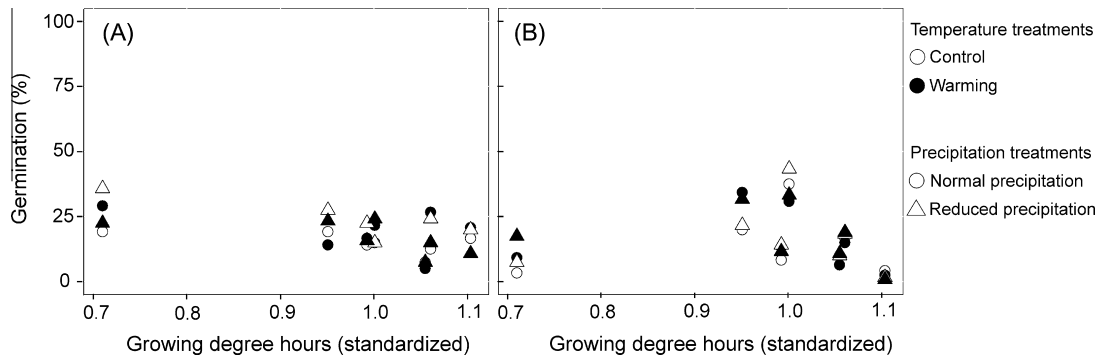
Fig. 4. Seed germination as a function of the standardized growing degree hours experienced by the mother tree and the experimental temperature and precipitation treatments for *A. platanoides* (A) and *A. pseudoplatanus* (B).
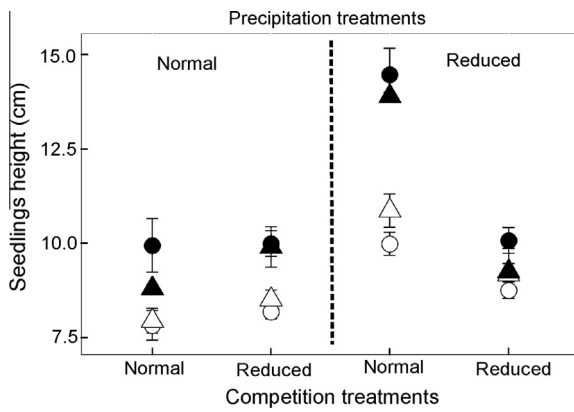

Fig. 5. Height reached by the seedlings of *A. platanoides* (white) and *A. pseudoplatanus* (black) and the end of the first (circles) and the second growing season (triangles) under a combination of precipitation and competition treatments. Error bars indicate standard error.

growing degree hours experienced by the mother tree during seed production (GDH) (Table 1). The number of leaves developed by the seedlings decreased from colder to warmer seed provenances.

The height of the seedlings of both species was still affected by some of the same factors as in the first growing season. However, in *A. pseudoplatanus* some factors that were important during the first growing season lost relevance (i.e. reduced precipitation and the interaction between competition and warming) (Table 1). During the second growing season, the positive effect of reduced precipitation in *A. platanoides* seedlings and the negative effect of reduced competition in *A. pseudoplatanus* seedlings were very similar to those of the first growing season (Fig. 5, Appendix B Table B2 and Table B3). During the second growing season, the seedlings growing under reduced precipitation and reduced competition were 13% and 4% taller than the ones growing under full precipitation and competition for *A. platanoides* and *A. pseudoplatanus* respectively (Table 1 and Fig. 5). For the seedling height of *A. pseudoplatanus*, reduced precipitation counteracted the negative effects of reduced competition (Table 1).

The biomass variables were influenced less by the experimental treatments than the height. The total biomass of *A. platanoides* the seedlings growing without the natural vegetation competition were 31% heavier than those surrounded by natural forest understory vegetation, respectively (Table 1 and Fig. 6A and Appendix B Table B2). Moreover, the root: shoot ratio of *A. platanoides* increased in seedlings growing surrounded by the understory vegetation. Reduced competition and precipitation decreased the root: shoot ratio with 19 % and 14%, respectively (Table 1 and Fig. 6B).

4. Discussion

The experimental assessment of direct abiotic effects of climate change (i.e. temperature and precipitation changes), the influence of the temperature experienced by the mother tree along the latitudinal gradient, and the impact of two levels of competition, allowed us to assess the effects of changing environmental conditions on early tree establishment and growth. We focused on two currently secondary *Acer* tree species which are predicted to change their performance under climate change (Hanewinkel et al., 2013; Zimmermann et al., 2013). Species-specific responses to changes in abiotic and biotic conditions during the recruitment stage were observed (e.g. Adler and HilleRisLambers, 2008; Milbau et al., 2009; Shevtosova et al., 2009). *A. platanoides* was more influenced by competition than *A. pseudoplatanus*, while the second species was more influenced by warming than *A. platanoides*. Moreover, both species were similarly susceptible to precipitation reduction.

4.1. Seed germination

With regard to establishment (germination and survival), *A. platanoides* was mainly influenced by competition, while *A. pseudoplatanus* responded to changes in both biotic and abiotic conditions. However, it is important to mention that the stronger influence of competition on establishment might be linked with the fact that the competition treatment was intense (complete elimination of all the surrounding vegetation) while the changes in abiotic conditions were less severe. The higher germination of *A. platanoides* recorded in plots where the surrounding vegetation was eliminated can be related to pulses of light (George and Bazzaz, 2014). However, despite the fact that the germination of some *Acer* species (*A. pseudoplatanus* and *A. rubrum*) is light sensitive (Webb and Wareing, 1972), *A. platanoides*' germination was expected to be equal under darker and lighter conditions (Baskin and Baskin, 1998). Despite that the light intensity under the different competition treatments was not directly measured it is likely that was significantly lower under the understory vegetation. The effect of the elimination of most aboveground plant–plant competition on germination can also be related to a reduction of insect predation due to decreased amount of vegetation cover (Jinks et al., 2006). Moreover, the regular weeding probably reduced the water uptake by the understory vegetation, favoring higher soil moisture content and nutrient availability, thereby providing the seeds with better conditions to germinate (Baskin and Baskin, 1998) and reducing mortality risks (Jinks et al., 2006). However, the explanation of a potential positive effect of reduced competition due to lower soil desiccation is partially contradicted by the absence of reduced precipitation effects on germination. Yet, it is possible that lateral belowground flow of infiltrated water reduced
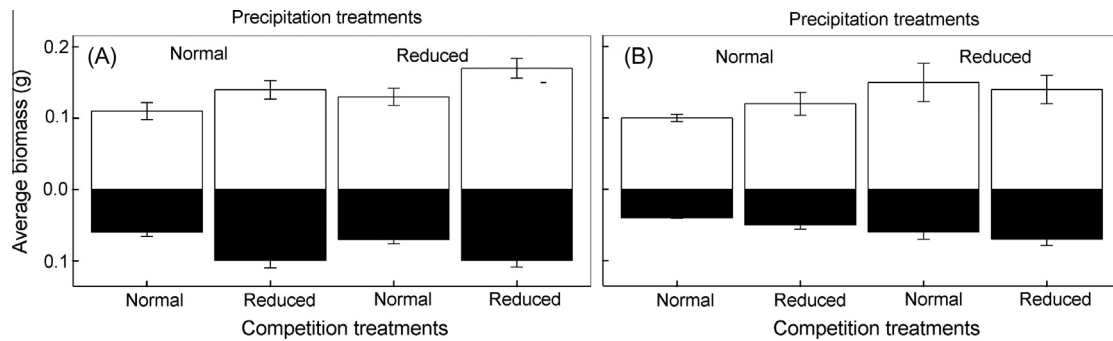
Fig. 6. Total, aboveground and belowground biomass of *A. platanoides* (A) and *A. pseudoplatanus* (B) under normal and reduced precipitation and competition. The white bars represent the aboveground biomass and the black bars the belowground biomass. Error bars indicate standard error.

the effects of the reduced precipitation treatment. It is not possible to directly link the positive effect of reduced competition with changes in the soil moisture content because this variable was not directly measured. Therefore it is highly recommended to consider this variable in future research. Finally, an alternative explanation of the positive effect of the removal of the surrounding vegetation on seed germination can be linked to a positive influence of disturbance on seed germination. However, due the thick litter layer present in the forest the impact of disturbance was probably limited. On the other hand, *A. pseudoplatanus* was unresponsive in terms of germination to the treatments applied. This indicates that, in terms of germination, this species will likely be less influenced by slightly warmer conditions, reduced precipitation and changes in competition intensity, than *A. platanoides* (Carón et al., 2014b). Moreover, the germination of both species was unresponsive to the temperature treatment, however it is important to consider that the warming simulated in this work was low compared to other studies that showed significant effects of warming on germination (e.g. Carón et al., 2014a).

4.2. Seedling survival

The survival of both species during the first growing season and the seedling survival of *A. platanoides* during the second growing season were negatively affected by competition. This indicates that the periodical elimination of the surrounding vegetation provided the seedlings with pulses of resources (water, light and nutrients) (Craine, 2005), facilitating growth and allowing the seedlings to better survive until the end of the first growing season and the following winter (Adler and HilleRisLambers, 2008; Milbau et al., 2009). This result is especially relevant in the context of climate change because under warmer conditions some herbaceous understory plants might enhance their growth, thereby increasing competition intensity (De Frenne et al., 2011a). However in this research, no interactive effects of warming and competition were observed in relation to the establishment variables. On the other hand, *A. pseudoplatanus*' survival was influenced by both, abiotic and biotic conditions. Seedlings of *A. pseudoplatanus* were negatively influenced by competition during the first growing season, when the seedlings are still less prepared to compete for resources. However, the effects of competition decreased during the second growing season, while warming enhanced seedling survival in both growing seasons. The different responses observed during the first and the second growing season imply that interactions with the understory vegetation have stronger effects on younger seedlings than on more established plants (Adler and HilleRisLambers, 2008). Moreover, the positive effects of warming might be related to lower exposure to freezing during winter when OTCs in forests

are more effectively warming due to the open deciduous tree canopies (De Frenne et al., 2011a). While due the similarities of herbivory levels observed along this work in the OTCs and control plots, probably the effects of the warming treatments were not related to changes in herbivory levels.

4.3. Seedling growth

Contrasting with the findings on the seedling establishment, growth was only influenced by the competition and the precipitation amount. Surprisingly, warming did not affect seedling growth despite the fact that warming enhances plant biochemical and physiological processes such as photosynthesis, respiration, and transpiration (Chmura et al., 2011; Wan et al., 2004). An interesting pattern emerging was that seedling height of both species increased with reduced precipitation. Previously, a positive effect of reduced precipitation on growth of some species has been reported (Dreesen et al., 2012). However, the positive effect of the rainout shelters was partially canceled out due to positive effect of competition on seedling height. It is possible that, when competing with the understory vegetation, the seedlings enhanced their height growth more than when growing without competition to have more access to light. Moreover, it is important to mention that the seedlings recorded in the second growing season were taller than the recorded during the first growing season but due the mortality of some big seedlings the average seedling size was lower. The mortality of big seedlings was probably link to herbivory. The different results observed under interacting abiotic and biotic factors demonstrates, once again, the relevance of its joint manipulation.

For *A. pseudoplatanus* seedlings, the reduced precipitation enhanced belowground biomass. A similar pattern was observed for low intensity reduced precipitation and extreme drought in herbs (*Malva neglecta*, *Myosotis arvensis* and *Solanum nigrum*) and tree seedlings (*A. platanoides* and *A. pseudoplatanus*) (Carón et al., 2014b; Dreesen et al., 2012). Additionally, the total biomass and the root: shoot ratio of *A. platanoides* was negatively affected by competition, probably linked to pulses of resources. The differential influence of the understory on seedling growth influenced the size structure among seedlings that might ultimately influence the outcome of future tree–tree competition.

Finally, the temperature experienced by the mother tree during seed production along the latitudinal gradient did not affect seed germination and seedling performance, except for the number of leaves recorded in the second growing season in *A. platanoides* seedlings. The seeds produced under colder conditions were bigger than the produced under warmer conditions. The higher seed mass of seeds produced at colder locations probably allow the seedlings to have more resources to growth better and develop more leaves.

Moreover, the native vs. non-native status of the mother trees did not influence any of the variables analyzed except for the height of *A. platanoides* in both growing seasons (results not shown). This means that, irrespective of the climatic conditions under which the seeds were produced, the responses to the treatments applied are very similar.

The lack of a pattern related with the temperature experienced by the mother tree, is surprising because generally the environmental conditions experienced by the mother tree affect early establishment and growth variables, including seed mass, viability and seed germination and seedling biomass (see Verheyen et al., 2009; González-Rodríguez et al., 2011). Moreover, the influence of the temperature experienced by the mother plant is species-specific (Graae et al., 2009) and, in some species, the influence of the conditions experienced by the mother tree on seed germination and seedling growth can change over time (Carón et al., 2014b).

These experimental results suggest that *A. platanoides* might be less influenced by changes in the climatic conditions (warming and reduced precipitation) than *A. pseudoplatanus*. However, considering the strong negative effect of competition on the regeneration of *A. platanoides*, it is likely that with potentially enhanced competition intensity in forest understorys due to the positive effect of warming on the growth of some understory plants (De Frenne et al., 2011b) this species may be less successful than *A. pseudoplatanus* despite its originally higher germination, survival and biomass. Moreover, it is important to consider that other co-occurring species might show different responses to climate change and affect these species' recruitment, especially when co-occurring with seedlings of more (climate change) resistant tree provenances (Thiel et al., 2014). The relevance of the interacting factors and the influence of abiotic factors on biotic interactions (i.e. competition) is clear, especially related to the growth variables.

5. Conclusion

In sum, our results highlight the complexity of understanding and anticipating the impact of climate change on forests. Climate-change experiments inferring the effects of direct abiotic and indirect biotic drivers constitute a step forward to better understand the response of tree species' regeneration to climate change. This information is essential to better comprehend and forecast changes in the structure and composition of plant communities and, consequently, develop adaptive management plans. Finally, these results are very relevant for species distribution modeling which is currently pointing at the importance of incorporating biotic interactions into species distribution models to improve future predictions on the impact of climate change on biodiversity. The effects of temperature, precipitation and competition treatments not only depended on each individual factor but also on their interactions and were highly species-specific. Moreover, species interactions may influence population dynamics more than the direct effects of changes in climatic variables. Nevertheless, further research is needed to understand the effect of changing climatic conditions as well as biotic interactions over longer temporal scales.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.01.003.

References

Abrams, M.D., 1990. Adaptations and responses to drought in Quercus species of North America. Tree Physiol. 7, 227–238. http://dx.doi.org/10.1093/treephys/7.1-2-3-4.227.

Adler, P.B., HilleRisLambers, J., 2008. The influence of climate and species composition on the population dynamics of ten prairie forbs. Ecology 89, 3049–3060. http://dx.doi.org/10.1890/07-1569.1.

Bai, W., Wan, S., Niu, S., Liu, W., Chen, Q., Wang, Q., Zhang, W., Han, X., Li, L., 2010. Increased temperature and precipitation interact to affect root production, mortality, and turnover in a temperate steppe: implications for ecosystem C cycling. Glob. Chang. Biol. 16, 1306–1316. http://dx.doi.org/10.1111/j.1365-2486.2009.02019.x.

Baskin, C.C., Baskin, J.M., 1998. Seeds. Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego, California, USA.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plat communities. Ecology 78, 1958–1965.

Carón, M.M., De Frenne, P., Brunet, J., Chabrerie, O., Cousins, S.A.O., De Backer, L., Diekmann, M., Graae, B.J., Heinken, T., Kolb, A., Naaf, T., Plue, J., Selvi, F., Strimbeck, G.R., Wulf, M., Verheyen, K., 2014a. Latitudinal variation in seeds characteristics of *Acer platanoides* and *A. pseudoplatanus*. Plant Ecol. http://dx.doi.org/10.1007/s11258-014-0343-xi.

Carón, M.M., De Frenne, P., Brunet, J., Chabrerie, O., Cousins, S.A.O., De Backer, L., Decocq, G., Diekmann, M., Heinken, T., Kolb, A., Naaf, T., Plue, J., Selvi, F., Strimbeck, G.R., Wulf, M., Verheyen, K., 2014b. Interacting effects of warming and drought on regeneration and early growth of *Acer pseudoplatanus* and *A. platanoides*. Plant Biol. 1–11. http://dx.doi.org/10.1111/plb.12177.

Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shaw, D.C., Brad St. Clair, J., 2011. Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. For. Ecol. Manage. 261, 1121–1142. http://dx.doi.org/10.1016/j.foreco.2010.12.040.

Craine, J.M., 2005. Reconciling plant strategy theories of Grime and Tilman. J. Ecol. 93, 1041–1052. http://dx.doi.org/10.1111/j.1365-2745.2005.01043.x.

Davis, M.A., Wrage, K.J., Reich, P.B., 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. J. Ecol. 86, 652–661. http://dx.doi.org/10.1046/j.1365-2745.1998.00087.x.

De Frenne, P., Schrijver, A., Graae, B.J., Gruwez, R., Tack, W., Vandelook, F., Hermy, M., Verheyen, K., 2010. The use of open-top chambers in forests for evaluating warming effects on herbaceous understorey plants. Ecol. Res. 25, 163–171. http://dx.doi.org/10.1007/s11284-009-0640-3.

De Frenne, P., Brunet, J., Shevtsova, A., Kolb, A., Graae, B.J., Chabrerie, O., Cousins, S.A., Decocq, G., De Schrijver, A.N., Diekmann, M., Gruwez, R., Heinken, T., Hermy, M., Nilsson, C., Stanton, S., Tack, W., Willaert, J., Verheyen, K., 2011a. Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. Glob. Change Biol. 17, 3240–3253. http://dx.doi.org/10.1111/j.1365-2486.2011.02449.x.

De Frenne, P., Kolb, A., Graae, B.J., Decocq, G., Baltora, S., De Schrijver, A., Brunet, J., Chabrerie, O., Cousins, S.A.O., Dhondt, R., Diekmann, M., Gruwez, R., Heinken, T., Hermy, M., Liira, J., Saguez, R., Shevtsova, A., Baskin, C.C., Verheyen, K., 2011b. A latitudinal gradient in seed nutrients of the forest herb Anemone nemorosa. Plant Biol. 13, 493–501. http://dx.doi.org/10.1111/j.1438-8677.2010.00404.x.

De Frenne, P., Graae, B.J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D.A., Verheyen, K., 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. J. Ecol. 101, 493–501. http://dx.doi.org/10.1111/1365-2745.12074.

Dermody, O., Weltzin, J.F., Engel, E.C., Allen, P., Norby, R.J., 2007. How do elevated [CO₂], warming, and reduced precipitation interact to affect soil moisture and LAI in an old field ecosystem? Plant Soil 301, 255–266.

Diekmann, M., 1996. Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. Can. J. Bot., 528–537

Dreesen, F.E., De Boeck, H.J., Janssens, I.A., Nijs, I., 2012. Summer heat and drought extremes trigger unexpected changes in productivity of a temperate annual/biannual plant community. Environ. Exp. Bot. 79, 21–30.

Fay, P.A., Schultz, M.J., 2009. Germination, survival, and growth of grass and forb seedlings: effects of soil moisture variability. Acta Oecologica 35, 679–684, http://dx.doi.org/10.1016/j.actao.2009.06.007.

Garten, J.C.T., Classen, A.T., Norby, R.J., 2009. Soil moisture surpasses elevated CO₂ and temperature as a control on soil carbon dynamics in a multi-factor climate change experiment. Plant Soil 319, 85–94. http://dx.doi.org/10.1007/s11104-008-9851-6.

George, L.O., Bazzaz, F.A., 2014. The Herbacesous layer as a filter determining spatial pattern in forest tree regeneration. In: Gilliam, F.S. (Ed.), The Herbacesous Layer in Forest of Eastern North America. Oxford University Press, New York, USA, pp. 340–355.

González-Rodríguez, V., Villar, R., Navarro-Cerrillo, R.M., 2011. Maternal influences on seed mass effect and initial seedling growth in four Quercus species. Acta Oecologia 37, 1–9. http://dx.doi.org/10.1016/j.actao.2010.10.006.

Graae, B.J., Verheyen, K., Kolb, A., Van Der Veken, S., Heinken, T., Chabrerie, O., Diekmann, M., Valtinat, K., Zindel, R., Karlsson, E., Ström, L., Decocq, G., Hermy, M., Baskin, C.C., 2009. Germination requirements and seed mass of slow- and fast-colonizing temperate forest herbs along a latitudinal gradient. Ecoscience 16, 248–257. http://dx.doi.org/10.2980/16-2-3234.

Graae, B.J., De Frenne, P., Kolb, A., Brunet, J., Chabrerie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., Nijs, I., Milbau, A., 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. Oikos 121, 3–19. http://dx.doi.org/10.1111/j.1600-0706.2011.19694.x.

Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P., Askew, A.P., Corker, D., Kielty, J.P., 2000. The response of two contrasting limestone grasslands to simulated climate change. Science 289 (80-), 762–765. http://dx.doi.org/10.1126/science.289.5480.762.

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.-J., Nabuurs, G.-J., Zimmermann, N.E., 2013. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Chang. 3, 203–207.

Hedhly, A., Hormaza, J.I., Herrero, M., 2008. Global warming and sexual plant reproduction. Trends Plant Sci. 14, 30–36.

Heisler-White, J.L., Knapp, A.K., Kelly, E.F., 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158, 129–140. http://dx.doi.org/10.1007/s00442-008-1116-9.

HilleRisLambers, J., Harsch, M.a., Ettinger, A.K., Ford, K.R., Theobald, E.J., 2013. How will biotic interactions influence climate change-induced range shifts? Ann. N.Y. Acad. Sci. 1297, 112–125, doi:10.1111/nyas.12182.

Jensen, M., 2001. Temperature relations of germination in *Acer platanoides* L. seeds. Scand. J. For. Res. 16, 404–414. http://dx.doi.org/10.1080/02827580152632793.

Jinks, R.L., Willoughby, I., Baker, C., 2006. Direct seeding of ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.): the effects of sowing date, pre-emergent herbicides, cultivation, and protection on seedling emergence and survival. For. Ecol. Manage. 237, 373–386. http://dx.doi.org/10.1016/j.foreco.2006.09.060.

Klady, R.A., Henry, G.H.R., Lemay, 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. Glob. Chang. Biol. 17, 1611–1624.

Klein Tank, A.M.G., Wijngaard, J.B., Können, G.P., Böhm, R., Demarée, G., Gocheva, A., Mileta, M., Pashiardis, S., Hejkrlik, L., Kern-Hansen, C., Heino, R., Bessemoulin, P., Müller-Westermeier, G., Tzanakou, M., Szalai, S., Pálsdóttir, T., Fitzgerald, D., Rubin, S., Capaldo, M., Maugeri, M., Leitass, A., Bukantis, A., Aberfeld, R., van Engelen, A.F.V., Forland, E., Mietus, M., Coelho, F., Mares, C., Razuvaev, V., Nieplova, E., Cegnar, T., Antonio López, J., Dahlström, B., Moberg, A., Kirchhofer, W., Ceylan, A., Pachaliuk, O., Alexander, L.V., Petrovic, P., 2002. Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. Int. J. Clim. 22, 1441–1453, doi:10.1002/joc.773.

Koch, G.W., Vitousek, P.M., Steffen, W.L., Walker, B.H., 1995. Terrestrial transects for global change research. Vegetatio 121, 53–65, doi:10.1007/bf00044672.

Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M.T., De Winter, W., 2010. Modelling exploration of the future of European beech (Fagus sylvatica L.) under climate change – range, abundance, genetic diversity and adaptive response. For. Ecol. Manage. 259, 2213–2222.

Milbau, A., Graae, B.J., Shevtsova, A., Nijs, I., 2009. Effects of a warmer climate on seed germination in the subarctic. Ann. Bot. 104, 287–296.

Paradis, M., Mercier, C., Boudreau, S., 2014. Response of *Betula glandulosa* seedlings to simulated increases in nutrient availability, temperature and precipitation in a lichen woodland at the forest-tundra ecotone. Plant Ecol. 215, 305–314. http://dx.doi.org/10.1007/s11258-014-0299-x.

R Core Team, 2013. R: A Language and Environment for Statistical Computing.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., Wilmking, M., 2011. Drought matters – declining precipitation influences growth of Fagus sylvatica L. and Quercus robur L. in north-eastern Germany. For. Ecol. Manage. 262, 947–961. http://dx.doi.org/10.1016/j.foreco.2011.05.026.

Shevtosova, A., Graae, B.J., Jochum, T., Milbau, A., Kockelbergh, F., Beyens, L., Nijs, I., 2009. Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. Glob. Change Biol. 15, 2662–2680.

Staelens, J., De Schrijver, A., Verheyen, K., Verhoest, N.E.C., 2006. Spatial variability and temporal stability of throughfall water under a dominant beech (Fagus sylvatica L.) tree in relationship to canopy cover. J. Hydrol. 330, 651–662. http://dx.doi.org/10.1016/j.jhydrol.2006.04.032.

Thiel, D., Kreyling, J., Backhaus, S., Beierkuhnlein, C., Buhk, C., Egen, K., Huber, G., Konnert, M., Nagy, L., Jentsch, A., 2014. Different reactions of central and marginal provenances of Fagus sylvatica to experimental drought. Eur. J. For. Res. 133, 247–260. http://dx.doi.org/10.1007/s10342-013-0750-x.

Vanhellemont, M., Baeten, L., Verheyen, K., 2014. Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium. Plant Ecol. Evol. 147, 22–32.

Verheyen, K., Adriaenssens, S., Gruwez, R., Michalczyk, I.M., Ward, L.K., Rosseel, Y., Van den Broeck, A., García, D., 2009. Juniperus communis: victim of the combined action of climate warming and nitrogen deposition? Plant Biol. http://dx.doi.org/10.1111/j.1438-8677.2009.00214.x.

Walck, J.L., Hidayati, S., Dixon, K.W., Thompson, K., Poschlod, P., 2011. Climate change and plant regeneration from seed. Glob. Change Biol. 17, 2145–2161. http://dx.doi.org/10.1111/j.1365-2486.2010.02368.x.

Wan, S., Norby, R.J., Pregitzer, K.S., Ledford, J., O'Neill, E.G., 2004. CO_2 enrichment and warming of the atmosphere enhance both productivity and mortality of maple tree fine roots. New Phytol. 162, 437–446. http://dx.doi.org/10.1111/j.1469-8137.2004.01034.x.

Webb, D.P., Wareing, P.F., 1972. Seed dormancy in *Acer pseudoplatanus* L.: the role of the covering structures. J. Exp. Bot. 23, 813–829. http://dx.doi.org/10.1093/jxb/23.3.813.

Zimmermann, N.E., Normand, S., Pearman, P.B., Psomas, A., 2013. Future ranges in European tree species. In: Fitzgerald, J., Linder, M. (Eds.), Adapting to Climate Change in European Forest – Results of the MOTIVE Project. Pensoft Publishers, Sofia, pp. 15–21.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA.