

RESEARCH PAPER

Interacting effects of warming and drought on regeneration and early growth of *Acer pseudoplatanus* and *A. platanoides*

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ABSTRACT

Climate change is acting on several aspects of plant life cycles, including the sexual reproductive stage, which is considered amongst the most sensitive life-cycle phases. In temperate forests, it is expected that climate change will lead to a compositional change in community structure due to changes in the dominance of currently more abundant forest tree species. Increasing our understanding of the effects of climate change on currently secondary tree species recruitment is therefore important to better understand and forecast population and community dynamics in forests. Here, we analyse the interactive effects of rising temperatures and soil moisture reduction on germination, seedling survival and early growth of two important secondary European tree species, *Acer pseudoplatanus* and *A. platanoides*. Additionally, we analyse the effect of the temperature experienced by the mother tree during seed production by collecting seeds of both species along a 2200-km long latitudinal gradient. For most of the responses, *A. platanoides* showed higher sensitivity to the treatments applied, and especially to its joint manipulation, which for some variables resulted in additive effects while for others only partial compensation. In both species, germination and survival decreased with rising temperatures and/or soil moisture reduction while early growth decreased with declining soil moisture content. We conclude that although *A. platanoides* germination and survival were more affected after the applied treatments, its initial higher germination and larger seedlings might allow this species to be relatively more successful than *A. pseudoplatanus* in the face of climate change.

INTRODUCTION

Models predict that mean annual temperatures in Europe are likely to increase more than the global mean (Christensen *et al.* 2007; Hansen *et al.* 2010), while changes in precipitation will differ geographically: increases are expected in Northern Europe and declines in Southern Europe (Christensen *et al.* 2007). Resulting decreases in soil moisture are expected in the Mediterranean and parts of Central Europe, while for other European regions no consensus on the direction of soil moisture change exist (Wang 2005).

Considering that the climate has a large influence on plant population dynamics (e.g. Woodward 1987), climate change can

be expected to affect plant populations across the globe (Hedhly *et al.* 2008; Walck *et al.* 2011). It is known that climate change can modify several aspects of the life cycle of plants (Farnsworth *et al.* 1995; Norby *et al.* 2003), including the sexual reproductive stage (Hedhly *et al.* 2008). For many plant species, seed germination and seedling establishment are considered a major bottleneck in regeneration (Lloret *et al.* 2005; Fay & Schultz 2009; Dalglish *et al.* 2010), but these phases also provide the plant with an opportunity to adapt to environmental changes (Hedhly *et al.* 2008). Increasing our understanding of the effects of climate change on regeneration is therefore particularly important (Jeltsch *et al.* 2008; Milbau *et al.* 2009) to better forecast future population dynamics (Milbau *et al.* 2009).

Most previous research on the effects of climate change on plant reproduction has been performed on the individual effects of changes in temperature (Milbau *et al.* 2009; Klady *et al.* 2011; De Frenne *et al.* 2012) and precipitation (Lloret *et al.* 2005; Kos & Poschlod 2008; Fay & Schultz 2009). These approaches provide valuable information but analyses of the interactive effects of these two global change drivers on tree species recruitment are largely lacking (Beier *et al.* 2012). Moreover, research on plant reproduction response to climate change has been mainly directed at tundra vegetation, boreal forest and tree line ecotones, with less emphasis on temperate regions (Walck *et al.* 2011). Specifically in temperate forests, a compositional change based on changes in dominance of currently dominant forest tree species due to climate change can be expected (Booth *et al.* 2012). The most abundant primary tree species from a management point of view, *e.g.* beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H.Karst.), are expected to decrease in fitness and abundance and consequently retreat from parts of their distribution range (Kramer *et al.* 2010; Hanewinkel *et al.* 2012). For this reason, currently less abundant, secondary forest tree species (*e.g.* *Acer* spp. and *Tilia* spp., *Quercus cerris* L. and *Quercus petraea* (Matt.) Liebl.) may become more important (Lloret *et al.* 2005; Hanewinkel *et al.* 2012).

There are several empirical approaches available to assess the impact of climate change on populations. One such is to use the natural temperature variation along latitudinal gradients (De Frenne *et al.* 2013). This approach provides an opportunity to evaluate the long-term effects of temperature on terrestrial organisms (Rustad 2008) and, using a space-for-time substitution procedure (*sensu* Fukami & Wardle 2005), study the effects of climate change on terrestrial organisms (see *e.g.* Daws *et al.* 2004; Reich & Oleksyn 2008; Ramírez-Valiente *et al.* 2009; Qiu *et al.* 2010; De Frenne *et al.* 2011, 2012). Yet the integration of techniques such as a combination of seed collection along a latitudinal gradient with experimental warming studies in common gardens represent a promising way forward in the quest for better understanding and forecasting the potential implications of global warming on plant populations and communities (Shaver *et al.* 2000; Dunne *et al.* 2003; Fukami & Wardle 2005; Rustad 2008; De Frenne *et al.* 2013).

Here we investigate the performance of regeneration from seed of two currently secondary tree species (*Acer pseudoplatanus* and *A. platanoides*) from nine regions along a 2200-km latitudinal gradient covering most of the distribution range of these species, including areas outside their natural range. We analysed the germination, seedling survival and growth of these two species using two common garden experiments, in which both temperature and soil moisture availability were manipulated. This set-up allowed evaluation of the effects of the temperature that the mother tree experienced during seed production as well as the response of germination, seedling survival and growth to projected changes in climate conditions. We specifically examined: (i) how differences in temperature and soil moisture content affect the germination, survival and growth of two congeneric *Acer* species; (ii) whether there is an interacting effect of the joint manipulation of temperature and soil moisture content; and (iii) whether the response to the experimental treatments depends on the temperature regime experienced by the mother trees.

MATERIAL AND METHODS

Study region and populations

In 2011, we collected seeds of *Acer platanoides* L. and *Acer pseudoplatanus* L. along a wide (2200 km) latitudinal gradient in Europe to allow study of a wide range of temperature effects on the mother tree. We 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 to fully represent possible maternal temperatures in Europe. These species were specifically selected since they (i) will likely become more important for European forestry in the context of future climate change (Hanewinkel *et al.* 2012); (ii) are characteristic for and abundant in broadleaved forests across Europe; (iii) have a large distribution range and occur along a wide latitudinal gradient in Europe; and (iv) tend to have high germination rates, ease of dormancy breaking and similar phenology. We sampled populations located in nine regions from Italy (43°49' N) via France, Belgium, Germany, Sweden to Norway (63°26' N). In each region, one landscape window of 40 × 40 km² was chosen, in which up to three forest patches were selected. In all cases, the forest patches were homogeneous in terms of canopy cover and soil characteristics. In each forest patch, one mature, well established, vital, seed-bearing healthy mother tree was selected. Seeds were collected using water-permeable nets (France, Belgium, Potsdam in Germany, Müncheberg in Germany and Skåne in Sweden) or picked from the forest floor immediately after seed dispersal (Italy, Bremen in Germany, Stockholm in Sweden and Norway; Fig. 1).

Climatic data from weather stations close to the sampling point (< 50 km distance) and available in the European



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

Climate Assessment and Dataset project (Klein Tank *et al.* 2002) were used for the calculation of the growing degree hours (GDH) experienced by the mother tree between the 1 April and 30 September 2011 (period between flowering and seed maturation). The GDH were calculated considering a base temperature of 5 °C and the following formulas (Graae *et al.* 2012).

$$\text{If } T_{\max_i} \leq 5^\circ\text{C} \rightarrow \text{GDH}_i = 0$$

$$\text{If } T_{\max_i} > 5^\circ\text{C} \text{ and } T_{\min_i} > 5^\circ\text{C} \rightarrow \text{GDH}_i \\ = 24 \times (T_{\min_i} - 5) + 12 \times (T_{\max_i} - T_{\min_i})$$

$$\text{If } T_{\max_i} > 5^\circ\text{C} \text{ and } T_{\min_i} \leq 5^\circ\text{C} \rightarrow \text{GDH}_i \\ = 12 \times \frac{(T_{\max_i} - 5)^2}{T_{\max_i} - T_{\min_i}}$$

$$\text{GDH} = \sum_{\text{August 1}}^{\text{September 30}} \text{GDH}_i,$$

where GDH_i , T_{\max_i} and T_{\min_i} are the GDH, maximum temperature and minimum temperature for day i , respectively. The GDH were standardised per location by dividing site-specific values by the overall mean across the gradient (Graae *et al.* 2009). The Pearson correlation between latitude and GDH was $r = -0.90$ ($n = 9$, $P < 0.0001$), between GDH (April and September 2011) and the mean annual GDH (average 1981–2011) was $r = 0.93$ ($n = 9$, $P < 0.001$), between GDH (April and September 2011) and the average single-seed mass (without dispersal structures) calculated from 30 seeds per mother tree, was -0.73 ($n = 9$ provenances, $P = 0.03$) and -0.37 ($n = 9$, $P = 0.32$) for *A. platanoides* and *A. pseudoplatanus*, respectively.

Experimental design

We performed two full factorial soil heating and moisture manipulation experiments to simulate a total of nine climate change scenarios. We based our two experiments on the A1B-IPCC scenarios that project an increase of the summer (June, July and August) temperature between +1.4 °C and +5.0 °C (average +2.7 °C) for Northern Europe. The expected summer (again June, July and August) temperature increase for Southern Europe is between +2.7 °C and +6.5 °C (average +4.1 °C) (Christensen *et al.* 2007). Concerning large-scale changes in precipitation, a change in summer precipitation between +16% and –21% is projected for Northern Europe while a reduction between –3% and –53% is forecast for Southern Europe (Christensen *et al.* 2007). We expressed our precipitation treatments as soil moisture rather than millimetres of rainfall, since (i) this is a stronger predictor of plant establishment than precipitation (Walck *et al.* 2011); and (ii) germination is highly dependent on available soil moisture (Kos & Poschod 2008).

Both experiments were performed with the collected seeds of *Acer platanoides* and *A. pseudoplatanus* from three mother trees (except *A. platanoides* from Bremen and Amiens with two mother trees), and ten and 25 seeds per mother tree for the first and second experiment, respectively (see below). In total, 27 *A. pseudoplatanus* and 25 *A. platanoides* mother trees were sampled. The seeds were randomly sown in plastic pots

(25 cm³ vol. for the first experiment and 112 cm³ vol. for the second experiment), filled with standard potting soil (mean pH 6, nutrient ratio NPK 15:10:11, organic matter 20% and water holding capacity 80%).

All seeds were cold stratified to break dormancy. Initially the seeds were soaked in water until the desired level of humidity was reached (*i.e.* 48% and 38% for *A. pseudoplatanus* and *A. platanoides*, respectively). Afterwards the seeds were placed in controlled cold conditions (at 0 °C to 1 °C and 90–95% humidity) for approximately 2 months until germination started. The stratification period depended on the species and the provenance, assuring that all the seeds were at the same development stage and at optimal conditions for germination. Seed lots that reached the correct development stage and started germinating were stored in a freezer at –2 °C until the moment of seed sowing.

For both experiments, warming was achieved through soil heating mats (ACD aluminium heating mats HMT-A; Oberweidbach Germany). The experiment was installed at the edge of a deciduous forest composed of *Fagus sylvatica*, *Fraxinus excelsior* L., *Quercus robur* L. and *Acer* sp. in Gontrode, Belgium (50°58' N, 3°48' E) under plastic roofs (70 cm above pots) to exclude natural precipitation and allow free air exchange. The soil temperature in the pots was measured every minute, and averaged and logged every 15 min using Decagon data loggers Em50 ECH₂O LOGGER, while the soil moisture was controlled by weighing each pot three times per week and adding the necessary amount of distilled water until the desired moisture content was reached.

We assessed the regeneration in terms of germination time (emergence above the ground), germination amount, survival (living seedlings at the end of the experiment) and seedling growth (number of leaves, biomass and height). Germination was recorded three times per week. At the end of the experiments, the seedlings were carefully removed from the soil, and for each seedling, the number of leaves was recorded. The belowground and aboveground plant parts were separated, dried at 60 °C for 24 h and weighed. In the second experiment only, the height reached by the seedlings was additionally measured.

First experiment

In the first experiment, which lasted for 36 days (starting on 16 July 2012), we sowed ten seeds per mother tree per species. The manipulations of temperature were as follows: (i) control at ambient temperature (average for the whole period was 16.5 ± 3.7 °C); (ii) average temperature increase of 2.5 °C (19.0 ± 2.5 °C); and (iii) average temperature increase of 7.2 °C (23.7 ± 3.1 °C). Additionally, the three soil moisture treatments were applied: (i) soil moisture constantly at 100% of field capacity (gravimetric soil moisture 65% and volumetric soil moisture 29%); (ii) soil moisture at 80% of field capacity (gravimetric soil moisture 52% and volumetric soil moisture 23%); and (iii) soil moisture at 60% of field capacity (gravimetric soil moisture 32% and volumetric soil moisture 17%). The total amount of water added during the experiment to maintain the desired level of soil moisture content was: +0 °C–8.9 l (control), 5.6 l (80%) and 4.3 l (60%); +2.5 °C–23.8 l, 14.9 l and 8.2 l; +7.2 °C–26.4 l, 15.2 l and 13.1 l.

Second experiment

The objective of this experiment was to evaluate possible changes in seedling establishment and growth over time using a longer experimental period (more than twice as long). This experiment was a replication of the intermediate temperature treatment (+2.5 °C) with the same three soil moisture content treatments as in the first experiment. The second experiment lasted for approximately 3 months (79 days, starting on the same day as the first experiment, 16 July 2012). In this experiment, we sowed 25 seeds per mother tree and the soil temperature was set at an average for the whole period of 19.0 ± 2.4 °C, while three levels of soil moisture content were applied (same procedure as above, *i.e.* 100%, 80% and 60% of field capacity). The total amount of water added during the experiment to maintain the desired level of soil moisture content was 180 l, 169 l and 133 l.

Data analysis

Mixed-effects models using the *lme* and *lmer* functions in R version 3.0.0 (R Core Team 2013) were applied. For the continuous variables (seedling height, total, aboveground and belowground biomass and root:shoot ratio), binomial data (germination and survival) and count data (germination time and number of leaves) we used Gaussian, binomial and Poisson error structures, respectively. All the continuous data were log-transformed prior to the analyses to fulfil the requirements of normality and homoscedasticity, except for the total, aboveground and belowground biomass of *A. platanoides* in the second experiment. As predictor variables, we included the temperature and soil moisture treatments and the standardised growing degree hours (GDH) experienced by the mother tree between the 1 April and 30 September as fixed effects, while the mother tree and the provenance were included as nested random effects (to account for the hierarchical structure of the data). For each variable analysed, first the maximal model was fitted and model simplification was achieved by comparing the deviance of the model, dropping one interaction and explanatory variable at a time.

RESULTS

First experiment

The germination and survival of the species showed different responses in relation to the temperature and soil moisture treatments and the GDH experienced by the mother tree during seed production (Table 1). The two species showed different responses to the treatments applied regarding germination time: germination was 24% earlier and 28% later for *A. platanoides* and *A. pseudoplatanus*, respectively, under the treatment (+7.2 °C × 80%) than at control moisture and temperature conditions (0 °C × 100%). Additionally, in *A. pseudoplatanus* the strong reduction in soil moisture content (60%) combined with GDH experienced by the mother tree affected the germination time: seedlings emerged on average 26% later under drier conditions than under the control treatment (Table 1).

Acer platanoides was more affected by the treatments applied and the GDH experienced by the mother tree during seed

production. Germination in this species was affected by experimental changes in temperature, soil moisture content, GDH experienced by the mother tree and their joint manipulation. The strong reduction in soil moisture content (60%) produced an average reduction of 5% in germination success. Moreover, the soil moisture reduction combined with rising temperature (+7.2 °C) increased germination success in comparison with the full moisture capacity at the same temperature (Fig. 2). Nevertheless for *A. platanoides*, the GDH experienced by the mother tree during seed production had a negative effect on germination success. The seeds from provenances with the lowest GDH showed 53% higher germination success than the seeds from the warmest provenance under control temperature treatment (Table 1, Table S1). However, rising temperatures (+2.7 °C and +7.2 °C) increased the difference between seeds from the colder and warmer provenances (lower and higher values of accumulated GDH) to 73% and 79% (Table 1, Table S1). In *A. platanoides* the joint manipulation of temperature (+7.2 °C) and soil moisture content reduction (80% and 60%) reduced survival 2.4- and 1.9-fold, respectively, compared with the control temperature and soil moisture conditions (Table 1, Fig. 2).

On the other hand, germination in *A. pseudoplatanus* only showed significant differences due experimental warming interacting with GDH experienced by the mother tree during seed production. The temperature treatments significantly increased the difference between the germination of *A. pseudoplatanus* seeds from colder and warmer provenances (Table 1, Table S1), while survival was only affected by the temperature increase of +7.2 °C (Fig. 2).

Regarding growth, both *Acer* species showed similar but not identical responses to the treatments applied. *A. platanoides* was sensitive to changes in temperature, moisture and the joint manipulation of these factors (Table 2). A small temperature increase had a positive effect on the biomass variables, but a higher increase in temperature (+7.2 °C) reduced total biomass by 35%, aboveground biomass by 30% and belowground biomass by 33% (Table 2). The strong soil moisture decrease (60%) produced an average reduction of 33% in total and aboveground biomass (Table 2). The joint manipulation of temperature and soil moisture content (+2.7 °C × 60%) produced a stronger reduction in the biomass variables than the individual modification of the two factors (Table 2, Fig. 3).

Acer pseudoplatanus showed changes in the growth variables related to changes in the temperature and soil moisture content, but did not show significant differences caused by the joint manipulation of temperature and moisture (Table 2). A temperature increase and reduced soil moisture content had a negative effect on most of the biomass variables. Total biomass was reduced by 21% when the temperature increased by 2.7 °C and 33% when the soil moisture content was 60% of field capacity. The belowground biomass was 41% and 39% lower when temperature increased by 2.7 °C and 7.2 °C, respectively, while the soil moisture reduction decreased belowground biomass by 20%. The aboveground biomass was only affected by moisture: the reduction was 23% and 32% for the 80% and 60% field capacity treatments, respectively (Table 2). The root:shoot ratio was reduced by 39% on average when the temperature increased by 2.7 °C and 7.2 °C, and increased by 18% when soil moisture was 80% of field capacity (Table 2, Fig. 3).

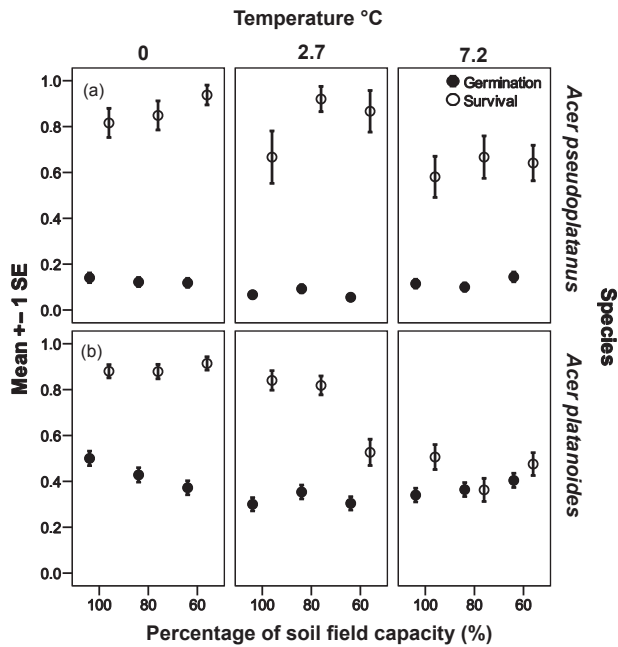


Fig. 2. *Acer pseudoplatanus* (a) and *A. platanoides* (b) germination and survival as a function of the applied temperature and soil moisture treatments in the first experiment.

Second experiment

In the second experiment, the number of GDH experienced by the mother tree reduced germination success in *A. platanoides*, while the soil moisture content reduction narrowed difference in germination time between the colder and warmest provenances (Table 3). For this species, germination was 75% lower in seeds from higher GDH than those produced under colder conditions (lower accumulated GDH). The germination time of *A. pseudoplatanus* increased by 18% and 26% when soil moisture content was 80% and 60% of field capacity, respectively (Table 3). Growth variables for both species were mainly affected by the soil moisture content. Drought negatively affected the total, aboveground biomass and height, while soil moisture reduction increased the root:shoot ratio (Table 4).

The soil moisture content at 60% of field capacity reduced total biomass by 20% and 30% for *A. platanoides* and *A. pseudoplatanus*, respectively. For both species, the root:shoot ratio was higher at 60% of field capacity than at field capacity (Table 4, Fig. 4). Additionally, the height reached by seedlings at the end of the experiment was 28% and 25%, 18% and 17% lower under treatments at 80% and 60% of field capacity for *A. pseudoplatanus* and *A. platanoides*, respectively (Table 4).

Finally, the temperature (+2.7 °C and +7.2 °C) and soil moisture reduction (80% and 60% of field capacity) treatments applied had different effects on germination, seedling survival and growth of both species. During both experiments, *A. platanoides* was more susceptible than *A. pseudoplatanus* to the treatments applied (Fig. 5).

DISCUSSION

By simulating moderate and extreme warming and drought (Chmura *et al.* 2011; Smith 2011) combined with the effect of

the temperature experienced by the mother tree along the latitudinal gradient (Johnsen *et al.* 2005; De Frenne *et al.* 2013), we were able to provide important information about the germination and seedling establishment of two currently secondary tree species in the face of climate change. The variable responses of germination, germination time and survival to the combination of temperature and soil moisture treatments indicates the relevance of jointly manipulating different climatic variables, and highlights the need for more complex full factorial experiments (Shaver *et al.* 2000; Dieleman *et al.* 2012). Across both experiments, two congeneric species, *Acer platanoides* and *A. pseudoplatanus*, showed divergent responses. This species-specific behaviour during the recruitment stage is relevant to better forecast and understand population dynamics (Milbau *et al.* 2009). Additionally, reliable information about the effects of climate change on early establishment, considering the temperature experienced by the mother tree and native *versus* non-native populations, might be especially relevant to better forecast future forest compositional changes and develop adaptive management plans (Chmura *et al.* 2011; Hanewinkel *et al.* 2012).

Life-stage transitions that are important for plant population dynamics (germination and survival) were especially sensitive to changes in temperature, the interaction with soil moisture content and the GDH experienced by the mother tree. Previous research indicated that for species with dormant seeds, climate warming may be favourable for germination and recruitment as long as the stratification requirements are satisfied (Chmura *et al.* 2011). Moreover, warmer temperatures enhance plant biochemical and physiological processes as long as threshold temperatures are not exceeded and moisture content is adequate (Chmura *et al.* 2011). In these experiments, the stratification requirements were specifically satisfied before the beginning of the experiments, and were therefore excluded from our analyses. Regardless of whether future stratification requirements will be met, our results suggest that the projected changes in temperature and soil moisture content will likely have negative effects on germination and/or survival of both *Acer* species. However, as indicated, there will likely be species-specific responses, dependent also on the level of change of the climatic variables. This highlights the complexity in understanding and anticipating the effects of climate change in plant communities.

The effects of the experimental temperature and moisture treatments on recruitment depended not only on the level of change in the climatic variables but also on their interactions. For example, in *A. platanoides*, the soil moisture reduction negatively affected germination. Yet, the negative effect of soil moisture content reduction on germination was partly compensated when interacting with a temperature increase. However, germination under dry and warm conditions did not reach the amount recorded under control conditions. Such partial compensation can be explained by the fact that at high temperatures and drier conditions the seeds are less exposed to fungi and pathogens than under warm and wet conditions (Blaney & Kotanen 2001), and are stimulated to germinate under higher temperatures. For both species, warming, drought and the GDH experienced by the mother tree affected germination time, an important factor in the potential regeneration of plants (Chmura *et al.* 2011). Under warm and wet conditions, germination was advanced, extending the growing season length and potentially improving the chances of seedlings to survive the following winter (Milbau *et al.* 2009; De

Table 2. Effects of warming (temperature increased by 2.7 °C and 7.2 °C) and drought (soil moisture reduced to 80% and 60% of field capacity; M80% and M60%) on the total, aboveground and belowground biomass and root:shoot ratio of *Acer platanoides* and *A. pseudoplatanus* in the first experiment. The effects of GDH were not significant and therefore excluded from the model.

	T + 0 °C	T + 2.7 °C	T + 7.2 °C	M100%	M80%	M60%	T + 0 °C* M100%	T + 2.7 °C x M80%	T + 7.2 °C xM80%	T + 2.7 °C xM60%	T + 7.2 °C xM60%
<i>Acer platanoides</i>											
biomass (g)											
mean	0.17	0.17	0.11	0.18	0.17	0.12	0.18	0.17	0.12	0.12	0.10
SE	0.005	0.007	0.007	0.007	0.007	0.005	0.018	0.020	0.020	0.019	0.014
t-value		2.20*	-4.46***		-0.09	-2.65**		-1.72	0.21	-2.73**	0.52
belowground biomass (g)											
mean	0.06	0.06	0.04	0.06	0.07	0.04	0.06	0.06	0.04	0.04	0.04
SE	0.003	0.004	0.003	0.003	0.005	0.002	0.002	0.004	0.002	0.002	0.002
t-value		1.13	-4.84***		0.64	-1.87(*)		-1.83(*)	0.27	-2.56*	1.08
aboveground biomass (g)											
mean	0.10	0.11	0.07	0.12	0.10	0.08	0.12	0.10	0.07	0.07	0.06
SE	0.004	0.004	0.005	0.004	0.003	0.006	0.004	0.003	0.003	0.002	0.003
t-value		2.32*	-3.95***		-1.29	-3.33***		-1.34	0.65	-2.41*	0.71
ratio											
mean	0.65	0.54	0.50	0.54	0.66	0.56	0.57	0.58	0.55	0.50	0.51
SE	0.034	0.027	0.068	0.019	0.052	0.046	0.025	0.054	0.085	0.031	0.160
t-value		-3.21**	-4.15***		2.34*	1.14		+	+	+	+
<i>Acer pseudoplatanus</i>											
biomass (g)											
mean	0.14	0.11	0.12	0.15	0.13	0.10	0.17	0.12	0.13	0.06	0.10
SE	0.108	0.080	0.060	0.010	0.009	0.007	0.016	0.012	0.018	0.013	0.012
t-value		-2.91**	-1.52		-0.63	-3.72***		+	+	+	+
belowground biomass (g)											
mean	0.05	0.03	0.03	0.04	0.05	0.03	0.06	0.03	0.04	0.02	0.02
SE	0.004	0.003	0.003	0.004	0.005	0.003	0.006	0.004	0.009	0.005	0.004
t-value		-4.05***	-3.59***		0.83	-2.32*		+	+	+	+
aboveground biomass (g)											
mean	0.09	0.08	0.08	0.10	0.08	0.07	0.11	0.07	0.08	0.06	0.07
SE	0.005	0.007	0.006	0.007	0.005	0.005	0.010	0.008	0.010	0.013	0.008
t-value		+	+		-2.35*	-3.49***		+	+	+	+
ratio											
mean	0.63	0.39	0.37	0.46	0.57	0.45	0.59	0.48	0.36	0.34	0.39
SE	0.045	0.027	0.031	0.052	0.044	0.032	0.095	0.040	0.048	0.031	0.063
t-value		-4.72***	-4.98***		3.50***	0.58		+	+	+	+

Results from mixed-effect models.

$P < 0.001$ ***, $P < 0.01$ ** , $P < 0.05$ * , $P < 0.10$ (*) .

Mean and SE are calculated on the untransformed variables.

+: Factors removed during model simplification.

Frenne *et al.* 2012). However, due the high early mortality under warm and wet conditions, the relative advantage of advanced germination might be suppressed and not provide advantages for the species analysed.

For both species, soil warming reduced seedling survival. However, the negative effect of temperature on the survival of *A. platanoides* increased when temperature and soil moisture content were jointly manipulated, while in *A. pseudoplatanus* survival was not affected by the soil moisture content. The high sensitivity of emerging seedlings to drought is well known, and because shoot growth continues later into the growing season, late season droughts may impact seedlings more than they affect mature trees (Dieleman *et al.* 2012). For this reason, it is likely that drought-related regeneration failures will increase under future climate regimes. However, explaining the differences in drought sensitivity observed, the effect of drought on survival depends on several factors, including

drought hardiness, evolutionary adaptation and drought acclimation (Abrams 1990, 1994; Martinez-Vilalta *et al.* 2004). As observed in these two closely related species, differences in drought hardiness have also been found between species, varieties and populations, which also points to the relevance of provenance-related tests (Martinez-Vilalta *et al.* 2004). In this work, we showed that two congeneric species exhibit different drought sensitivities. *A. pseudoplatanus* survival was not affected by the soil moisture, indicating this species is more drought-tolerant than *A. platanoides*. As these two species can occur in the same sites, we can expect that under drought stress, *A. pseudoplatanus* will be relatively advantaged.

The germination and seedling survival of *A. platanoides* from colder provenances (lower GDH) were much higher than those from warmer provenances (higher GDH) when the seeds were placed under equal conditions. Thus, seeds from warmer provenances may be less provisioned (as indicated by the negative

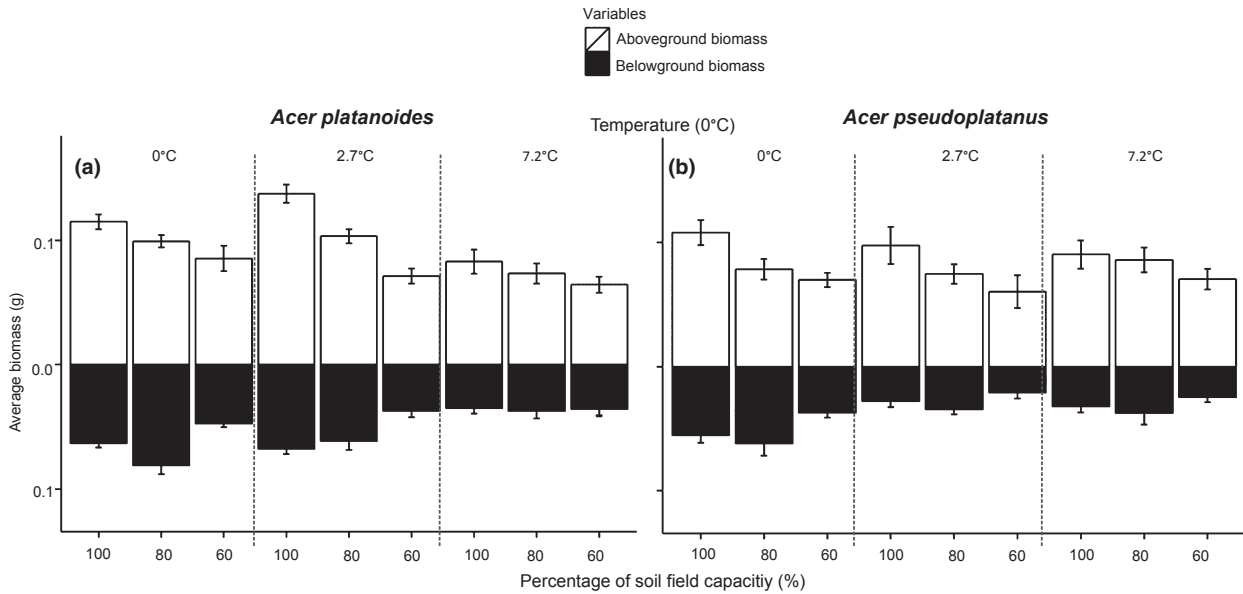


Fig. 3. Average aboveground and belowground biomass of *Acer pseudoplatanus* (a) and *A. platanoides*. (b) Error bars indicate SE.

Table 3. Effects of drought (soil moisture content reduced to 80% and 60% of field capacity; M80% and M60%) and the standardised number of growing degree hours between April and September (GDH) on the germination, survival, number of leaves and germination time for *Acer platanoides* and *A. pseudo-platanus* in the second experiment.

	<i>Acer platanoides</i>						<i>Acer pseudoplatanus</i>					
	M100%	M80%	M60%	GDH	M80% × GDH	M60% × GDH	M100%	M80%	M60%	GDH%	M80% × GDH	M60% × GDH
germination (%)												
mean	23	25	24				6	6	5			
SE	1.68	1.72	1.72				0.89	0.89	0.81			
z-value		+	+	-3.06**	+	+		+	+	-0.989	+	+
survival (%)												
mean	58	61	60				66	63	47			
SE	4.13	3.96	4.01				7.79	7.95	8.27			
z-value		+	+	0.85	+	+		0.779	-1.582	+	+	+
number leaves												
mean	5.9	4.6	3.7				4.8	4.0	3.1			
SE	0.65	0.48	0.39				0.33	0.37	0.26			
z-value		-3.52***	-6.41***	+	+	+		-1.16	-2.11*	+	+	+
germination time (days)												
mean	9.3	9.6	11.3				14.6	17.9	19.9			
SE	0.77	0.78	0.93				1.27	1.02	1.38			
z-value		1.11	-1.43	0.51	-0.93	2.35*		2.19*	4.47***	+	+	+

Results from mixed-effect models.

$P < 0.001$ ***, $P < 0.01$ ** , $P < 0.05$ *.

Mean and SE are calculated on the untransformed variables.

+: Factors removed during model simplification.

correlation between seed mass and GDH along the latitudinal gradient). The higher seed mass recorded under colder conditions might be related to a lower rate of seed ripening and a longer seed filling process that allows higher total assimilation (Fenner & Thompson 2005). Conversely, the effects on populations that were native *versus* non-native were limited and there were no clear directional effects on the studied response variables (results not shown). This matches with observations of Skrøppa *et al.* (2010), who reported rapid adaptation in *Picea*

abies regarding seedling timing of bud set at the end of the first growing season. These authors compared seedlings obtained from seeds from Central European and Norwegian parents that produced seeds in Norway with seedlings from seeds of mother trees producing seeds at their geographic origin. They argued that the rapid change in this adaptive trait is related to the influence of day length and temperature conditions during embryo formation and maturation on the phenotypic performance of Norway spruce seedlings.

Table 4. Effects of drought (soil moisture content reduced to 80% and 60% of field capacity; M80% and M60%) and the standardised number of growing degree hours between April and September (GDH) on the total, aboveground and belowground biomass and root:shoot ratio of *Acer platanoides* and *A. pseudoplatanus* in the second experiment.

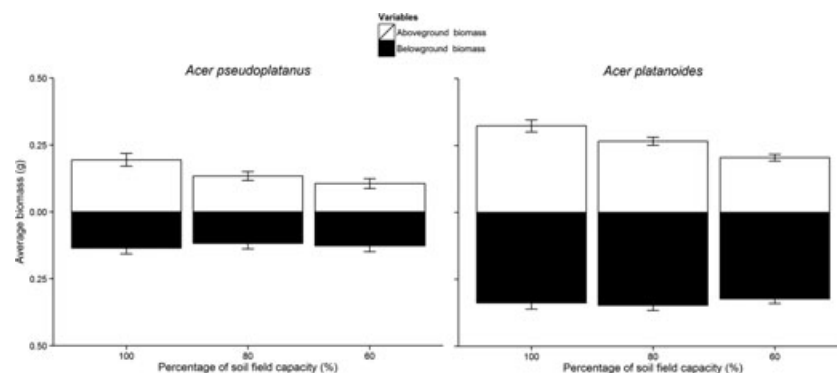
	<i>Acer platanoides</i>						<i>Acer pseudoplatanus</i>					
	M100%	M80%	M60%	GDH	M80% × GDH	M60% × GDH	M100%	M80%	M60%	GDH	M80% × GDH	M60% × GDH
biomass (g)												
mean	0.66	0.61	0.53				0.33	0.25	0.23			
SE	0.04	0.03	0.03				0.04	0.04	0.03			
t-value		-0.93	-2.58*	+	+	+		-1.98(*)	-1.40	+	+	+
belowground biomass (g)												
mean	0.34	0.35	0.32				0.14	0.12	0.13			
SE	0.03	0.02	0.02				0.02	0.02	0.02			
t-value		-0.10	1.96(*)	0.439	0.181	-2.134*		-1.49	-0.03	+	+	+
aboveground biomass (g)												
mean	0.32	0.27	0.21				0.20	0.13	0.11			
SE	0.02	0.02	0.01				0.02	0.02	0.01			
t-value		-2.38*	-4.89***	+	+	+		-2.34*	-3.02**	+	+	+
ratio												
mean	1.06	1.33	1.77				0.65	0.76	1.32			
SE	0.03	0.05	0.12				0.04	0.07	0.144			
t-value		3.26**	7.32***	+	+	+		0.41	3.95***	+	+	+
height (cm)												
mean	8.21	6.8	6.13				7.67	6.30	5.56			
SE	0.32	0.24	0.19				0.44	0.33	0.26			
t-value		-3.41***	-4.84***	+	+	+		-2.43*	-3.41***	+	+	+

Results from mixed-effect models.

$P < 0.001$ ***, $P < 0.01$ ** , $P < 0.05$ * , $P < 0.10$ (*) .

Mean and SE are calculated on the untransformed variables.

+ : Factors removed during model simplification.

**Fig. 4.** Effects of drought treatments on aboveground and belowground biomass of *Acer pseudoplatanus* (a) and *A. platanoides* (b) in the second experiment. Error bars denote SE.

Furthermore, in the two *Acer* species, differences between colder and warmer provenances in germination and survival success increased under the treatments applied in our experiment, showing the importance of bigger seeds and, consequently, higher nutrient reserves, on the early regeneration success under climate change. Finally, it is important to mention that the response of tree survival to soil moisture reductions can change over longer time periods. For instance, it is possible that seedlings and saplings resulting from seeds taken from warmer regions perform better under drought stress, as previously reported for other species (Atzmon *et al.* 2004; O'Brien *et al.* 2007).

Concerning the growth variables, warming and drought affected height and biomass growth of both *Acer* species. The

influence of the GDH of different provenances appears to be important only at the very start of the recruitment stage. However, after germination, the role of the provenance loses relevance in terms of growth, which is mainly conditioned by the experimental conditions. Again, these results show that species-specific responses are especially relevant in terms of the population dynamic variables (germination and survival) and indicate how different aspects of plant life can be differentially affected in congeners. Drought and warming reduced the growth of both *Acer* species (total, above- and belowground biomass and height). The root:shoot ratio generally increased as drought intensified, as reported before for low-severity drought (Kramer *et al.* 2010) and extreme drought (Dreesen *et al.* 2012). Our results thus equally confirm that under stress

Effect of the treatments on the variables analysed		Variables analysed		
		Germination	Seedling survival	Seedling total biomass
<i>Acer platanoides</i>	Positive	↑Temperature*↓Moisture		
	Positive and/or negative		↑GDH mother tree*↓Moisture*↑Temperature ↑Temperature*↓Moisture	↑Temperature
	Negative	↓Moisture ↑GDH mother tree ↑Temperature*↑GDH Mother tree		↑Temperature*↓Moisture
<i>Acer pseudoplatanus</i>	Positive	↑Temperature	↑Temperature	
	Positive and/or negative			
	Negative	↑Temperature*↑GDH mother tree		↑Temperature ↓Moisture

Fig. 5. Scheme of the main experimental outcomes. In the first column, effects of the treatments on germination, survival and biomass are indicated (positive, negative and a combination of positive and negative). The small arrows indicate increases and decreases in the level of the treatments; stars indicate the interaction between treatments.

conditions there is a differential allocation of resources in favour of belowground biomass.

To conclude, our results suggest that increasing temperatures might negatively affect critical life stages, such as germination and survival, of *Acer pseudoplatanus* and *A. platanoides*. The negative impact of soil moisture was especially important in constraining biomass production and growth. However, especially when the two global-change drivers act together, these might strongly modify population dynamics of our study species. The germination success of *A. platanoides* was more than twofold higher than that of *A. pseudoplatanus*. An additional potential future advantage of the former species is that under all the treatments applied, seedlings of *A. platanoides* were larger than seedlings of *A. pseudoplatanus*, especially regarding root biomass, which may allow this species to colonise a larger soil volume for nutrient and water uptake. Together, these results suggest that *A. platanoides* might be better able to cope with changing climate conditions, which is especially relevant since deciduous trees are gaining in dominance, *e.g.* in several Central European forests, because of higher conifer mortality caused by climate change-related drought stress (Gimmi *et al.* 2010). This is particularly important when considering that potential novel regional communities might emerge in the context of climate change (Williams & Jackson 2007). However, it is necessary to stress that we

focused only on the germination, survival and early growth of the seedlings and that information about the subsequent life stages will be key to fully understand and forecast the population dynamics of these *Acer* species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Provenance-specific responses to the temperature treatments (Control, 2.7 °C and 7.2 °C) and the moisture treatments (100% field capacity, reduced to 80% and 60% of field capacity; M100%, M80%, M60%) on germination and survival probabilities and biomass.

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