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A transplantation experiment along climatic gradients suggests limitations of experimental warming manipulations

Sabrina Backhaus[1,*], Juergen Kreyling[2], Carl Beierkuhnlein[2], Constanze Buhk[3], Laura Nagy[1,4], Daniel Thiel[2,5], Anke Jentsch[1]

[1]Department of Disturbance Ecology, University of Bayreuth, 95440 Bayreuth, Germany
[2]Department of Biogeography, University of Bayreuth, 95440 Bayreuth, Germany
[3]Geoecology/Physical Geography, University of Koblenz-Landau, 76829 Landau, Germany
[4]Institute for Landscape Biogeochemistry, Leibniz Center for Agricultural Landscape Research, 15374 Müncheberg, Germany
[5]Bavarian Office for Forest Seeding and Planting, 83317 Teisendorf, Germany

ABSTRACT: Transplantation to a warmer site and experimental passive warming are powerful tools for predicting plant responses to climate change. Both techniques are widely applied for the study of plant species and community response to temperature increase. We investigated differences in height increment of *Fagus sylvatica* seedlings between 2 different techniques: experimental warming (passive warming) and transplantation to a warmer site. Additionally, the plants were exposed to an extreme drought to further examine the influence of the different warming techniques in combination with an additional climatic driver. We found significant differences between the 2 warming techniques for height increment, which were mainly attributed to the case with additional drought exposure (significant interaction between warming and drought). Surprisingly, when subjected to drought, experimental warming had no negative effect on height increment of seedlings, while transplantation decreased height increment by 32% when subjected to drought. Growth did not show a linear dependence on the magnitude of warming. Differences between the warming techniques can therefore not be explained by differences in realized temperature increases. The results of this study emphasize the complexity of simulating global warming, as required for accurate prediction of shifts in plant performance. The role of co-varying parameters, such as evapotranspiration, photosynthetically active radiation, and wind speed, in addition to experimental temperature increases should be acknowledged when analyzing ecological responses to climate warming.

KEY WORDS: Beech · EVENT experiment · Experimental manipulation · Global warming

1. INTRODUCTION

Simulating global warming is currently a fundamental topic in ecological climate change research (Leuzinger et al. 2011). Different techniques are used in this context, such as transplantation to a warmer site (e.g. Joshi et al. 2001, Link et al. 2003, Turetsky et al. 2008, Gonzalo-Turpin & Hazard 2009, Saarinen & Lundell 2010, Haggerty & Galloway 2011) or passive warming techniques (Henry & Molau 1997, Marion et al. 1997, Beier et al. 2004, Dabros et al. 2010, De Boeck et al. 2012, Kreyling et al. 2012a, Thiel et al. 2012). However, the question of which technique is more realistic and useful when predicting the effects of warmer temperatures in the future is difficult to answer. Obvious limitations in experimental warming techniques exist: passive warming can induce chamber overheating, alter moisture, light, gas concentrations and wind, or underestimate simulated temperature at tissue level (Marion et al. 1997, De

*Corresponding author: sabrina.backhaus@uni-bayreuth.de

Boeck et al. 2012). Furthermore, edge effects, such as an increased heat loss near the edges compared with the plot center, occur for passive nighttime warming by aluminum curtains (Beier et al. 2004). Regarding warming by transplantation, the respective plant species experience a step change of the entire environmental conditions in comparison to passive warming techniques. In addition, a transplantation shock (Tetsumura et al. 1998), the size of monoliths or new biotic interactions — especially herbivory (Kile et al. 2013) — might impact on the plant performance. These side-effects can blur the true warming response, yet they might also reveal ecologically important processes by their holistic nature of change.

In this study, we focus on the different effects of experimental warming (passive warming by wind shelters and black floor covers) versus warming by transplantation (across several hundred kilometers) in comparison to ambient conditions. To our knowledge no study has so far directly compared passive warming and warming by transplantation.

Climate change includes more than gradual warming; more frequent and stronger extremes are also an important aspect to consider (IPCC 2012). These extreme events are thought to have high ecological importance (Easterling et al. 2000, Jentsch et al. 2007). Recent multi-factor climate change experiments (which include different manipulations such as warming and drought as single factors and in combination) imply that single-factor effects are often not additive, i.e. the interaction of climate parameters results in unexpected effects (Shaw et al. 2002, De Boeck et al. 2011, Larsen et al. 2011, Kreyling et al. 2012b). Therefore, in the present study, we tested potential limitations of warming manipulations not only as a single factor, but also in combination with drought extremes.

The impact of global warming on ecosystems is indisputable (IPCC 2007); however, developing an accurate prediction of the consequences of climate change is very challenging. It is difficult, for example, to scale up experimental results, which describe a certain temporal and spatial scale, to realistic scenarios (Leuzinger et al. 2011, Wolkovich et al. 2012). A dampening of effect size is known to occur with increased scale and treatment complexity, which leads to an overestimation of the influence of a changing climate based on small-scale and short-scale experiments (Leuzinger et al. 2011). Inconsistencies in climate predictions might also be caused by experimental artifacts. A thorough investigation of potential artifacts, for example from the warming technique used, is needed to improve these predictions. Therefore, we compared the performance of *Fagus sylvatica* L. (European beech) seedlings in response to 2 different warming techniques: experimental warming (passive warming by wind-shelters and black floor covers) and transplantation to a warmer site. Both warming techniques were compared to ambient conditions. We chose *F. sylvatica* because this deciduous forest tree is naturally dominant in Central European forests.

We hypothesized that (1) experimental warming and warming of similar magnitude by transplantation would lead to the same increase in height increment. As warming by transplantation depends on actual weather conditions, it cannot be controlled in its magnitude. To circumvent this potentially confounding effect, we expected the effect sizes of our response variable to correlate linearly with the magnitude of warming, irrespective of warming technique. Furthermore, we assumed that (2) different warming techniques would not influence the temperature sensitivity of plant growth under additional pulsed drought stress.

2. MATERIALS AND METHODS

2.1. Experimental sites

The main experimental site was established in Bayreuth, Germany, in the Ecological-Botanical Garden of the University of Bayreuth (49° 55′ 19″ N, 11° 34′ 55″ E) in March 2010 (Beierkuhnlein et al. 2011, EVENT 3). The long-term mean annual temperature at this site is 8.2°C and the long-term mean annual precipitation is 724 mm with a precipitation peak in December/January and July/August (data: German Weather Service, www.dwd.de/klimadaten).

The second experimental site was established in April 2010 next to the campus Siebeldingen (University Koblenz-Landau) at the experimental sites of the Julius Kühn-Institut (JKI) (Federal Research Center for Cultivated Plants) (49° 13′ 03″ N, 8° 02′ 47″ E), Germany. The long-term mean annual temperature at the site is 10.2°C, i.e. 2.0°C warmer than the main experimental site, and the long-term mean annual precipitation is 643 mm, which is distributed bimodally with a major peak in May/June and in November/December (data: German Weather Service, www.dwd.de/klimadaten).

2.2. Plant material

We used 7 *Fagus sylvatica* provenances — 3 from Germany, 3 from Bulgaria, and 1 from Hungary — in order to improve the generality of the observations. Specific geographic origin of the provenances is provided (Table A1 in the Appendix). Despite differing in their general performance, the provenances showed no difference in their sensitivity to experimental warming at the main experimental site (Kreyling et al. 2012b) and at the transplantation site (tested in a pre-analysis). The seedlings were cultivated at the Bavarian Institute for Forest Seeding and Planting (ASP) in Teisendorf, Germany from February 2009 to March 2010. In March 2010 the seedlings were transported bare-root to Bayreuth and individually planted in 12 l plastic pots filled with sandy silt (pH 7.73, total C 1.58%, total N 0.13%). The plants were planted and watered until they were saturated on March 23. Further watering was applied on March 25 and 29. On April 12, 2010, 126 planted seedlings were transported to the second experimental site in Siebeldingen. In total, there were 252 planted seedlings in Bayreuth. Nine seedlings per provenance and treatment (ambient, ambient with drought, experimental warming, experimental warming with drought, warming by transplantation, warming by transplantation with drought) were selected randomly from all plants alive at planting date. The irrigation simulated the local daily 30 yr average precipitation, which was applied twice a week using collected rainwater at the main experimental site and groundwater at the transplantation site.

2.3. Experimental design

At the main experimental site in Bayreuth, the 4 climate treatments resulted from fully crossed twofold factorial combination of 2 temperature regimes, i.e. ambient and experimental warming, and 2 moisture regimes, i.e. ambient and drought, conducted from April to October 2010. Each of the 4 climate treatments (ambient, ambient with drought, experimental warming, experimental warming with drought) were replicated 3 times, resulting in 12 experimental units in total. Each provenance was represented by 3 plants in each experimental unit (7 provenances × 4 climate treatments × 3 plants per experimental unit × 3 replications = 252 plants in total). The available plants were assigned randomly to the experimental units. Each experimental unit (10.5 × 7 m) was covered by a single rain-out shelter with a steel frame (GlasMetall Riemer GmbH) and covered by a transparent polyethylene sheet (0.2 mm, SPR5, Hermann Meyer KG). The edges of the rain-out shelters were at a height of 80 cm and the polyethylene sheet permitted nearly 90% penetration of photosynthetically active radiation. Due to the sensitivity to solar radiation of *Fagus sylvatica* seedlings, shading nets (Quadra 105 ME, 105 g, DM-Folien GmbH) were attached inside the polyethylene sheet, resulting in a penetration of about 55% of the photosynthetically active radiation, which resembles natural forest floor conditions in beech stands (Ellenberg 1996). The warming treatment was mainly achieved by passive warming via additional wind breaking around the shelters and black floor covers (in comparison to white floor covers in the ambient and ambient with drought treatments). The windbreaker nets (type Z, 330 g m^{-2}, 70% wind speed reduction, DM-Folien GmbH) were installed around the experimental units reaching up to the roof height of 80 cm aboveground. Note that all climate treatments including ambient were installed under rain-out shelters in order to control precipitation. In addition, each experimental unit had 8 evenly distributed infrared (IR) heating lamps (IOT/90, 250 W, 230 V, Elstein) placed at 2 m height, theoretically resulting in roughly 30 W m^{-2}. However, these affected warming only marginally (by 0.1°C in comparison to passive warming alone; Thiel et al. 2012). The applied experimental warming (passive warming, IR-heating) increased the average air temperature at plant height by 1.6°C.

At the transplantation site in Siebeldingen only 1 rain-out shelter (see above) was set up. Below this shelter, all 126 plants were kept completely randomized in 2 climate treatments: warming by transplantation and warming by transplantation with additional drought (×7 provenances, ×9 replications).

At both sites the air temperature at plant height was measured hourly. At the main experimental site in Bayreuth, 2 thermistores (B57863-S302-F40, EPCOS) connected to a dl2 datalogger (Delta) were used per experimental unit. At the transplantation site in Siebeldingen, 2 Tinytag Plus 2 Data Loggers (Gemini Data Loggers, Chichester) were used (Fig. 1). At both sites, soil moisture was measured hourly at a depth of 5 cm with 3 Ech2o EC-5 moisture sensors (Decagon Devices) per climate treatment (Fig. 2). Regarding the entire experimental time period (April to October 2010), 'experimental warming' resulted in a temperature increase by 1.9°C in comparison to 'ambient', while 'warming by transplantation' resulted in a temperature increase by 3.2°C (Fig. 1; Table 1). The air temperature sums (see section 2.5) of both warming techniques and ambient conditions are also provided in Table 1.

The drought manipulation took place from 14 May until 16 or 17 July 2010. The plants at the main ex-

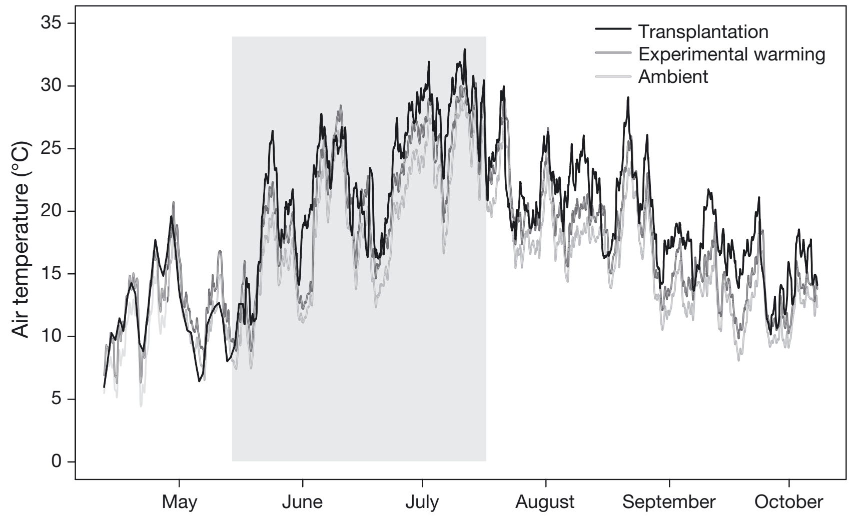

Fig. 1. Air temperature at plant height in the different warming treatments over the course of the experiment in 2010. The grey area represents the drought period

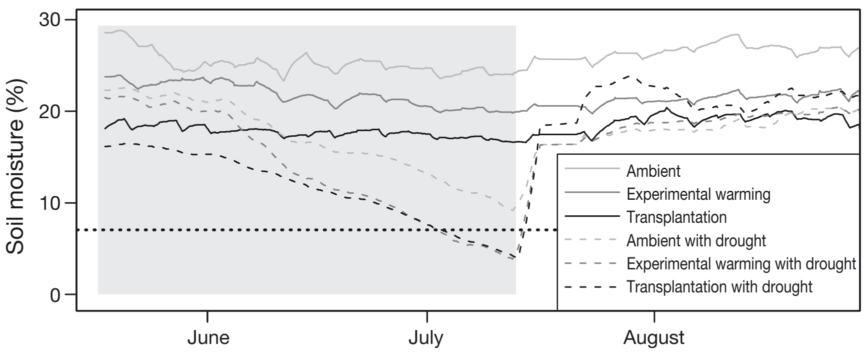

Fig. 2. Soil moisture at a depth of 5 cm for the different warming treatments over the course of the experiment in 2010. The grey area represents the drought period. The permanent wilting point (pF = 4.2) is indicated by the dotted black line

perimental site in Bayreuth reached the stopping criterion (20% of the plants showed strong drought damage; 76 to 100% of the leaves damaged) one day earlier than at the transplantation site in Siebeldingen. After the drought the plants received additional water (600 ml per pot) on 16, 19, and 23 July 2010.

2.4. Response variable

We used height increment (height measured in October minus height measured in April/May) as our response variable.

2.5. Statistical analyses

Analysis of variance (ANOVA) combined with linear mixed effect models was applied to test for main effects and interactions of the treatments 'warming technique' (levels: 'ambient', 'experimental warming', and 'warming by transplantation') and drought (levels: yes or no) on height increment. The provenance identities were included as a random factor in the mixed models, as no significant interactions of this factor with 'warming technique' were present in a pre-analysis. Data on height increment were square root transformed to improve the normality of residuals and the homogeneity of variances prior to analysis (Faraway 2006). In case of significant main effects of the linear mixed effect model, pairwise post-hoc comparisons (Tukey's test) were performed according to Hothorn et al. (2008).

The air temperature sum was calculated as the sum of daily mean temperatures from 12 April to 8 October 2010. All daily mean temperatures were above a 5°C threshold value for all treatments (ambient, ambient with drought, experimental warming, experimental warming with drought, and transplantation) at both experimental sites. Using growing degree days with the commonly applied threshold would therefore have no impact on the results. The respective air temperature sums are pro-

Table 1. Mean air temperature (C°) and air temperature sum of both warming techniques and ambient conditions during the period from the start of the experiment to the final height measurements for height increment (April to October 2010)

Mean air temperature (C°)			Air temperature sum				
Transplantation	Experimental warming	Ambient	Transplantation	Experimental warming	Ambient	Ambient in combination with drought	Experimental warming in combination with drought
19.3	18.0	16.1	3387	3158	2830	2874	3123

vided in Table 1. Warming by transplanting to a different site does not allow for a pre-defined amount of warming as weather conditions often vary from the long-term mean conditions at the given site. In order to enable a direct comparison between the 2 warming techniques, we therefore needed to acknowledge the slight differences between realized warming in both techniques. This was done by assuming the most simple, i.e. a linear, response to warming and checking if this assumption is met by the data. For a parameter A the linear construction yields

$$A(T) = \frac{A_{\exp} - A_{amb}}{T_{\exp} - T_{amb}} \times (T - T_{amb}) + A_{amb}$$

where A_{amb} and A_{exp} are the parameter means for the cases 'ambient' and 'experimental warming'. T_{amb} and T_{exp} are the corresponding temperature sums. The assumption of linearity is tested by comparing the predicted parameter mean for the 'transplantation' temperature sum A (T_{trans}) with the experimentally determined mean for this site.

All statistical analyses were conducted with the statistical software R v. 2.11.1 (R Development Core Team 2010) including the packages 'nlme' (Pinheiro et al. 2012) and 'multcomp' (Hothorn et al. 2008).

3. RESULTS

3.1. Warming technique

Regarding height increments of all *Fagus sylvatica* plants, there was a significant difference between the 2 warming techniques (Table 2; post-hoc test: p = 0.0016). Furthermore, a difference between the observed temperature effect and the one based on expected linear extrapolation was observed for 'warming by transplantation' (see arrow in Fig. 3A).

3.2. Warming technique in combination with drought

When additionally subjected to drought, 'experimental warming' was significantly different from 'warming by transplantation' and from 'ambient' (Table 2; Fig. 3B), resulting in 56% relative growth difference between warming techniques. Plants warmed by transplantation only showed a height increment average of 36%, whereby the plants of the 'experimental warming' had a height increment average of 92%. When subjected to drought there was no significant difference between the plants of the 'warming by transplantation' and the plants under 'ambient' conditions

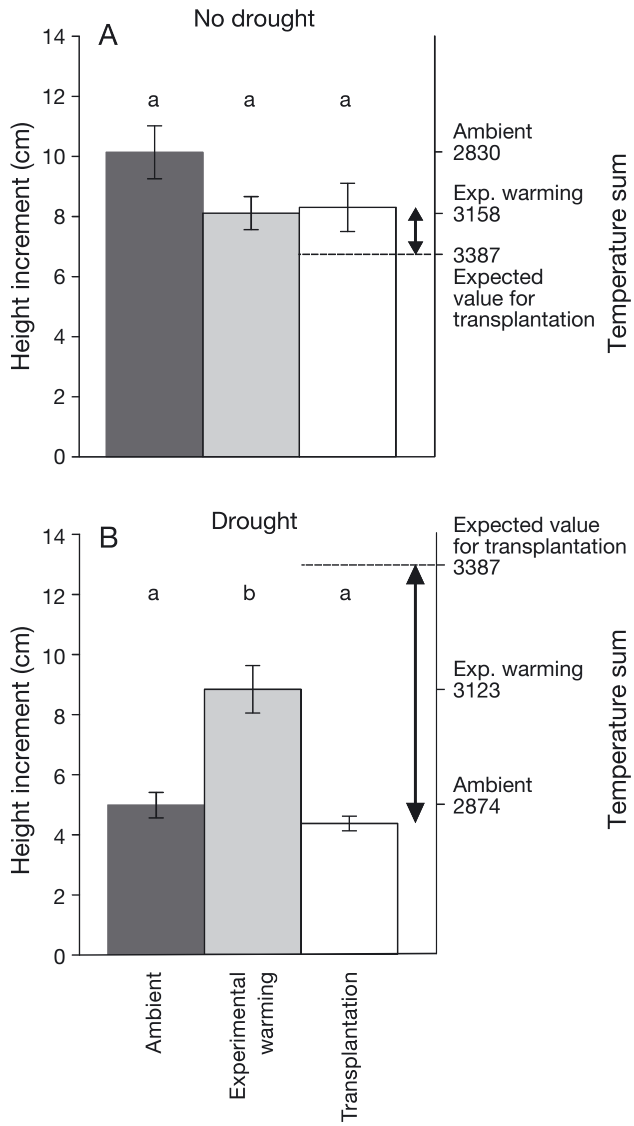

Fig. 3. Height increment of the *Fagus sylvatica* seedlings in response to the different warming techniques without drought (A) and under drought (B) (mean ± SE). The respective temperature sum is indicated on the right hand side. The temperature sums for 'ambient' and 'experimental warming' are positioned at the respective height of the corresponding bar. Relative to these 2 points, the expected value for 'warming by transplantation' is shown, together with the dashed horizontal line, at the position where the response effect size would be expected based on the linear extrapolation. The vertical arrow indicates the difference between the expected and actually realized response for the case of 'warming by transplantation'. Lower case letters represent significant differences as revealed by the post-hoc test of the interaction warming technique:drought

(Fig. 3B). The 'experimental warming' in combination with drought had no negative effect on height increment, contrary to the transplanted and ambient plants subjected to drought, which showed a decrease in height increment by 32% ('warming by transplanta-

Table 2. *Fagus sylvatica.* ANOVA results for the effects of warming technique and drought (experimental warming, warming by transplantation, ambient, experimental warming with drought, warming by transplantation with drought, and ambient with drought) on height increment. All values are significant ($p < 0.05$)

Factor	*F*	p
Warming technique	6.4	0.0019
Drought	31.0	<0.0001
Interaction warming technique:drought	11.2	<0.0001

tion') and 50% ('ambient'), respectively. Again, the observed temperature effect in the 'warming by transplantation' differed more strongly in height increment than expected (see arrow in Fig. 3B).

4. DISCUSSION

4.1. Influence of warming technique

Plant performance (i.e. height growth) of juvenile beech trees differed among warming techniques, i.e. 'experimental warming' (mainly passive warming with marginal effectiveness of IR radiation) and 'warming by transplantation' (across several hundred kilometers). This finding contradicts our first hypothesis: experimental warming and warming of similar magnitude by transplantation would lead to the same increase in height increment. In particular, we compared the plant response of the transplantation technique to an expected response for the achieved warming based on a linear extrapolation in the temperature sum between the 'experimental warming' and 'ambient' conditions. This was done because the 2 warming techniques yielded different mean air temperatures due to unpredictable weather conditions at both sites. The linear extrapolation was done to take this into account and to test whether the temperature difference had explanatory power in this experiment. The transplanted plants experienced a temperature that was, on average, 1.3°C higher than under the 'experimental warming' conditions over the period the growth took place (Fig. 1; Table 1). Nevertheless, no linear dependence on the magnitude of warming could be found (Fig. 3). In summary, the respective effect sizes of both warming techniques for height increment could not be explained by the difference in temperature sum between the 2 warming treatments. Warming reduced height growth in our experiment, which can be explained by the reduced soil moisture in the warmed pots—leading to a generally mild yet chronic drought stress in comparison to ambient conditions (McLaughlin & Downing 1995).

The lack of linear dependence of plant growth on temperature sum suggests further complexity. Factors such as the vapor pressure gradient (VPG) from inside the leaves to the air outside (Kimball 2005), the duration, intensity, and spectral distribution of the radiation, the water potential in the soil, the content of atmospheric CO_2 as well as gravity and pressure effects (wind, flow of water, pressure of snow) may have impacts on plant performance (Larcher 2003). A different VPG in the case of infrared heating leads to an increased water loss (Kimball 2005). As testing the VPG was not at our disposal, we compared the soil moisture content of the different sites and treatments. Only under the control treatment was soil moisture higher in the 'experimental warming' pots compared to the pots of the transplanted plants without the drought treatment. Under drought conditions, both techniques showed a similar decline in soil moisture (Fig. 2). This suggests that the evapotranspiration was similar in the pots of the 'experimental warming' plants. Thus, evapotranspiration might have played a secondary role associated with the difference between warming techniques in our study.

Another potentially important climatic parameter is solar radiation. The fraction of photosynthetically active radiation (PAR) within the solar radiation depends on time and location (Amthor 2010) and might be one reason for the differences between warming techniques. In this study, the curves of the solar radiation (short-wavelength radiation of the global radiation; daily sums) were close together at both sites (see Fig. A1 in the Appendix). The average of the daily sums of the solar radiation was 4324 W m^{-2} at the 'experimental warming' site and 4869 W m^{-2} at the 'warming by transplantation' site during the time span of the experiment (April to October 2010). The resulting difference of about 12% in solar radiation could contribute to the difference between both warming techniques.

Another possible explanation for the difference between the warming techniques could be the 70% reduction of wind speed due to passive warming. This is, however, an unavoidable side effect of passive warming and can thus be taken as a further argument against these techniques. Future studies will show to what extent the above-mentioned parameters (evapotranspiration, photosynthetically active radiation, and wind speed) may be responsible for the observed differences in warming techniques.

In addition, other factors of importance, such as species-specific effects, are improbable explanations, as we used *Fagus sylvatica* from 7 different provenances, and thus covered a broad spectrum of intraspecific variability. Furthermore, the interaction of warming technique and provenance was not significant (F = 1.4; p = 0.162). Overall, our results strengthen the argument that an interpretation of global warming experiments should be made very carefully in relation to climate change predictions.

4.2. Influence of warming technique interacting with drought

'Experimental warming' and 'warming by transplantation' had different effects on plant performance when superimposed by drought (Fig. 3B). In our study, the plants in the 'experimental warming' revealed high resilience, showing no decrease in height increment, whereas the plants grown under ambient conditions and those transplanted had a growth reduction under drought. An explanation for the growth stimulation after drought in the 'experimental warming' could be a compensatory growth after the re-watering phase at the end of the drought. Spieß et al. (2012) carried out a long-term drought during 2 growing seasons and detected a strong compensation growth in *Quercus robur* L. (pedunculate oak) after re-watering. However, in our experiment only the plants subjected to 'experimental warming' under drought showed an increase in growth. The plants of 'ambient' (drought exposed plants without the warming treatment) and the transplanted plants did not respond in the same way. Hence, further research is needed to understand the complex response of plants under drought and heat stress. Nevertheless, our results strengthen the conclusions from several multi-factor experiments (Shaw et al. 2002, De Boeck et al. 2011, Larsen et al. 2011, Kreyling et al. 2012b), i.e. that different climatic drivers are not additive. The significant interaction of warming and drought in our study, which implies non-additivity of both factors, further depended on the warming technique, a factor which complicates the comparability of different warming techniques.

5. CONCLUSIONS

In climate change experiments, the selected warming technique, i.e. experimental warming (mainly passive warming with marginal effectiveness of IR-radiation) versus warming by transplantation influences plant performance differently. Thus, prediction of global warming effects on plant performance is highly influenced by the choice of technique. These differences among warming techniques were further exacerbated when warming was combined with manipulation of another climate parameter, here an extreme drought event. The findings of this study suggest that experimental warming should include the control or consideration of further parameters such as evapotranspiration, photosynthetically active radiation, and wind speed, aside from temperature, in order to provide a deeper insight.

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Appendix

Table A1. *Fagus sylvatica.* Geographic origin of the 7 provenances used in the experiment

Provenance	Country	Latitude (N)	Longitude (E)
Gotze Delchev	Bulgaria	41°38′08″	23°35′08″
Petrochan	Bulgaria	43°15′18″	23°14′20″
Strumjani	Bulgaria	41°40′55″	23°00′42″
Kisbárapáti	Hungary	46°35′19″	17°51′12″
Hengstberg	Germany	50°08′00″	12°11′00″
Elchingen	Germany	48°27′21″	10°03′48″
Weildorf	Germany	47°50′45″	12°52′56″

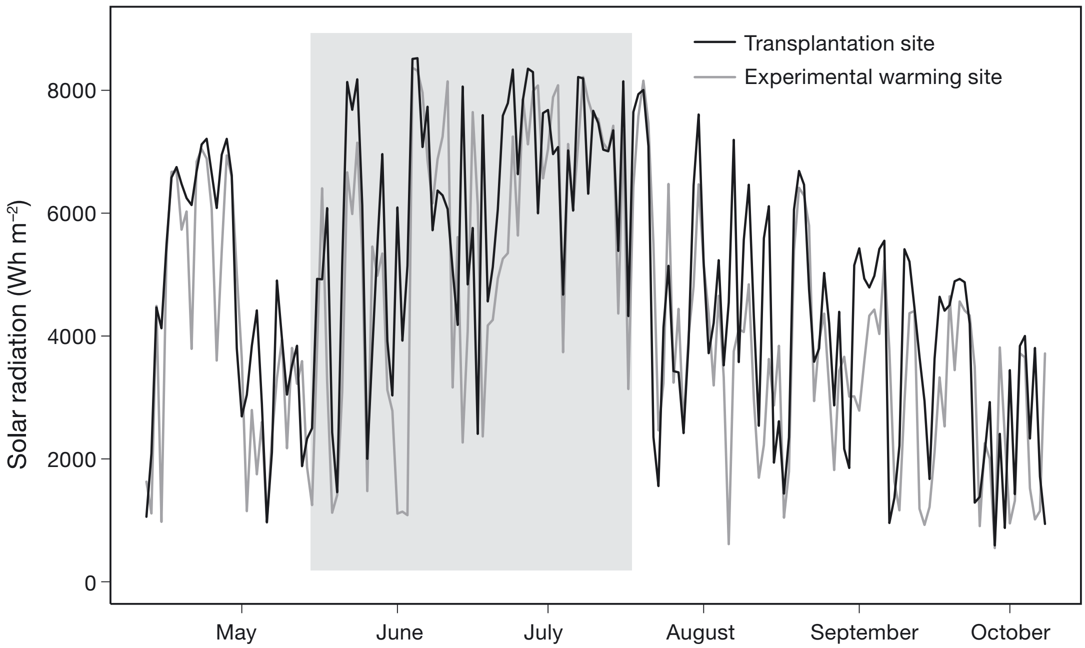

Fig. A1. Solar radiation (short-wavelength radiation of the global radiation; daily sums) at the different sites over the course of the experiment in 2010. The grey area represents the drought period

Editorial responsibility: Nils Chr. Stenseth, Oslo, Norway

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