LETTER

Climate warming will reduce growth and survival of Scots pine except in the far north

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Abstract

Tree growth and survival were assessed in 283 populations of Scots pine (*Pinus sylvestris* L.) originating from a broad geographic range and grown at 90 common-garden experimental sites across Europe, and in 101 populations grown at 14 sites in North America. Growth and survival were analysed in response to climatic transfer distance, the difference in mean annual temperature (MAT) between the site and the population origin. Differences among populations at each site, and across sites for regional groups of populations, were related to climate transfer distance, but in opposite ways in the northern vs. southern parts of the species range. Climate transfers equivalent to warming by 1–4 °C markedly increased the survival of populations in northern Europe (≥ 62°N, < 2 °C MAT) and modestly increased height growth ≥ 57°N but decreased survival at < 62°N and modestly decreased height growth at < 54°N latitude in Europe. Thus, even modest climate warming will likely influence Scots pine survival and growth, but in distinct ways in different parts of the species range.

Keywords

Climate-change impacts, genetic variation, global warming, growth, intraspecific differentiation, *Pinus sylvestris*, population adaptation, provenance, survival.

INTRODUCTION

Given that current climate projections are for warming by 1.4–5.8 °C globally and 2.0–6.3 °C in Europe by 2100 (EEA 2004; IPCC 2007), climate change impacts on growth and survival of temperate and boreal trees are likely in the coming century (Matala *et al.* 2006; Scholze *et al.* 2006). It is generally thought that warming will enhance growth of trees in cold regions, unless temperature-induced drought stress becomes disproportionately important in controlling growth (Barber *et al.* 2000; Rehfeldt *et al.* 2004; Wilmking *et al.* 2004). However, accurately predicting such effects represents a critical research gap (Persson & Beuker 1997; Davis & Shaw 2001; Rehfeldt *et al.* 2002; Stromgren & Linder 2002; EEA 2004; Davis *et al.* 2005; Matala *et al.* 2006; Scholze *et al.* 2006).

Evidence regarding tree responses to climate warming has come from analyses of tree-rings (Briffa *et al.* 1998; Vaganov *et al.* 1999; Wilmking *et al.* 2004; Driscoll *et al.* 2005), direct soil or air warming experiments (Peltola *et al.* 2002; Stromgren & Linder 2002; Kilpeläinen *et al.* 2004) or from forestry experiments in which individuals of given populations were planted and studied across climate gradients,

using multiple common garden experiments (Hanninen 1996; Persson & Beuker 1997; Rehfeldt *et al.* 1999b, 2002; Salminen & Jalkanen 2005). Collectively, evidence from these studies suggests that temperate and boreal trees may grow faster with modest warming (Davis & Shaw 2001; Peltola *et al.* 2002; Rehfeldt *et al.* 2002, 2004; Stromgren & Linder 2002; Kilpeläinen *et al.* 2004; Norby & Luo 2004), although evidence to the contrary has also been reported (Rehfeldt *et al.* 2004; Wilmking *et al.* 2004).

It is not yet clear whether the different approaches used or the different geographic and bioclimatic contexts can explain the divergent results. Regardless, some of these results are difficult to extrapolate over the mid- to long-term or across a broad geographic range. For instance, manipulative experiments have been short term (often 1–3 years, always < 7 years) and typically involve only soil warming (Jarvis & Linder 2000; Melillo *et al.* 2002; Stromgren & Linder 2002; Norby & Luo 2004) or growth chamber grown seedlings (Oleksyn *et al.* 1998; Olszyk *et al.* 1998) or, rarely, treatment of individually enclosed trees (Peltola *et al.* 2002; Kilpeläinen *et al.* 2004; Volanen *et al.* 2006). Moreover, there are too few warming experiments to assess whether trees in colder and warmer ends of a species range will respond

differently. Common garden climate gradient experiments, in contrast, do typically employ multiple sites, but have other limitations.

Climate gradient experiments typically consist of individuals of populations from different locations planted in numerous common sites, and have been used to assess possible effects of climate change (Matyas & Yeatman 1992; Persson & Beuker 1997; Rehfeldt et al. 1999a,b, 2002) based on the assumption that conditions at sites with milder climate resemble those expected after climatic warming. However, it is difficult to distinguish between photoperiodic and climate effects associated with latitudinal shifts in climate-gradient experiments; this issue has been largely (Matyas & Yeatman 1992; Rehfeldt et al. 1999a,b, 2002; Wang et al. 2006) but not always ignored (Persson & Beuker 1997).

A modelling study suggested that 90% of Scots pine populations inhabit sites at less than their thermal optima (Rehfeldt et al. 2002), but that work did not attempt to separate photoperiodic from climate effects (Oleksyn et al. 1998), and included European populations from high latitudes grown at much lower latitudes in North America. To begin to separate temperature and latitudinal effects would require a broad range of both temperatures and geography of planting sites and populations for the common-garden experiments, but most prior studies using forestry gradient experiments do not have enough planting sites to satisfy such requirements. For example, one prior paper did attempt to separate temperature from photoperiodic effects (Persson & Beuker 1997). However, that study used 34 populations and 26 sites, all within Sweden, providing a relatively biogeographically limited survey.

In contrast to the growing number of reports relevant to tree growth in response to climate change, evidence relevant to potential climate effects on tree survival is relatively scarce (Rehfeldt et al. 1999a). To extend the scope of studies of tree growth cited above and to additionally address responses of survival to potential climate warming, we compiled a comprehensive data set based on more than 20 000 trees that includes 283 wide-ranging populations of the dominant Eurasian tree, Scots pine (Pinus sylvestris L.) grown at 90 sites distributed across much of Europe (Fig. 1). In this report we use that large, long-term climate gradient data set, spanning multiple sites ranging from 46 to 68°N latitude, to assess the potential response to climate change of Scots pine. We also compare those results to similar data from experiments with 101 European Scots pine populations planted at 14 sites in North America. With these large data sets, we were able to assess the response of trees from different latitudinal zones and, to an extent, limit potential confounding with photoperiod effects. Herein, this research demonstrates that modest warming will likely enhance growth and survival of Scots pine in northern Europe (> 62°N), but reduce its growth and survival at lower latitudes.

METHODS

Pinus sylvestris data were taken from seven series of European (established by the IUFRO in 1907, 1938 and 1982, by the State Forestry Committee of the Former USSR, and several Swedish series) and two series of North American common-garden experiments. Information on sites included in the study and on literature sources is presented in Table S1, and their location in relation to the Scots pine range in Europe is shown in Fig. 1. More detailed facts on seed collection, plantation establishment and measurements can be found in the publications listed in Table S1.

Figure 1 Location of experimental common-garden provenance sites. Sites are coded by the seven different experimental series shown in the lower right. Darker colour denotes range of Scots pine. Different symbols denote distinct major provenance experiments. Base map: http://www.ipgri.cgiar.org/Networks/euforgen/Distribution_Maps/Maps/Pinus%20sylvestris%20big.jpg.
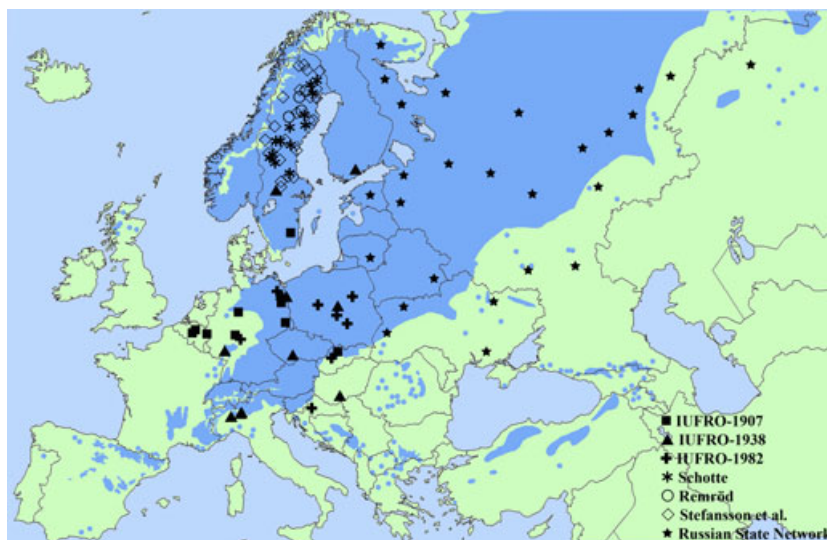
For European sites, the data set was limited to sites for which sufficient climatic data were available, and for sites where a local population (or a population from a similar climatic region) was among those planted. We used the Worldclim data base (Hijmans *et al.* 2005) as a source of climatic data for sites and populations. Given a lack of reliable high-elevation climatic data, the data set was limited to lowland populations from locations < 400-m a.s.l. for locations ≥ 65°N and to ≤ 1000-m a.s.l. for all remaining populations. For Europe, the data set includes 90 sites, ranging in latitude (46–68°N), longitude (4–70°E), mean annual temperature (MAT; –1.7 to 12.2 °C) and mean annual precipitation (MAP; 323–1160 mm year^{-1}), and 283 populations; the data set contains 1950 site × genotype contrasts. The population origins ranged in latitude (41 to 70°N), longitude (5°W to 138°E) and origin MAT (–10.1 to 12.7 °C). Hereafter for brevity, we refer to the latitude (or MAT) of experimental sites and of the home site (origin) of each population as 'site latitude (or MAT)' and 'population latitude (or MAT)', respectively. For every population at every site, a mean transfer distance in MAT units (ΔMAT) was calculated by subtracting the population MAT from the site MAT. The average age (at time of measurements) for all sites was 18.1 ± 1.3 (SE) years; annual height increment was used as the growth metric.

We also compare European data with data from North America that includes 14 sites, ranging in latitude (43 to 50°N), longitude (65 to 78°W), MAT (–0.8 to 7.7 °C) and MAP (323 to 1160 mm year^{-1}), and includes a total of 101 European populations that range in climate origin MAT from −3.2 to 10.8 °C; this North American data set contains 447 site × genotype contrasts.

As several climate factors are known to be generally important for tree growth and survival, including the means and variability of temperature and precipitation, we examined the relations of several of these to each other and to the observed Scots pine growth and survival data. These climate variables were MAT, MAP, the highest and lowest mean monthly and quarterly temperature and precipitation, respectively, and the ranges between the highest and lowest mean monthly temperatures and precipitation. Among the 90 European sites, the seasonal and range values were significantly correlated with the mean values. Therefore, the coldest and warmest monthly or quarterly temperature and MAT contain similar information content, as do MAP and the wettest and driest months or quarters. MAT, MAP and the temperature range (T_{range}) overlap least. Survival of local populations was not significantly related to any climate metric. Absolute height and mean annual height increment of local populations were much better correlated with MAT than with either MAP or T_{range}, and were generally similarly or better correlated with MAT than with the covarying seasonal temperature metrics; hence the remainder of the

analyses focussed on MAT. This approach is further supported by multiple regression analyses. In models of height growth vs. various climate metrics (with population origin of latitude as a covariate), MAT and MAT transfer explained more of the overall variance than all other climate metrics, and inclusion of additional climate metrics such as MAP or MAP transfer explained only a very small additional amount of the variance.

Several types of analyses were performed. First, as described above, data for all populations and sites were used in the correlation and multiple regression analyses that determined that MAT explained the greatest variation in tree response and would be the focus of further analyses. Second, multiple regression was used to assess whether there were significant interactions between site latitude or population latitude and mean climate transfer distance (ΔMAT), which would indicate different responses in different regions of the species range. Given that these analyses showed significant interactions (see below), two different means of exploring these were used that, respectively, focus on (i) responses across populations within individual sites – representing a geographic gradient in population origin and called a 'transfer function' (cf. Rehfeldt *et al.* 1999a) and (ii) responses for groups of populations assessed across sites – called a 'response function' (cf. Rehfeldt *et al.* 1999a).

Comparing populations planted in a given site is relatively straightforward, as common site and cultural conditions (e.g. all populations planted at the same time, with same spacing, similar cultural practices, in the same soil and under identical climate regimes) allow the phenotypic responses of each genotype to be expressed in a common environment. Having multiple common gardens (as in this study) can help to alleviate problems with common-garden studies where some genotypes have been moved further than others from their home locations. In this data base, there are an average of ≈20 populations with height or survival data included in each common-garden experiment and, for many sites except in the extreme south or north, these include populations from both colder and warmer regions than the experimental site. Our analytical approach was as follows.

First, the relationships of growth increment and survival with mean transfer distance (in MAT units) were assessed for every site with appropriate data ($n = 78$ for height, $n = 55$ for survival). One outlier was removed from 10 of the 133 data sets. There were 80 significant linear relations of the 133 tests; 11 were better fit nonlinearly (including eight of those that were significant linearly). Although growth at sites markedly warmer or colder than their home site often results in poor performance (and hence a nonlinear relation to ΔMAT), tree populations often have a very broad 'fundamental niche' (Rehfeldt *et al.* 1999a) and are often not grown very far from home – thus both transfer

and response functions often have uni-directional responses across a large climate space (Rehfeldt *et al.* 1999a). This was largely the case for the Scots pine data in this study. Additionally, sites with the largest range in ΔMAT, both in positive and negative directions, showed little evidence of greater nonlinearity than the remaining sites. Hence, we assume that the observed slopes are representative surrogates for responses to ΔMAT in the vicinity of 0 °C ΔMAT; i.e. the relevant range for modest temperature change. Second, the slopes of all significant linear relations were expressed in relation to the mean value of growth or survival of all populations at that site, resulting in a measure of percent change in growth or survival per degree change in MAT. These percentage change values were nearly identical to those derived when the slopes were related to the values of growth and survival at 0° ΔMAT (i.e. the intercept). Using data from all sites with significant ($P < 0.1$) linear relations, the percent change in growth and survival was related to the MAT and latitude of the site (see Figures 3 and 4). Restricting this regression to those sites that included populations with both positive and negative MAT ($n = 32$ for height) did not change the fit nor the relationship (data not shown).

Developing response functions for individual populations across sites is more problematic with these data. Heterogeneity among sites (due to differences in soils, planting practices, diseases, extreme storm events and other possibilities) decreases the 'signal' to 'noise' ratio (if the 'signal' is for MAT shift and 'noise' includes variance due to factors unrelated to MAT). Given this, one would expect that a relatively large number of sites would likely be required to adequately characterize the response of a single population to an inferred gradient, such as in ΔMAT, across multiple sites. The European data base includes a large number of populations (283), but each was replicated on average across a small number of sites (mean of ≈ 6 for both height growth and survival). Although there were 26 populations with height increment data from > 10 sites, very few populations from the southern half of the species range were grown at more than 1–2 sites with MAT greater than their origin MAT, and very few populations from the northern part of the range were grown at more than 1–2 sites with MAT less than their origin MAT. Hence, population-specific relationships cannot be used to assess how individual southern populations respond to warming (and as a result, to assess whether southern populations respond differently to warming than northern populations).

Instead, responses of populations were assessed by pooling populations and sites across latitudinal bands (i.e. populations and experiments serve as replicates), and data were binned into classes in Δ 0.5 °C increments for analyses. This approach was used to increase replication and provide a sufficient range of ΔMAT, and has additional advantages of averaging out site heterogeneity that is unrelated to the questions of interest and limiting covariance of MAT and latitude. Such groupings averaging across many populations minimize potential bias related to possible differences in the genetic quality of any particular population, as well as to differences in measurement ages and growth conditions among sites.

In dividing populations and sites into these latitudinal bands, an attempt was made to balance the latitudinal range of each band and the number of experimental sites within each, as well as to match disjunctions in the distribution of sites and shifts in the response of growth and survival to MAT transfer among populations within sites (Fig. 3). Thus we assessed responses of northern populations (71 from ≥ 61.5°N) to ΔMAT differences among northern sites (37 from ≥ 61.5°N), central populations (72 from 57–61°N) to ΔMAT differences among central sites (17 from 56.5–61.5°N) and southern populations (49 from 50–53°) to ΔMAT differences among southern zone sites (24 from 50–53°N). Largely due to the location of the Baltic Sea, there were few experimental sites at 54–56°N. Similarly, the extreme southern part of the range (45–49°N) contains disjunct populations and few experimental sites (Fig. 1). As a result of the lack of sites and populations at these latitudes, there is a gap between the southern and central bands that were used. The mean (and SE) MAT and MAP of the sites for these three groups suggest that they are strongly contrasting in temperature (MAT, °C mean (SE) = 0.7 (0.2), 3.9 (0.3), 7.5 (0.4) for northern, central and southern site groups), but not precipitation (MAP, mm year^{-1} = 575 (12), 638 (11), 626 (33), respectively. The height and survival data for these groups were related to ΔMAT (between −6 and 6 °C ΔMAT) using simple linear or second-order polynomial regression. The data were restricted to cases where there were data for at least two populations in a given °C class (average sample size for those included ≈11); two outliers (with samples sizes of 2 and 3, respectively) were removed before analysis.

The grouping of populations and sites into northern, central and southern zones reduced the covariance in MAT and latitude differences among sites, and among site by population origin combinations, compared with those that exist for the entire data set. For all sites pooled ($n = 90$), covariation of MAT and latitude (assessed as the correlation coefficient of the among-site regression of MAT and latitude) was 0.84, whereas site-to-site covariation of MAT and latitude was 0.67, < 0.01 and 0.14 for northern, central and southern zones, respectively. For all site x population origin contrasts ($n = 1950$), the covariation between ΔMAT and Δlatitude was 0.48, while this was 0.24, 0.33 and 0.48 for northern, central and southern zones considered separately, respectively. Furthermore, longitude of the experimental site explained very little of the MAT shift (between origin and

experimental site) of populations across or in the three zones, indicating that the MAT variation among sites within geographic zones is largely unrelated to continentality. Contrasts of responses to climate transfer in Europe vs. North America (see Results) were made to provide a more direct test of potential temperature vs. photoperiodic effects.

All analyses were made using JMP 7.0 (SAS Institute, Cary, NC, USA). For presentation, linear and nonlinear regression was used but we do not assume that direct casual relations are involved.

RESULTS

The importance of temperature for Scots pine growth is shown by comparing local populations growing across the ≈25° latitudinal gradient (and an associated 14 °C MAT gradient), representing the north–south range of the study sites in Europe (Fig. 2). Growth varies by almost 40-fold, with far northern trees growing slower than trees located in warmer southern climate zones. In contrast, local populations are similarly adapted for survival to local conditions, as no geographic or MAT-related pattern of survival was detected (Fig. 2). Differences in growth along existing climate gradients reflect both the relative suitability and optimality of the growth environment and ecotypic adaptations made by populations growing along the entire climate gradient, both of which contribute to the enormous growth differences (Matyas & Yeatman 1992; Loehle 1998; Rehfeldt *et al.* 2003).

Given our objective of testing whether response to warming differs geographically, multiple regression analysis was used to test whether the response to temperature transfer differed with latitude (of site and of population origin). Results indicate that interactions occur, i.e. response to a similar climate transfer was different in colder northern areas and populations than in warmer southern ones. In a multiple regression model with height increment as the dependent variable, and site latitude, population latitude and ΔMAT (and all interactions) as the independent variables, there were significant interactions ($P < 0.0001$) between site latitude and ΔMAT, and between population latitude and ΔMAT (data not shown). When the same model was run with survival as the dependent variable, the interactions were again significant ($P < 0.0001$ for site latitude × MAT; $P = 0.05$ for population latitude × MAT). These interactions indicate that the response to ΔMAT is different in northern sites and populations than in southern sites and populations. The interactions were similarly significant using the MAT of sites and populations instead of their latitudes as independent variables, but these latter analyses are problematic because of extreme collinearity between site MAT, population MAT and delta MAT.
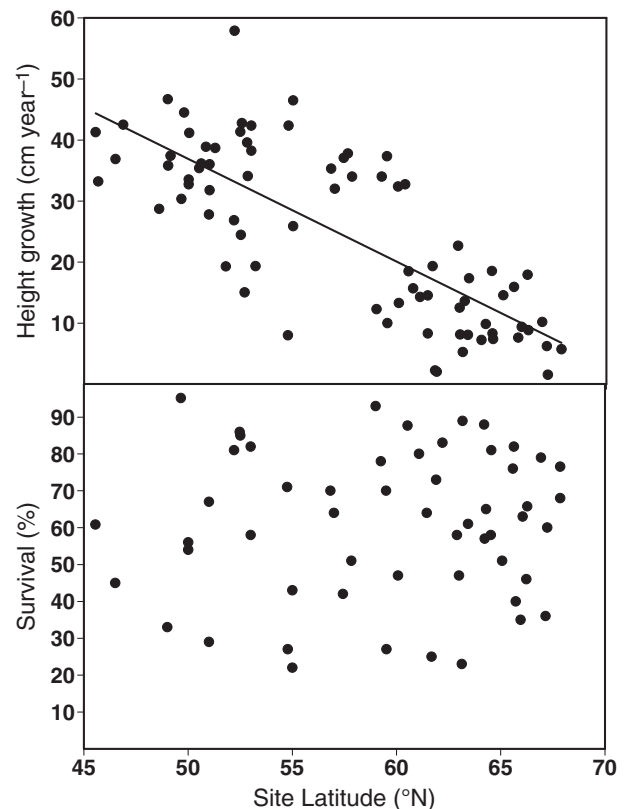

Figure 2 Height growth and survival in relation to site latitude (°N). Height growth increment (cm year^{-1}) and survival (%) of local populations (population that originated closest to each site, on an average within 0.5° latitude and 0.9° longitude) in relation to site latitude (°N) ($R^2 = 0.83$, $P < 0.0001$ for height growth and $R^2 = 0.02$, $P = 0.64$ for survival). Trees were 18 years old on an average at time of measurements. Latitude is inversely related with MAT, but not precisely (data not shown).

To further explore the nature of the differing response of northern and southern populations at northern and southern sites, the response of height and survival to ΔMAT was examined at every individual European site ($n = 78$ for height, $n = 55$ for survival). Each analysis was therefore a cross-population contrast that compared responses of populations (from various locations) to transfer (i.e. ΔMAT) to that particular common garden.

At 49 sites, there were significant linear relationships between height increment and ΔMAT. For these sites, the proportional change in height increment per unit ΔMAT was significantly related ($P < 0.0001$) to the site MAT ($R^2 = 0.50$, Fig. 3) or the site latitude (data not shown). At all sites at with MAT > 4.0 °C or latitudes < 62°N, height growth decreased as ΔMAT increased (i.e. populations transferred from warmer locations grew fastest). At sites with MAT < 4.0 °C, increasing ΔMAT of transferred
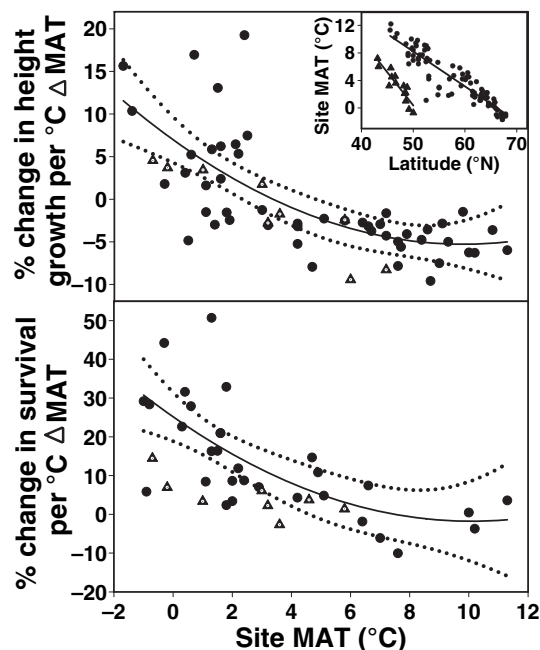
Figure 3 The relationship of height growth and survival transfer functions across the mean annual temperature (MAT) gradient of the experimental sites. For each site, the datum represents the percent change in height growth or survival per 1 °C change in ΔMAT. See Methods for details. The relationship of those transfer function slopes to site MAT was significant (< 0.05) for both height growth ($R^2 = 0.50$ and 0.84) and survival (0.48 and 0.50) of the European (closed circles) and North American (open triangles) data sets, respectively. Simple polynomial regressions (and associated 95% confidence intervals of the lines) of the European data are shown. Inset in upper panel is the relation of site MAT to latitude among sites for each of the continents.

populations was related to greater height growth, and the further north the more positive the response. Thus at these locations, populations transferred from colder locations grew fastest.

At 31 sites, there were significant linear relationships between survival and ΔMAT. For these sites, the proportional change in survival per unit ΔMAT was significantly related to site MAT ($P < 0.0001$, $R^2 = 0.48$, Fig. 3). At the warmer, more southerly sites, survival was only modestly related to ΔMAT, whereas at colder, higher latitude sites survival was positively related with ΔMAT. Hence, at these northern sites, populations transferred from colder locations survived best.

Site-specific height increment responses to ΔMAT were generally similar for Scots pine transplanted to North America as for those tested in Europe (Fig. 3). At sites with MAT < 3–4 °C MAT, populations moved from colder sites grew fastest, whereas at sites warmer than 3–4 °C MAT, populations moved from warmer sites

grew fastest. The responses to ΔMAT varied with site MAT in a similar way in North America as in Europe, as the North American data fit within the same general response surface described by the relationship for the more numerous European sites (Fig. 3). Similarly, the transfer function for survival was most positive at colder sites in both North America and Europe (Fig. 3), although the data from North America occupied the lower bound of the response surface established by the European data. The generally similar relationship of the growth and survival transfer functions to ΔMAT across site MAT gradients on the two continents suggests similar response to ΔMAT despite different photoperiods, which can be visualized by comparing the differing relations of site MAT with latitude on the two continents (inset, Fig. 3).

As it was not possible to adequately assess responses of individual populations in relation to ΔMAT (i.e. a strictly cross-site response function analysis), sites and populations (by origin) were grouped into three latitudinal bands (see Methods). We assessed responses of northern populations (> 62°N) to ΔMAT among northern experimental sites (> 62°N) only, responses of central populations (57–61°N) to ΔMAT among central zone experiments (57–61°N) only and responses of southern populations (50–53°N) to ΔMAT among central zone experiments (50–53°N) only. These analyses therefore represent combined cross-site and cross-population contrasts. Additionally, by analysing responses for populations grouped by climate zones and tested within those climate zones, temperature effects were partially decoupled from photoperiod effects, because dividing sites (and populations) into northern, central and southern zones resulted in modest within-zone covariation in latitude and MAT (see Methods).

Populations in diverse parts of the species range responded differently to ΔMAT (Fig. 4). Survival and height growth of northern populations at northern sites (> 62°N) were both positively related to ΔMAT, with the growth responses flattening out with very modest warming. In contrast, survival and height growth of southern populations at southern sites (50–53°N) were both negatively related to ΔMAT, especially at ΔMAT > 0 °C. (Fig. 4). Responses of central populations at central sites were intermediate.

DISCUSSION

The results from multiple experiments in Europe with many wide-ranging populations of Scots pine are useful for examining several questions: (i) are local populations the best performers? (ii) could populations hypothetically be moved to better match current or future climate? (iii) how will performance at a given climate regime (herein a given MAT) change as that MAT 'migrates' north? and (iv) what
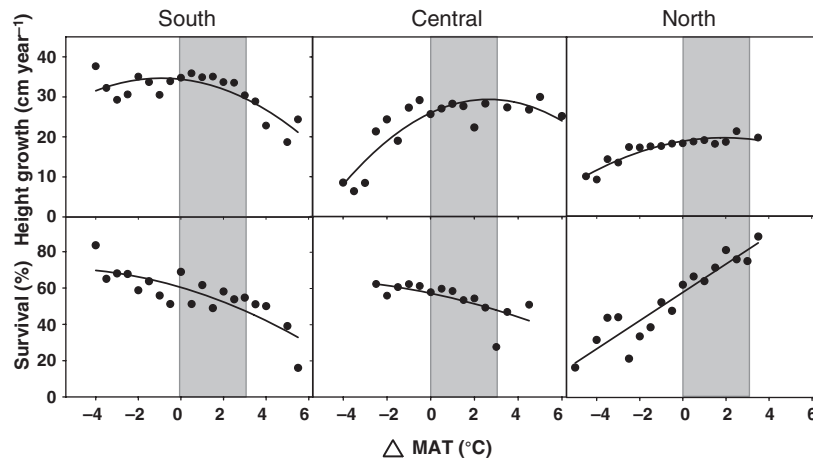
Figure 4 Mean height growth increment and survival vs. climate transfer by geographic zones. Mean height growth increment (cm year^{-1}) and survival (%) of Scots pine populations (at 18 years age on an average) in relation to differences between experimental site and seed origin mean annual temperatures (ΔMAT), for populations both originated and growing within three latitudinal bands (50–53, 57–61 and ≥ 62°N, with average site origin MAT of 7.0, 3.5 and 1.0 °C, respectively). Linear and second-order polynomial regressions were used. The individual population by ΔMAT responses were grouped by 0.5° ΔMAT increments. The relation of survival to ΔMAT was significant for the ≥ 62°N ($R^2 = 0.87$, $P < 0.0001$), 57–61°N ($R^2 = 0.46$, $P < 0.03$) and 50–53°N ($R^2 = 0.67$, $P = 0.0001$) groups. The relation of height increment growth to ΔMAT was significant for the ≥ 62°N ($R^2 = 0.87$, $P < 0.0001$), 57–61°N ($R^2 = 0.77$, $P < 0.0001$) and 50–53°N ($R^2 = 0.65$, $P < 0.0001$) groups. Gray shaded areas represent the shift from population site origins to sites warmer by 0–3°C, which is a conservative estimate of the expected climate warming during the coming century.

are likely responses to *in situ* warming? Both the transfer functions from specific sites (Fig. 3) and the regional response functions (Fig. 4) suggest that responses vary in the northern and southern part of the species range, which has implications for all four questions.

At many sites, populations moved from slightly different MAT regimes were the best performers (Fig. 3). Populations moved from warmer locations were the best performers (especially for height growth) in the warm southern part of the range. Conversely, populations transferred from colder locations were the best performers in the cold northern part of the range. With climate warming, 'adaptive transfers' of populations would need to be made at increasingly larger distances in the south and across narrower distances in the north. Note that we do not recommend that the results of this study or of ones with similar results (Rehfeldt *et al.* 1999a) be used to develop such practices, as far as too many other unknown variables could make such practices unwise.

Assuming a northward march of MAT zones, our results suggest that growth performance at a given MAT will deteriorate as that zone moves north in the southern part of Scots pine range, and that growth and survival will initially improve as a given MAT zone moves north in the northern part of the range. This follows from the transfer functions that showed populations moved from a colder site performed better than local ones in the north. It is not clear why this should be the case, as northern populations

are often considered to have limited growth potential compared with ones from much further south (Giertych & Oleksyn 1981; Shutyaev & Giertych 1997). However our study focusses on modest differences in height growth of relative near neighbours. Additionally, it is possible that the poor growth of far northern populations in common garden studies is most notable when they are moved to radically different photoperiods (and climates), which is not the case herein. Finally, it is known that Scots pine populations from colder environments often show higher tissue nitrogen concentrations and higher metabolic rates than populations from warmer environments when grown in common gardens (Reich *et al.* 1996; Oleksyn *et al.* 2003). These kinds of responses are often interpreted as being a result of selection for high potential metabolic rate in order to maintain even a modest achieved metabolic rate under the cold temperatures of northern sites (Reich *et al.* 1996). Although such traits of northern ecotypes could contribute to the responses seen in this study, data are unavailable to test this idea.

The regional response function results (Fig. 4) demonstrate that transfer to a warmer site reduces growth and especially survival in southern populations while increasing growth and survival in northern populations. Examination of relationships with a variety of seasonal and annual climate metrics suggests that temperature is the environmental factor that best explains these responses, with MAT the best measure of temperature for these purposes in this data set.

The differences in response to increasing ΔMAT between the northern (positive) and southern (negative) populations support the likelihood of a temperature-dependent response, as photoperiodic effects are not known to result in divergent responses. Congruence of ΔMAT transfer functions at European and North American sites, despite marked differences in latitude and photoperiod, also supports the idea that growth and survival responses to warming vary largely with the thermal environment of the site. It seems reasonable therefore to interpret these results as suggesting that anticipated climate warming will likely influence Scots pine survival and growth, with responses varying markedly with geography. In the following paragraphs, we discuss whether these results are consistent with theory and prior empirical results, as well as presenting possible mechanisms by which warming might have divergent impacts in southern vs. northern parts of the species range.

Northern hemisphere tree species are expected to move both their southern and northern range margins to the north in a warming world (Iverson & Prasad 1998; Tchebakova et al. 2004; Soja et al. 2007), but poor performance at the southern limit in a warming climate is often considered likely because of heightened competition and not necessarily due to direct adverse effects of warming (Loehle 1998). This may be especially true in mid-latitude regions where cold conditions, including long winters, have been shown to directly constrain carbon uptake and productivity (Goulden et al. 1996). This notion, of southern range limit retreats (to the north) occurring with warming due to heightened competition even in the face of potentially enhanced growth, is consistent with the studies of climate effects on growth from temperature manipulations and tree ring analyses, which also suggest that modest warming will increase growth (Briffa et al. 1998; Peltola et al. 2002; Stromgren & Linder 2002; Kilpeläinen et al. 2004; Norby & Luo 2004). However, our results suggest that even in the absence of interspecific competition, trees in their southern range region may experience modestly reduced growth and markedly reduced survival with modest warming. Hence, shifts in natural communities, and/or dysfunction in managed communities, may be more pronounced with climate warming than would occur due solely to altered competitive conditions.

The idea that tree growth responses to anticipated warming will likely differ in the southern vs. northern parts of a species range has been reported previously for Scots pine (Rehfeldt et al. 2002). In that study, tree growth was modelled based on responses to climate transfer, with results suggesting that 90% of Scots pine populations inhabit sites at less than their thermal optima (Rehfeldt et al. 2002). In contrast, our study suggests that growth and survival will be enhanced by warming only at cold locations

in the far north, and that in much of the range, warming will reduce growth, and especially survival. It is not clear why the results of these two studies, although agreeing in general on the notion of biogeographically divergent responses, should disagree somewhat on where the switch from positive to negative would occur. The approaches of the two studies were distinct, which could contribute to their variation. Perhaps a more likely explanation involves differences in the populations used in each study. Only a small fraction of the data in the two studies overlapped, with Rehfeldt et al. (2002) focussing more on eastern European and Asian populations and our study more on European populations, including 177 populations originating from < 20°E longitude, not represented in the former study. Recent phylogeographic findings (Naydenov et al. 2007) suggest distinct evolutionary heritage and genetic composition for eastern (dominant in Rehfeldt et al. 2002) vs. European populations (dominant in our study) of Scots pine. It is at the very least possible that the distinct lineages might respond differently to climate transfer.

The divergent growth and survival responses to climate transfer of Scots pine in southern vs. northern Europe are likely a result of physiological processes and biogeographically varying limitations to growth and survival. In the far north, trees are growth-limited and cold-stressed both by cold conditions and effects of cold on soil resource supply, and warming likely alleviates such limits (Chapin et al. 1993), resulting in enhanced growth and survival. In contrast, in central and southern Europe, warming may enhance heat stress and heat-induced moisture stress more than alleviate cold stress (Kjellström 2004), which would be consistent with decreased growth and survival. Thus, warming will likely relieve extreme cold stress in the far north but enhance heat and moisture stress in southern and central Europe, leading to distinct responses of Scots pine to warming in different parts of its range. The idea that variation in relative moisture limitation may be a critical factor governing response to warming is supported by modelling, empirical trends analyses and dendrochronological findings (Barber et al. 2000; Soja et al. 2007). Dendrochronological studies in Alaska, moreover, also suggest that local site moisture gradients and warm temperature-induced drought can lead to divergent responses to climate warming even in the far north (Lloyd & Fastie 2002). Thus, drought-stress may accompany increased warming in the boreal forest (Barber et al. 2000; Lloyd & Fastie 2002), and in the European range of Scots pine such stresses may be more frequent and severe in the southern rather than the northern extent of the species range.

The results of these long-term experiments indicate that other than at far northern locations in Europe (> 62°N), Scots pine trees will likely have reduced growth, reduced survival or both, upon experiencing increases in MAT

predicted to occur in the coming century. Climate warming, however, is both distinct from and more gradual than moving a plant to a different site than its parents occupied, but it is unclear how that would influence or alter results observed herein. Regardless of the causes, which may be manifold (Persson & Beuker 1997; Davis & Shaw 2001; Rehfeldt *et al.* 2002; Stromgren & Linder 2002), these results suggest that even modest climate warming may have negative consequences for the dominant Eurasian tree species across much of the southern portion of its range. Given the vast land coverage of pine and other temperate and boreal species, and the likelihood of climate change, such responses will likely have considerable importance for environmental and human future well-being.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Source of data used in the study.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01172.x

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