Responses of temperature changes on survival and growth in mountain birch populations.

by

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1. Introduction

During the last 100 years mean annual temperatures on the northern hemisphere have increased by about 1.5°C but with a temporary warm period in the 1930-ies followed by a colder period in 1965-80 (see Chapter 1, this volume). The last 20 years there has been a strong increase of about 1.0°C in global temperatures. The temperature has shown cyclic variations due to the activity of the North Atlantic Oscillation (NOA), expressed by annual mean temperatures or annual temperature range (Crawford et al. 2002). During the last 50 years a steady increase in the CO_2 concentrations in the atmosphere from 315 to 360 ppm has been recorded (Mitchell et al. 1990)). The recent increase in global CO_2 is mainly due to increased output of fossil fuel. Increased CO_2 is in turn expected to lead to higher absorption rates of long wave radiation in the atmosphere (the greenhouse effect), thereby increasing temperatures. According to predictions, a future doubling of the CO_2 concentrations from 360 to 720 ppm would result in a 3-4°C increase in mean winter temperatures and 1-2°C increase in summer temperatures on the northern hemisphere (Mitchell et al. 1990)).

The raised temperature impact on sensitive stages like seed reproduction, winter dormancy, migration rates and soil conditions (Heide 1993, Huntley 1997) is expected to affect subarctic plant species. Increased CO_2 level will normally cause increased growth rates due to a combination of increased photosynthetic rates and increased water use efficiency (Hall et al. 1993). In most deciduous trees, e.g. birch, shoot growth will take place over the whole season ("free growth") and there will be no sink limitation on photosynthesis (Bliss 1971, Skre 1993b).

Thornley (1972) developed a model for balanced shoot/root growth at varying temperatures by regulating the C/N ratio. The expected CO_2 increase would lead to higher C/N ratio, that would have to be balanced by increased root growth. The most pronounced effects of increased CO_2 is therefore increase in root biomass (Mousseau 1993). In birch these compensation mechanisms have also been found. Most of these experiments have been carried out at considerably higher temperatures (15-30°C) and lower photosynthetic active radiation than in ambient field conditions at higher latitudes (cf. Mortensen 1998). Higher summer temperatures would also lead to temperature acclimation, i.e. the temperature responses of the Rubisco enzyme will be changed, leading to a higher temperature optimum for photosynthesis (Skre 1993a). Low Rubisco activity as a result of high temperature acclimation (Crawford 1989) is also probably related to a decreased leaf-N content, since

most of the leaf protein is associated with the Rubisco enzyme (Salisbury and Ross 1991). In accordance with this, Hikosaka (1997) and Weih and Karlsson (1999, 2001) concluded that the optimal N content (area based) would tend to decrease with increasing air temperature. On long terms this acclimation would lead to genetic adaptation of plant species and ecotypes. Higher soil temperatures would cause more rapid decomposition and uptake rates of nitrogen in soil (see Chapter 5 this volume), and increased summer temperatures would also lead to better seed quality, and thereby to improved seed reproduction in forest tree species (e.g. Mork 1957)

Genetic ecotypes have also developed in response to daylength and temperature regarding dormancy induction and to temperature regarding dormancy breaking (chilling requirements). The chilling requirements increase with decreasing latitude due to longer growing season (Myking and Heide 1995). When plants have entered out of dormancy, higher temperatures would lead to earlier dehardening, that may lead to higher frequency of spring frost damage (Hänninen 1996), particularly in ecotypes from northern and inland areas (Larsen 1976). These damages may lead to reduced growth the following season.

In the present review the effects of raised winter temperatures because of increased CO_2 level on growth and carbon balance in some birch provenances have been studied. Mountain birch (*Betula pubescens* ssp. *czerepanovii*) is a major constituent of northern forests in northern Europe (see Chapter 1 this volume), and because it is an old inhabitant of Scandinavia it had also evolved climatically adapted ecotypes.

In order to elucidate the mountain birch responses on the expected changes in winter temperature levels, three different aspects of the climate x birch relationships will be discussed in more detail, i.e.
- to see how birch growth and carbon balance is influenced by summer and winter temperatures in field (and greenhouse) experiments.
- to compare the responses of mountain birch seedlings from different origin to different temperature and CO_2 levels in order to investigate possible adaptation mechanisms, and see how the winter temperature responses are modified by different CO_2 levels.
- to see how different winter temperature levels may influence dormancy, frost hardiness and growth in birch seedlings the following season.

2. Responses to summer temperatures.

To investigate the influence of the expected climate change on tree growth and carbon balance, Skre (1993b) transplanted birch seedlings of different origin (Table 1) grown in fertilized peat (see Skre 1991 for composition) to two oceanic sites in southwestern Norway (60°N), one lowland site (50 m) and another upland site near the treeline at 450 m altitude. A comparison between sites show approximately twice as high growth rates at the former locality as compared with the other (Fig. 1). Another important result was that at the lowland site the highest growth rates were found in seedlings from the southern lowland mountain birch (BAM) and silver birch (*Betula pendula*) provenances (BAL), while at the treeline site the seedlings originating from the southern alpine provenance (BH) and the local provenance from western Norway (BS) were most successful. At the treeline site, the southern lowland provenances were found to suffer frost damages (Skre 1993b) because of too late growth cessation in fall.

Growth rates as measured by biomass values were four times higher at the lowland site than at the high altitude site by the end of the two-year period (Table 2). In accordance with Mäenpää et al. (2001) there was a sharp drop in total carbohydrates in the stem and root tissue after budbreak, as related to shoot growth, and the strongest carbohydrate depletion was found at the low-elevation Fana site (see Fig. 1) where growth rates were strongest. The nitrogen content in roots (Skre 1993b) showed an almost inverse relationship to the carbohydrate content, i.e. when root nitrogen content is high, indicating root growth, the carbohydrates tend to be incorporated into structural tissue and used for growth.

Experiments in a controlled environment (Skre 1993a) showed that the carbohydrate content in root tissue of arctic as well as the southern alpine ecotypes was higher than in southern lowland ecotypes. This agrees well with earlier findings on alpine plants in e.g. Alaska, because in a nutrient-poor environment with low competition for light and water, plants tend to avoid growth rather than producing nutrient-deficient tissue (Chapin 1979). The seedlings from the northern population (BJ) also had slightly higher photosynthesis rates than the southern populations (Fig. 2). This is called metabolic compensation (Mooney and Billings 1961, Crawford 1989) and is looked at as a compensation for relatively shorter growing season in northern areas. Strong short-time temperature acclimation effects were also found (cf. Billings et al. 1971). At medium temperatures (10-15ºC) when photosynthesis rates were high, the shoot/root ratios as well as the specific leaf areas and leaf area ratios were low, indicating a higher proportion of structural tissue than when temperatures were higher and less favourable for photosynthesis (see Figs 2-3). By increasing root growth at high temperatures, plants may be able to absorb more nitrogen from the soil (Karlsson and Nordell 1996) and compensate for the high temperatures by increasing their photosynthetic capacity (cf. Thornley 1972). In field experiments with birch seedlings the uptake rates of nitrogen in roots have been found to be strongly affected by soil temperatures, leading to increased leaf productivity and increased growth rates (see Chapter 5 this volume).

Respiration rates increased in leaf and stem tissue in birch seedlings grown for six weeks at low temperatures, and decreased in roots, as compared with plants grown at high temperatures (Skre 2001). Most of this low-temperature induced increase has been shown to be cyanide-resistant, i.e. not related to growth, particularly at low nutrient level. The high-temperature induced respiration increase in roots, however, was mostly growth-related. The ecological implication is that increased growth in fine root biomass at high soil temperatures may increase nitrogen absorption (Karlsson and Nordell 1996) and leaf nitrogen content (Weih and Karlsson 2001) and increased Rubisco activity in leaves, while at low air temperatures and low nutrient levels in soil, increased cyanide-resistant respiration rates in shoot and leaf tissue would prevent growth at unfavourable conditions (see Skre 2001). Chemical analysis of birch tissue (Fig. 3) confirmed the results from the growth measurements. Mountain birch seedlings increased their nitrogen and chlorophyll concentration in leaves in response to elevated temperatures, at the same time as there was a strong decrease in the total nitrogen and carbohydrate concentration in stem and root tissue.

3. Winter temperature and CO_2 responses.

Seeds of mountain birch (*Betula pubescens*) from one of the same populations (BH) as in the former experiment and two other populations, one (NH) northern and one (IH) from Iceland (see Table 1) were sown in plastic pots the first year and added two different levels of nutrients (Skre and Naess 1999). The seedlings were kept during the winter at ambient and

+4°C raised winter temperatures. The following spring the plants were moved into four open top chambers at 350 and 650 ppm CO_2 with two replicates. The shoot elongation was followed during the season, and shoot and root biomass sampled by the end of the season. Light, temperature and photoperiod was kept as close as possible to ambient conditions at the habitat (see Skre and Naess 1999).

One important result from the experiment in the open top chambers was that plants from the southern alpine population increased their growth during the following season after treated in elevated winter temperatures, while plants from the two northern birch populations (IH and NH) showed negative responses (Fig.4). The southern alpine plants also showed a positive response on shoot elongation rates when grown at elevated CO_2 levels, while there was no significant responses in the Icelandic population (IH). All three populations showed a positive response on added nutrients, and in the southern birch population there was also a strong increase in CO_2 responses after nutrient addition, this response was weaker in the two northern populations. As a consequence, increased winter temperatures may extend the growth season (cf. Myking and Heide 1995), particularly in southern ecotypes, leading to increased growth. The results agree well with previous studies (e.g. Murray et al. 1994, Skre 1993a), indicating that ecotypes and species that are competetive and adapted to a high-growth strategy may take advantage of the expected climate change, because they would tend to put more of their carbon and nutrients into new growth, while the northern populations tend to use their resources for storage and defence against climatic and herbivore stress, which seems to be more important as selective factors in northern areas than competition (Chapin 1980, Ågren 1985). (see also Figs 1-3 and Chapter 5 this volume). As for the Icelandic population, a higher degree of inbreeding with slow-growing *Betula nana* is also possible (Elkington 1968, Anamthawat-Jonsson and Tomasson 1990), probably as a result of selective sheep grazing (Blöndal 1993), see also Ch. 1, this volume.

4. Dormancy and frost hardiness in mountain birch provenances as influenced by winter temperatures.

The winter dormancy in forest tree species (e.g. Håbjørg 1972, Skre 1988) is induced mainly by short days, and is only slightly influenced by temperature. When the low temperature requirements for dormancy breaking are fulfilled, however, high temperatures would promote budbreak and metabolic activity in buds (Ritchie 1982, Heide 1993). Earlier budbreak may in turn make trees more susceptible to spring frost damage (e.g. Hänninen 1996, Tenow 1996), but the dehardening process is often slower and partly independent on dormancy breaking (Skre 1988). In some species higher winter temperatures may lead to delayed budbreak because they will need more time to have their low temperature requirements fulfilled (Murray et al. 1994). In birch, however, the chilling requirements have been shown to be relatively low, and the overall effect of the expected increased winter temperatures is earlier dormancy breaking and a longer growth period (Myking and Heide 1995). On the other hand very few investigations have been carried out to see how the dehardening process in birch might be influenced by the expected increase in winter temperatures, i.e.

(a) to investigate the winter dormancy and spring frost resistance in birch provenances as influenced by winter temperatures
(b) to see how these changes in winter dormancy and spring frost resistance may influence growth during the following season.

Seedlings from five different mountain birch populations (the last five in Table 1) were raised in a greenhouse at 69°40'N during the summer of 2000 (Nilsen, unpubl.). The seedlings were kept three months for hardening and dormancy induction, and then transferred to another greenhouse with temperature control at 60°24'N where they were subdivided between two greenhouse compartments, according to temperature treatment, i.e. ambient and +4°C above ambient. The stems were subjected to controlled freeze-thaw cycles prior to frost hardiness test based on electrolyte leakage (Taulavuori et al. 2001). The time to budbreak and the growth after budbreak was recorded by destructive and non-destructive methods.

The LT50, i.e. the temperature at 50% lethality of tissue, showed that the southern alpine population (BH) was generally much less hardy than the northern populations. In these plants high winter temperature treatment seemed to have had a strong negative effect on frost hardiness. In the Icelandic population (IH), however, the high temperature treated plants stayed hardy during most of the winter, until March. In accordance with the frost hardiness data the northernmost high temperature treated plants were entering out of dormancy much earlier than those from Iceland. The budbreak in all populations except the southern alpine plants occurred earlier in plants treated with elevated winter temperatures than in plants grown at ambient temperatures. Biomass of stem and leaf tissue in the two northernmost populations was significantly higher after growing the plants at elevated winter temperatures than after ambient winter temperature treatment at 60°24'N (cf. Weih and Karlsson 2002). The total biomass as well as the total accumulated shoot lengths, however (Skre, unpubl.) were significantly higher after elevated winter temperature treatment in the southern populations than in the two northern populations, while the Iceland (IH) population was indifferent. The results are in accordance with Skre and Naess (1999). Corresponding plants grown at ambient winter temperatures at 69°40'N (Igeland, unpubl.) kept their hardiness much longer than plants overwintering at 60°24'N, probably as a result of 3-4°C lower temperatures, and even in mid-April the LT50 was below -25°C.

The observations on date of budbreak were partly in agreement with the dehardening conditions, i.e. the most hardy populations and treatments were also those with the latest budbreak. The plants stayed with winter buds for a long time after they had lost their frost hardiness. At low (ambient) temperature treated plants the time of budbreak corresponded with the time when they lost their hardiness. In earlier studies on e.g. Douglas fir the needles stayed in hardened condition for a long time after they had entered out of dormancy (Ritchie 1982). The present study indicate that southern subalpine boreal trees may in the future lose their hardiness before they enter out of dormancy, which is expected to leave bark and needles more unprotected against spring frost damage. Comparisons with ambient temperatures at the origin of the seed populations indicate that northern lowland and coastal populations (NMe and NH) also may become more exposed to spring frost damage in the future, while the extreme oceanic Iceland population (IH) as well the extreme continental Kevo population (BJ) look more protected, by having adapted a high spring frost tolerance (IH) or by large differences between ambient winter temperatures and the critical temperatures (LT50) for spring frost damage (BJ). In comparison Larsen (1976) found that coastal provenances of Douglas fir *(Pseudotsuga menziesii)* from British Columbia were more resistant against spring frost than inland provenances from the Rocky Mountains. He explained this as an adaptation to a long spring season with varying temperatures, in contrast to the inland Douglas fir populations.

5. Conclusions.

Generally, in northern areas where competition from other plants about light and water is low and climate and herbivore stress is high, it is more important for plants to invest carbon and nutrients into storage and defence substances than into new growth (cf. Chapin et al. 1993). The present case studies seem to support these conclusions, and it also agrees well with earlier studies on mountain birch by e.g. Partanen et al. (2001), Körner (1989) and Mäenpää et al. (2001). The summer temperature strongly affects growth and carbon balance during the season in birch seedlings according to temperature and daylength conditions at their habitat, but the plants are to a certain degree able to compensate for these changes in order to maintain a balanced shoot and root growth and reallocate nutrients and carbon to actively growing sites. The shoot and biomass growth is limited by soil temperatures through its effect on nitrogen and phosphorus uptake rates. Increased winter temperatures seem to promote growth in fast-growing southern ecotypes and reduce shoot and biomass growth in northern ecotypes, partly by exposing plants more frequently to spring frost damage. CO_2 and nutrient levels may to a certain extent modify the temperature responses, and the responses to CO_2 and nutrients are found to be strongest in southern fast-growing populations, in accordance with the stress resistance syndrome (SRS) hypothesis suggested by Chapin et al. (1993) . Extreme oceanic and continental ecotypes seem to be more protected from spring frost damages as a result of elevated winter temperatures than intermediate mountain birch populations.

6. References.

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Table 1

Localities and altitudes of seed populations.

BAL	Løten, SE Norway	60°51'N	11°20'E	200 m
BAM	Løten, SE Norway	60°51'N	11°20'E	200 m
BS	Fana, SW Norway	60°16'N	5°22'E	50 m
BH	Blefjell, SE Norway	59°45'N	9°28'E	750 m
IH	Hafnaskogur, Iceland	64°23'N	21°40'W	50 m
NMe	Melbu, N Norway	68°37'N	14°27'E	20 m
BJ	Kevo, N Finland	69°44'N	27°00'E	200 m
NH	Hammerfest, N Norway	70°40'N	23°41'E	50 m

BAL = Silver birch (*Betula pendula*)

Table 2
Total biomass (g/plant) at peak season in 2-year old seedlings of mountain birch *(Betula pubescens)* and silver birch (*Betula pendula*) grown in fertilized peat at two different altitudes, i.e. Fana (50 m) and Kvamskogen (450 m) in western Norway (60°N). Means with ± 2 s.e. See Table 1 for origin of seed populations.

Origin	Kvamskogen	Fana
BJ	1.6 ± 0.2	1.9 ± 0.4
BH	3.0 ± 0.4	7.9 ± 1.4
BS	6.8 ± 0.7	17.5 ± 2.7
BAM	4.6 ± 0.6	25.2 ± 4.0
BAL	3.2 ± 0.6	26.1 ± 3.8

Figure legend

Fig. 1
Total non-structural carbohydrate content as percentage dry weight in roots of birch seedlings during two seasons (1986-87) at Fana and Kvamskogen (see Table 2 for locations)
Means with 2 s.e. See Table 1 for origin of seed populations (cf. Skre 1993b).

Fig. 2. Shoot/root ratios (top) and leaf area ratios (LAR) and specific leaf area (SLA) as $cm^{-2}mg^{-1}$ (bottom) with 2 s.e. in 6 weeks old mountain birch seedlings from a subalpine area in southern Norway (BH). See Skre (1993a) for details and Table 1 for origin of seed populations.

Fig. 3. Photosynthesis rates (μM CO_2 $m^{-2}s^{-1}$) as a function of temperature in discs of mature leaves from three mountain birch populations (see Table 1). Leaves were kept three weeks at 18 hours photoperiod and at 21°, 15° and 9^oC respectively. Irradiance was 100 μM $m^{-2}s^{-1}$. See Skre (1993a) for details.

Fig. 4. Shoot elongation (mean length longest shoot L_{max} in cm) during the 1994 season in the three investigated populations. Significant differences are shown by asterisks where *p<0.05. After Skre and Naess (1999). Fertilized plants grown at elevated (left) and ambient (right) CO_2 levels (CO2+ and CO2-) and at two different winter temperatures (T1 = ambient and T2 = ambient + 4^oC). See Table 1 for origin of seed populations.