Combined Effects of Elevated Winter Temperatures and CO_2 on Norway Spruce Seedlings

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A total of 1800 3-year old seedlings of Norway spruce (*Picea abies* (L.) Karst.) from two Norwegian and one German provenance were treated with two different nitrogen levels during the 1992 growth season. The plants were kept during the following winter at two different temperature levels. In the spring of 1993 the nutrient application was resumed, and the plants were divided between three different treatments, 350 and 650 p.p.m. in open top chambers and a control plot outside the chambers. This treatment was repeated also during the following 1994 growth season.

The growth and primary production was studied by photosynthesis experiments and by non-destructive growth measurements.

The results indicate that raised winter temperatures may lead to increased needle loss and reduced growth the following season, particularly in northern provenances.

Carbon dioxide significantly influenced growth in addition to nutrient level and winter temperature. High CO_2 also seemed to cause increased photosynthesis at early season, and earlier budbreak and growth cessation than in control plants.

1 Introduction

One of the major topics of present-day research is the growing concern about the effects of the expected rise in greenhouse gases, particularly CO_2. According to climatological models (GCM) a doubling of the CO_2 concentration would cause a 3–4°C increase in winter temperatures and about 2°C in summer temperatures (Pedersen 1993). A side-effect of raised temperatures would be a more rapid decomposition and uptake rates of nitrogen in soil.

In the present study the emphasis has been placed on the combined effect of raised winter temperature and increased CO_2 level on trees.

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As test plant has been chosen Norway spruce (*Picea abies* (L.) Karst.).

In spruce and other evergreens the excess of assimilated carbon is usually stored in evergreen leaves. The carbon reserves are mobilized next spring, and enable the plants to overcome the critical period with negative photosynthesis, and to produce new leaves, that eventually take over as carbon producer (Rutter 1957).

The induction of winter dormancy in fall takes place through photoperiodic reactions and is only slightly influenced by temperature (Håbjørg 1972, Heide 1974).

When the low temperature requirements for dormancy breaking are fulfilled, however, usually in January, high temperatures would lead to earlier budbreak, and induce higher metabolic activity in buds and needles (Ritchie 1982, Heide 1993). As a result of a longer growth period, plants would therefore increase their growth potential, but at the same time earlier budbreak would more easily expose plants to frost damages due to sudden cold periods in spring, particularly in continental areas and ecotypes (Jalkanen and Nikula 1993).

Another effect of high winter temperatures would be a longer period with negative carbon balance at mid-winter, due to high winter temperatures combined with low light intensities (Printz 1933) This could lead to a temporary shortage of carbohydrates in plants during the growth period in spring (Stewart and Bannister 1973). On the other hand earlier dormancy breaking would lead to increased photosynthesis in evergreen needles when light conditions are improving in February and March after dormancy breaking (Hagem 1947, Aalvik 1939). The overall effect on the carbon balance could therefore become positive in some woody species and negative in others.

In an earlier study (Skre 1995) high winter temperatures were found to cause a lower carbohydrate level in needles and heavy needle loss, particularly of old needles, the following spring. Consequently, a strong reduction was found in growth and biomass the following season.

The aim of the present study is to follow the growth processes in the investigated spruce plants, and to see to what extent the expected rise in CO_2 level would help resuming growth after a winter with exceptionally high temperatures, by increasing photosynthetic rates and biomass production.

2 Material and Methods

Three years old spruce seedlings, raised from mixed seed populations within three provenances, were transplanted into plastic containers (diameter 12 cm) with fertilized peat in the spring of 1992. For peat composition see Skre (1991). The provenances were as follows:

Harz, Germany (52°N), 420–470 meter (H5)
Östfold, Norway (59°N), 50–150 meter (C1)
Hedmark, Norway (61°N), 250–350 meter (B3)

The C1 provenance was intermediate in its responses between the B3 and H3 provenances (Skre 1995), and the actual results from the growth measurement are therefore not shown for the C1 plants, but they are included in the variance analysis.

The plants were placed under a birch canopy (light intensity 300–400 μmolm^{-2}s^{-1} PPFD) and added two strengths of SUPERBA nutrient solution, equivalent to 1 or 10 gm^{-2}year^{-1} nitrogen once a week over the season (May-October). For composition of nutrient solution, see Skre (1991). The ratios between the concentrations of nutrients were kept unchanged. In late November the plants were moved into two greenhouse compartments, simulating ambient temperature conditions and 4°C raised winter temperature (see Fig. 1a). A constant temperature difference of about 4°C was achieved by means of a differential temperature controller.

In late April 1993 the plants were moved into six open top chambers with normal (350 p.p.m.) and high (650 p.p.m.) CO_2 level, and with control plants outside the chambers.

The CO_2 treatment continued until early November. The remaining plants, eight per replicate and with three replicates per treatment, were moved into the two greenhouse compartments, and the winter temperature treatment was repeated (Fig. 1b). In early May 1994 the plants
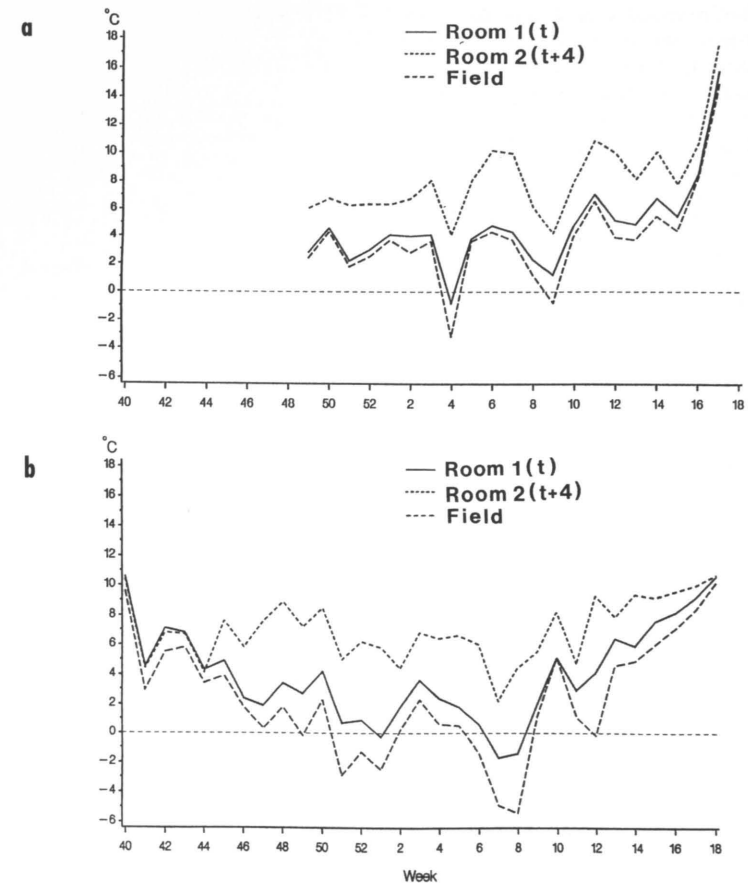

Fig.1. Weekly mean and extreme temperatures during the winter 1992/93 (a) and 1993/94 (b) in the low (t) and high (t+4) temperature rooms, and in field. Fig. 1a is a redrawn from Skre (1995).

were moved into open top chambers and the CO_2 treatment was repeated until late October.

Subsamples of plants and needles were taken for biomass determination throughout the experiment, and shoot length, stem base diameter and needle density were measured at intervals.

The temperature and CO_2 content in the open top chambers and in the greenhouse were monitored continuously and data stored in a datalogger. Also the data from one light probe (Lambda LI-185B quantum sensor) and the humidity probe were recorded, the probes were placed in one open top chamber during the summer and in the greenhouse during the winter season.

The CO_2 exchange measurements of net photosynthesis and respiration rates were made in a closed system using a Li-COR 6200 transportable system with a clear plexiglass chamber (volume 1190 cm^2) equipped with a Lambda Li-185B quantum sensor, thermocouple and humid-

ity sensors. 2-year-old shoots from the upper whirl were used. The total area of the shoot was estimated from the length and width of needles, needle density and shoot length. After an equilibration time, that was found to be three minutes for photosynthesis and ten minutes for dark respiration measurements, six measurements, once every 5 ppm subsequent drop in the CO_2 level, were taken at 10–40 seconds intervals.

The fitted light response curves at early and late season at a given temperature (16–20°C) were found according to Farquhar and Caemmerer (1982) and Leverenz (1994). The temperatures were close to the measured optimum temperatures at saturation light levels (Skre unpubl.). All variables were tested by GLM variance analysis (Goodnight 1976) in order to find significant effects and interactions.

Table 1. Variance ratios (F) and significance levels for needle density (cm^{-1}) of shoots from the 1991 age class (n_2), measured Dec. 28, 1992 and June 12, 1993, and shoots from the 1992 age class (n_3), measured June 12, 1993. The plants have been subjected to different nutrient levels and winter temperatures. Significant levels are * = $p < 0.001$; + = $p < 0.01$; ° = $p < 0.05$. DF = degrees of freedom. R_2 = square multiple correlation coefficient. SS = sum of squares.

Source	DF (n_2)	Dec. 28. (n_2)	June 12. (n_3)	June 12.
Provenance	2	102.5*	54.1*	10.6*
Nutrient level	1	0.2	3.0	11.6*
Winter temp.	1	0.0	125.4*	72.1*
Prov × nut	2	1.5	1.3	1.2
Prov × temp	3	1.2	14.5*	12.0*
Nut × temp	1	1.7	6.1°	9.4+
Prov × nut × temp	2	0.7	0.7	0.6
Block	9	0.7	3.2+	1.0
Error SS	99	116.2	422.3	407.7
Total SS	119	373.4	1718.8	1029.6
R^2		0.69	0.75	0.60

3 Results

The observations on needle density from the first winter (1992/93) were evaluated by running a three-way variance analysis on the observed values before and after the winter season on age class 1991. In addition a separate test was run on age class 1992 after the winter season. The results are presented in Table 1.

The stem base diameter underneath the lowest side branch (means of two measurements at right angels) was measured on October 27, 1994 after
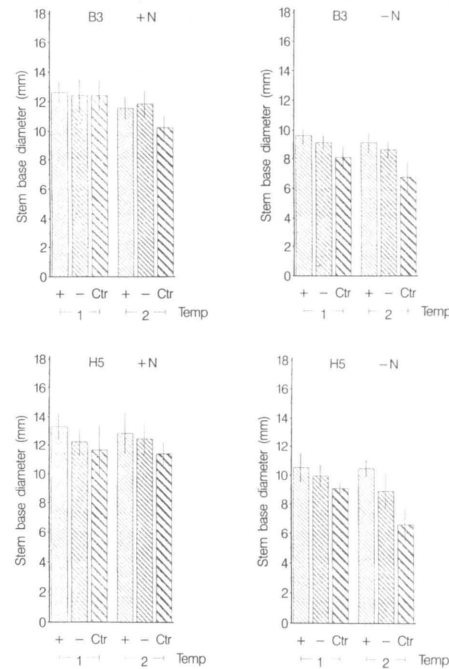

Fig. 2. Stem base diameter (mm) in October 1994 in fertilized (+N) and non-fertilized plants (–N) from a German (H5) and a Norwegian (B3) provenance, grouped according to CO_2 and winter temperature treatment, where the symbols are: high CO_2 (+), low CO_2 (–), outside open top chamber (Ctr.). High (2) and low (1) winter temperature. Means of 24 observations per treatment and provenance, with ±2 s.e.

two summers with normal and raised (650 ± 50 ppm) CO_2 level and two winters with normal and 4°C raised winter temperatures on the same plants. The stem base diameter is a measure of the accumulated growth during the whole 2-year period. Fig. 2 shows the results, as compared with measurements on control plants outside the open top chamber.

The needle density measurements of April 1994 presented in Fig. 3 are only shown for plants grown at normal CO_2 level, because CO_2 had
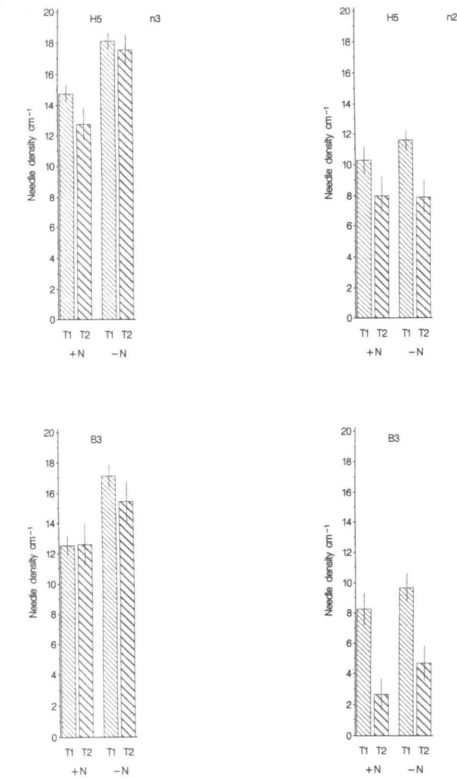

Fig. 3. Needle density (cm^{-1}) in the 1992 (n_2) and 1993 (n_3) needles measured in April 1994, grouped according to provenance, nutrient level and winter temperature treatment, symbols are: high (T_2) and low (T_1) winter temperature. High (+N) and low (–N) nutrient level. Means of 24 observations per treatment and provenance, with ±2 s.e.

only slight and hardly significant influence on this growth parameter. The needle densities are mainly influenced by nutrient levels and winter temperatures. The density in young 1993 needles (n_3) is influenced by the temperature during the preceeding 1993/94 winter (Fig. 1b), while the densities in the 1992 age class (n_2) are also influenced by the extremely mild 1992/1993 winter (Fig. 1a), that caused heavy needle loss the following spring (Skre 1995).

The length of the apical shoot at May 26, 1994 (Fig. 4) may be used as a measure of budbreak time. The result is only shown for fertilized Norwegian spruce plants.

The growth of annual shoots usually took place from May to July, after which there was a period with only secondary growth in stem and root, and bud development. In some plants, however, there was a new short period with apical growth in late August and early September. This is called Lammas growth. The length of these "Lammas shoots" may be used as a measure of the budset time, or time of growth cessation in shoots. Fig.
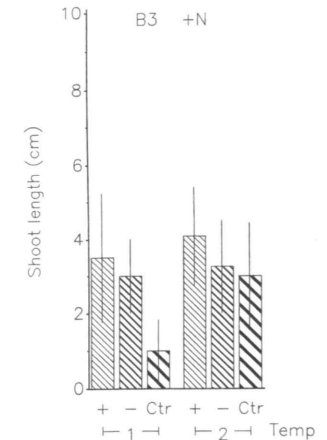

Fig. 4. Length of annual shoots (cm) on May 26, 1994 in fertilized seedlings of the Norwegian provenance (B3). The plants are grouped according to CO_2 and winter temperatures, where the symbols are: High CO_2 (+), low CO_2 (–). outside open top chamber (Ctr.). High (2) and low (1) winter temperatures. Means of 24 observations per treatment and provenance, with ±2 s.e.

Table 2. Variance ratios (F) and significant levels for annual shoot length (cm), measured May 26 (L_{41}) and August 3 (L_{42}), 1994. (L_{41}), length of Lammas growth (ΔL), and stem base diameter (d), measured October 27, 1994, in three Norway spruce provenances, as a function of winter temperature, nutrient level and CO_2 concentration of the previous summer. * = $p < 0.001$; + = $p < 0.01$; ° = $p < 0.05$. DF = degrees of freedom. Only significant interactions are included.

Source	DF	L_{41}	L_{42}	ΔL	d
Provenance	2	2.9°	10.0*	7.6*	11.1*
Temperature	1	8.0+	35.3*	26.8*	10.8*
Nutrient	1	9.3+	108.8*	1.0	215.4*
CO_2	1	16.6*	9.2+	19.8*	19.4*
Temp × CO_2	1	1.4	3.0+	2.7	3.2°
Model	23	2.2*	4.2*	3.0*	9.2*
Error m.s.	72	2.44	6.66	1.46	2.33
R^2		0.233	0.546	0.294	0.562

5 shows the length of "Lammas shoots" in fertilized plants on August 30, 1994 (control plants are not shown).

The measurements of apical shoot lengths on May 26 and August 3 (L_{41} and L_{42}), 1994, the length of the "Lammas growth" at August 30, 1994 and the stem base diameters October 27, 1994 of the total plant material were transformed to logarithmic values and subjected to a variance analysis. The result of this analysis is shown in Table 2.

In the presentation of net photosynthesis measurements in Tables 3–4 only the results from the fertilized plants are shown, and all three provenances are combined because there was no significant provenance effect on the photosynthesis values. The results are therefore based on measurements on net photosynthesis at temperatures close to optimum values, given in the tables. In Table 3 are shown the estimated maximum net photosynthesis rates in 2-year-old shoots at early (July) and late season (September) 1994, and the corresponding optimum temperatures and saturation light levels. At late season measurements were also made on spruce shoots grown in high CO_2 concentrations, but measured at normal CO_2 level. In Table 4 are shown the maximum net photosynthesis rates in dormant shoots January 1994, grown in

Table 3. Estimated maximum net photosynthetic rates, P_{max} (μmol $CO_2 m^{-2}s^{-1}$), saturation light intensity of photosynthesis, I_{max} (μmol m^{-2} s^{-1}) and temperature, T (°C) during measurements of light response in 2-year-old fertilized spruce shoots at early (July 4–7) and late season (September 2–4) 1994, measured at two different CO_2 levels (C_2). Optimum temperatures, T_{opt} and light intensity, I (μmol m^{-2} s^{-1}) during the measurements of temperature response. Means with ±2 s.e. are given on the P_{max} values. The mean CO_2 concentration (ppm), the month before (C_1) and during the measurements (C_2), and relative humidities RH (%) during the measurements are also given.

C_1	C_2	P_{max}	I_{max}	T	T_{opt}	I	RH
Early season							
668	614	4.5±0.5	500	16.5	22	600	60
355	373	1.5+0.4	300	19.0	19	450	59
Late season							
667	622	2.5±0.4	700	19.7	19	750	53
667	372	2.9±0.4	800	18.4	18	700	62
382	367	2.9±0.5	400	18.8	21	500	64

Table 4. Maximum net photosynthetic rates, P_{max} (μmol $CO_2 m^{-2}s^{-1}$), saturation light intensity of photosynthesis, I_{max} (μmol $m^{-2}s^{-1}$) and optimum temperatures, T_{opt} (°C) in daylight with supplementary light in fertilized 2-year-old spruce shoots at mid-January 1994 at ambient (T) and 4°C raised temperatures (T+4). All three provenances are combined. Seedlings were grown at ambient CO_2 concentration. Means with ±2 s.e. The mean CO_2 levels (ppm), temperatures T (°C), light levels I (μmol m^{-2} s^{-1}) and relative humidities RH (%) during the measurements are also given.

Temperature treatm.	CO_2	P_{max}	I_{max}	T	T_{opt}	I	RH
T	368	0.7±0.2	100	8.8	9.5	140	70
T+4	371	1.1±0.3	120	9.6	9.0	135	61

normal and 4°C raised temperatures.

The saturation light is defined as the light level corresponding to a photosynthetic rate equal to 90 % of the estimated maximum value.
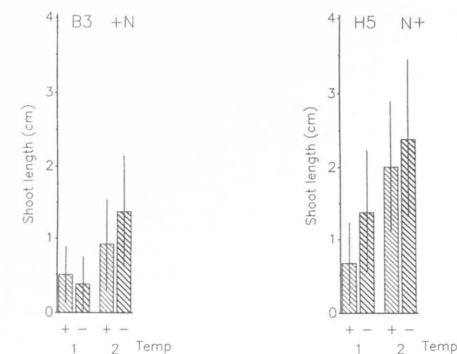

Fig. 5. Lammas growth (cm) on August 30, 1994 in fertilized spruce seedlings of a German (H5) and a Norwegian (B3) provenance. The plants are grouped according to CO_2 and winter temperature, where the symbols are: high CO_2 (+), low CO_2 (–). High (2) and low (1) winter temperatures. Means of 24 observations per treatment and provenance, with ±2 s.e.

Table 3 indicates a strong positive CO_2 effect on photosynthesis in spruce shoots at early season, while there was a slight negative effect at late season. In winter the photosynthetic rates were slightly higher at 4°C raised temperatures than at normal temperatures (Table 4).

4 Discussion

The nutrient level increased growth and biomass in both provenances (see Fig. 2). The reason is probably prolonged secondary growth in fall (Pümpel et al. 1975, Skre 1988) and partly earlier budbreak (Larsen 1976, Murray et al. 1994).

Because of high temperatures during the first winter, the needles suffered an increased carbon loss, as demonstrated by decreased C/N ratio (Skre 1995). At the same time heavy needle damages were observed in plants from the high temperature treatment. The damage was strongest in fertilized plants (Fig. 3). The damaged needles developed necrotic spots in March and eventually fell off. As a result of this needle loss

the annual production during the 1993 season was lower in fertilized plants grown at high winter temperature than in low temperature (Skre 1995). This growth reduction was still significant also in 1994 (Fig. 2, Table 2).

The higher degree of needle loss in plants grown at high nutrient level than at low level, is another indication that the damage may be related to low C/N ratio and high dark respiration rates, as a result of stronger fertilization and growth (Skre 1992). Damages on spruce needles during winter storage in low temperatures above zero have been reported by e.g. Venn (1980). Sandvik (1968) found that dark respiration rates during winter storage of five year old Norway spruce were about twice as high at +0.5°C than at –2°C, and that the respiration increased in late April, probably due to increased metabolic activity (see also Ritchie 1982). Navratil and Dye (1978) studied white spruce and black spruce seedlings and found 12 % dry weight loss after 40–70 days of winter storage at +2.5–4.0°C, equivalent to about 50 % depletion of food reserves (Venn 1980).

The growth increase due to elevated CO_2 is often overestimated because of the CO_2 acclimation that takes place at the same time (Mortensen 1993). The reason for CO_2 acclimation may be attributed to limited pot volume (Kerstiens and Hawes 1994), substrate limitation (Poorter 1993) or enzymatic adaptations (Crawford 1989).

After two seasons with different CO_2 treatment a significant increase due to raised CO_2 level was found in the stem base diameter (Table 2), particularly in the German provenance (Fig. 2). This agrees well with the results of Mortensen (1994a, b) who also found that elevated CO_2 levels increased biomass and growth rates in *Picea abies*. There was a strong positive CO_2 effect on photosynthesis at early season, and a corresponding negative CO_2 effect at late season (Table 3). This down regulation of photosynthesis may be seen by comparing spruce shoots grown at high or normal CO_2 concentrations, measured at normal CO_2 level, but also by comparing shoots grown at high CO_2, but measured at high or normal CO_2 level. This so-called "CO_2 acclimation" may be attributed to sink limitation (Poorter 1993).

The strong increase in net photosynthesis rates at normal CO_2 level during the season is proba-

bly related to the development of new, photosynthetically active needles without any sink limitation as in the CO_2 treated needles.

In contrast to the extremely warm winter of 1992/93 the following winter 1993/94 was relatively cold, or about 2°C below the first winter (Fig. 1b). In accordance, needle densities were only slightly lower on annual shoots (n_3) from the high temperature treatment than in the corresponding shoots from the low temperature treatment (Fig. 3) in contrast to the 1-year-old needles (n_2).

High CO_2 seemed to induce early growth cessation as indicated by the significantly lower Lammas growth (Fig. 5). The early budbreak in CO_2 treated plants (Fig. 4) was confirmed by the F-values on the variance ratio (Table 2). This is in contrast to the results of Murray et al. (1994) in *Picea sitchensis*. According to some authors (Sandvik 1978, Heide 1974), however, plants that are induced by short days to early growth cessation would also have a tendency towards earlier budbreak next spring. The relatively early growth cessation in CO_2 treated plants, particularly in the German provenance (Fig. 5), may be a result of accumulation of photosynthetic products. Driessche (1969) concluded from experiments with Douglas fir (*Pseudotsuga menziesii*) that light promotes hardening (and early growth cessation) by synthesis of cryoprotective substances.

Early growth termination in spruce (*Picea abies*) might result in better bud development and stronger growth next year (Heide 1974). This is in good agreement with the present results (Fig. 2). The increased stem base diameter in CO_2 treated plants indicates higher root growth, since a close connection has been found between root biomass and stem base diameter (Rutter 1955).

The CO_2 level also seemed to increase apical growth, but the affect, as indicated by the F-values, was not as strong as for the stem base diameter (Table 2).

Photosynthesis measurements (Table 4) during the 1993/94 winter showed that spruce grown in elevated winter temperatures to a certain degree is able to balance the carbon loss due to increased respiration rates during dark periods, when grown at saturating light levels. This is in accordance with earlier long-term experiments on spruce seedlings (Hagem 1947). Further ex-periments are needed, however, to evaluate the effect of the predicted 4°C increase in winter temperatures on the carbon balance on Norway spruce in West Norway.

References

Aalvik, G. 1939. Über Assimilation und Atmung einiger Holzgewachee in westnorwegishen Winter. Meddr. Vestland. forstl. ForsSta. 6(4): 1–266.

Crawford, R.M.M. 1989. Studies in plant survival. Studies in Ecology 11. Blackwell Scientific Publications, Oxford. 296 p.

Driessche, R. van den. 1969. Influence of moisture supply, temperature, and light on frost-hardiness changes in Douglas fir seedlings. Can. J. Bot. 47: 1765–1772.

Farquhar, G.D. & Caemmerer, S. von. 1982. Modelling of photosynthetic response to environmental conditions. In: Lange, O.L., Nobel, P.S., Osmond, C.S. & Ziegler, H. (eds.) Physiological plant ecology II, vol. 12B. Water relations and carbon assimilation. p. 549–588.

Goodnight, J.H. 1976. The new general linear modes procedure. Proceedings of the First International SAS Users Conference, Cary, NC: SAS Institute Inc.

Hagem, O. 1947. The dry matter increase in coniferous seedlings in winter. Meddr. Vestland. forstl. ForsSta. 8(1): 1–317.

Heide, O.M. 1974. Growth and dormancy in Norway spruce ecotypes (Picea abies) I. Interaction of photoperiod and temperature. Physiol. Plant. 30: 1–12.

— 1993. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. Physiol. Plant. 88: 531–540.

Håbjørg, A. 1972. Effects of photoperiod and temperature on growth and development of three latitudinal and three altitudinal populations of Betula pubescens Ehrh. Meld. Nor.Landbr. hogsk. 51(2): 1–27.

Jalkanen, R. & Nikula, A. 1993. Forest damage in Northern Finland in 1992. In: Jalkanen, R., Aalto,T. & Lahti, M.L. (eds.) Forest pathological research in northern forests with special reference to abiotic stress factors. Finnish Forest Research Institute, Research Papers 451: 30–35

Kerstiens, G. & Hawes, C.V. 1994. Response of growth and carbon allocation to elevated CO_2 in young cherry (Prunus avium L.) samplings in relation to root environment. New Phytol. 128: 607–614.

Larsen, J.B. 1976. Untersuchungen über die Frostempfindlichkeit von Douglasienherkünften und über den Einfluss der Nährstoffversurgung auf die Frostresistenz der Douglasie. Der Forst- und Holzwirtschaft 31(15): 299–302.

Leverenz, J.W. 1994. Factors determining the nature of the light dosage response curve of leaves. In: Baker, N.R. & Bowyer, J.R. (eds.) Photoinhibition of photosynthesis from molecular mechanisms to the field. p. 239–254. Bios Sci. Publ. Oxford.

Mortensen, L.M. 1993. Effekter av global CO_2-økning på ulike terrestriske økosystemer i Norge. Norsk Landbruksforskning 7: 1–19.

— 1994a. The influence of carbon dioxide or ozone concentration on growth and assimilate partitioning in seedlings of nine conifers. Acta Agric. Scand. Sect. B, Soil and Plant Sci. 44: 157–163.

— 1994b. Effects of carbon dioxide concentration on assimilate partitioning, photosynthesis and transpiration of Betula pendula Roth. and Picea abies (L.) Karst. seedlings at two temperatures. Acta Agric. Scand. Sect. B, Soil and Plant Sci. 44: 164–169.

Murray, M.B., Smith, R.I., Leith, I.D., Fowler, D., Lee, H.S.J., Friend, A.D. & Jarvis, P.G. 1994. Effects of elevated CO_2, nutrition and climatic warming on bud phenology in Sitka spruce (Picea sitchensis) and their impact on the risk of frost damage. Tree Physiology 14: 691–706.

Navratil, S. & Dye, D. 1978. Survey of the quality of planting stock stored in storages in Northern region in the spring of 1977. Ont. Min. Nat. Res. Internal Report, 28 p.

Pedersen, K. 1993. Climatic models and feedback mechanisms. Climatic scenarios. In: Holten, J.I. & Oechel, W.C. (eds.): Impacts of climatic change on natural ecosystems, with emphasis on boreal and arctic/alpine areas, p. 9–11. NINA/DN, Trondheim, Norway.

Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. In: Rozema, J., Lambers, H., Van der Geijn, S.C. & Cambridge, M.L. (eds.): CO_2 and biosphere. p. 77–98. Kluwer Acad. Publ., Dordrecht. 484 p.

Printz, H. 1933. Granens og furuens fysiologi og geografiske utbredelse. Nyt. Mag. Naturvid. 73: 169–219.

Pümpel, B., Gobl, F. & Tranquillini, W. 1975. Wachestum, Mykorrhiza und Frostresistenz von Fichtenjungplanzen bei Düngung mit verschiedene Stickstoffgaben. European J. of Forest Pathology 5: 83–97.

Ritchie, G.A. 1982. Carbohydrate reserves and root growth potential in Douglas-fir seedlings before and after cold storage. Can. J. For. Res. 12: 905–912.

Rutter, A.J. 1955. The relation between dry weight increase and linear measures of growh in young conifers. Forestry 28: 125–135.

— 1957. Studies in the growth of young plant of Pinus sylvestris L. I. The annual cycle of assimilation and growth. Ann. Bot. 21: 399–425.

Sandvik, M. 1968. Bygging av kjølelager for skogplanter. Årsskr. norske Skogpl. Sk. 1967: 55–96.

— 1978. Gjødningens innflytelse på plantenes etablering etter utplanting. Årsekrift for Nordiske Skogplanteskoler 1977: 41–56.

Skre, O. 1988. Frost resistance in forest trees: a literature survey. Medd. Nor. inst. skogforsk. 40(9): 1–35.

— 1991. Chemical composition of mountain birch (Betula pubescens Ehrh.) and lowland birch (Betula pendula Roth.) seedlings grown at varying temperature, light intensity and daylength. Medd. Skogforsk. 44(8): 1–28.

— 1992. Nutrient limitation in three birch populations and the possible function of alternative respiration as a growth-regulating mechanism. Medd. Skogforsk 45(11): 1–28.

— 1995. The effect of raised CO_2 and winter temperatures on growth and carbon balance in Norway spruce seedlings. Report from Global Change and Arctic Terrestrial Ecosystems: an International Conference 21–26 August 1993, Oppdal, Norway. Ecosystems Research Report 10: 171–180. European Commission.

Stewart, W.S. & Bannister, P. 1973. Dark respiration rates in Vaccinium spp. in relation to altitude. Flora 163: 415–421.

Venn, K. 1980. Winter vigour in Picea abies (L.) Karst. VII. Development of injury during over-winter cold storages. A literature review. Medd. Nor. inst. skogforsk. 35(9): 1–48.

Total of 31 references