Effect of Accumulated Duration of the Light Period on Bud Burst in Norway Spruce (*Picea abies*) of Varying Ages

Jouni Partanen, Ilkka Leinonen and Tapani Repo

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One-year-old seedlings (two sowing times), two-year-old seedlings and 14- and 18-year-old cuttings of Norway spruce (*Picea abies* (L.) Karst.) were exposed to shortening photoperiod (initially 16 h), lengthening photoperiod (initially 6 h) and constant short photoperiod (6 h) treatments with uniform temperature conditions in growth chambers. The timing of bud burst was examined. In all plants, shortening photoperiod treatment seemed to promote bud burst compared with other treatments. This effect was clearest in the oldest material. The results suggest that, in addition to temperature sum, the accumulated duration of the light period may promote bud burst of Norway spruce.

Keywords growth initiation, phenology, photoperiod, Norway spruce
Authors' addresses *Partanen*, Finnish Forest Research Institute, Punkaharju Research Station, Finlandiantie 18, FIN-58450 Punkaharju, Finland; *Leinonen* and *Repo*, University of Joensuu, Faculty of Forestry, P.O. Box 111, FIN-80101 Joensuu, Finland
Fax +358 15 644 333 **E-mail** jouni.partanen@metla.fi
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1 Introduction

Light conditions control various events in the annual cycle of development of several tree species. Light is the primary source of energy for them and their morphogenic development is strongly affected by light conditions. The effects of photoperiod on growth cessation and dormancy have been observed for example by Wareing (1950a, 1950b), Vaartaja (1959), Heide (1974) and Ekberg et al. (1979). In this kind of response, the role of photoperiod is to act as an environmental signal which ensures the initiation of the hardening processes already before the occurrence of low autumn temperatures.

In dormancy release and growth initiation the role of temperature is more important than the role of light conditions. However, photoperiod may have effects similar to those of low temperatures for rest break. Long days compensate partially for a lack of chilling during rest break in *Pinus sylvestris* L. (Jensen and Gatherum 1965,

Hoffman and Lyr 1967), *Picea abies* (L.) Karst. (Nienstaedt 1967, Worrall and Mergen 1967) and several other tree species (Nienstaedt 1966, Farmer 1968, Campbell and Sugano 1975, Hinesley 1982, Garber 1983). Some results indicate that there is a critical photoperiod for bud burst in beech (*Fagus sylvatica* L.) seedlings, even when they are fully chilled (Heide 1993a). In these cases, the photoperiodic signal may reduce the effect of temperature variation and stabilise the timing of bud burst in spring (Heide 1993a, 1993b). In addition, the results obtained by Häkkinen et al. (1998) suggest that mechanisms based on both light and temperature conditions control bud development in *Betula pendula* Roth.

It has recently been suggested that growth initiation in Norway spruce is affected by the direction of a change in the photoperiod, not its length per se (Partanen et al. 1998). In the event of climatic warming, this mechanism would be ecologically significant in autumn before winter solstice (December 21). It would prevent the ontogenetic development of buds and thus premature bud burst would be avoided. The delaying effect of shortening photoperiod on bud burst detected by Partanen et al. (1998) was especially pronounced in fluctuating temperature conditions.

The aim of this study was to test the effect of different light conditions on the timing of bud burst in Norway spruce. The effect of direction of change in the photoperiod (shortening, lengthening and constant photoperiod) was tested in uniform fluctuating temperature conditions. In light treatments, the duration of the light period, and consequently the accumulation of light hours, was different. The possible effects of the maturation of trees on the photoperiodic responses were also examined.

2 Materials and Methods

2.1 Plant Materials

The material consisted of seedlings and cuttings of Norway spruce of varying ages, forming five treatment groups. The youngest group consisted of one-year-old Norway spruce seedlings. The seeds produced at seed orchard number 111 in Kangasniemi (61°56´N, 26°41´E; 100 m a.s.l.) were sown on June 12, 1997 into PS-608 paper pots containing commercial fertilized peat (Vapo peat for forest trees) in the nursery at the Suonenjoki Research Station of the Finnish Forest Research Institute (62°40´N, 27°00´E; 130 m a.s.l.). The seedlings were grown in a plastic greenhouse and fertilized twice with 10 g/m^2 of the commercial fertilizer Kekkilä Superex-9 (N 19%, P 5%, K 20% and micronutrients).

The second youngest group also consisted of one-year-old Norway spruce seedlings. The seeds produced at seed orchard number 111 in Kangasniemi (61°56´N, 26°41´E; 100 m a.s.l.) were sown on April 28, 1997 into PS-508 paper pots containing commercial fertilized peat (Vapo peat for forest trees) in the nursery at Suonenjoki Research Station. The seedlings were grown in a plastic greenhouse with a shading net (30% shade). The seedlings were fertilized four times with 10 g/m^2 of the commercial fertilizer Kekkilä Superex-9 (N 19%, P 5%, K 20% and micronutrients), and once with 10 g/m^2 of Kekkilä Superex-5 (N 11%, P 4%, K 25% and micronutrients).

The third group consisted of two-year-old Norway spruce seedlings. The seeds produced at seed orchard number 111 in Kangasniemi (61°56´N, 26°41´E; 100 m a.s.l.) were sown on June 10, 1996 into PS-608 paper pots containing commercial fertilized peat (Vapo peat for forest trees) in the nursery at Suonenjoki Research Station. The seedlings were grown in a plastic greenhouse until October. During the second growing season the seedlings were grown outdoors on a rack 15 cm above the ground. Between the middle of June and the beginning of August a shading net was used (30% shade). During the first growing season, the seedlings were fertilized twice with 10 g/m^2 of the commercial fertilizer Kekkilä Superex-9 (N 19%, P 5%, K 20% and micronutrients). During the second growing season, the seedlings were fertilized six times with 15 g/m^2 of the commercial fertilizer Kekkilä Superex-9, and once with 10 g/m^2 of Kekkilä Superex-5 (N 11%, P 4%, K 25% and micronutrients).

The fourth group consisted of Norway spruce cuttings cut from the hedged motherplant V4208 in Haapastensyrjä Tree Breeding Centre. This

plant was selected in 1990 from seedlings in early test number 1130/2. The seeds were sown in 1984 and the seedlings were planted in 1986 in Haapastensyrjä Tree Breeding Centre of the Foundation for Forest Tree Breeding (60°37´N, 24°27´E; 120 m a.s.l.). The seeds originated from plus clone E137 in Kalvola (61°05´N, 24°00´E; 120 m a.s.l.), which was pollinated by the trees from clone experiment number 125 in Haapastensyrjä (60°37´N, 24°26´E; 110 m a.s.l.). The cuttings were taken in autumn 1994. They were rooted in spring 1995 and grown in plastic trays of 45 cells filled with fertilized peat. The size of each cell was 5.0 cm × 5.4 cm × 10 cm (depth).

The fifth group consisted of Norway spruce cuttings from the hedged motherplant V3702 in Haapastensyrjä Tree Breeding Centre. This plant was selected in 1982. The seeds were sown in 1980 in Haapastensyrjä Tree Breeding Centre. The seeds originated from plus stand number 44 in Miehikkälä (60°47´N, 27°30´E; 60 m a.s.l.). The cuttings were taken in autumn 1994 and rooted in spring 1995. They were grown in plastic trays of 45 cells filled with fertilized peat. The size of each cell was 5.0 cm × 5.4 cm × 10 cm (depth).

2.2 Chilling Conditions

The seedlings were moved from the nursery at Suonenjoki Research Station to the Botanical Gardens of the University of Joensuu (62°36´N, 29°43´E; 81 m a.s.l.) on September 18, 1997. The cuttings were moved from Haapastensyrjä Tree Breeding Centre to the Botanical Gardens on October 14, 1997. After moving, the seedlings and cuttings were transplanted into plastic pots of 450 cm^3 volume containing commercial fertilized peat (Vapo B2, 1.2 kg m^{-3}: N 10%, P 8%, K 16%). After transplanting, the seedlings and cuttings were moved outdoors and exposed to natural chilling and freezing temperatures until December 5, 1997. On this date the material was presumed to be fully chilled (Worrall and Mergen 1967, Sarvas 1974, Hänninen 1990). The pots were isolated from each other with sand. The air temperature from the chilling conditions outdoors was monitored by a thermograph. The maximum and minimum air temperatures were 13 °C and –23 °C respectively. The seedlings and cuttings were moved indoors for two weeks into the growth room of the University of Joensuu (temperature 3 °C, relative humidity 90%, daylength 6 h, photon flux density approximately 100 μmol m^{-2} s^{-1}).

2.3 Forcing Conditions

The experimental material was moved and distributed evenly between the three growth chambers (Conviron PGW 36) of the University of Joensuu on December 19, 1997. In each of the three light treatments, 20 seedlings from each of the first three groups and five cuttings from each of the two other groups were used as experimental material. The treatments were: 1) shortening photoperiod (starting from a 16 h photoperiod, changing 6 min 40 s day^{-1}); 2) lengthening photoperiod (starting from a 6 h photoperiod, changing 6 min 40 s day^{-1}); and 3) constant 6 h photoperiod. At the beginning of treatment 1, the lights were switched on at 4 a.m. and off at 8 p.m. In treatment 3 and at the beginning of treatment 2, the lights were switched on at 9 a.m. and off at 3 p.m. Fluorescent (type F96T12/CW/VHO) and tungsten incandescent lamps (Sylvania 100W/227V) were used to give a photon flux density of approximately 200 μmol m^{-2} s^{-1}.

The accumulated duration of the light period was clearly different in the different light treatments. The number of accumulated light hours was greater in the shortening photoperiod treatment than in the lengthening photoperiod and much greater than in the constant 6 h photoperiod treatment. At the beginning of the experiment, the shortening photoperiod treatment presented long day conditions, whereas the lengthening and the constant photoperiod treatments presented short day conditions. With the shortening and lengthening photoperiod treatments the effect of direction of change in the photoperiod could also be tested.

In order to achieve the same temperature sum accumulation in all light treatments, the temperature conditions were identical in all treatments. During the whole experiment, the temperature was maintained at 20 °C between 8 a.m. and 4 p.m. and at 10 °C between 8 p.m. and 4 a.m. During the intervening times the temperature was

changed steadily 2.5 °C per hour. The temperature data were recorded hourly. The water vapour pressure deficit was maintained at a maximum of 0.5 kPa during daytime and at 0.25 kPa during the night.

2.4 Observations and Calculations

The developmental stage of the terminal bud of one- and two-year-old seedlings and the terminal buds of the four uppermost twigs and the main shoot of the cuttings were checked at an interval of two days. Thus, the number of observed buds in each group in each treatment was 20 in the case of seedlings and 25 in the case of cuttings. A bud was considered to have burst if new needles were visible.

The temperature sum accumulation required for the bursting of the observed buds was calculated as the mean daily temperature sum (5 °C threshold) in degree days (d.d.) for each treatment and for each group. The number of days, the temperature sum and the number of light hours required for the bursting of 50% of the observed buds (pooled data) were calculated for each treatment and for each material group.

3 Results

In all plants, shortening photoperiod treatment seemed to promote bud burst compared with other treatments (Table 1). Furthermore, the higher number of accumulated duration of light period in the shortening photoperiod treatment seemed to reduce the temperature sum requirement of bud burst (Fig. 1). This phenomenon was clearest in the oldest material.

Table 1. Mean number of days required for 50% bud burst in Norway spruce seedlings and cuttings of varying ages in different light treatments.

Photoperiod in light treatment	One-year-old seedlings (June)	One-year-old seedlings (April)	Two-year-old seedlings	14-year-old cuttings	18-year-old cuttings
Shortening	19	21	21	21	27
Lengthening	25	25	24	25	33
Constant 6 h	21	23	24	25	35

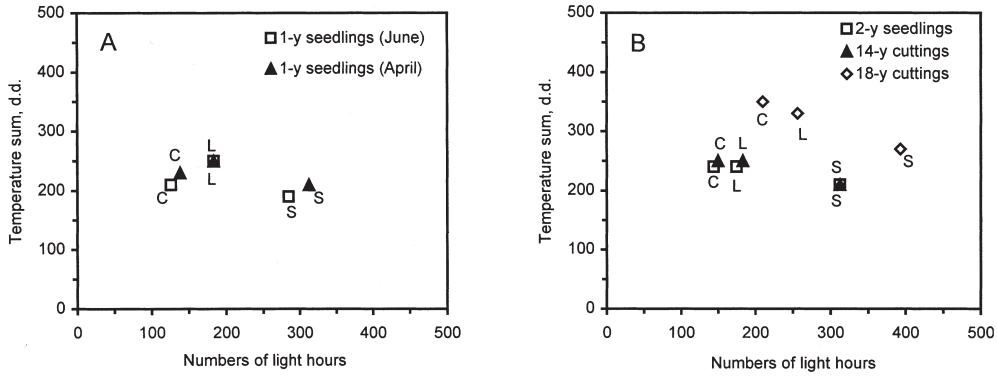

Fig. 1. Temperature sums and numbers of light hours required for 50% bud burst in one-year-old seedlings (A) and two-year-old seedlings and cuttings (B) in constant (= C), lengthening (= L) and shortening (= S) photoperiod. For one-year-old seedlings, the sowing time of the seeds is presented in parentheses.

Compared with other treatments, the shortening photoperiod treatment seemed to promote bud burst in all plant materials, but with respect to the other light treatments there were differences in timing of bud burst between the plant materials (Table 1). In 18-year-old cuttings bud burst was earliest in the treatment with a shortening photoperiod and latest in the constant 6 h photoperiod. With 14-year-old cuttings and two-year-old seedlings bud burst occurred first in the shortening photoperiod. In these material groups, however, there was no difference in timing of bud burst between the treatments with lengthening and constant photoperiod. With one-year-old seedlings (two sowing times) bud burst occurred first in the shortening photoperiod and last in the lengthening photoperiod.

4 Discussion

In this study, growth initiation in Norway spruce seemed to be more dependent on the accumulated duration of the light period than on the direction of a change in the photoperiod. Thus, the results are controversial to the results where bud burst in Norway spruce cuttings was delayed several weeks in shortening photoperiod treatments (Partanen et al. 1998). However, because the photoperiod had to be changed abruptly from 6 h (in controlled chilling conditions) to 16 h (in forcing conditions), the seedlings and cuttings in the shortening photoperiod treatment might have received a signal to the effect that the photoperiod is lengthening. Therefore, the results of this study do not exclude the possibility that the direction of a change in the photoperiod determines the response of bud development to forcing temperatures.

In the present study, bud burst of the four youngest material groups took place in the constant short photoperiod only two to four days later than in the long (= shortening) photoperiod (Table 1). This is in accordance with the results obtained with adult Scots pine trees (Hänninen 1995). In a study carried out by Leinonen et al. (1997) in elevated temperature conditions in midwinter, however, growth onset occurred approximately at the same time in a natural short photoperiod and in an artificially lengthened 17 h photoperiod. In the study by Leinonen et al. (1997) the initial growth rate of new shoots and the rate of dehardening of needles from the previous year were higher under the lengthened than the natural photoperiod. The difference was proposed to be due to the amount of total absorbed radiation, not to the photoperiodic effect itself.

The effect of the accumulated duration of the light period on photosynthetic production might explain the observed differences in timing of bud burst between long and short day conditions, assuming that the development and development rate of the bud is dependent on the carbohydrate level. The reduced photosynthetic production and the increased respiratory loss of carbohydrates in short day conditions lead to the low levels of carbohydrates (Ögren 1997, Ögren et al. 1997). In a study carried out with white spruce (*Picea glauca* (Moench) Voss) bareroot seedlings the delayed bud burst detected in fall-lifted seedlings stored at –2 °C could be related to low carbohydrate levels (Jiang et al. 1994) and/or slow photosynthetic recovery (Jiang et al. 1995). The reason for low levels of carbohydrates in fall-lifted seedlings compared with those lifted in spring could be respiration during cold storage (Cannell et al. 1990, Ögren et al. 1997). In a another study carried out with bareroot white spruce seedlings (Wang and Zwiazek 1999) the seedlings with higher carbohydrate levels produced more roots but the carbohydrate levels did not significantly affect the timing of bud burst following planting. In our study carried out with ball seedlings, however, the accumulated carbohydrates were more likely to be used for shoot growth and bud burst than for root growth.

The warming effect of the absorbed radiation energy might also be an explanation for the observed differences in the timing of bud burst between long and short day conditions (Repo et al. 1991). The possible warming effect of the absorbed radiation energy is stronger in treatments with long photoperiod than in treatments with short photoperiod. As a result, the actual temperature sum, based on the bud temperature, may be higher in long day conditions than in short day conditions during the same time period. In natural conditions during a sunny day, the temperature in the buds of Norway spruce graft may

rise up to 7.5 °C above that of the air (Pukacki 1980). In the present study, a relatively low light level (approximately 200 μmol m^{-2} s^{-1}) was used in order to minimise the effects of light other than the photoperiodic signal effect. It has, however, been found earlier that light levels even below 140 μmol m^{-2} s^{-1} increase the bud temperature of Scots pine by about 2 °C compared to the surrounding air temperature (Repo et al. 1991).

The warming effect of the illumination on bud burst was possibly the largest in 18-year-old cuttings, because in this material group the differences in timing of bud burst between light treatments were the clearest. We estimated the presumed warming effect of the illumination on bud burst by using the differences in temperature sums and numbers of light hours and by supposing the physiological response of the bud to the temperature to be linear. According to our estimation the bud temperature of the 18-year-old cuttings in the shortening photoperiod should have been 10.5 °C higher during the light period than during the dark period in order to explain the results solely by the warming effect of illumination. According to the previous data, however, the bud temperature would have been elevated by 4 °C only at light level of 200 μmol m^{-2} s^{-1}. Thus, it seems that the warming effect of the absorbed radiation energy did not alone explain the observed differences in timing of bud burst between long and short day conditions.

In this study, the 18-year-old cuttings required a longer time for bud burst than the other groups (Table 1, Fig. 1). This refers to change in environmental responses of bud burst as trees get older and is in accordance with the results obtained in Norway spruce by Ununger et al. (1988). In the present study the differences in origin of the cuttings might also affect the timing of bud burst, in addition to age.

The results obtained from this study suggest that, in addition to temperature sum, the accumulated duration of the light period may promote bud burst of Norway spruce. This means that beside temperature, light conditions might also have an effect on bud burst in Norway spruce. The experiment used in this study could not, however, prove this effect unambiguously. Further studies concerning the accumulated duration of the light period and absorbed radiation energy are needed to explain the actual role of light conditions in the timing of bud burst.

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