# The influence of temperature on the cessation of height growth of Sitka spruce (Picea sitchensis (Bong.) Carr.) provenances

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(Received September / December 1975)

## Introduction

Sitka spruce is a native of West North America occurring in a narrow coastal belt from Kodiak Island and the Kenai Peninsula (61° N) to Mendocino County, California (39° N). Although of major importance in British forestry this species has been only recently the subject of physiological research.

The common occurrence of photoperiodic ecotypes in Northern Hemisphere tree species with a large north-south range was demonstrated by Sylven (1940) and was confirmed in Picea by Vaartaja (1959).

The decrease in daylength after mid summer is an important factor in initiating seasonal rest periods in conifers (Downs and Borthwick, 1956). Using artificial photoperiods Vaartaja (1959) showed that the critical daylength, for extension growth cessation in Sitka spruce, was greater for a northern (60° N) source than four a southern (43° N) and that the endogenous growth pattern was entirely overruled by the effects of photoperiod. This interaction between latitude of seed origin and photoperiod substantiated the presence of ecotypes in this species.

Provenance trials of Sitka spruce in the field have confirmed the photoperiodic control of apical growth cessation (Lines and Mitchell, 1966). Northern provenances, when grown in Britain, cease growth while other environmental factors remain favourable. The time of bud formation in Sitka spruce is closely correlated with latitude of seed origin and, in a nursery and glasshouse study (Burley, 1966) extended over 120 days for year-old seedlings of 47 provenances.

The regulation of the seasonal growth cycle of Sitka spruce has received less attention than other coniferous species in which continentality and altitude of seed origin have been shown to influence the photoperiodic response (Vaartaja, 1959; Irgens-Muller, 1957).

Growth and dormancy in Nonvay spruce (Picea abies (L.) Karst.) has been more widely studied (Dormling et al., 1968; Robak and Magnesen, 1970). Extension of daylength did not compensate for unfavourable temperatures in the growth of Nonvay spruce seedlings (Magnesen, 1969) and an abnormally short photoperiod reduced growth regardless of temperature. Heide (1974) found that temperatures between 12 and 24° C did not alter appreciably the critical daylength of various Norway spruce provenances but higher temperatures accelerated the short day response.

This paper reports an experiment on the interaction of temperature and photoperiod on the setting and maturation of buds in a range of provenances of Sitka spruce.

## Methods

1-year old seedlings of the eight provenances, detailed in Table 1, were potted in April 1973 and 'plunged' out of doors until midsummer. At the time of maximum natural photoperiod (19.75h on 24 June 1973) the plants were allocated randomly to treatments and transferred to four growth rooms. The plants were arranged in eight randomised blocks with 15 seedlings per provenance in each treatment.

*Table 1.* — Provenances of Sitka spruce (**I.U.F.R.O** Collection)

| I.U.F.R.O. No. | Provenance Location | Latitude N | Elevation (m) |
|---|---|---|---|
| 3022 | Dyea, Alaska | 59°50' | 0 |
| 3032 | Kitwanga, Skeena/Nass R. | 55°17' | 670 |
| 3050 | Copper Creek, Moresby Is. | 53°13' | 80 |
| 3059 | Fair Harbour, Vancouver Is. | 50°05' | 30 |
| 3061 | Vedder, Chilliwnck, H.C. | 49°12' | 30 |
| 3002 | Port Angeles, Washington | 18°15' | 110 |
| 3013 | Tillamook, N. Oregon | 45°33' | 90-120 |
| 3017 | Gold Beach, Oregon | 42°50' | 30 |

*Table 2.* — Experimental treatments in controlled environment rooms

| Temperature °C | | Humidity % | | Vapour pressure deficit (mb) | |
|---|---|---|---|---|---|
| Day | Night | Day | Night | Day | Night |
| 20 | 11 | 91 | 96 | 2.0 | 0.5 |
| 16 | 9 | 89 | 96 | 2.0 | 0.5 |
| 12 | 7 | 86 | 95 | 2.0 | 0.5 |
| 8 | 5 | 82 | 82 | 1.9 | 1.9 |

The 4 temperature treatments and associated conditions (Table 2), were selected to relate to those at the latitudes of origin and to the suggested optimal temperature for photosynthesis in Sitka spruce (Nielsen et *al.*, 1971). All temperature treatments received the same photoperiod which was progressively reduced from 19h, at the start of the experiment, by hourly decrements to 17h and then by 30 min. wk$^{-1}$. The daily illumination cycle was as follows: —

e.g. a 17h day 2.5h daylight bulbs
12h bright fluorescent light (14,000 lux at plants)
2.5h daylight bulbs
7h dark

Decrements were made in the bright period. The soil was maintained at field capacity by daily watering and additions of liquid fertilizer made twice weekly.

Height measurements and recordings of the condition of the terminal apices were made weekly. As there was considerable variation in weekly height increment within provenances, and in individual plants in successive weeks, it was desirable to have some objective criterion of growth cessation. Extension growth was considered to have ceased, when the difference between the sample means of successive measurements did not exceed 1.6 mm, which was the detection limit of any change in height (detection limit = 3 X standard deviation of repeated measurement).

*Table 3.* — **Photoperiod at time of extension growth cessation (h)**

| Treatment<br>Provenance | 8/5° | 12/7° | 16/9° | 20/11° |
|---|---|---|---|---|
| 3022 | 17 | 16 | 16 | 15.5 |
| 3032 | - | 16.5 | 15.5 | 15.5 |
| 3050 | 16 | 16 | 16 | 14.5 |
| 3059 | 16 | 16 | 16 | 15 |
| 3064 | 16 | 16 | 15 | 15 |
| 3002 | 16 | 16 | 14.5 | 14.5 |
| 3013 | 16.5 | 16 | 14 | 13.5 |
| 3017 | 16.5 | 16 | 12 | 12 |

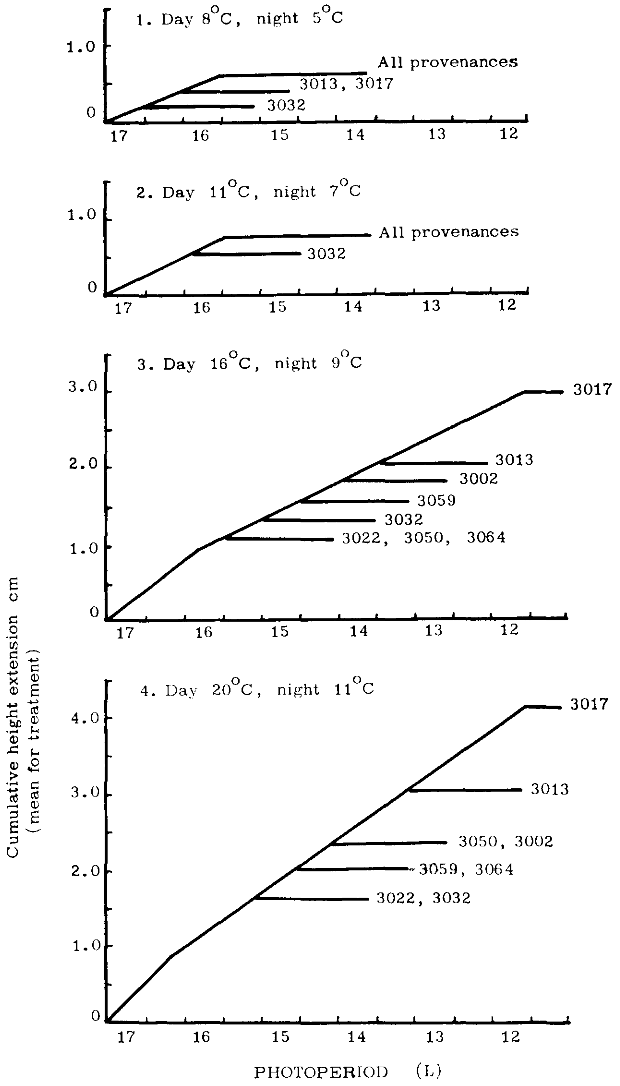

*Figure 1.* — **Interaction of temperature and photoperiod on cessation of shoot extension of Sitka spruce provenances.**

When extension growth had ceased in all provenances in all treatments the plants were removed from the growth rooms and wintered outdoors.

## Results

The effect of the temperature treatments on the duration of extension growth and the photoperiod at its cessation are given in Table 3. The interaction of temperature and photoperiod on the rate of cumulative height growth and the order of its cessation in the different provenances is shown in *Figure 1.*

At the two cooler temperature regimes (8/5° C, 12/7° C), all provenances ceased height growth when the photoperiod reached 16h, whereas growth of southern provenances continued until the photoperiod was reduced to 12h in the warmer regimes (16/9° C, 20/11° C).

Shoot extension, in the two most northerly provenances, ceased at a photoperiod of 15.5h in all temperature treatments. The southern provenances displayed a wider range of temperature effects with the cooler regimes resulting in cessation of height growth at the relatively long daylength of 16.5h.

Differences in rate of shoot extension were noted for each provenance in the four temperature treatments. This, coupled with the differences in time of growth cessation, accounts for the large variation in height attained between treatments. Although the limit of detection of height increment provided a useful criterion of growth cessation for each provenance sample, many plants continued to make additional extensions during the remainder of the experiment. These additional increments are shown in *Table 4.* The 20/11° C treatment resulted in the greatest height increments due to greater growth rates and, particularly, longer periods of growth.

To take the variation in successive height increments of individual plants into account an analysis of variance was performed in which the cessation of growth for each plant was assumed to occur when its weekly increment first fell below 1.6 mm.

| Source of variation | DF | SS | MS | VR |
|---|---|---|---|---|
| Provenance | 7 | 102.3 | 14.6 | 5.0 |
| Temperature | 3 | 685.4 | 228.5 | 79.0 |
| Interaction | 20 | 484.9 | 24.2 | 8.4 |
| Residual | 387 | 1119.1 | 2.9 | |
| Total | 417 | 2391.8 | 5.7 | |

All the variance ratios are highly significant ($p \leqslant 0.01$) but the overriding influence of the temperature treatments on the time of cessation is clear.

The mean duration of growth in weeks after the summer solstice, based on individual plants, is given by provenance and temperature treatment in *Table 5.* The provenances show a latitudinal trend in termination of extension growth comparable with the field results of LINES and MITCHELL (1966), while the duration of growth doubles between the coolest and warmest treatments.

*Table 4.* — **Mean height growth of provenances (cm)**

| Treatment | 8/5° | | 12/7° | | 16/9° | | 20/11° | |
|---|---|---|---|---|---|---|---|---|
| Provenance | a | b | a | b | a | b | a | b |
| 3022 | 0.6 | 0.9 | 1.2 | 1.6 | 1.8 | 1.9 | 2.4 | 2.5 |
| 3032 | 0.0 | 0.3 | 0.5 | 0.8 | 1.8 | 2.0 | 1.9 | 2.0 |
| 3050 | 1.3 | 1.5 | 1.2 | 1.7 | 1.7 | 2.4 | 2.7 | 2.8 |
| 3059 | 1.2 | 1.4 | 1.7 | 2.3 | 2.3 | 2.6 | 3.1 | 3.4 |
| 3064 | 1.1 | 1.4 | 1.2 | 1.9 | 1.6 | 2.2 | 2.6 | 2.8 |
| 3002 | 1.0 | 1.2 | 1.4 | 1.9 | 2.5 | 2.7 | 3.2 | 3.3 |
| 3013 | 0.7 | 1.2 | 1.5 | 2.2 | 2.4 | 2.6 | 3.7 | 3.9 |
| 3017 | 0.8 | 1.2 | 1.4 | 2.3 | 3.0 | 3.0 | 4.8 | 4.8 |

a) when weekly extension no longer detectable.

*Table 5.* — **Mean duration of height growth (weeks) for individual plants**

| Treatment<br>Provenance | 8/5$^{\circ}$ | 12/7$^{\circ}$ | 16/9$^{\circ}$ | 20/11$^{\circ}$ | Overall Mean |
|---|---|---|---|---|---|
| 3022 | 3.38 | 5.50 | 4.86 | 5.83 | 4.89 |
| 3032 | 3.02 | 4.39 | 5.61 | 5.18 | 4.55 |
| 3050 | 5.00 | 5.20 | 6.07 | 6.20 | 5.62 |
| 3059 | 4.67 | 5.20 | 6.53 | 6.40 | 5.02 |
| 3064 | 4.13 | 4.14 | 5.27 | 6.53 | 5.70 |
| 3002 | 4.20 | 5.46 | 5.67 | 7.60 | 5.73 |
| 3013 | 3.54 | 4.79 | 5.73 | 8.47 | 5.63 |
| 3017 | 2.51 | 4.67 | 4.58 | 12.25 | 6.00 |
| Overall Mean | 3.84 | 4.93 | 5.56 | 7.18 | |

Bud development was enhanced by the higher temperatures; terminal buds becoming visible 1—3 weeks after height growth ceased in the 20/11$^0$ C treatment and 2—6 weeks later in the 16/9$^0$ C treatment. In the two cooler treatments buds could only be detected visually 8—9 weeks after cessation of growth.

The influence of the different temperature regimes during bud maturation on flushing in the spring of 1974 was recorded in the open. Breaking of bud dormancy followed a latitudinal trend from northern to southern provenances, while the northern provenances subjected to the cooler bud maturation temperatures (also the longest periods after bud development) flushed first. Southern provenances flushed up to 1 month later and displayed greater variation between treatments.

## Discussion and Conclusions

Bud formation in Norway spruce tends to occur slightly earlier in nursery than in glasshouse grown plants and Dormling (1973) attributes this to a temperature effect once a critical night length has made the plants receptive to lower temperatures. In Magnesen's (1971) experiments some Norway spruce of southerly provenances (Ca. 48$^0$ N) showed no response to short periods of lowered night temperatures until late summer, when bud formation was enhanced. In the experiment reported here, although the temperature regimes were constant and did not include night temperatures below 5$^0$ C, they had marked effects on the photoperiod at which apical shoot growth ceased. As the experiment began at midsummer, it is unlikely that any photoperiodic conditioning could have taken place yet the lower temperature regimes resulted in no further shoot extension after the photoperiod had reached 16h. An exception might be the Kitwanga provenance (3032) from a high elevation (670 m) at latitude 55$^0$ N in an area of introgression with white spruce (*P. glauca* (Moench.) Voss.). At the start of the experiment a high proportion of these plants had already formed buds by the longest photoperiod of 19.75h in the Edinburgh area (56$^0$ N), indicating an adaptation to a short warm season. A similar instance for a Norway spruce provenance from latitude 64$^0$ N is discussed by Heide (1974).

The plants used in this experiment were lifted from the same bed of a nursery provenance trial and potted before flushing in their second year. They thus had buds which would be extended into shoots of a predetermined length after flushing in early May and the experiment was designed to start before extension growth would normally be expected to cease. Growth continuing beyond that predetermined in the bud has been termed 'free' and shown to occur in the early years of several species and has recently been demonstrated for 4-year old Black spruce (*Picea mariana* (Mill) B.S.P.) provenances in Canada (Pollard and Logan 1974). These authors further demonstrated (1975) that 'free' growth could be induced in the second growth cycle of Black spruce by a high temperature treatment (25$^0$ C) at photoperiods in excess of 12h. It seems probable that the Sitka spruce provenances in this experiment at the higher temperatures were in 'free' growth.

This is supported by a comparison of duration of growth between these 2-year seedlings and two vegetatively propagated clones of older Sitka spruce included in the experiment. Neither clone, of probable Queen Charlotte Island provenance, grew for more than 3—4 weeks in any treatment indicating that they had little or no capacity for free growth in these conditions.

From *Table 3* it appears that the highest temperature had the greatest effect on duration of growth and that it was related inversely to latitude of origin. Conversely the southern provenances seem to be more sensitive to low temperatures (*Table 5*) than those origins from the middle of the range. These results support Pollard and Logan's contention that 'free' growth is environmentally controlled.

In general the results show that photoperiod does not control cessation of apical shoot extension in Sitka spruce absolutely but that higher temperatures may be important in shortening the critical daylength while low temperature appears to upset the commonly accepted latitudinal relationship between photoperiod and growth cessation.

Bud development to the stage where it becomes visible is clearly affected by the ruling temperature regime and the results with Sitka spruce are similar to those published by Magnesen (1969) for Norway spruce. At low temperatures the process of development is slower.

Flushing, in the spring following the experiment, followed the general pattern, described by Burley (1966), of northern provenances first with greater variation in the southerly provenances. This makes it difficult to assign any effects to the experimental treatments although it appeared that low temperatures advanced flushing dates.

Of necessity controlled environment experiments are conducted on newly germinated seedlings, or as in this case, young transplants which are still capable of free growth in suitable conditions. Older trees tend to have predetermined annual growth and this age effect and the relationship between meristems responsible for shoot extension, leaf initial formation and cambial activity require further investigation before results of controlled environment experiments can be extrapolated to field conditions.

## Acknowledgements

The authors are grateful to the Forestry Commission for provision of growth room facilities and supply of the plants used.

## Summary

The observed time of bud formation in Sitka spruce is closely linked with the latitude of seed origin and shows a north-south progression. The effect of 4 different temperature regimes on cessation of apical shoot extension has been investigated in controlled environments.

Eight provenances covering the latitudinal range of the species were transferred to growth rooms, at mid summer

1973, where day/night temperatures were 20/11° C, 16/9° C, 12/7° C and 8/5° C respectively. Photoperiods were reduced progressively at 0.5h wk$^{-1}$ while weekly height measurements were made to determine growth cessation.

At the cooler temperatures shoot extension in all provenances ceased at 16h, whereas the higher temperatures allowed growth in southern provenances to continue until a 12h photoperiod was reached. The northern-most provenances ceased growth at 15.5h in all treatments. It was concluded that the critical photoperiods for shoot extension could be markedly affected by temperature in southern provenances but less so in those from the north. Bud development was delayed by low temperature but this appeared to advance flushing dates in the following year.

*Key words:* Provenance, Sitka spruce, growth cessation, temperature, photoperiod.

### Zusammenfassung

Im Jahre 1973 wurden in Schottland 1jährige Sämlinge von *Picea sitchensis* (Bong.) Carr. aus 8 Provenienzen, von Oregon bis Alaska = 42° 50' bis 59° 50' nördlicher Breite und 0 bis 670 m Seehöhe, auf die Beendigung des Triebwachstums während der Vegetationsperiode untersucht. Die Behandlung erfolgte in Klimaräumen unter vier verschiedenen Tag/Nacht Temperaturbedingungen ab 24. Juni. Die Belichtungsdauer wurde danach fortschreitend um 30 Min. wöchentlich gesenkt.

Die nördlichen Provenienzen stellten in allen Behandlungsarten das Triebwachstum ab einer Tageslänge unter 15,5 Stunden ein, während die südlichen Provenienzen bei genügend hoher Temperatur das Wachstum bis herunter zu 12 Stunden fortsetzten.

### References

Burley, J.: Provenance variation in growth of seedling apices of Sitka spruce. Forest Sci. **12** (2), 170—4 (1966 a). — Burley, J.: Genetic variation in seedling development of Sitka spruce, *Picea sitchensis* (Bong.) Carr. Forestry **39** (1), 68—94 (1966 b). — Dormling, I., Gustafsson, A. and Wettstein, D. von: The experimental control of the life cycle in *Picea abies* (L.) Karst. I. Some basic experiments on the vegetative cycle. Silvae Genet. **17**, 44—6 (1968). — Dormling, I.: Photoperiodic control of growth and growth cessation in Norway spruce seedlings. I.U.F.R.O. Div. 2 Symp. Dormancy in trees, Kornik, 1973. — Downs, R. J., Borthwick, H. A.: Effects of photoperiod on growth of trees. Bot. Gaz. **117**, 310—26 (1956). — Heide, O. M.: Growth and dormancy in Norway spruce ecotypes *(Picea abies)*. I. Interaction of photoperiod and temperature. Physiologia Plant. *30* (1), 1—12 (1974). — Irgens-Moller, H.: Ecotypic response to temperature and photoperiod in Douglas fir. Forest Sci. 3, 79—83 (1957). — Lines, R. and Mitchell, A. F.: Differences in phenology of Sitka spruce provenances. Rep. Forest. Res. 1965. For. Commn. Lond. 178—84 (1966). — Magnesen, S.: (Ecological experiments regarding growth termination in seedlings of Norway spruce. 1. Effect of daylength and temperature conditions during growth season). Meddr. Vestland. forstl. ForsStn. **14** (1), 1—50 (1969). — Magnesen, S.: (2. Effect of autumn temperature and periods of low nigth temperature). Ibid. **14** (4), 227—69 (1971). — Nielsen, R. E., Ludlow, M. M. and Jarvis, M. G.: Photosynthesis in Sitka spruce *(Picea sitchensis* (Bong.) Carr.). II. Response to temperature. J. Appl. Ecol. **9** (3), 721—45 (1972). — Pollard, D. F. W. and Logan, K. T.: The role of free growth in the differentiation of provenances of Black spruce, *Picea mariana* (Mill.) B.S.P. Can. J. Forest Res. **4** (3), 308—311 (1974). — Pollard, D. F. W., and Logan, K. T.: The free growth phenomenon. Paper presented to I.U.F.R.O. Division 2 Meeting on Physiological Genetics, Edinburgh July 1975. — Robak, H. and Magnesen, S.: Contribution to the knowledge of the ecology of growth termination in spruce seedlings of Norwegian and Central European provenances. Silvae Genet. **19**, 188—90 (1970). — Sylven, N.: Long day and short day types of Swedish forest trees. Svensk Papptidn. **43**, 317—24; 332—42 (1940). — Vaartaja, O.: Evidence of photoperiodic ecotypes in trees. Ecol. Monogr. **29** (2), 91—111 (1959).

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# Pinus nigra Provenance Variation and Selection in New Zealand

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(Received September 1975)

### Introduction

*Pinus nigra* was one of the first exotic timber species to be widely used in New Zealand. Plants were being sold 20—30 years prior to the inception of State plantations in 1896—98 (Weston, 1957). Many forms of the species were brought to New Zealand, their origins being mostly unrecorded. However, a distinction was made at the outset between provenances of two general types, *P. nigra (austriaca)* and *P. nigra (laricio)*. These subsequently became known among foresters as "austriaca" and "Corsican" pines respectively.

The first use of *P. nigra* in State plantations was as a "nurse" species, for which it was highly rated because of its reliability and health during and after establishment. By 1909, "austriaca" was second and "Corsican" third behind European larch in total area planted in New Zealand. As these early plantings developed, broad differences between the two types became increasingly appreciated, in particular the slower growth and coarser branching habit of "austriaca", which was generally dropped from planting programmes after 1925 in favour of "Corsican" pine, radiata pine, ponderosa pine, and Douglas fir. In contrast, plantings of "Corsican" pine were increased with the assistance of substantial bulk seed imports. During the period 1927—1951, 1422 kg of seed was collected from the Dumgree plantation in Marlborough in the South Island of New Zealand, and 2610 kg was imported from Corsica.

In 1970, *P. nigra* stands amounted to 30 000 ha (New Zealand Forest Service, 1970) making it in area the third ranking exotic species after radiata pine and Douglas fir. Since the late 1960s the area of *P. nigra* has steadily declined as mature stands have been clearfelled for the local sawn timber and pole market, and for export as logs and chips. Further planting has almost ceased meanwhile due mainly to high susceptibility of "Corsican" pine to *Dothistroma pini* needle blight, and uneconomic growth rates compared with radiata pine.

Provenance trials of *P. nigra* were planted in New Zealand in 1956—58 to systematically study the variation in

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