# INFLUENCE OF EXTENDED PHOTOPERIOD ON GROWTH OF WHITE AND ENGELMANN SPRUCE SEEDLINGS IN COASTAL BRITISH COLUMBIA NURSERIES

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Abstract.--Current knowledge of the effects of photoperiod on vegetative growth of northern hemisphere tree species is reviewed. The effects of extended daylength versus night interruption, minimum light intensity required and interaction with low night temperatures on growth of 1-0 white spruce (*Picea glauca* [Moench] Voss) and Engelmann spruce (*P. engelmannii* [Parry]) seedlings are discussed. Photoperiod regimes currently used for spruce in British Columbia nurseries are described.

Résumé.--On fait un survol des connaissances actuelles sur les effets de la durée d'éclairement sur la croissance végétative des arbres de l'hémisphère nord. On discute des effets de la prolongation de la durée du jour en regard de l'interruption de la nuit, de l'intensité lumineuse minimale requise et de son interaction avec les basses températures au cours de la nuit sur la croissance de semis 1-0 d'épinette blanche (*Picea glauca* [Moench] Voss) et d'épinette d'Engelmann (*P. engelmannii* [Parry]). On décrit les photopériodes couramment employées pour l'épinette dans les pépinières de la Colombie-Britannique.

## I. PHOTOPERIODISM AND TREE SEEDLING GROWTH - A REVIEW

The effect of photoperiod on tree seedling growth has been known for a long time. The following section reviews the subject for participants in this symposium, and provides background information for the research done in British Columbia which is described in section II of this paper.

### Daylength

The growth and development of many tree species is regulated by photoperiod. In general, continuous light and long days promote increased height growth, accompanied by increased diameter and dry weight. Bud determination, Lammas growth, and root development are also affected by long days in some species. Short days of 8-9 hours usually promote the cessation of height growth, and reduce leaf size and number, and root growth.

Dormancy may also be affected by photoperiod. Continuous light and/or long days may cause the breaking of dormancy. Short days generally induce the formation of buds and the onset of dormancy. More detailed information on the above, by species, is provided in Table 1.

### Provenance and Altitude

Provenance and geographic (topographic) location modify the effect of photoperiod. Under similar conditions of temperature and photoperiod, southern provenances of a species grow better than northern ones (Jester and Kramer 1939; Vaartaja 1954, Magnesen 1969, 1971). Northern provenances have longer critical daylengths (Table 2).

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Table 1. Effects of daylength on tree growth.

| Common name | Scientific name | Day length[a] | Effects | Authority |
|---|---|---|---|---|
| European silver-fir | *Abies alba* Mill. | LD | increased height | Leibundgut and Heller (1960) |
| Sakhalin fir | *A. sachalinensis* Fr. Schm. | LD | increased height | Satoo (1961) |
| | | LD | promoted lammas | Shibakusa and Kimata (1975) |
| | | SD | fewer leaf primordia | Asakawa et al. (1974) |
| Gray birch | *Betula lutea* Michx. | SD | induced dormancy | Loveys et al. (1974) |
| Paper birch | *B. papyrifera* Marsh. | SD | stopped growth | Powell (1976) |
| European white birch | *B. pendula* Roth | SD | induced dormancy | Kelly and Mecklenburg (1978) |
| European larch | *Larix decidua* Mill. | LD | increased growth | Simak (1970) |
| Norway spruce | *Picea abies* (L.) Karst. | SD | induced dormancy | Robak (1962) |
| Engelmann spruce | *P. engelmannii* (Parry) | LD | increased height | Arnott (1974) |
| White spruce | *P. glauca* (Moench) Voss | CL | increased height | Fraser (1962) |
| | | LD | no height increase | Vaartaja (1957) |
| | | LD | increased height | Arnott (1974) |
| | | SD | induced dormancy | Pollard (1974) |
| Black spruce | *P. mariana* (Mill.) B.S.P. | CL | increased height | Fraser (1962) |
| Sitka spruce | *P. sitchensis* (Bong.) Carr. | LD | increased root growth | Stahel (1972) |
| | | SD | decreased height | Stahel (1972) |
| Jack pine | *Pinus banksiana* Lamb. | LD | no height increase | Vaartaja (1957) |
| Lodgepole pine | *P. contorta* var. *latifolia* Engelm. | CL | increased height, weight | Wheeler (1979) |
| Japanese red pine | *P. densiflora* Sieb. & Zucc. | CL | increased height | Ikemoto and Shidei (1963) |
| | | SD | induced dormancy | Ikemoto and Shidei (1963) |
| Austrian pine | *P. nigra* Arnold | CL | increased height | Read and Bagley (1967) |
| | | LD | increased height | Read and Bagley (1967) |
| Ponderosa pine | *P. ponderosa* Laws. | CL | increased height | Downs and Piringer (1958) |
| | | CL | increased height | Read and Bagley (1967) |
| | | LD | increased height | Read and Bagley (1967) |
| Eastern white pine | *P. strobus* L. | CL | increased root weight | Fowler (1961) |
| | | LD | increased height | Fowler (1961) |
| Scots pine | *P. sylvestris* L. | CL | increased height | Jester and Kramer (1939) |
| | | CL | increased height | Vaartaja (1951) |
| | | CL | no height increase | Balut and Zelawski (1955) |
| | | CL | broke dormancy | Wareing (1956) |
| | | LD | increased height | Jester and Kramer (1939) |
| | | LD | increased height | Downs and Borthwick (1956) |
| | | LD | increased diameter | Wareing (1951) |
| | | LD | induced dormancy | Wareing (1956) |
| | | SD | reduced growth | Jester and Kramer (1939) |
| Loblolly pine | *P. taeda* L. | CL | increased height | Downs & Piringer (1958) |
| Douglas-fir | *Pseudotsuga menziesii* (Mirb.) Franco | LD | increased height | Lavender et al. (1968) |
| | | SD | induced dormancy | Lavender et al. (1968) |
| Giant sequoia | *Sequoia gigantea* (Lindl.) Decne. | SD | reduced height | Skok (1961) |
| Eastern white cedar | *Thuja occidentalis* L. | LD | increased height | Bagley and Read (1960) |
| Western red cedar | *T. plicata* Donn | LD | no height increase | Vaartaja (1957) |
| Western hemlock | *Tsuga heterophylla* (Raf.) Sarg. | SD | induced dormancy | Cheung (1973) |

[a] CL = Continuous light  LD = Long days  SD = Short days.

Table 2. Critical daylengths for northern and southern provenances of several species.

| Species | Critical daylength (hr) Northern | Critical daylength (hr) Southern | Authority |
|---|---|---|---|
| *Picea abies* | 20 | 14 | Dormling et al. (1968) and Håbjørg (1978) |
| *Picea sitchensis* | 14 | 10 | Pollard et al. (1975) |
| *Tsuga canadensis* (L.) Carr. (Eastern hemlock) | 16 | 15 | Nienstaedt and Olson (1961) |

As the critical daylength is approached, the variation within a provenance increases (Vaartaja 1959). The longer critical daylength observed for northern provenances indicates that initiation of budset in nature occurs at an earlier date and that the time required for the yearly vegetative growth cycle is shorter. In Norway spruce, southern European provenances have a 15-week cycle while northern ones set bud in 13 weeks (Dormling et al. 1968). It has been suggested (Simak 1975) and proven (Watt and McGregor 1963) that the use of supplementary illumination to meet the critical daylength requirement enables the growing of trees from northern latitudes in nurseries much farther to the south with good results.

The elevation at which the provenance is found also affects the response to photoperiod. High altitude provenances have longer critical daylengths for the cessation of apical growth and formation of terminal buds than do those from low altitudes (Holzer 1960, 1962; Simak 1970; Heide 1974; Habjorg 1978). A difference of 150 m in provenances of loblolly pine was enough to make a difference in growth under long days (McGregor and Kramer 1957).

## Intermittent Light

### One interruption

It has been known for a long time that 1 hr of low-intensity illumination in the middle of the dark period will delay the onset of dormancy in conifer seedlings. Wareing (1956) has described this for Scots pine, Vaartaja (1957) for jack pine and white spruce, Skok (1962) for giant sequoia and Irgens-Moller (1962) for Douglas-fir. An experiment comparing 10-hr days with 9.5-hr days plus 0.5-hr light at night showed that jack pine and lodgepole pine attained twice the height, total dry weight, leaf weight and root weight, and showed increased absorption and utilization of nitrogen when given the supplemental light at night (Giertych and Farrar 1961).

### Repeated interruption

As a result of research it has been found that repeated short bursts of light *throughout* the dark phase are as effective as long days or a 1-hr night break for maintaining vegetative growth in conifer seedlings (McCreary et al. 1978). Tinus (1970) initially found that 323 lux of incandescent light given 3% of the time was sufficient to maintain growth of ponderosa pine and blue spruce *(Picea pungens* [Engelm.]), provided that no dark period exceeded 30 min. White spruce and Engelmann spruce given 1600 lux of incandescent light at different frequencies throughout the dark period responded best to a light break of 2 min for every 30 min of darkness (Arnott 1974) which was also found to delay the onset of terminal resting buds of mountain hemlock *(Tsuga mertensiana* [Bong.] Carr.), Noble fir *(Abies procera* [Rehd.]) and amabilis fir *(Abies amabilis* [Dougl.] Forbes) (Arnott 1976).

## Quality and Intensity of Light

### Quality of light

Many investigators have experimented with the quality and intensity of supplemental light required to extend the photoperiod for tree seedlings (Asakawa et al. 1974). Several experiments have compared the effectiveness of fluorescent versus incandescent supplemental light to extend the photoperiod for tree seedlings (Downs and Borthwick 1956, Downs 1957). While it has been demonstrated that fluorescent light does stimulate growth when used for supplemental photoperiodic lighting (Vaartaja 1957, 1959), incandescent light is generally more effective, as Downs and Piringer (1958) found for pines.

The spectral quality of the light supplement has a marked effect on seedling growth (Ceschi 1965). Using both red and far-red light to interrupt the dark period at various times, for various lengths of time, Dinus (1968) found that red light enhanced growth, leaf size, and leaf number of Douglas-fir, and the degree of response varied directly with the length of treatment. There was a small effect with a 2 min interruption, a better effect with 5 min and the best effect with a 30 min exposure. The effect also increased as the treatment approached the middle of the dark period. Far-red light also increased growth, but exposure of less than 15 min proved ineffective in preventing dormancy.

The use of alternative types of lights, other than fluorescent or incandescent, is not widely reported. Sodium vapor lamps have been used effectively to extend the photoperiod of Sitka spruce (Russell 1974, Johnstone and Brown 1976), mountain hemlock, amabilis fir, white and Engelmann spruce (Arnott 1979).

### Intensity of light

There is a wide range in effective light intensities which will maintain vegetative growth in tree species (Table 3). There is also a strong interaction between the intensity of supplemental light used to extend daylength and the latitudinal source of the species. Three populations of European white birch *(Betula pubescens* Ehrh.) from latitudes 70°20', 63°20' and 56°20' had critical light intensities of 250-500, 100-250 and 15 lux, respectively. Thus, the northern populations required higher light intensities than the southern ones (Habjorg 1972).

Light intensity also interacts with night temperature (Habjorg 1972). The effect of light intensity is more pronounced at low than at high night temperatures. At a night temperature of 8°C, an increase in light intensity from 15 to 500 lux led to an increase in dry weight from 1.4 to 2.7 g per plant. The corresponding increase in dry weight at 13 and 18°C night temperatures was from 1.8 to 2.9 and from 2.0 to 2.7 g per plant, respectively. In Norway spruce, Magnesen (1969) found that short days overruled temperature in the induction of dormancy. Some species are sensitive to a very slight stimulus, and the effect of the light intensity is on the degree of elongation of the cotyledons and primary needles (Kozlowski and Borger 1971).

## Mode of Action

Wareing (1949, 1950, 1951, 1956), in a series of experiments using Scots pine, laid

Table 3. Effective light intensities to extend photoperiod for several species.

| Species | Intensity (lux) | Authority |
|---|---|---|
| *Abies sachalinensis* | 1000 | Satoo (1961) |
| *A. amabilis* | 20 | Arnott (1979) |
| *Betula pubescens* | 15-500 | Håbjørg (1972) |
| *Larix laricina* | 40-110 | Simak (1975) |
| *Picea abies* | 1000 | Simak (1975) |
| *P. engelmannii* | 20-40 | Arnott (1979) |
| *P. glauca* | 80 | Arnott (1979) |
| | 400 | Tinus and MacDonald (1979) |
| *P. pungens* | 400 | Tinus and MacDonald (1979) |
| *P. sitchensis* | 7000 | Johnstone and Brown (1976) |
| | 6000 | Russell (1974) |
| *Pinus contorta* | 400 | Tinus and MacDonald (1979) |
| *P. densiflora* | 120 | Ikemoto and Shidei (1963) |
| *P. ponderosa* | 215-2150 | Read and Bagley (1967) |
| | 400 | Tinus and MacDonald (1969) |
| *P. strobus* | 270-4300 | Fowler (1961) |
| *P. sylvestris* | 40-1000 | Simak (1975) |
| | 220 | Cathey and Campbell (1975) |
| *Pseudotsuga menziesii* | 100 | McCreary et al. (1978) |
| *Tsuga heterophylla* | 400 | Owston and Kozlowski (1976) |
| *T. mertensiana* | 80 | Arnott (1979) |

the foundations of the currently accepted theory to explain the effects of photoperiod on growth and cambial activity. He attributed the effects to the production and availability of auxin, noting that low light intensities were enough to cause a response. A growth promoter, produced in the light, was balanced by some inhibitor produced in the dark, provided that the dark period was longer than 4 hr. Wareing's 1951 hypothesis was that "when the daily dark period exceeds 4 hr, there is a gradual accumulation of an inhibitor which promotes dormancy, and that when the duration of the dark period is less than 4 hr, there is a gradual reduction in the inhibitor and the suppression of dormancy."

The "Beltsville group" of the USDA Agriculture Research Service, including Hendricks, Borthwick, Parker, and others, did much of the basic research that led to the currently accepted explanation of the photoperiodic response of plants and the mechanism controlling it (Anon. 1961). These workers established that the part of the spectrum governing the inhibition of flowering in soybean *(Glycine sofa)* and cockelbur *(Xanthium* sp.) plants is from about 580 to 720 nm, i.e., the red light band. In further work on germination of lettuce seed the group found that germination was sensitive to the same wavelengths as those affecting flowering in the above plants. Red wavelengths promoted germination; far-red wavelengths inhibited it. They determined that a pigment, which they called phytochrome, was responsible for controlling these physiological responses. This light-sensitive protein converts to an active form, called Pfr, when exposed to red light (660 nm) and this prevents dormancy initiation. Far-red light (735 nm) reverses the effect of the red light and converts the phytochrome to the inactive form called Pr. It was discovered that phytochrome also reverts slowly to the inactive form in the dark. In addition to preventing dormancy, active phytochrome retards stem elongation as Meijer (1959) found when exposing certain plants to red light. Studies of the inhibitor-promoter mechanism in Douglas-fir by Dinus (1968) led him to conclude that• the active pigment Pfr was responsible for the prevention of dormancy in these tree seedlings. Plant growth responses were attributable to the levels of Pfr activity and not to their concentration. Dinus (1968) also found that responses of Douglas-fir to 30 and 55 min of far-red light resembled those of red light. Apparently, excessive far-red light reversed the normal photoreaction of phytochrome and caused the accumulation of the active form (Pfr) of the pigment.

As Tinus and MacDonald (1979) point out, "there are several important differences between light required for photosynthesis and that required for dormancy prevention. For the latter, wavelengths shorter than 550 nm are of no value, and wavelengths between 700 and 770 nm reverse the effect of red light. As red light intensity increases from zero, there is a threshold below which there is no growth response. Above the threshold, height growth increases rapidly and then tapers off at an upper limit above which there is no further response."

Cathey and Borthwick (1964) had shown that the conversion of the phytochrome from Pr to Pfr was influenced by the filtering action of chlorophyll and by anatomical differences in the leaves. Habjorg (1972) found that the northern sources of birch had a higher chlorophyll content than the southern ones, and as a result, less radiation would penetrate the interior of their thick, firm leaves. As the Pfr in these thick leaf cells would be far below that produced in the thinner leaves from the southern sources, Pfr would revert to its inactive form sooner, and this would lead to the induction of growth cessation. Habjorg (1972) concluded that this may be the reason for the higher light intensities required to maintain growth of the northern populations of birch.

## Seedlings More Than One Year Old

Much of the research described above deals with the effects of photoperiod on seedlings during their first year of growth. The effects of extended photoperiod on older seedlings are varied. Scots pine given supplemental light in their second growing season showed an increase in leaf length and internode extension in response to long days, but there was no effect on leaf number (Wareing 1950). If a long day treatment is begun after leaf elongation has ceased in the second year, cambial activity is continued, but if the seedlings have below average vigor, there is no response (Wareing 1949). Japanese red pine given continuous light in August and September of the second year showed increased height and fresh weight in response to treatment (Ikemoto and Shidei 1966). Nagata (1967) noted that in second year Japanese red pine only internode extension was affected by photoperiod. Continuous light of 250 lux slowed early bud burst in the second year but enhanced bud development of this species (Nagata 1968).

### Cold Hardiness

The induction of frost hardiness has often been linked to photoperiod. Alden and Hermann (1971) summarized research on the mechanism of the response.

The processes of dormancy and hardening seem related, in that apical bud development, a first sign of dormancy, must precede the low temperature treatment. Presumably, the conversion of amino acids and peptides to soluble proteins marks the hardy plants, and indeed some photosynthates may be required for this, as plants grown in the dark do not develop hardiness even though they are exposed to low temperatures. The hypothesis is, therefore, that some phytochrome-like compound reacts to promote hardiness. Furthermore, photoperiod must affect the development of hardiness because, if the dark period is broken, then hardiness may not develop, even though the trees were exposed to hardening temperatures of 5°C (McCreary et al. 1978), and long days may inhibit the hardening process even if temperatures are low (Christersson 1978). The process of dehardening may, however, be almost wholly controlled by temperature (Aronsson 1975). The above is not meant to be an exhaustive review of literature on cold hardiness as the subject will be covered in depth by others at this symposium.

## II. PHOTOPERIOD EXPERIMENTS ON WHITE SPRUCE AND ENGELMANN SPRUCE SEEDLINGS IN BRITISH COLUMBIA

### Continuous Versus Intermittent Light

When northern latitude and/or high-elevation provenances of the white/Engelmann spruce complex are grown in low-elevation nurseries in southern (coastal) British Columbia, the seedlings become dormant early in the growing season. The literature review above indicates that trees can be kept in a state of continuous growth by extending the daylength with low-intensity artificial light or by interrupting the dark period with light of low intensities. An experiment was undertaken to determine the minimum duration of dark period interruption required to maintain growth of four provenances of white/Engelmann spruce (Table 4), comparing such treatments with the growth response obtained using extended and natural daylengths in an outdoor container nursery at Victoria, British Columbia (Lat 48°28'N).

Details of the experiment have been described elsewhere (Arnott 1974) and are summarized as follows:

Five photoperiod treatments were evaluated, viz:

a) 2 min light every 30 min darkness
b) 1 min light every 10 min darkness
c) 15 sec light every 6 min darkness
d) An 18-hr photoperiod (natural daylength extended by supplemental light)
e) Control (natural daylength)

The supplemental incandescent light source consisted of two 300-watt incandescent reflector flood lamps suspended above the seedlings to provide a light intensity of 1600 lux. Seeds were sown on 10 March in BC/CFS styroblocks. The photoperiod experiment, which began on 20 April 1972, was conducted in an unheated shelterhouse.

Height growth of all four spruce provenances was significantly greater under the four supplemental light treatments than in the control, and interrupting the darkness with 2 min of light every 30 min was the most effective treatment. Within the interrupted dark treatments, a) produced significantly greater shoot weight but not root weight. All light treatments produced significantly greater shoot and root weights than the control.

Cessation of height growth and formation of terminal resting buds occurred as early as mid-May for control treatment e) of proven-

Table 4. Geographic origin of the four spruce provenances used in the 1972 experiment (Arnott 1974).

| Provenance no. | B.C. Min. For. seedlot no. | Latitude | Longitude | Elevation (m) | Location |
|---|---|---|---|---|---|
| 1 | 779 | 54°07' | 122°03' | 640 | Aleza Lake |
| 2 | 1548 | 53°36' | 122°07' | 1220 | Jerry Cr. |
| 3 | 905 | 51°36' | 119°54' | 430 | Birch Island |
| 4 | 1675 | 49°13' | 117°41' | 1770 | China Cr. |

ante 4, giving the trees a rosette appearance. Supplemental light delayed formation of these terminal buds, and maintained leaf production and internodal growth, thereby producing a 1-year-old seedling suitable for outplanting. Even within the light treatments, terminal buds appeared on some of the spruce provenances, particularly No. 4, before the end of the treatment period. Also, these terminal buds did not necessarily signify a continuous dormancy, as some flushed intermittently throughout the experiment. Height growth had practically ceased on all seedlings given supplemental light 14 days after the lights were turned off on 31 August.

In conclusion, the northern and high-elevation provenances (4, 2, and 1 - Table 4) grown at this southern, low-elevation nursery formed terminal resting buds very early in the growing season and ceased shoot growth unless given extended photoperiod treatments. At an intensity of 1600 lux, interrupting the darkness 2 min out of every 30 (i.e., 6.6% of the time) provided the best growth response for all provenances.

## Minimum Light Intensities

The initial experiment above with white and Engelmann spruce used a supplemental light intensity of 1600 lux. However, the literature indicated that a wide range of light intensities was required for effective supplemental lighting. Therefore, an experiment was conducted in 1976 to determine the minimum light intensity required to maintain shoot growth of these species (Arnott 1979).

A 400-watt high-pressure sodium vapor lamp was used as the supplemental lighting source because, from an operational perspective, lights with higher luminous intensities are more desirable as they cover a greater nursery area. Spectral energy distribution of the sodium vapor source peaks in the 500-625 nm range which is considered to be close to the optimum for producing the effect of long photoperiod (Bickford and Dunn 1972).

The light experiment began on 24 May 1976 in the British Columbia Ministry of Forests shadehouse nursery at Duncan on southern Vancouver Island (Lat. 48°47'N). At 20 m above sea level, the nursery has a mild climate and long growing season (273 frost-free days) and is one place at which the Ministry grows white and Engelmann spruce seedlings for reforestation in the interior of the province.

The light source was positioned 2 m above the ground at one end of the shadehouse nursery. The light was tilted downward 3° toward the seedlings. The first seven light-treatment stations were positioned along the length of the shadehouse nursery at 6 m intervals in a direct line away from the light source. As a result of this linear distribution the light intensity at each station was progressively less with increasing distance from the lamp as shown below.

| Treatment station | Distance from light source (m) | Light intensity (lux) |
|---|---|---|
| 1 | 6 | 220 |
| 2 | 12 | 80 |
| 3 | 18 | 40 |
| 4 | 24 | 20 |
| 5 | 30 | 12 |
| 6 | 36 | 8 |
| 7 | 42 | 5 |
| 8 (control) | - | 0 |

The control treatment was located in an adjacent corner of the same shadehouse where it received no supplemental light. The light itself was controlled by an automatic time clock to provide illumination throughout the dark period; i.e., a 24-hr photoperiod was used. It was turned off on 7 September 1976. On 24 May 1976, the four spruce seedlots (Table 5) were placed on a wooden pallet at each of the eight light-treatment stations. Throughout the experiment, they were grown under the standard operational container nursery regime used in shadehouses.

Table 5. Geographic origin of seed and seedlots used in the 1976 experiment (Arnott 1979).

| Species | B.C. Min. For. seedlot no. | Latitude | Longitude | Elevation (m) | Location |
|---|---|---|---|---|---|
| *Picea engelmannii* (1) | 1819 | 49°50' | 120°45' | 1130 | Coquihalla |
| *Picea engelmannii* (2) | 1379 | 51°50' | 120°10' | 1370 | Moira Lake |
| *Picea glauca* (3) | 1957 | 53°50' | 126°45' | 1040 | Ootsa Lake |
| *Picea glauca* x *engelmannii* (4) | 2507 | 49°10' | 117°15' | 1610 | McIntyre Creek |

The occurrence of terminal resting buds was noted and seedling height measurements were recorded biweekly throughout the experiment until 30 October 1976, when a destructive sample was taken for shoot and root dry weight.

Extending the photoperiod and increasing the light intensity had highly significant effects on seedling shoot growth of all four spruce seedlots. Shoot length and weight declined as the light intensity decreased. The effect of extended photoperiod and increasing light intensity on root weight was usually negative, although the differences were significant only in seedlots 2 and 3. The greatest shoot length response to light intensity was attained at the highest level (220 lux). The critical minimum intensity (the minimum level that yielded shoot lengths significantly different from the controls) varied by seedlot as follows:

| Seedlot | Critical minimum (lux) |
|---|---|
| 3 | 80 |
| 1,4 | 40 |
| 2 | 20 |

The trend in shoot weight was somewhat different. Minimum light intensity levels usually had to be one treatment level higher in order to produce a response which was significantly different from that of the controls. The smaller average shoot length and weight at the lower light intensities is a result of many of the seedlings forming terminal resting buds and ceasing shoot growth before the lights were turned off on 7 September. This effect was minimal on those seedlings growing with 220 lux. By 7 September seedlots receiving less than 40 lux of supplemental lighting were not significantly different from the controls in the proportion of terminal buds formed. Seedlings from all treatments were fully dormant by 7 October 1976.

From the experimental evidence, it can be generally concluded that northern-latitude and high-elevation populations of the white/Engelmann spruce complex can be successfully grown at southern, low-elevation container nurseries in coastal British Columbia by extending the photoperiod with a sodium vapor lamp that provides a minimum light intensity of 80 lux at seedling level.

## Light Intensity and Provenance Interaction

The above evidence indicated that the minimum intensity required to maintain growth of the seedlings was in the range of 20-80 lux. However, the maximum intensity levels were not clearly defined. A series of experiments was conducted in 1980 to bracket this upper limit on a wide range of provenances grown under both greenhouse (heated) and shelterhouse (unheated) conditions. Experimental methods are summarized as follows.

Seedlings from seven seedlots from the white/Engelmann spruce complex, covering a range of 10 degrees of latitude, were selected from operational sowings in the B.C. Ministry of Forests' container nurseries and shipped to Victoria. They were held in a heated greenhouse (min temp 18°C) with a 19-hr photoperiod until the initiation of the experiment.

The seven seedlots were randomly assigned to four light intensity treatments (0, 100, 200, and 400 lux) in both a heated greenhouse and an unheated shelterhouse on 13 June 1980. These light intensities were provided to extend the photoperiod to a constant 19 hr throughout the experiment. Incandescent lightbulbs were suspended above the seedlings and the bulb height and number were adjusted to provide the treatment intensities of 100, 200 and 400 lux. Time clocks activated the lights 1 1/2 hr before sunset. Standard cultural practices of seedling fertilization and irrigation as described by Van Eerden (1974) for container nurseries were employed throughout the experiment.

The treatment replicates were measured every 2 weeks to record a) frequency of terminal resting buds and b) shoot length of the seedlings. The supplemental photoperiod lights were shut off on 15 September 1980 and measurements continued until seedlings in all treatments had formed a terminal resting bud, after which a destructive sample was taken for a) seedling height, b) root collar diameter and c) seedling dry weight.

In summary, the results were as follows (Arnott, unpublished data):

1. Height growth of all provenances grown under extended daylength was significantly different from that of the controls.

2. There were no significant differences in seedling height among all three extended daylength treatments. The trend, however, was for a reduction in seedling height at the 400 lux light level, and this substantiates claims made by Tinus and MacDonald (1979) that too much supplemental light is detrimental to seedling height growth.

3. The more northerly populations of white spruce and the high elevation population of Engelmann spruce did not require higher intensities of light than the southern/low elevation populations to maintain shoot growth. A light intensity of 100 lux was sufficient to provide significantly larger seedlings for all populations. As noted above, intensities of 400 lux provided no significant increase in growth response and generally (over 71% of the time) created a negative trend in height growth.

4. Seedling height growth was significantly greater in the greenhouse than in the shadehouse for all treatments (including the control). Normal daylight intensities were similar in these two growing areas but temperatures were not. The differences in mean minimum and mean maximum temperatures between the two units are shown in Table 6. Clearly, warmer conditions in the greenhouse accounted for the significantly larger seedlings.

Table 6. Temperature differences between greenhouse and shadehouse (°C).

| | Mean maximum | | | Mean minimum | | |
|---|---|---|---|---|---|---|
| Month | G.H.[a] | S.H.[b] | Diff. | G.H. | S.H. | Diff. |
| June | 26 | 20 | 6 | 19 | 11 | 8 |
| July | 27 | 24 | 3 | 18 | 14 | 4 |
| August | 26 | 25 | 1 | 18 | 14 | 4 |
| Sept. | 25 | 23 | 2 | 19 | 15 | 6 |

[a] G.H. = Greenhouse
[b] S.H. = Shadehouse

### Low Night Temperature Effects

As low night temperature is known to have a significant interaction with extended photoperiod treatments in birch (Habjorg 1972) and spruce (Brix 1972), further experiments with the same seven spruce provenances were conducted the same year in controlled environment chambers to define the effects of low night temperature on the growth response of spruce under an extended photoperiod with a light intensity of 200 lux. (The effects of low night temperature could not be clearly separated from the results of the greenhouse/shadehouse comparison owing to the confounding effect of higher mean maximum day temperatures.) Growing conditions in the growth rooms are summarized as follows:

| Growth chamber/ treatment | Day temp. (°C) | Night temp. (°C) | Extended photoperiod light intensity (lux) |
|---|---|---|---|
| A-control | 21 | 18 | 0 |
| B-warm nights | 21 | 18 | 200 |
| C-cold nights | 21 | 7 | 200 |

The experiment was initiated simultaneously with the aforementioned greenhouse/shadehouse trial and the same seedling measurement schedule was followed.

Results are summarized as follows (Arnott, unpublished data):

1. Extending the daylength to 19 hr with 200 lux produced significantly larger seedlings.

2. Cool 'nights' of 7 °C produced smaller seedlings than those grown under 18 °C nights.

3. Seedlings grown under cool night temperatures did not set terminal resting buds any sooner than those grown under warm night temperatures. In other words, 200 lux of extended daylight prevented terminal budset on seedlings growing under both night temperature regimes. On the basis of the work of others (Habjorg 1972), it had been anticipated that those seedlings grown under cooler night temperatures would have set a terminal resting bud sooner. If anything, the cooler night regime tended to delay the formation of terminal buds in spruce.

## CURRENT OPERATIONAL PROCEDURES

The findings from the above research have been used as guidelines by the B.C. Ministry of Forests for operational production of containerized interior spruce seedlings in their southern nurseries. Although specific details vary according to nursery location, the main features are common to all and are as follows:

All nurseries use the 400-watt high-pressure sodium vapor lamp in a 'Power Flood' reflector as the source of light for extending

2. There were no significant differences in seedling height among all three extended daylength treatments. The trend, however, was for a reduction in seedling height at the 400 lux light level, and this substantiates claims made by Tinus and MacDonald (1979) that too much supplemental light is detrimental to seedling height growth.

3. The more northerly populations of white spruce and the high elevation population of Engelmann spruce did not require higher intensities of light than the southern/low elevation populations to maintain shoot growth. A light intensity of 100 lux was sufficient to provide significantly larger seedlings for all populations. As noted above, intensities of 400 lux provided no significant increase in growth response and generally (over 71% of the time) created a negative trend in height growth.

4. Seedling height growth was significantly greater in the greenhouse than in the shadehouse for all treatments (including the control). Normal daylight intensities were similar in these two growing areas but temperatures were not. The differences in mean minimum and mean maximum temperatures between the two units are shown in Table 6. Clearly, warmer conditions in the greenhouse accounted for the significantly larger seedlings.

Table 6. Temperature differences between greenhouse and shadehouse (°C).

| Month | Mean maximum G.H.[a] | Mean maximum S.H.[b] | Mean maximum Diff. | Mean minimum G.H. | Mean minimum S.H. | Mean minimum Diff. |
|---|---|---|---|---|---|---|
| June | 26 | 20 | 6 | 19 | 11 | 8 |
| July | 27 | 24 | 3 | 18 | 14 | 4 |
| August | 26 | 25 | 1 | 18 | 14 | 4 |
| Sept. | 25 | 23 | 2 | 19 | 15 | 6 |

[a] G.H. = Greenhouse
[b] S.H. = Shadehouse

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## CURRENT OPERATIONAL PROCEDURES

The findings from the above research have been used as guidelines by the B.C. Ministry of Forests for operational production of containerized interior spruce seedlings in their southern nurseries. Although specific details vary according to nursery location, the main features are common to all and are as follows:

All nurseries use the 400-watt high-pressure sodium vapor lamp in a 'Power Flood' reflector as the source of light for extending the photoperiod. The lamps are positioned to provide as uniform coverage as is possible within the physical limitation of each type of production facility (which ranges from greenhouses to unheated outdoor shadeframes). They are mounted on the shadeframe walls or, more usually, on the greenhouse irrigation booms. The Koksilah shadeframe, measuring 48 m x 30 m, which holds approximately 1 million seedlings in styroblocks, uses four lamps fixed to the shadeframe supports to provide a minimum light intensity of 20 lux at seedling level. Cross-fit houses, which do not have irrigation booms, and are 60 m long, have one lamp at either end plus a third one mounted towards the centre.

Most nurseries use a fixed lighting system programmed to extend the photoperiod to a constant 18- or 19-hr from the time of seed germination to early August. Minimum light intensities at seedling level are usually 40 to 120 lux although some nurseries provide as little as 20 lux. Those nurseries using an 18- or 19-hr photoperiod provided by lamps mounted on irrigation booms simply move the boom to the centre point of the greenhouse for the night. Two lamps on the top of the boom, directed to opposite ends of the unit, provide adequate light (>20 lux) for half the length of the house.

Only two nurseries--Surrey and Green Timbers--use night interruption on spruce. Unlike many horticultural nurseries which use a fixed series of lights programmed to light the unit sequentially throughout the night, the B.C. seedling nurseries move the light source. The sodium vapor lamps are stationed on the irrigation booms which travel back and forth throughout the darkness. The boom passes over the seedlings every 25-30 min and seedlings are never subjected to total darkness for periods exceeding 30 min. The travelling light system is more economical than the fixed system as it requires fewer numbers of sodium vapor lamps. However, it does depend on 100% reliability of the moving boom which, through mechanical failure, could result in a nursery unit being in total darkness for an entire night. The effect of such a system failure on growth of white and Engelmann spruce is not known. However, failure of the intermittent light source for two nights has resulted in formation of terminal resting buds on other tree species (R.W. Tinus, personal communication).

The sodium vapor lamps are usually turned off in early August to allow the seedlings sufficient time to form terminal buds, grow sufficient roots and develop winter hardiness throughout the latter part of the year. Prolonged use of lights beyond early August delays budset and has detrimental effects on the above-mentioned seedling characteristics. Sodium vapor lamps, for extended photoperiod or night interruption, have been used since 1974 by the B.C. Ministry of Forests to grow white and Engelmann spruce from northern and high elevation sources at southern B.C. nurseries where the long growing season and favorable temperatures can be used to advantage in seedling production.

## LITERATURE CITED

Anon.
1961. Plant and light-growth discoveries. USDA Spec. Rep. 22-64.

Alden, J. and Hermann, R.K.
1971. Aspects of the cold hardiness mechanism in plants. Bot. Rev. 37:37-142.

Arnott, J.T.
1974. Growth response of white-Engelmann spruce to extended photoperiod using continuous and intermittent light. Can. J. For. Res. 4:69-75.

Arnott, J.T.
1976. Container production of high elevation species. Proc. Joint meeting of Western Forest Nursery Council and Intermountain Nurserymen's Assoc. Aug. 10-12, Richmond, B.C.

Arnott, J.T.
1979. Effect of light intensity during extended photoperiod on growth of amabilis fir, mountain hemlock and white and Engelmann spruce seedlings. Can. J. For. Res. 9:82-89.

Aronsson, A.
1975. Influence of photo- and thermoperiod on the initial stages of frost hardening and dehardening of phytotron-grown seedlings of Scots pine *(Pines sylvestris* L.) and Norway spruce *(Picea abies* [L.] Karst.). Stud. For. Suec. 128:1-20.

Asakawa, S., Sasaki, S. and Morikawa, Y.
1974. Growth of tree seedlings under lights of different spectral compositions. J. Jap. For. Soc. 56:441-447.

Bagley, W.T. and Read, R.A.
1960. Some temperature and photoperiod effects on growth of Eastern Redcedar seedlings. Iowa State Coll. J. Sci. 34: 595-602.

Balut, S. and Zelawski, W.
1955. [The annual growth cycle of *Pinus sylvestris* and *Picea abies* seedlings under continuous illumination.] Sylwan 99:501-504.

Bickford, E.D. and Dunn, S.
1972. Lighting for plant growth. Kent State Univ. Press. 221 p.

Brix, H.
1972. Growth response of Sitka spruce and white spruce seedlings to temperature and light intensity. Dep. Environ., Can. For. Serv., Victoria, B.C. Inf. Rep. BC-X-74.17 p.

Cathey, H.M. and Borthwick, H.A.
1964. Significance of dark reversion of phytochrome in flowering of *Chrysanthemum morifolium.* Bot. Gaz. 125:232-236.

Cathey, H. and Campbell, L.E.
1975. Effectiveness of five vision-light sources on photo-regulation of 22 species of ornamental plants. J. Am. Hort. Soc. 100:65-71.

Ceschi, I.
1965. [The variability of some characters of Douglas-fir under different light regimes.] Schweiz. Z. Forstw. 116:46-59.

Cheung, K.-W.
1973. Induction of dormancy in container-grown western hemlock *(Tsuga heterophylla* [Raf.] Sarg.). B.C. For. Serv. Res. Notes No. 59.

Christersson, L.
1978. The influence of photoperiod and temperature on the development of frost hardiness in seedlings of *Pinus sylvestris* and *Picea abies.* Physiol. Plant., Copenhagen. 44:288-294.

Dinus, R.J.
1968. Effect of red and far-red light upon growth of Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco) seedlings. Dis. Abstr. 29B:6-7.

Dormling, I., Gustafsson, A. and Von Wettstein, D.
1968. The experimental control of the life cycle in *Picea abies* [L.] Karst. I. Some basic experiments on the vegetative cycle. Silv. Genet. 17:44-64.

Downs, R.J.
1957. Photoperiod control of growth and dormancy in woody plants. p. 529-537 *in* Thimann, K.V., *Ed.* Physiology of forest trees. Ronald Press Co., N.Y.

Downs, R.J. and Borthwick, H.A.
1956. Effects of photoperiod on growth of trees. Bot. Gaz. 117:310-326.

Downs, R.J. and Piringer, A.A., Jr.
1958. Effects of photoperiod and kind of supplemental light on vegetative growth of pines. For. Sci. 4:185-195.

Fraser, D.A.
1962. Growth of spruce seedlings under long photoperiods. Can. Dep. For., Tech. Note No. 114.

Fowler, D.P.
1961. Effect of photoperiod on white pine seedling growth. For. Chron. 37:133-143.

Giertych, M.M. and Farrar, J.L.
1961. The effect of photoperiod and nitrogen on the growth and development of seedlings of jack pine. Can. J. Bot. 39:1247-1254.

Habjorg, A.
1972. Effects of light quality, light intensity and night temperature on growth and development of three latitudinal populations of *Betula pubescens* Ehrh. Inst. Den. and Nursery Manage., Agric. Univ. Norway, Rep. No. 47.

Habjorg, A.
1978. Photoperiodic ecotypes in Scandinavian trees and shrubs. Meld. Nor. Landbrukshoegskole 57:33.

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

Holzer, K.
1960. [Results of tests on spruce seedlings in culture chambers]. Silv. Genet. 9:137-138.

Holzer, K.
1962. [Genetically determined photoperiodic reactions of spruce seedlings.] Proc. 13th Congr. Internatl. Union For. Res. Orgn., Vienna 1961 Pt. 2(1), Sect. 22/7, 1962.

Ikemoto, A. and Shidei, T.
1963. Studies on the photoperiodism in woody plants. Effect of photoperiodic treatment of different duration given at different growth periods on the development of one-year-old seedlings of *Pinus densiflora.* J. Jap. For. Soc. 45:174-180.

Ikemoto, A. and Shidei, T.
1966. Studies on the photoperiodism of woody plants. Utilization of photoperiodic treatment to shorten the nursery bed period of *Pinus densiflora.* Memoirs of the College of Agric., Kyoto Univ., Kyoto. 88:49-64.

Irgens-Moller, H.
1962. Genotypic variation in photoperiodic response of Douglas-fir seedlings. For. Sci. 8:360-362.

Jester, J.R. and Kramer, P.J.
1939. The effect of length of day on height growth of certain forest tree seedlings. J. For. 37:796-803.

Johnstone, R.C.D. and Brown, W.
1976. Low pressure sodium (SOX) tube lights as a source of supplementary lighting for improved growth of Sitka spruce seedlings. U.K. For. Comm. Res. and Dev. Pap. No. 111.

Kelley, R.J. and Mecklenburg, R.A.
1978. The effect of photoperiod on root growth of European birch *(Betula pendula)* seedlings. HortScience 13:369.

Kozlowski, T.T. and Borger, G.A.
1971. Effect of temperature and light intensity early in ontogeny on growth of *Pinus resinosa* seedlings. Can. J. For. Res. 1:57-65.

Lavender, D.P., Ching, K.K. and Hermann, R.K.
1968. Effect of environment on the development of dormancy and growth of Douglas-fir seedlings. Bot. Gaz. 129:70-83.

Leibundgut, H. and Heller, H.
1960. [Photoperiodic reaction, light requirements and shoot development of young Silver fir plants.] Beih. Z. Schweiz. Forstver. 30:185-198.

Loveys, R., Leopold, A.C. and Kriedmann, P.E.
1974. Abscisic acid metabolism and stomatal physiology in *Betula Zutea* following alteration in photoperiod. Ann. Bot. 38:85-92.

Magnesen, S.
1969. [Experimental ecological studies on the termination of growth in *Picea abies* seedlings. 1. The effect of day-length and temperature relationships during the growing season.] Medd. Vestland. Forstl. Forsokssta. 14(48):1-50.

Magnesen, S.
1971. [Experimental ecological studies on the termination of growth in *Picea abies* seedlings. 2. The effect of different autumn temperatures and periods of low night temperature.] Medd. Vestland Forstl. Forsokssta. 14(51):229-269.

McCreary, D.D., Tanaka, Y. and Lavender, D.P.
1978. Regulation of Douglas-fir seedling growth and hardiness by controlling photoperiod. For. Sci. 24:142-152.

McGregor, W.H.D. and Kramer, P.S.
1957. The effect of photoperiod on photosynthesis respiration and growth of Loblolly pine seedlings from two sources. Abstr. in Plant Physiol. 32 (Suppl.):x-xi.

Meijer, G.
1959. Photomorphogenesis in different spectral regions. p. 101-109 in Proc. Conf. Photoperiodism and Related Phenomena in Plants and Animals, Gatlinburg, Tenn., 1957.

Nagata, H.
1967. Studies on the photoperiodism in the dormant bud of *Pinus densiflora* Sieb. et Zucc. I. Effects of photoperiod on the growth of first- and second-year seedlings of *P. densiflora.* J. Jap. For. Soc. 49:279-285.

Nagata, H.
1968. Studies on the photoperiodism in the dormant bud of *Pinus densiflora.* III. Photoperiodism in the terminal buds of second-year seedlings. J. Jap. For. Soc. 50:174-180.

Nienstaedt, H. and Olson, J.S.
1961. Effects of photoperiod and source on seedling growth of eastern hemlock. For. Sci. 7:81-96.

Owston, P.W. and Kozlowski, T.T.
1976. Effects of temperature and photoperiod on growth of western hemlock. p. 108-117 in Atkinson, W.A. and Zasoski, R.J., *Ed.* Proceedings of the Western Hemlock Management Conference. Coll. of For. Resour., Univ. Wash., Contrib. No. 34.

Pollard, D.F.W.
1974. Bud morphogenesis of white spruce *Picea glauca* seedlings in a uniform environment. Can. J. Bot. 52:1569-1571.

Pollard, D.F.W., Teich, A.H. and Logan, K.T.
1975. Seedling shoot and bud development in provenances of Sitka spruce, *Picea sitchensis* (Bong.) Carr. Can. J. For. Res. 5:18-25.

Powell, L.E.
1976. Effect of photoperiod on endogenous abscisic acid in *Mahus* and *Betula.* Hort-Science 11:498-499.

Read, R.A. and Bagley, W.T.
1967. Response of tree seedlings to extended photoperiods. USDA For. Serv., Rocky Mt. For. Range Exp. Stn., Res. Pap. No. RM-30.

Robak, H.
1962. [New nursery studies on the relation between summer daylength and termination on the first year's growth in Norway spruce and Douglas-fir.] Medd. Vestland. Forstl. Forsokssta. 11(36):199-246.

Russell, K.W.
1974. Growing container Sitka spruce under high pressure sodium lights. Dep. Nat. Resour., Washington. DNR Notes No. 9.

Satoo, S.
1961. [Effect of long-day treatment under various nutritional conditions on the growth of *Abies sachalinensis* seedlings.] J. Jap. For. Soc. 43:320-324.

Shibakusa, R. and Kimata, M.
1975. [Studies on the dormancy of *Abies sachalinensis* Masters. I. Effect of long-day treatment on the formation of lammas shoots and the breaking of initial dormant buds.] J. Jap. For. Soc. 57:224-227.

Skok, J.
1961. Photoperiodic responses of *Sequoia gigantea* seedlings. Bot. Gaz. 123:63-70.

Skok, J.
1962. Further aspects of the photoperiodic responses of *Sequoia gigantea.* Bot. Gaz. 124:17-19.

Simak, M.
1970. Photo and thermo periodic responses of different larch provenances *(Larix decidua* Mill.) Stud. For. Suec. Skogshogsk. No. 86.

Simak, M.
1975. [Intermittent light treatment of forest plants in a plastic greenhouse produces better plant material.] Sver. Skogs. Tidsk. 73:373-381.

Stahel, J.B.
1972. The effect of daylength on root growth of Sitka spruce. For. Sci. 18:27-31.

Tinus, R.W.
1970. Response of *Pinus ponderosa* Laws. and *Picea pungens* Engelm. to extension of photoperiod with continuous and intermittent light. Abstr. in Plant Physiol. 46 (Suppl.):25.

Tinus, R.W. and MacDonald, S.E.
1979. How to grow tree seedlings in containers in greenhouses. USDA For. Serv., Rocky Mt. For. Range Exp. Stn., Gen. Tech. Rep. RM-60. p. 96-99.

Vaartaja, O.
1951. [Photoperiodism in Finnish trees.] Metst. Aikak 4:105-107.

Vaartaja, O.
1954. Photoperiodic ecotypes of trees. Can. J. Bot. 32:392-399.

Vaartaja, O.
1957. Photoperiodic responses in seedlings of northern tree species. Can. J. Bot. 35:133-138.

Vaartaja, O.
1959. Evidence of photoperiodic ecotypes in trees. Ecol. Monogr. 29:91-111.

Van Eerden, E.
1974. Growing season production of western conifers. p. 93-103 in R.W. Tinus, W.I. Stein, and W.E. Balmer, *Ed.* Proceedings of the North American Containerized Forest Tree Seedling Symposium. Great Plains Agric. Counc. Publ. No. 68.

Wareing, P.F.
1949. Photoperiodic control of leaf growth and cambial activity in *Pinus sylvestris.* Nature 163:770-771.

Wareing, P.F.
1950. Growth studies in woody species. I. Photoperiodism in first-year seedlings of *Pinus sylvestris.* II. Effect of daylength on shoot-growth in *Pinus sylvestris* after the first year. Physiol. Plant., Copenhagen 3:258-276, 300-314.

Wareing, P.F.
1951. Growth studies in woody species. III. Further photoperiodic effects in *Pinus sylvestris.* Physiol. Plant., Copenhagen 4:41-56.

Wareing, P.F.
1956. Photoperiodism in woody plants. Ann. Rev. Plant Physiol. 7:191-214.

Watt, R.F. and McGregor, W.H.
1963. Growth of four northern conifers under long and natural photoperiods in Florida and Wisconsin. For. Sci. 9:115-128.

Wheeler, N.
1979. Effect of continuous photoperiod on growth and development of lodgepole pine seedlings and grafts. Can. J. For. Res. 9:276-283.