STUDIA FORESTALIA SUECICA

Nr 128 · 1975

Influence of photo- and thermoperiod on the initial stages of frost hardening and dehardening of phytotron-grown seedlings of Scots pine (*Pinus silvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.)

Foto- och termoperiodens inverkan på frosthärdningens inledningsskeden samt på avhärdningen hos fytotron-odlade plantor av tall (Pinus silvestris *L.*) *och gran* (Picea abies (*L.*) *Karst.*)

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Abstract

ODC 181.212: 181.222: 181.221.1—174.7(485)

Seedlings of Pinus silvestris *(L.) and* Picea abies *((L.) Karst.), 16 weeks old, were hardened under various photo- and thermoperiods. Dehardening after a period of chilling was followed by exposure to various temperatures under long and short day conditions. The degree of frost hardiness of the seedlings was determined in freezing tests at −7°, −11° and −17°C. Damage caused by freezing was evaluated by measurement of conductivity.*

Short day conditions were of importance to hardening in both species, the most effective photoperiods being 6—12 hours. Shorter photoperiods (2—4 hours) were less effective.

Low temperatures did not cause hardening under long-day conditions, but increased hardiness under short photoperiods, especially in pine. Night temperature had a greater influence on hardening in pine than did day temperature.

Dehardening appeared to depend more on temperature than on photoperiod. Dehardening was a much faster process than hardening.

Ms received 2nd June, 1975

LiberFörlag/Allmänna Förlaget

ISBN 91-38-02564-7

Berlingska Boktryckeriet, Lund 1975

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1 Introduction

The capacity of woody plants to withstand a severe winter climate depends on a series of physiological changes which result in increased frost hardiness (Weiser 1970). Many workers consider that these processes can be divided into two stages. According to Tumanov (1967), the plant must have entered dormancy before the first stage of hardening, while e.g. Weiser (1970) considers it enough that growth has ceased. The first stage is thought to occur at temperatures down to about 0°C, and the second stage at temperatures below 0°C. Weiser (1970) stated that a third stage occurs at temperatures between −30 to −50°C. During the first stage many biochemical changes occur, such as conversion of starch to sugars, changes in the sugar composition and in the amount of soluble nitrogen compounds, etc. (Parker 1963, Tumanov 1967, Weiser 1970).

The most important external factors that influence the first stage of hardening are probably photoperiod, light intensity and temperature. However, knowledge of the effects of these factors is incomplete. There are also differences between species as regards response to these factors; McGuire and Flint (1962) reported for four conifer species that photoperiod had no effect on frost hardening. Hardening was, however, increased by light, and McGuire and Flint concluded that light operated by way of photosynthesis. Similar results were obtained by Steponkus and Lanphear (1968) for *Hedera helix*. Van den Driessche (1969a, 1970) found that seedlings of Douglas fir hardened more at short photoperiods if the light intensity was high, while at low light intensity hardening increased with increasing daylength. Lowering of the night temperature also promoted hardening. For *Picea abies* and *Pseudotsuga menziesii,* Scheumann and Börtitz (1965) reported that light was a prerequisite for hardening, and that hardening was induced by short day and low temperature. According to results obtained by Zehnder and Lanphear (1966), both light and low temperature are necessary for hardening in *Taxus cuspidata.* Schwarz (1970) has shown for *Pinus cembra* that photoperiod has a dominating influence during the first stage of hardening.

The influence of photo- and thermoperiod on dehardening has been far less studied; of the relatively few papers dealing with these topics, may be mentioned that of Zehnder and Lanphear (1966), who reported for *Taxus cuspidata* that hardiness was lost at high temperatures approximately twice as rapidly as it could be developed under the most favourable conditions. Van den Driessche (1969b) found for Douglas fir that dehardening depended much more on temperature than on photoperiod.

In the present investigation, the influence of some photo- and thermoperiods on the first stage of hardening and dehardening has been studied.

2 Material and Methods

The seedlings were grown from seeds of Scots pine (*Pinus silvestris* L.) (Södra Ydre Latitude 57°45′, altitude 200—300 m), and Norway spruce (*Picea abies* L. Karst.) (Älvan Latitude 58°45′, altitude 90 m). The seeds were sown in plastic containers (40×48×16 cm) with low-humified *Sphagnum* moss peat (degree of humification 2—3 according to the scale of von Post et al. 1926). The containers were filled with peat to a depth of about 14 cm. Each container was divided into two; one half was sown with pine and the other half with spruce. The plants were thinned after germination, in order to obtain uniform material.

Before seeds were sown, the peat in each container was mixed with 30 g dolomite meal (about 22 per cent Ca and 12 per cent Mg as carbonates) and 28 ml Wallco 1L 65/13 nutrient solution (for composition, see Ingestad 1967). The plants were fertilised weekly from the third week; thereafter, for the remainder of their growth, at the same time as they were watered: 5 ml Wallco 1L 65/13 was applied weekly to every container. Plants were watered three times a week by a system of tubes with outlets at a depth of 2—3 cm in the peat. The water content of the peat was checked once a week by weighing, and was maintained constant during growth and hardening. The water content was 60—80 per cent of the saturation capacity (Elowson and Perttu 1970). The growth period before the hardening treatment was 16 weeks (in a few cases 13 weeks). During the growth period the plants received 18 hours' light a day. Light intensity at plant level was 18—20 000 Lux (Light source Sylvania Gro Lux WS 215 W). Day/night temperature was 20°/15°C and relative humidity 70—75 per cent. After the initial growth period, the seedlings were transferred to different thermo- and photoperiods for hardening (see table 1), and maintained at the same light intensity and relative humidity as during their initial growth.

Table 1. Photo- and thermoperiods used during hardening. Two asterisks denote that the treatment was repeated in other occasion on separate material.

Day/night	Hours light per day						
temp. °C	18	16	12	8	6	4	2
20/15	*	*	*	*	*	*	*
20/10			*				
20/ 5				*			
20/ 0	*			*			
15/10	*			**			
15/ 0				*			
10/10			*	**	*		
10/ 5	*			**	*	*	
10/ 0				*			
10/20				**			

Dehardening was studied on hardened plants exposed to a hardening and chilling period under an eight hour daylength regime. This period was in one case 11 weeks and in the other eight weeks. The treatments are shown in figure 1.

Samples were taken for testing frost hardiness at three, six and nine weeks after the start of treatment. On every sampling occasion, 16 seedlings from each treatment were cut above the peat surface. The seedlings were divided into a basal and an apical part. The 32 fractions thus obtained were divided into four groups, in such a way that fractions from eight separate seedlings were included in all of the four test temperatures.

The determination of frost hardiness was carried out as described by Aronsson and Eliasson (1970), with the following modifica-

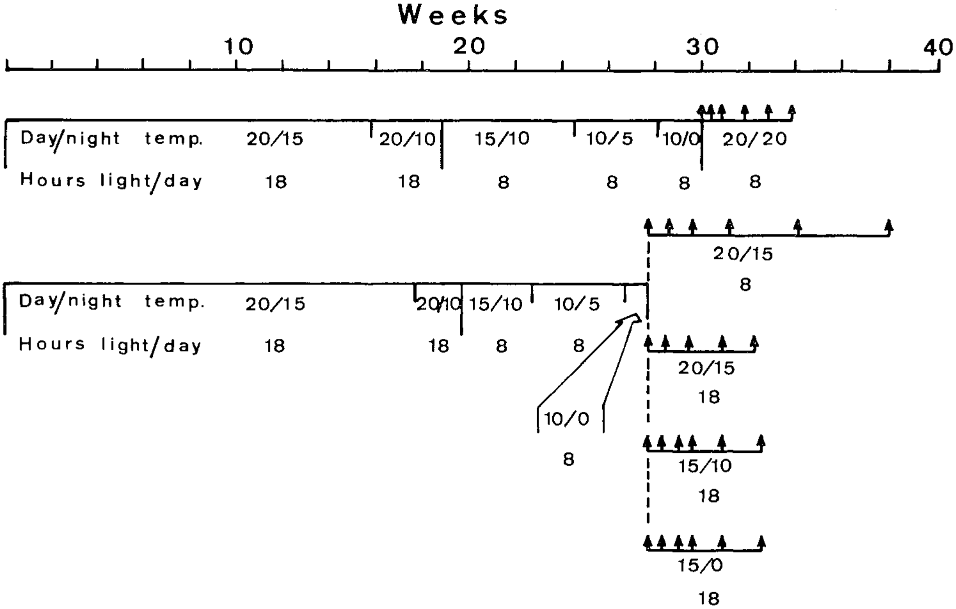

Figure 1. Schedule from sowing to the completion of the experiments for thermo- and photoperiodic treatment used in the dehardening experiments. ↑ denotes the time at which a sample was collected for testing frost hardiness.

tions: Plywood boxes (35×26×42 cm) were placed in deep-freezes. The air in the boxes was circulated by fans, to maintain a uniform temperature, and to counteract supercooling of the tissues. During freezing treatment, the plant material was placed on a plastic net 5 cm above the bottom of the box. The amount of plant material was between 20 and 30 g. To decrease the effect of different amounts of test material on the course of temperature lowering, and to ensure a more uniform lowering of temperature, a plastic bag containing a disk of foam plastic that had absorbed 50 ml water was attached to an inside wall of the plywood box. Before freezing, the plant material and the plastic bag were placed in a refrigerator for 18 hours. About two hours after freezing started, all three boxes had reached their final temperatures: −7°, −11°, and −17°C. After six hours in the boxes the plant parts were kept for 18—22 hours in a refrigerator while thawing.

To estimate the damage caused by freezing, conductivity measurements were made on water extracts of the plant material according to the method of Aronsson and Eliasson (1970). For extracting electrolytes, to a weighed sample was added 20 times its own weight of distilled water, and it was then shaken for 18—20 hours. The conductivity of the water was measured at 25°C ($\varkappa_{frozen}$). The tissues were then killed by boiling and shaken for a further 18—20 hours. A new conductivity measurement was carried out ($\varkappa_{boiled}$). "Relative Conductivity" (RC) was calculated as follows:

$RC = \frac{\varkappa_{frozen}}{\varkappa_{boiled}} \times 100$. Low RC values indicate that the plants had suffered little or no damage during freezing. High values indicate that the tissues were severely damaged or killed by the treatment.

In the case of pine secondary needles, which were cut into 8 mm lengths, were used in the conductivity measurements. In the case of spruce, the entire shoot was used (both stem and needles), the shoot being then cut into 5 mm lengths.

Abbreviations: Day and night temperatures are shown by figures only, the day temperature being first, e.g. 20/15 for 20°C during the day and 15°C during the night. The daylight period is given as "hours light".

3 Results

3.1 **Hardening**

Changes of the RC values during hardening

A hardening period of three weeks induced only slight hardening. Depressed RC values were obtained only at −7°C in spruce and in pine at −11°C (Table 2). In non-hardy plants the RC values were 90—95. After six weeks' hardening, plants from those treatments that hardened fastest were little damaged by freezing to −7° and −11°C. After a further period of three weeks, most of the treatments resulted in appreciable hardiness, the differences in the RC values between the treatments then being smaller than after six weeks. For this reason, the main emphasis will here be laid on the results referring to six weeks' hardening.

All values in tables and figures are mean values of eight RC determinations.

Influence of photoperiod

From figures 2 and 3 it is clear that the seedlings hardened fastest at a photoperiod of 6—12 hours. At the higher day/night temperature (20/15, the same as during the initial growth period) the pine seedlings hardened fastest at six to eight hours' light. At the lower temperature (10/5), hardening increased with increasing length of the light period, from four to 12 hours. The spruce seedlings were influenced by the temperature to a lesser extent, although the tendency was the same as for pine.

Influence of temperature

Figures 4 and 5 and table 3 show results of temperature effects at a photoperiod of eight hours' light after six weeks' treatment. Pine hardened considerably more when both day and night temperature were lowered at the same time, while spruce was little influenced by this (Figure 4). At a day temperature of 10°C and a variable night temperature, the pine seedlings (Figure 5) hardened almost to the same extent as when the day/night temperatures were changed (Figure 4). The spruce seedlings hardened more at lower night temperatures (Figure 5).

Table 2. RC values when the growth temperature was gradually or instantly lowered to the hardening temperature applied. Eight hours' light per day.

	Pine									Spruce								
Freezing test temperature	−7°			−11°			−17°			−7°			−11°			−17°		
Test week no.	3	6	9	3	6	9	3	6	9	3	6	9	3	6	9	3	6	9
Day/night temp. °C																		
15/10	83	29	12	94	70	72	—	82	62	87	31	—	92	58	34	—	81	—
gradually* lowered	49	23	20	80	44	15	95	65	31	69	19	17	90	45	28	94	74	42
15/0	41	18	15	74	26	16	92	56	38	68	19	20	91	58	21	93	72	36
10/0	29	20	14	56	21	17	90	35	38	78	26	19	85	52	26	91	69	29

* One week at 20/15 (same as growth temperature) 15/10, 10/5 respectively, followed by 10/0 during the remainder of the time to nine weeks.

Table 3. Effect of temperature on RC-values after six weeks' hardening at eight hours' light/day. Regression coefficients and t-values for the equation RC = a + b (day-temperature) + c (night-temperature).

Day/night temp. °C	RC-values Pine				Spruce			
	Not frozen	– 7°	– 11°	– 17°	Not frozen	– 7°	– 11°	– 17°
20/15	11	36	80	91	13	24	54	80
20/ 5	9	31	40	69	10	32	39	63
15/10	8	29	70	82	13	31	58	81
15/10	12	27	59	73	11	20	52	72
15/ 0	9	18	26	56	10	19	58	72
10/10	10	43	59	78	12	35	75	85
10/ 5	12	22	36	56	12	36	54	78
10/ 5	10	23	44	75	11	38	53	71
10/ 0	13	20	21	35	13	26	52	69
Reg. coeff.								
Day temp.		– 0.1	0.4	0.6		– 0.9	– 1.6	– 0.9
Night temp.		1.3	4.1	2.8		0.4	1.0	1.1
t-values								
Day temp.		0.18	0.94	0.68		1.44	2.20	2.11
Night temp.		2.81*	10.83***	4.09**		0.67	1.63	3.08*

t-value for probits of significance: 5 % (*) 2.45, 1 % (**) 3.71 and 0.1 % (***) 5.95

Figures 4 and 5 show RC-values after six weeks' treatment. Three and nine weeks' hardening gave similar results, although hardiness increased continuously. In Table 3 a larger material is shown than that in figures 4 and 5. For pine, night temperature had a greater effect on hardening than did day temperature. Calculation of t-values shows significantly greater hardiness at lower night temperatures for the three freezing test temperatures. Day temperature had no effect. In the case of spruce, it is uncertain whether there were any effects (only one of six t-values was significant at the five per cent level), but if such effects exist, the regression coefficients indicate that high day and low night temperature increase hardiness.

Since 18 hours' light did not increase hardiness after six weeks' treatment at low temperatures, the treatment in three experiments was modified to eight hours' light and 10/0 during a further two weeks.

The hardiness of pine was greater the lower the temperature had been during the 18 hours' photoperiod. For spruce, no effect of the previous low temperature could be detected (Table 4).

Gradual lowering of the hardening temperature

At the beginning of the treatment, the plants were moved directly from growing to hardening conditions, which in some cases implied large changes of both photoperiod and temperature. However, in one experiment temperature was gradually lowered during the first four weeks of hardening. The photoperiod was eight hours. During the first week the seedlings grew at the same temperature as during growth, viz. 20/15. The temperature was then lowered step by step, one week at each of the regimes 15/10, 10/5 (first sampling) and 10/0 for the remainder of the hardening period.

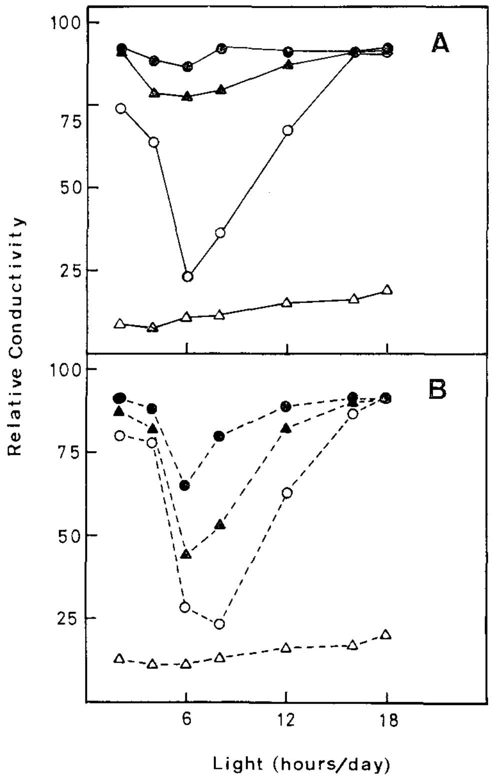

Figure 2. Photoperiodic influence on hardiness after hardening during six weeks. Day/night-temperature during hardening 20/15. A. Pine, B. Spruce. Freezing treatments: △ not frozen, ○ −7°, ▲ −11° and ● −17°C.

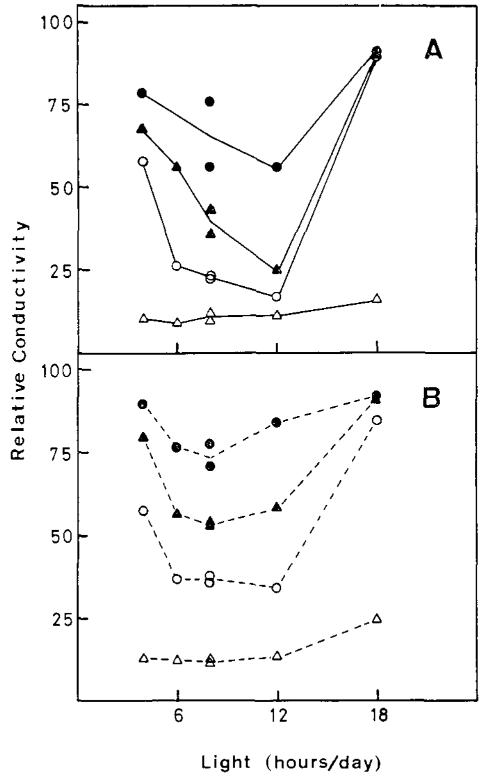

Figure 3. Photoperiodic influence on RC-values after six weeks' hardening at the day/night-temperature 10/5 (except 12 hours' light at 10/10). (A) Pine, (B) Spruce. Symbols as in figure 2. The double symbols for each freezing test temperature at eight hours' light indicate experiments which were repeated, using different material, on another occasion.

Table 4. Influence of different day/night temperatures during six weeks at 18 hours' light, followed by two weeks at eight hours' light and temperature 10/0 for all treatments, RC-values at six and eight weeks.

Day/night temp. during the first six weeks of hardening	RC-values															
	Pine								Spruce							
	Not frozen		−7°		−11°		−17°		Not frozen		−7°		−11°		−17°	
	6	8	6	8	6	8	6	8	6	8	6	8	6	8	6	8
15/10	19	14	91	70	91	89	92	91	22	26	89	85	93	75	93	90
10/ 5	15	14	89	57	91	83	91	91	25	17	85	58	91	89	92	93
20/ 0	17	13	92	31	92	73	93	72	17	19	80	78	93	83	93	92

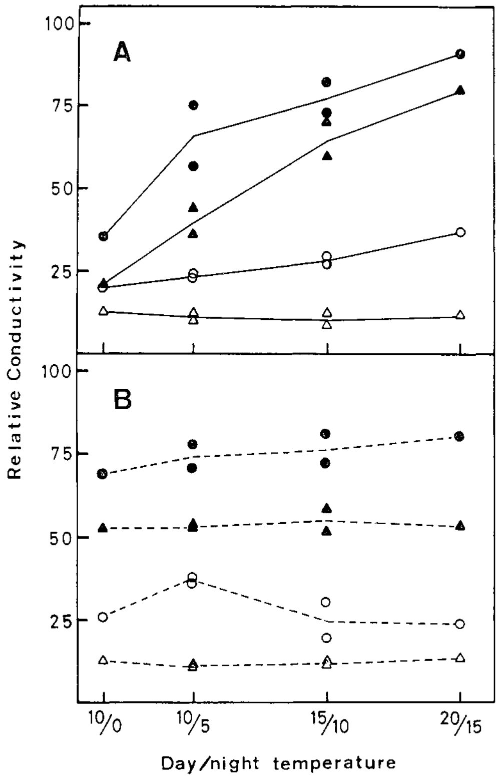

Figure 4. Effect on frost hardiness of lowering the day/night-temperature. RC-values after six weeks' hardening at eight hours' light. (A) Pine, (B) Spruce. Symbols as in figure 2. The double symbols for each freezing test temperature at eight hours' light indicate experiments which were repeated, using different material, on another occasion.

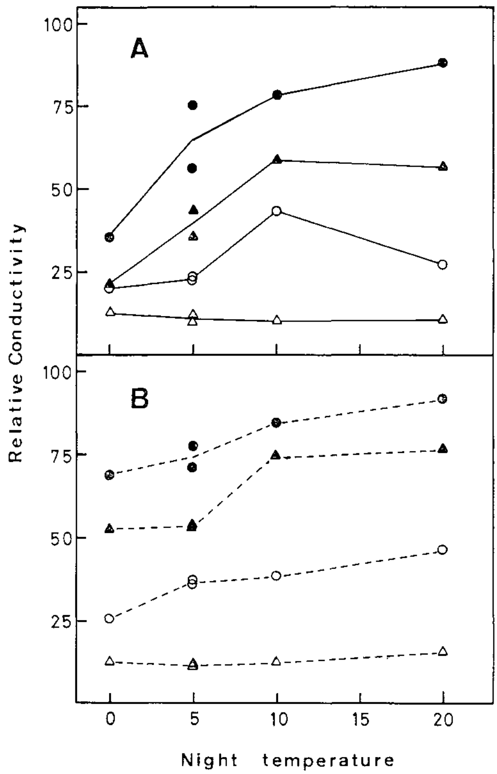

Figure 5. Effect on frost hardiness of different low night temperatures. RC-values after six weeks' hardening at eight hours' light and a day temperature of 10°C. (A) Pine, (B) Spruce. Symbols as in figure 2. The double symbols for each freezing temperature at eight hours' light indicate experiments which were repeated, using different material, on another occasion.

Table 5. Influence of plant age on hardening treatment. RC-values after six weeks' hardening at the temperature given and eight hours' light.

Growth period in weeks	Day/night temp. °C	Pine				Spruce			
		Not frozen	−7°	−11°	−17°	Not frozen	−7°	−11°	−17°
16	15/10	12	27	59	73	11	20	52	72
13	15/10	9	28	74	87	11	46	62	72
16	10/10	10	43	59	78	12	35	75	85
13	10/10	9	46	74	84	9	28	42	66
16	10/20	11	27	57	89	15	47	77	92
13	10/20	9	68	82	93	11	45	68	91

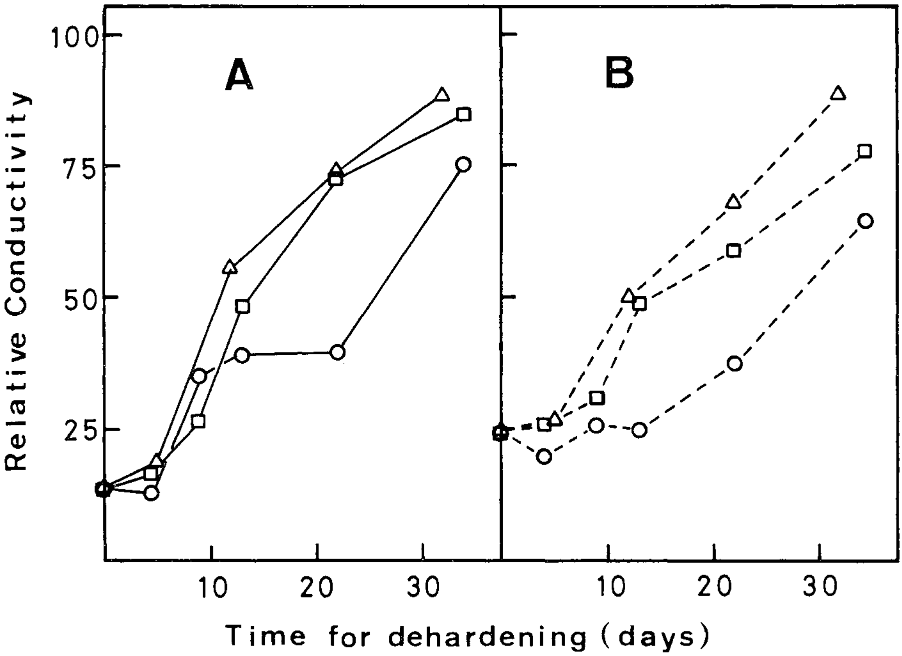

Figure 6. Dehardening at different temperatures at 18 hours' light. Freezing test temperature – 11°C. (A) Pine, (B) Spruce. Symbols: Day/night temperatures ○ 10/5, □ 15/10, △ 20/15.

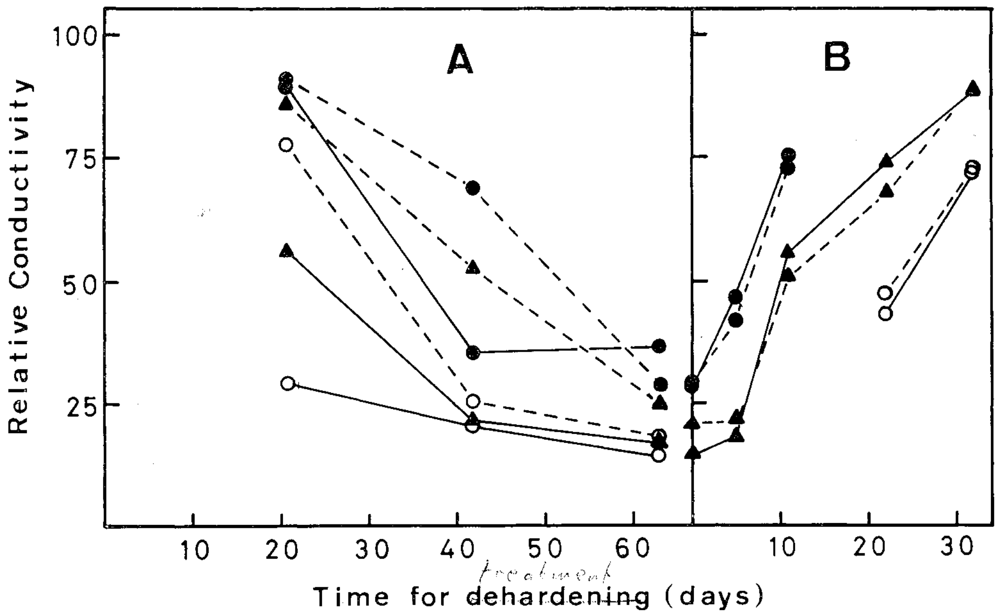

Figure 7. Comparison between hardening and dehardening. (A) Hardening after changing light and temperature from 18 hours' light, 20/15 to eight hours' light, 10/0. (B) Dehardening in the reverse situation, changing from eight hours' light, 10/0 to 18 hours' light, 20/15. Hardening and chilling treatment eight weeks. Symbols: —— pine, - - - spruce; other symbols as in figure 2.

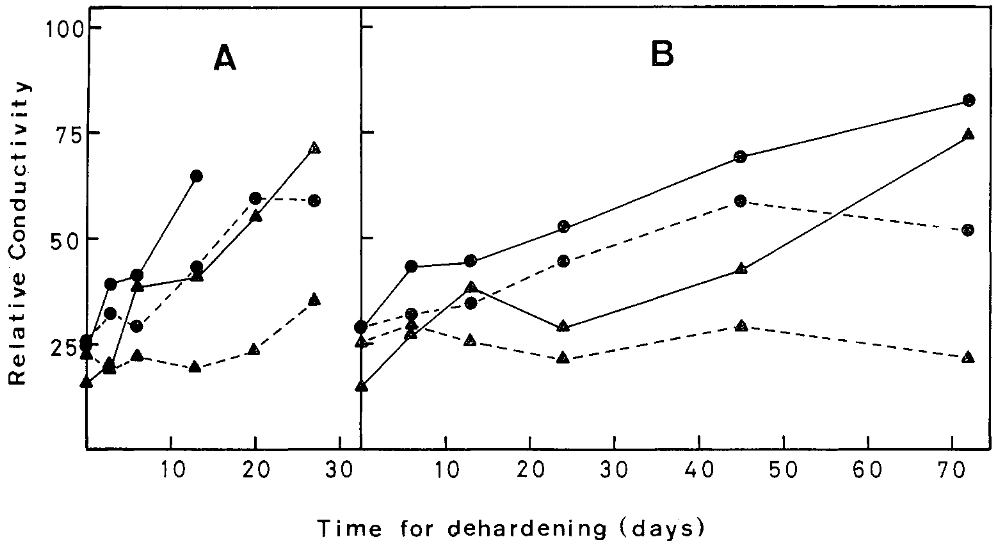

Figure 8. Dehardening at eight hours' light. (A) At day/night temperature 20/20, hardening and chilling period 11 weeks. (B) At day/night temperature 20/15, hardening and chilling treatment eight weeks. Symbols: —— pine, - - - spruce; other symbols as in figure 2.

This gradual lowering of temperature did not harden the plants faster than the method normally used (Table 2).

Length of the growth period

In some experiments the period between sowing and the hardening treatments was reduced from 16 to 13 weeks. Pine hardened faster at the longer growth period, while no difference was found for spruce (Table 5).

3.2 **Dehardening**

At 18 hours' light, dehardening was faster the higher was the temperature, and there were no differences between the two species. Figure 6 shows the results of freezing tests at −11°C. Freezing to −7° and −17°C gave similar results. Bud flushing also was faster at higher temperatures. On the latest sampling occasion, after 34 days, the pine seedlings had leading shoot lengths of 1—4 cm for 10/5 and 3—10 cm for 20/15; for 15/10 and 20/15 needles were developing. The spruce seedlings at 10/5 had only swollen buds (about stage 1—2 according to Krutzsch 1973), at 15/10 the needles were developing (Krutzsch stage 3), and at 20/15 the needles were almost of full size (Krutzsch 4—5). These buds were not included in the conductivity measurements.

When the plants were taken from eight hours' light (10/0), and placed in 18 hours' light (20/15), dehardening was much faster than hardening when the transfer was reversed (Figure 7). Figure 7A also shows that spruce hardened far more slowly than pine 10/0 (cf. also Table 3).

Even at eight hours' light, dehardening occurred, but was less complete than at 18 hours' photoperiod. While the pattern of dehardening was very similar for both species at 18 hours' light, there was a considerable difference at eight hours' light (Figure 8). Pine lost hardiness far more rapidly than spruce, which exhibited a very small increase of RC values at the −11°C freezing treatment. After a hardening and chilling period of eight weeks' duration, dehardening took place considerably more slowly than after this treatment for 11 weeks.

4 Discussion

4.1 **Hardening**

The influence of photo- and thermoperiod on the first stage of hardening of different woody species varies from almost total dependence on temperature to almost complete control by photoperiod (McGuire and Flint 1962, Steponkus and Lanphear 1968, Scheumann and Börtitz 1965, van den Driessche 1969a, 1969b, 1970, Schwarz 1970).

For both pine and spruce, the present investigation showed that short photoperiod had considerably more effect on frost hardening than did low temperature. This agrees with results reported by Schwarz (1970) for *Pinus cembra* and *Rhododendron ferrugineum,* by van den Driessche (1969a, 1969b, 1970) for *Pseudotsuga menziesii,* and by Scheumann and Börtitz (1965) for *Picea abies* and *Pseudotsuga menziesii.*

Before a plant can be hardened, it has to cease growth (Weiser 1970). Many workers also are of the opinion that the plant must be in dormancy (cf. Tumanov et al. 1973), while others consider that it is sufficient that growth has ceased (Irving and Lanphear 1967). For pine and spruce it is possible to induce both growth cessation and budset by shortening the photoperiod under a certain critical day length (Dormling et al. 1968). For the spruce material used here, this critical photoperiod is between 15 and 17 hours (Dormling, personal communication, cf. also Dormling 1973). In this investigation the normal treatment of the plants was to change abruptly from growth conditions to hardening conditions after 16 week's growth. Thus the seedlings were at the growing stage when hardening treatment began. The slower hardening of pine seedlings when the growth period was reduced from 16 to 13 weeks, while spruce was not affected (Table 5), may be explained by differences in the growth pattern of the two species. Pine seedlings do not grow continuously even at long days and optimal temperatures, but alternate between periods of active growth and periods of more or less inactivity (cf. Christersson 1971). One can therefore expect hardening to go on at different rates, depending on the stage attained by the plants. It is likely that pine plants grown for 16 weeks were in an inactive growth phase, and for this reason hardened more rapidly. Spruce seedlings, on the other hand, grow continuously for long periods, at least during the first growing season (Dormling et al. 1968), and therefore show the same response to hardening treatment at any time.

After three weeks' hardening, some treatments led to slight hardening, while after six weeks' hardening, many of the treatments had made the seedlings considerably more hardy. Similar results were reported by van den Driessche (1970), who found that it was necessary to treat seedlings of Douglas fir for four to five weeks before detectable hardening occurred. Since the seedlings were growing more or less actively when the hardening treatment started, and since the development of dormancy takes some time (Perry 1971), these results may indicate that frost hardiness and dormancy can develop simultaneously. That this is so for *Acer negundo* and *Viburnum plicatum tomentosum* has been clearly shown by Irving and Lanphear (1967).

The highest degree of hardiness was achieved at a 6—12 hour photoperiod. The first stage of hardening is energy-consuming (Weiser 1970); and a photoperiod of 2—4 hours may induce a lesser degree of hardiness than one of 6—12 hours, because photosynthesis may be low at the shorter periods. Van den Driessche (1970) reports for Douglas fir that light intensity may limit the rate of hardening, owing to the low rate of photosynthesis. Under such conditions, an increase in the photoperiod will accelerate the rate of hardening by increasing photosynthesis. Although the effects of light intensity were not studied in the present investigation, the slow hardening at the shortest photoperiods may be explained as a result of lack of products of photosynthesis. At the longest photoperiods (16 hours and longer), the seedlings did not stop growing, and consequently could not be hardened.

There was a distinct difference between the species in their reaction to low temperatures. Pine hardened more rapidly if it was exposed to low temperatures before short-day treatment, while spruce did not react to this treatment. At short photoperiods, the pine seedlings hardened more at low night temperatures, while the day temperature did not affect hardening. Van den Driessche (1969a) obtained similar results for seedlings of Douglas fir at temperatures 7.5—24°C. Spruce, however, seems to harden more at relatively high day and low night temperatures.

4.2 **Dehardening**

Before the dehardening experiments started, the seedlings were exposed to a hardening and chilling period at short photoperiod (8 hours) and low temperature. The length of this period was in the one case eight weeks, and in the other, eleven weeks. In the treatment having the longer period, it was sufficient to increase the temperature and to maintain the same photoperiod as during the chilling period (8 hours), to obtain rapid dehardening, while in the treatment having a hardening and chilling period of eight weeks, dehardening was far slower. Effects of the length of the period also became apparent at flushing. The pine seedlings in figure 8A had on the latest sampling occasion leading shoots 1—4 cm long, while apical buds of the pine in figure 8B were only slightly swollen. However, buds on the lower half of the stem had in many cases begun to flush. The spruce in figure 8A had flushing buds at the top, while for that spruce in figure 8B, only a few seedlings had flushing buds on the lowest part of the stems. The way in which flushing began indicates that eight weeks was too a short period for the seedlings to have become prepared for a new growing season, while an 11-week period was sufficient for this. The spruce dehardened more slowly than pine at both chilling periods.

If the photoperiod was increased to 18 hours, dehardening was very fast for both chilling periods. The higher was the temperature, the more rapid was dehardening, and there was no difference between the two species. It has been reported for different species that dehardening is a much faster process than hardening (Parker 1963). Figure 7 shows that dehardening for pine and spruce was about twice as fast as hardening under the prevailing conditions.

Van den Driessche (1969b) has found for Douglas fir that loss of hardiness is not influenced by photoperiod and is dependent only on temperature. Although dehardening for the plants with the longer chilling period did not go as fast at eight hours' light as at 18 hours' light, the results indicate that dehardening for pine at least, as for Douglas fir, depends more on temperature conditions than on the light period.

5 Summary

In this investigation, the influence of some photo- and thermoperiods on the initial stages of frost hardening and dehardening were studied on seedlings of Scots pine and Norway spruce grown in the phytotron at the Royal College of Forestry, Stockholm. The seedlings were grown for 16 weeks from the date of sowing, before hardening treatment at different photo- and thermoperiods was applied. In some experiments the seedlings were treated for eight or eleven weeks at low temperature and short days to induce hardiness, then dehardened. For evaluation of frost hardiness, the seedlings were frozen to $-7°$, $-11°$ or $-17°C$. The damage caused by freezing was estimated by conductivity measurements on water extracts of the plant material.

The seedlings were only slightly hardened by treatment for three weeks, after which the increase in hardiness was rapid. Most of the results reported here refer to six weeks' hardening. Pine seedlings grown for 13 weeks from the date of sowing hardened more slowly than 16-week-old seedlings. For spruce no such difference could be observed. The dissimilar behaviour of spruce and pine may depend on differences in the growth pattern, since pine has a discontinuous growth pattern; the older pine seedlings may have been at a stage more suitable for hardening.

Under long-day treatment (16—18 hour photoperiod), the seedlings could not be hardened by lowering the temperature. If the photoperiod was afterwards decreased to eight hours, pine hardened more the lower the night temperature had been during the preceding long-day treatment. The most rapid hardening occurred at 6—12 hours' photoperiod, whereas 2—4 hours was less effective, probably because products of photosynthesis became limiting at these photoperiods.

Hardiness resulting from treatment at short photoperiods, could be improved by treatment at low temperatures; relatively little for spruce, considerably more for pine. For pine the night temperature had a greater influence on hardening than had the day temperature.

Gradual lowering of the hardening temperature during the first four weeks of hardening did not harden the plants more than a direct change from growing to hardening conditions.

Dehardening was a much faster process than hardening and was more influenced by temperature than by photoperiod.

6 Acknowledgements

The present investigation was supported by grants No. S 72, S 109, S 153/P 54 from the Swedish Council for Forestry and Agricultural Research.

I wish to express my sincere thanks to Professor Carl Olof Tamm, head of the Department of Forest Ecology, for constant support, advice and criticism during this study. I am also very much indebted to Professor Lennart Eliasson, head of the Department of Plant Physiology, University of Umeå, for many valuable discussions and encouragement. The technical assistance of Mrs. Elsa Fryklund is gratefully acknowledged. Thanks are also due to Dr. Jeremy Flower-Ellis for linguistic correction of the manuscript.

7 Sammanfattning

Vedväxternas förmåga att uthärda ett ogynnsamt vinterklimat beror på att de under hösten genomgår en serie fysiologiska förändringar, som leder till ökad frosthärdighet. Av de yttre faktorer, som styr dessa förändringar, är troligen fotoperiod, ljusintensitet och termoperiod de viktigaste.

I denna undersökning har studerats några foto- och termoperioders inflytande på den första härdningsfasen samt avhärdningen hos tall- och granplantor uppodlade i Skogshögskolans fytotron. De använda fröerna var för tall Södra Ydre (Lat. 57°45′, 200—300 m ö. havet) och från gran Älvan (Lat. 58°45′, 90 m ö. havet). Plantorna odlades i torv. Efter 16 veckors odling placerades plantorna i olika foto- och termoperioder för härdning. I några fall har plantorna avhärdats efter en period på 8 eller 11 veckor vid kort dag och låg temperatur. För att pröva plantornas frosthärdighet har de frusits ned till −7°, −11° eller −17°. Därefter har de uppkomna skadorna bestämts med ledningsförmågemätningar på vattenextrakt med växtdelar.

De mest effektiva foto- och termoperioderna gav efter tre veckors behandling endast obetydlig härdning, men därefter ökade härdigheten snabbt. Huvuddelen av här redovisade resultat är efter sex veckors härdning. För tallen inverkade plantornas ålder på härdningen, så till vida som tre veckor yngre plantor härdades långsammare. För granen kunde någon sådan åldersinverkan inte noteras. Denna skillnad mellan tall och gran kan bero på att tallen har en mer utpräglad periodicitet i sitt sätt att växa och att de äldre tallplantorna befunnit sig i en för härdning gynnsammare period.

Vid lång fotoperiod (16—18 tim. ljus/dygn) kunde plantorna ej härdas av sänkt temperatur. Vid efterföljande avkortning av fotoperioden härdades emellertid tallplantorna snabbare om de fått låg nattemperatur under långdagsbehandlingen. Snabbast härdades plantorna vid 6—12 timmar fotoperiod. 2—4 timmar gav sämre härdighet, troligen därför att fotosyntsen blir otillräcklig vid dessa korta fotoperioder.

Den härdning som åstadkoms av kort fotoperiod kunde förstärkas genom behandling vid låga temperaturer, relativt måttligt för gran, betydligt mer för tall. För tallplantorna hade nattemperaturen avgjort större inverkan än dagtemperaturen.

Stegvis sänkning av härdningstemperaturen under en fyra veckors period gav inte snabbare härdning än en direkt omställning från odlings- till härdningsförhållanden.

Avhärdningen gick betydligt snabbare än härdningen och påverkades mer av temperatur än fotoperiod.

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