were grown under 4 different temperature conditions for 23 weeks. Daylength in the 4 controlled-growth rooms was adjusted to correspond to that prevailing at 45° N. latitude. Statistically significant differences among sources were found in terminal elongation and needle size, but no meaningful relationship could be established between these growth characteristics and geographic origin of the seed. High temperatures caused roduced height growth but increased needle elongation; whereas low temperatures caused increased height growth but reduced needle elongation. The suggested cause of this inverse relationship was the influence of temperature on the distribution and utilization of assimilates, primarily reserve foods.

Statistically significant differences among sources were also found in most wood growth characteristics examined. However, these were not directly related to geographic origin of the seed. They appeared to be more closely associated with certain aspects of vegetative growth and varied accordingly. Careful consideration should be given to growth correlations when evaluating measurement data obtained either from seed source or from controlled-growth room experiments.

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Chilling Requirements in Seven Picea Species

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Woody plants in the temperate zones frequently require exposure for several weeks or months to low temperature in order to resume growth and develop normally the following spring. Current knowledge on the subject largely stems from work with orchard trees, particularly *Prunus persica* (L.) Batsch. (For general reviews see Doorenbos, 1953; Samish, 1954; Romberger, 1963; and Smith and Kefford, 1964.) Little is known regarding the need for exposure to cold of forest tree species native to North America. However, such information is essential if intensive studies of the physiology of tree growth are to be undertaken under greenhouse or controlled growth conditions. It would also be of considerable basic value to understand within- and between-species variation in a genus in this respect. Therefore, study of the chilling requirements of seven species of spruce was undertaken. The results are reported in this paper.

Review of Literature

A plant is said to be dormant when a tissue (bud) predisposed to elongate fails to do so. Several types of dormancy are recognized. Since responses of plants to environmental stimuli depend on their type of dormancy, the dormancy condition of experimental material must be clearly stated. Until recently, different distinct phases of dormancy have been considered. The three main types are: (1) Quiescence – dormancy imposed directly by an adverse external environment; growth is resumed as soon as the environment again becomes favorable to growth. (2) Correlated inhibition – a type of physiolagical dormancy maintained by agents or conditions originating within the plant, but not within the dormant organ itself; apical dominance is an example. (3) Rest – physiological dormancy maintained by agents or conditions within the organ itself (Romberger, 1963). Quiescence and correlated inhibition can be interrupted readily by a change in the environment or in the plant. In resting plants the resting organ must be exposed to prolonged chilling treatments or other forcing treatments such as hot water, extended photoperiods, or chemicals such as ethylene chlorohydrin.

More recently Smith and Kefford (1964) have stresced that dormancy development involves a succession of processes – some transitional and some steady-state phases. The spring period of elongation growth is a steady-state and terminates in a transitional phase of dormancy de-

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velopment. This is a stage of great meristematic activities. It is followed by the dormant steady-state, and the subsequent transitional dormancy release. Sometime during the winter months the release of dormancy is completed; the plants then remain in a nondormant steady-state until the transitional spring burst and finally the growth phase is reached. Past definitions have often led to ambiguities; the Smith and Kefford hypothesis overcomes these and appears to present a more realistic explanation for the annual sequence of events. In this study, dormancy signifies the dormant steady-state of late summer, fall, and early winter.

Although dormancy phenomena have been studied in many North American forest trees in connection with photoperiodic studies, actual chilling requirements have been determined for only a few. Results indicate that exposure to temperatures of 45° F. (7° C.) or less for periods of 4 weeks or more meets chilling requirements. Any temperature below 45° F. is equally effective, but warm temperatures interrupting the chilling period during the early phases of dormancy release actually counteract previous low temperature treatments. It has also been demonstrated for several species that long photoperiods compensate for lack of chilling (Romberger, 1963; Samish, 1954).

Two papers are particularly pertinent in connection with the present work. They have shown that different provenances of *Acer saccharum* Marsh. and *Acer rubrum* L. have different chilling requirements (Kriebel and Wang, 1962; Perry and Wang, 1960). With *Acer saccharum* Kriebel and Wang computed the number of hours the plants had been exposed to 7° C. or lower and compared this with the length of time required until budbreak was reached. Prompt budbreak resulted when Georgia plants had been exposed to 7° C. or less for 1800 hours, while provenances from Tennessee, Ohio, and Michigan required 2100 hours. Northern provenances of *A. rubrum* also require more chilling than their southern counterparts, and Perry and Wang describe the variation as clinal. Some information on provenance differences in the chilling requirements of *Pinus strobus* L. has been mentioned by Mergen (1963). Not enough critical and comparable data have been published on the chilling requirements of different species of the same genus of forest trees, but considering the rather striking differences between varieties of the same species (*Prunus persica* — from very little to 1200 hours), one would perhaps expect at least comparable differences between species of the same genus.

Chilling requirements of *Picea glauca* (Moench) Voss. have been given considerable attention (Holst, 1956, 1962; Holst *et al.*, 1956; Nienstaedt, 1966). This species requires 4 to 8 weeks of chilling, depending on the physiological conditions of the plants at the time of treatment. Furthermore, long photoperiods will compensate for the lack of chilling and permit unchilled resting plants to resume growth. We apparently have little or no information on the chilling requirements of other spruce species, but it has been reported that *Picea abies* (L.) Karst., responds more readily to long photoperiods than does *P. glauca*.

Material and Methods

The plant material consisted of seven species of spruce and one variety. Four of the species were represented by 2 or 3 provenances. The various seed sources and some information regarding their origin are listed in *Table 1*.

Approximately 25 seeds of each species or provenance were planted in 2½-inch pots during early August 1958. During and after germination in the greenhouse the plants were grown under long-day conditions. On November 28 they were moved to short-day conditions and thinned to 4 plants per pot. On January 27 after 2 months on short-days the plants were dormant, and the chilling treatments were begun. Three pots with 4 plants per pot were exposed to each treatment. Chilling was at 40° F. and 13 hours of light (100 foot-candles or less) and lasted 0, 2, 4, 6, and 8 weeks. Therefore, the last group was chilled until March 24 when it was returned to the greenhouse.

The plants were then exposed to two photoperiodic regimes. Plants of all seedlots were exposed to long-days (natural daylength extended to 20 hours with 300 foot-candles of a combination of fluorescent and incandescent light). Plants of only 8 of the 14 seedlots, representing 5 species (*Table 2*) were exposed to short-days (8 hours daylength) during budbreak and growth. Fluctuating temperatures in the greenhouse were 70—75° F. during the day and 55—60° F. at night. Toward the end of the experiment considerably higher temperatures were experienced during sunny days.

Data on bud growth were collected at 1- to 2-week intervals until May 22. Four classes of activity were considered: (1) Dormant, (2) swelling, (3) green, and (4) elongated. These

Table 1. — Seed sources of *Picea* species exposed to chilling treatments.

Source number	Species	Latitude	Longitude	Elevation (feet)	Name of location
1628	*P. glauca* (Moench) Voss	44° 10'N	103° 55'W	6,400	Lawrence Co., S. Dakota
1669	*P. glauca*	47° 30'N	94°W	1,350	Itasca Co., Minnesota
1677	*P. glauca*	54°N	123°W	2)	Ft. McLeod, B. C., Canada
1683	*P. engelmannii* Parry	37° 30'N	108°W	2)	San Juan Nat'l. Forest, Colorado
1679	*P. engelmannii*	40° 25'N	111° 00'W	9,500	Wasatch Co., Utah
1680	*P. engelmannii*	44° 30'N	117° 55'W	2)	Bald Mt. Tollgate Area, Oregon
1682	*P. pungens* Engelm.	37° 30'N	106° 30'W	2)	Rio Grande Nat'l. Forest, Colorado
1694	*P. breweriana* S. Wats.	42° 15'N	123° 45'W	4,500—5,000	Josephine Co., Oregon
1689	*P. abies* (L.) Karst.	47° 30'N	13°E	2)	Salzburg Area, Austria
1690	*P. abies*	53°—63°N1)	60°E	2)	Ural Mts., U.S.S.R.
1693	*P. jezoensis hondoensis* (Mayr) Rehd.	36° 30'N	138° 20'E	4,430	Ohdaki, Nagano Pref., Honshu
1691	*P. jezoensis* (Sieb. & Zucc.) Carr.	43° 30'N	143° 12'E	2)	Rikumbetsu, Hokkaido
1698	*P. jezoensis*	43° 50'N	141° 50'E	1,300—2,600	Yamabe, Hokkaido
1692	*P. glehnii* (Fr. Schmidt) Mast.	43° 14'N	143° 33'E	2)	Asyoro, Hokkaido

1) The exact origin not known, but it is definitely from a more northern latitude than collection nr. 1689.

2) Data unavailable.

classes were given the numerical values 0, 2, 4, 8 respectively. On the basis of the total possible scores, the average percentage of activity for a group of plants in a particular treatment and date was computed, and the results were plotted over date. From this graph the date at which 50 percent activity was reached by the particular group of plants was interpolated. The time at which 50 percent of the plants became dormant was determined in the same way. The time interval between these two dates was then determined and used as a relative value for the length of the growth period.

Results and Discussion

Evidently all species tested require some chilling in order to break dormancy promptly. Without a minimum of 2 weeks of chilling, all four species tested failed completely to break dormancy under short-day conditions *(Table 2)*. Under long-day conditions, the increased number of days required for the plants to reach 50 percent growth activity is evidence of the chilling requirements of all seven spruce species *(Table 2)*. Furthermore, it is clear that long photoperiods can compensate for lack of chilling in all the spruce species studied *(Table 2-A)*.

The magnitude of the response to chilling is similar in the different species. On unchilled plants flushing is delayed 2 to 4 weeks under long-day conditions (compare 0-week chilling with 6 or 8 weeks in *Table 2 — A)*, and for all species the first 2 weeks of chilling are relatively more effective than are subsequent additional days of chilling. For a few seedlots, notably *P. jezoensis* from Yamabe and Rikumbetsu on Hokkaido, 2 weeks of chilling practically fulfill all chilling requirements; while in the other species, additional chilling will reduce the period required to reach 50 percent activity by 5 to 12 days.

The rate of response under greenhouse conditions of fully chilled plants of all species is almost identical with the exception of the two *P. abies* collections and the collection of *P. jezoensis hondoensis*. For these collections, the response time (measured in terms of bud activity) under the experimental conditions was close to 3 weeks while in the other species it varied between 14 and 16 days. The response time of fully chilled plants is of course not a measure of the degree of dormancy — it probably reflects different temperature requirements for the spring burst. It is mentioned here because it accounts for some of the differences between species.

Within a particular species or provenance collection, the delay in response resulting when partially chilled plants are placed in the greenhouse can be assumed to reflect differences in dormancy. Therefore, if the increase in response time is expressed as a percent of the response of fully chilled plants, it is possible to compare species directly. These percentages show a consistent difference in chilling requirements between the various groups of species *(Table 3)*; and what is more, the differences fall into a meaningful pattern. The 4 North American species have the greatest chilling requirement. Therefore, they are most delayed — 20 to 30 days or 233 to 314 percent more than promptly responding plants — in development when chilling is withheld. The Eurasian species in contrast are delayed only 1 to 21 days (190 to 221 percent of prompt response) when chilling is withheld.

The sampling within the individual species is, of course, much too limited to permit any general conclusions to be drawn. However, the available data *(Table 3)* do show some within-species variation, and they may indicate that this variation follows patterns established for other species (PERRY and WANG, 1960; KRIEBEL and WANG, 1962; and MERGEN, 1963), i. e., southern and presumably mild-climate seed sources require less chilling than genotypes from more northern colder climates.

Table 2. — The responses of *Picea* species to chilling treatments and photoperiod.

Seed source	Species	Chilling treatments in weeks					Chilling treatments in weeks				
		0	2	4	6	8	0	2	4	6	8
A. Long Day		*Days to 50 percent activity*					*Growth period (days)*[1]				
1628	*P. glauca*	37	21	20	14	9?[2]	42	46	50	56	45?
1669	*P. glauca*	40	23	16	14	15	58	63	57	52	59?
1677	*P. glauca*	44	24	22	17	15	36	33	29	39	38
1683	*P. engelmannii*	41	24	22	18	15	32	34	27	38	37
1679	*P. engelmannii*	36	21	18	14	—[3]	22	30	28	36	—
1680	*P. engelmannii*	45	27	23	19	16	22	38	25	51	31
1682	*P. pungens*	35	21	20	16	15	38	42	52	40	35
1694	*P. breweriana*	44	—	24	14	14	71+	—	56+	54+	45+
1689	*P. abies*	35	30	26	25	18	55	57	52	50?	—
1690	*P. abies*	38	25	24	25	20	61	59	50	50?	46?
1693	*P. jezoensis hondoensis*	44	30	31	25	23	57	57	42	41	40
1691	*P. jezoensis*	28?	17	18	14	14	56	56	40	41	31
1698	*P. jezoensis*	31	14	10	14	14	40	71	63	—	—
1692	*P. glehnii*	38	24	24	17	23	77+	77+	63+	53+	36+
B. Short Day											
1628	*P. glauca*	∞[4]	30	22	15	—	—	30	38	—	—
1669	*P. glauca*	∞	—	17	—	—	—	—	30	—	—
1677	*P. glauca*	∞	—	25	—	—	—	—	21	—	—
1682	*P. pungens*	—	—	24	—	—	—	—	21	—	—
1639	*P. abies*	∞	—	27	—	—	—	—	20	—	—
1690	*P. abies*	∞	28	28	20	—	—	21	22	20	—
1693	*P. jezoensis hondoensis*	∞	38	31	25	—	—	13	27	—	—
1692	*P. glehnii*	∞	30	31	25	—	—	21	14	19	—

[1] Number of days between 50 percent activity and resumption of dormancy.

[2] ? = Graphical determination doubtful as 50 percent level was poorly fixed.

[3] Treatment not included in experiment.

[4] ∞ plants never resumed growth.

Table 3. — The effects of incomplete chilling on subsequent growth of seven species of spruce under long-day conditions.

Seed source	Species	Chilling treatments in weeks				
		0	2	4	6	8
		*Days to 50 percent activity-percent*1)				
1628	*P. glauca*	264	150	142	100	64
1669	*P. glauca*	286	164	114	100	107
1677	*P. glauca*	293	160	147	113	100
1683	*P. engelmannii*	273	160	147	120	100
1679	*P. engelmannii*	257	150	128	100	—
1680	*P. engelmannii*	281	168	144	119	100
1682	*P. pungens*	233	140	133	107	100
1694	*P. breweriana*	314	—	171	100	100
1689	*P. abies*	195	167	144	139	100
1690	*P. abies*	190	125	120	125	100
1693	*P. jezoensis hondoensis*	191	130	135	109	100
1691	*P. jezoensis*	200	121	129	100	100
1698	*P. jezoensis*	221	100	72	100	100
1692	*P. glehnii*	223	141	141	100	135

1) The number of days required to reach 50 percent activity expressed in percentages of the period required for prompt flushing by plants which have received complete chilling.

The data on the relative period of growth for the species and treatments vary considerably *(Table 2);* therefore, detailed conclusions are impossible. The behavior of *Picea breweriana* and *P. glehnii,* however, is extremely interesting. Under long photoperiods of the experiment, these species grow continuously. All the other species show extended growth but eventually return to dormancy. The evidence is too meager to permit any more detailed conclusions. It is, however, a phenomenon which deserves further investigation.

The results presented here, as well as other published work, invite speculations regarding the adaptive value and in turn the evolution of chilling requirements or, more correctly, rest phenomena in plants. In terms of adaptation to climatic extremes, rest could perhaps be considered as an adaptation increasing the survival value of the plant by protecting it against injury from (1) late spring frost, (2) extreme low temperatures during the winter months, or (3) early fall frost. However, NIENSTAEDT (1966) has pointed out that the white spruce in northern Wisconsin probably enters quiescence during the first 3 weeks of December, and it is generally acknowledged that many other species also enter the nondormant steady-state during the midwinter. During this state, high temperatures (MERGEN, 1963), photoperiod (IRGENS-MOLLER, 1957), or a combination of both (OLMSTED, 1951) are the factors controlling growth. Therefore, rest would not be of any adaptive value as a protection against late spring frosts; neither would it be expected to help in resistance to extreme low midwinter temperatures. Apparently, its adaptive value is associated with the protection it gives the plants against early fall frost. Unless dormant, the plants would reflush during warm spells in early fall. The resulting growth would be in danger of injury during nights with below freezing temperatures.

Physiologically, the initiation of rest is probably associated with changes in the concentrations or proportions of growth-controlling substances. But while much evidence has been presented in recent years to support such a view, very little is known about the factors which are directly responsible for the changes in the growth substances (KRAMER and KOZLOWSKI, 1960). Low temperatures in late summer cannot be responsible. For one thing growth cessation takes place before temperatures are low enough to check growth (KRAMER and KOZLOWSKI, 1960). Second, it may be argued teleologically that if the changes in growth substances were brought about by low temperatures, rest would not assure resistance to early fall frost. High night temperatures or a decreasing photoperiod may be involved (KRAMER and KOZLOWSKI, 1960).

The evolution of genotypes resistant to early fall frosts apparently has been brought about by the selection resulting from below freezing temperatures occurring in early fall and causing damage to nondormant plants with considerable regrowth. Dormancy and therefore the resistance very likely are mediated by physiological processes controlled by entirely different climatic factors, perhaps high night temperature or decreasing photoperiods during July and August. Obviously much additional research will have to be carried out before these relationships can be fully explained. In the meantime, their great complexity should be kept in mind when planning future research along these lines.

Summary

The chilling requirements at 40° F. (4.4° C.) were determined for 3 seed sources each of *Picea glauca* and *P. engelmannii,* for 2 seed sources each of *P. abies* and *P. jezoensis,* and for one each of *P. jezoensis hondoensis, P. pungens, P. breweriana,* and *P. glehnii.* Subsequent to chilling, the plants were exposed either to long-day or to short-day condition. In all species, treatment with long photoperiod compensates for lack of chilling. All species require from 6 to 8 weeks of chilling in order to break dormancy promptly when returned to growing conditions, but there is an indication that the North American species go into a somewhat deeper stage of rest than do the Eurasian species. Within-species variation in chilling requirement was observed and is believed to follow the pattern described for other species, in which northern cold-climate seed sources require more chilling than southern sources.

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