Discussion

The difference in time of bud burst of 15 to 18 days found between plants originating from areas separated by only 20—40 miles is of considerable importance in the selection of a seed source. Of equal importance is the lack of relationship between the time of bud burst and amount of growth since this permits selection of late types without necessarily also selecting for poor growth. However, this is true only when considering trees native to the area west of the Cascades. Continental sources from areas east of the Cascades and the Rocky Mountains are considerably earlier and also more slow growing. In any selection for early or late types recognition should be given to the obvious age dependency of the relative time of bud burst with younger plants being earlier. The great variability in time of bud burst indicates that the genetic control probably is multifactorial. The differences among the plants from the various sources with regard to the relationship between the times of initiation and cessation of height growth need further observations, including plants from other sources, before the possible biological meaning of these differences can be understood in terms of the environments of their native habitats.

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Effects of Temperature on the Growth and Wood Formation of Ten Pinus resinosa Sources

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Red pine (Pinus resinosa AIT.) is often considered an extremely homogeneous species. The literature on the extent of red pine variability has been comprehensively reviewed and critically evaluated by FOWLER (1964). On the basis of this literature survey and results of his own experiments, FOWLER reached the following conclusion: "Red pine, regardless of its origin, was observed to be morphologically uniform. With few exceptions, the variation observed could be attributed more easily to environmental than to genetic differences. A survey of the literature revealed that, although genetic differences undoubtedly do occur among red pines from different origins, the magnitude of these differences is not great."

Results of the present study, conducted during the 1962 growing season on 3-year-old red pine seedlings, agree in some respects with those of FOWLER. Although statistically significant differences among sources were found in the characteristics examined, no meaningful relationship could be established between any of these growth characteristics and geographic origin of the seed. On the contrary, sourcc differences in vegetative growth characteristics, such as terminal elongation and needle size, suggested a random distribution that may be attributed to the variability among local populations. However, source differences in most wood growth characterislics appeared to be more closely associated with certain aspects of vegetative growth and varied accordingly.

Material and Methods

Red pine seedlings, representing seed collections from 10 widely separated natural stands, were used as test material. The 10 sources selected for this study were fairly representative of the original 77 collections used by WRIGHT et al. (1963) and extend across the natural range of the species (Table 1). Procedures for seed collection and for sowing and rearing in the nursery have been previously described (WRIGHT et *al.*, 1963).

In the fall of 1961, after two growing seasons in the nursery, the seedlings were transplanted to clay pots and placed in a cold room maintained at about 5° C. After approximately 5 months of cold exposure, 20 seedlings of each source were randomly divided into lots of 5 and transferred to 4 growth rooms. The growth rooms were maintained on identical daylengths but ,different temperature regimes.

In each room 48 eight-foot fluorescent lamps supplemented with incandescent lamps provided a total light intensity of about 3500 foot-candles at plant height. The daylength was adjusted to correspond, as closely as possible, to that prevailing at Rhinelander, Wisconsin (approximately 45° N. latitude). Thus, the daylength increased from 12-3/4 hours at the start of the experiment to 15-3/4 hours at mid-season, and then decreased. In addition, a standard ½-hour "twilight" of about 250 foot-candles intensity was added to the beginning and end of each day.

The following temperature schedule was maintained throughout the experiment:

	Day °C	Night °C
Room 1	23.8 (75° F)	12.8 (55° F)
Room 2	18.3 (65° F)	12.8 (55° F)
Room 3	29.2 (85° F)	18.3 (65° F)
Room 4	23.8 (75° F)	18.3 (65° F)

The daily changes in temperature coincided with the changes in daylength. All changes in temperature and daylength were controlled automaiically by preset time clocks.

Since the rooms were not provided with humidity controls, humidity tended to vary with temperature. For example, the high temperature Room 3 was more humid following watering, but also dried out somewhat faster than the lower temperature rooms. However, by watering the trees in all rooms twice daily, soil moisture and atmospheric humidity were maintained at acceptable levels.

Height growth and needle elongation were measured weekly on every seedling. Three needles to be measured

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Table 1. — Origin of red pine sources.

Source no.	North latitude	West longitude	Location
703	44°00'	84°30'	Gladwin Co., Michigan
738	44°30'	74°00'	Franklin Co., New York
739	44°30'	73°00'	Chittenden Co., Vermont
740	46°30'	88°30'	Baraga Co., Michigan
749	46°48'	73°76'	Berthier, Quebec, Canada[1]
752	46°48'	73°76'	Berthier, Quebec, Canada[2]
755	47°30'	93°45'	Itasca Co., Minnesota
760	43°00'	71°00'	Hillsboro Co., New Hampshire
768	47°00'	67°05'	Victoria, New Brunswick, Canada
769	45°05'	89°05'	Oneida Co., Wisconsin

[1] Plantation established in 1925.

[2] Plantation established in 1926.

at the base, middle, and apex of the current-year internode of 1962 were identified by colored threads. All measurements were made to the nearest millimeter.

At the end of 23 weeks, the seedlings were harvested, the 1961 and 1962 needles removed, and the ovendry weights of each year's needles determined separately. Permanent slides were made from transverse microtome sections cut from the mid-points of the 1960 and 1961 internodes between branch whorls and from the lower 1/3 point of the 1962 internode. The apical 2/3 of each 1962 internode was used for determining wood specific gravity. Earlywood, latewood, and total ring widths were measured for every annual growth ring on each transverse section. From these data and measurements of internode lengths, volume data for each seedling could be computed. In addition, lumen diameter and cell wall thickness of the last 3 fully mature tracheids were measured at 5 radial positions on the 1962 internode sections.

Results and Discussion

Height Growth

Recent evidence suggests that once the physiological barriers of bud dormancy have been removed by adequate cold exposure, most trees of the North Temperate Region will begin growth when certain minimum temperature conditions are attained (Smith and Kefford, 1964). These minimal temperature criteria are apparently genetically controlled, since some workers have observed considerable variability in the initiation of height growth among provenances subjected to the same (Irgens-Moller, 1957; Silen, 1962; Hanover, 1963) or to a series of different (Grüll and Wettstein, 1955; Jensen and Gatherum, 1965) temperature conditions.

In this study, measurable bud elongation began in all seedlings about a week after the start of the experiment. No differences were noted in the breaking of bud dormancy and the initiation of extension growth among either the different sources or temperature conditions. However, once initiated, the rate of growth in height was quite different among sources and also among growth rooms.

Cumulative height growth curves for all sources in a room combined show significant effects of temperature regimes (*Figure 1*). Height growth of seedlings in the high-temperature Room 3 was rapid for the first 3 weeks, but then it slowed down and ceased completely by week 6. In contrast, height growth of seedlings in the low-temperature Room 2 began more slowly, continued steadily, and did not cease until week 8. Height growth of seedlings in the intermediate-temperture Rooms 1 and 4 approximated the typical sigmoid growth curve and ceased after 7 weeks. Analysis of variance revealed that seedlings of Room 3 were significantly shorter at date of harvest than those of the remaining rooms, but no differences existed among the other rooms (*Table 2*).

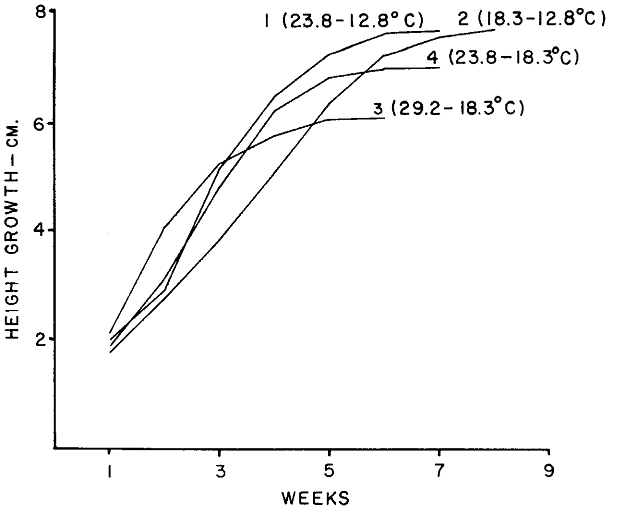

Fig. 1. — Average cumulative height growth for all sources in 4 day-night temperature regimes.

The most obvious explanation of the shorter height growth of trees in Room 3 would be high respiration. However, the only difference in the controlled environment between Rooms 3 and 4 was in day temperature, and it is difficult to rationalize how a higher daily respiration rate could account for the difference not only in level but also in shape of these height growth curves. The problem becomes even more complex when the shape of the growth curve from Room 2 is also considered. A more plausible interpretation of these differences involves growth interactions between internode extension and needle elongation. These correlative growth mechanisms will be discussed in the next section.

When mean weekly height growth was plotted by sources, all rooms combined, considerable between-source differences were evident (*Fig. 2*). Some of the sources differed significantly from others when tested by analysis of variance (*Table 2*), but the groupings by height growth did not suggest a close relationship with either geographic origin of the seed or with latitude. Although there was general agreement with the regional grouping of Wright *et al.* (1963), too few sources were included in this study for a valid comparison. An analysis of covariance (Wishart, 1950), in which current height growth (1962) was adjusted for the previous year's height growth (1961), showed essentially the same array by sources as *Table 2*. Thus, sources that grew most in 1961 under nursery conditions invariably grew most in 1962 under growth-room conditions. Furthermore, no significant interaction between growth-room temperature and sources was revealed by the covariance analysis. For example, in *Figure 1*, when all sources within a room were combined, the curve for Room 1 lay above that of Room 4. In a like manner, when all sources within a room were plotted separately and the graphs superimposed, each source in Room 1 lay just above its counterpart in Room 4. Certain slight variations did exist, such as the transposition of sources 703 and 769 in Rooms 1 and 4, but transpositions were always between closely adjacent sources that did not differ significantly. These results are somewhat analogous to the findings of Walters and Soos (1963) who studied a number of coniferous species growing in natural environments. They noted considerable varia-

Table 2. — Analyses of variance among geographic sources and growth rooms for selected tree growth measurements.

Height growth (1962)		Needle length (1962)		Needle weight (1962)		Needle weight (1961)		Basal tree increment2)		Volume increment3)	
Source	Mean1)	Source	Mean	Source	Mean	Source	Mean	Source	Mean	Source	Mean
	cm		*cm*		*gm*		*gm*		*mm^2)*		*mm^3)*
768	4.82	738	5.81	768	1.78	749	.80	768	2.88	768	300
749	4.88	752	6.02	769	1.92	768	.83	749	3.08	749	311
755	5.63	760	6.08	749	2.22	769	.89	769	3.38	769	382
769	5.67	739	6.45	755	2.33	755	1.03	740	3.48	755	457
703	6.22	740	6.47	740	2.40	740	1.05	755	4.01	740	461
740	7.08	755	6.79	703	2.61	703	1.30	760	4.31	703	544
752	8.64	768	7.00	760	2.74	760	1.34	703	4.43	760	634
738	9.14	769	7.03	752	3.49	739	1.72	739	5.04	739	796
739	9.50	703	7.14	738	3.56	752	1.87	738	5.11	738	812
760	9.60	749	7.41	739	3.67	738	1.90	752	5.23	752	845
F=	36.38**	F=	5.86**	F=	9.47**	F=	17.85**	F=	10.56**	F=	20.66**
Room		*Room*		*Room*		*Room*		*Room*		*Room*	
3	6.16	2	5.87	4	2.52	1	1.17	3	3.54	3	444
4	7.14	4	6.24	2	2.55	4	1.27	2	3.60	2	504
1	7.58	1	6.64	3	2.57	3	1.30	4	4.49	4	613
2	7.59	3	7.72	1	3.04	2	1.35	1	4.75	1	656
F=	11.03**	F=	32.16**	F=	3.20*	F=	1.48ns	F=	13.22**	F=	11.32**

Total ring width4)		Earlywood width4)		Latewood width4)		Latewood percent4)		Specific gravity5)		Cell wall thickness4)	
Source	Mean	Source	Mean	Source	Mean	Source	Mean	Source	Mean	Source	Mean
	mm		*mm*		*mm*		%				μ
768	.580	768	.286	768	.294	738	45.4	738	.359	768	5.63
749	.628	769	.308	749	.304	739	46.1	739	.368	755	5.80
740	.648	740	.320	739	.326	703	46.4	703	.370	703	5.93
769	.661	749	.324	740	.328	749	48.0	752	.372	740	6.06
760	.676	755	.330	760	.329	752	48.0	749	.380	769	6.06
739	.702	760	.347	738	.331	760	48.3	760	.382	738	6.10
755	.706	739	.376	703	.335	768	49.2	740	.390	749	6.26
703	.720	703	.385	769	.353	740	50.3	755	.397	739	6.27
738	.726	738	.395	755	.376	769	52.7	768	.398	752	6.27
752	.778	752	.401	752	.377	755	52.9	769	.405	760	6.86
F=	5.70**	F=	6.95**	F=	2.52*	F=	22.96**	F=	3.69**	F=	2.51*
Room		*Room*		*Room*		*Room*		*Room*		*Room*	
2	.565	2	.329	2	.236	2	41.7	3	.343	3	5.13
3	.683	4	.340	3	.338	3	49.3	2	.382	2	6.24
4	.729	3	.345	1	.378	1	50.4	4	.402	1	6.51
1	.752	1	.374	4	.389	4	53.5	1	.402	4	6.62
F=	30.91**	F=	4.04*	F=	40.96**	F=	21.38**	F=	31.22**	F=	26.34**

1) All values interconnected by the same vertical line do not differ significantly. * = significant at 5-percent level; ** = significant at 1-percent level; ns = not significant.

2) Basal area, 1962 increment only, determined at mid-point of 1960 internode.

3) Total 1962 volume increment for entire tree.

4) Measured on transverse sections from current-year (1962) internode.

5) Determined on apical 2/3 segment of current-year (1962) internode.

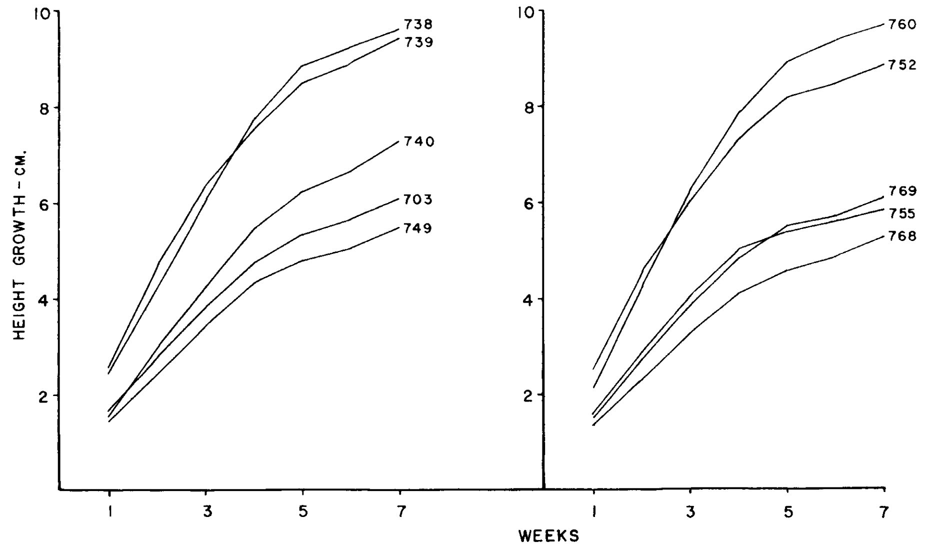

Fig. 2. — Average cumulative height growth of individual sources in four growth rooms.

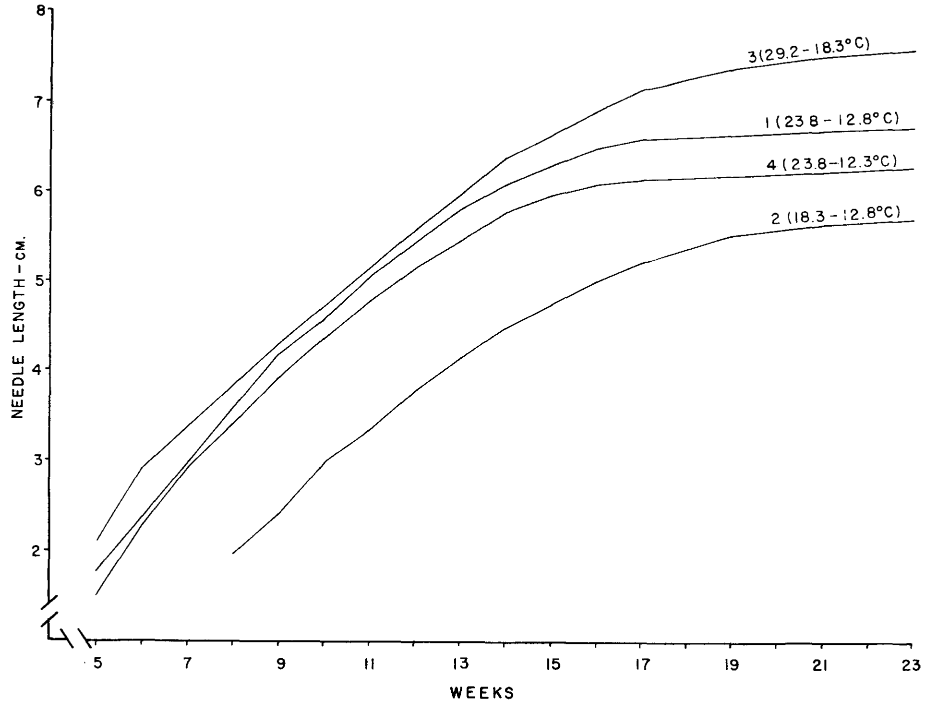

Fig. 3. — Average cumulative needle elongation for all sources in 4 day-night temperature regimes.

Fig. 4. — Differences in needle elongation after 7 weeks at high temperatures in Room 3 *(left)*, intermediate temperatures in Room 1 *(center)*, and low temperatures in Room 2 *(right)*.

bility in the growth of individual trees, but the general form of the growth curves were similar from year to year indicating strong hereditary controls.

Needle Elongation

Vigorous needle elongation does not normally occur in red pine until terminal extension growth has almost ceased. The typical example is illustrated by trees in Rooms 1 and 4 *(Fig. 3)* in which rapid needle elongation began during week 5. In Room 3 the needles exceeded 2 cm. in length at the first measurement in week 5. This indicates that active elongation began the preceding week at about the same time that height growth ceased. On the contrary, in Room 2 the initiation of needle growth was delayed until week 7 or 8, presumably because of the prolongation of height growth *(Figs. 3 and 4)*.

Needle growth in the high-temperature Room 3 not only began earlier than in the intermediate-temperature Rooms 1 and 4, but also continued at a more vigorous rate towards the end of the experiment resulting in significantly longer needles *(Table 2)*. In the low-temperature Room 2, the delayed start in needle growth was not completely compensated for by an increased rate of elongation although the initial gap did close towards the latter part of the experiment *(Fig. 3)*. Data for individual trees as well as the combined data of *Figure 3* indicated that the needles of trees in all rooms were beginning to slow down and approach cessation of growth at about the same rate during the final 3 to 4 weeks. This trend appears to be more a function of daylength than temperature, at least within the limits of this experiment. By week 19 daylength was 14½ hours, and by week 23 it was down to 13½ hours. These daylengths, however, are still rather long for bringing about the cessation of needle growth in red pine. Declining photoperiod probably acts in conjunction with seasonal endogenous processes as suggested by WAREING (1949) and VAARTAJA (1962).

An inverse relationship may be noted between needle length and height growth *(Table 2)*; that is, trees with the shortest internodes produced the longest needles. The statistical correlation between these two measures of tree growth was highly significant and negative *(Table 3)*. HESSELMAN (1904) observed a similar growth correlation in Scots pine and attributed the long shoot of 1902 to the previous favorable summer and the short needles of 1902 to the unfavorable cold, wet summer of the current growing season.

A number of recent studies have attempted to clarify the influence of temperature on height growth and/or needle elongation (HELLMERS, 1962; PERRY, 1962; MERGEN, 1963; LANNER, 1964). Principal emphasis has been placed on the variation between day and night temperatures, and it appears that best growth occurs when day temperatures exceed night temperatures — for example, by 12° to 13° C. in *Pinus taeda* (KRAMER, 1957). However, other factors such as photoperiod, light intensity, tree age, and particularly species differences tend to influence this response and make it difficult to compare the results of one study with those of another.

In the present study, the combination of high day and night temperatures caused reduced height growth but in-

Table 3. — Correlations between growth characteristics over all growth rooms and geographic sources.

x_1-variable[1]	x_2-variable[1]	Correlation Coefficient[2]
		r
Height growth	Needle length	—.658**
Height growth	Needle weight (1962)	.708**
Height growth	Total volume	.836**
Height growth	Total ring width	.296ns
Height growth	Earlywood width	.540**
Height growth	Latewood width	.034ns
Height growth	Latewood percent	—.274ns
Height growth	Specific gravity	—.074ns
Needle length	Needle weight (1962)	—.286ns
Needle length	Earlywood width	—.141ns
Needle length	Latewood width	.191ns
Needle weight (1962)	Total volume	.868**
Needle weight (1962)	Total ring width	.547**
Needle weight (1962)	Earlywood width	.809**
Needle weight (1962)	Latewood width	.202ns
Needle weight (1962)	Latewood percent	—.248ns
Needle weight (1962)	Specific gravity	—.321*
Needle weight (1962)	Cell wall thickness	.058ns
Needle weight (1961)	Height growth	.717**
Needle weight (1961)	Needle length	—.428**
Needle weight (1961)	Needle weight (1962)	.841**
Needle weight (1961)	Total volume	.807**
Needle weight (1961)	Total ring width	.373*
Needle weight (1961)	Earlywood width	.685**
Needle weight (1961)	Latewood width	.048ns
Needle weight (1961)	Latewood percent	—.341*
Needle weight (1961)	Specific gravity	—.458**
Needle weight (1961)	Cell wall thickness	.065ns
Total ring width	Latewood percent	.487**
Total ring width	Specific gravity	.057ns
Earlywood width	Latewood width	.308ns
Latewood percent	Specific gravity	.389*
Cell wall thickness	Specific gravity	.672**

[1]) All measurements refer to values for the 1962 internode except total volume, which is the volume of the 1962 increment over the entire tree, and the weight of the previous years' (1961) needles where indicated.

[2]) * = significant at 5-percent level; ** = significant at 1-percent level; ns = not significant.

creased needle elongation; whereas, low day and night temperatures caused increased height growth but reduced needle elongation. Since these results cannot be explained simply by temperature effects on photosynthesis and respiration, other temperature-induced factors must also be considered as suggested by Kramer (1958). Jensen and Gatherum (1965) observed identical temperature-related phenomena in *Pinus sylvestris* seedlings and suggested that temperature influenced the distribution of assimilates within the tree. This interpretation may be elaborated on to help explain the height growth-needle elongation interaction encountered in the present study.

Evidence has been presented previously (Larson, 1964 b) indicating that terminal extension growth in young red pines depends almost exclusively on reserve foods. During the first few weeks of growth, elongation of the new needles also depends to a certain extent on reserve foods in addition to the current photosynthetic contribution of the older needles. The data of the present experiment suggest that the relative distribution of reserve foods for internodal extension and needle elongation was influenced in some way by the growth room temperatures. By considering this relationship as a correlative growth interaction, the following interpretation may be offered.

In the high-temperature Room 3, the internode expanded rapidly from the bud and the entire complement of needle primordia was precociously exposed for development. Under these conditions of forcing, the needles began growing and competing for reserve foods while the internode was still elongating. In the low-temperature Room 2, on the contrary, the internode expanded slowly from the bud. Because of the delayed development of the needle primordia, a greater proportion of reserve foods was available for internode extension, and less for subsequent needle elongation. This conclusion is partially borne out by the needle measurement data. Needles along the entire internode of trees in Room 3 began growth almost simultaneously, and they maintained this uniformity. In Room 2 needles at the base of the internode not only began growth earlier but grew more rapidly than those at the apex (*Table 4* and *Fig. 4*).

Although the evidence suggests that precocious needle elongation can influence internodal extension growth, the relationship between the two processes cannot be envisioned as a simple competitive interaction involving nutrients alone. The fact that internodal growth of trees in the high-temperature room ceased when the needles began elongating, coupled with the fact that needle elongation of these same trees continued at a rapid rate in spite of high respiratory requirements, indicates a much more subtle relationship. The internode and the needles are integral components of the new shoot, and an interplay undoubtedly exists among a number of physiological processes that are similarly influenced by the external environment. Therefore, it appears quite probable that intra-seasonal competition between growth centers within the tree may be an important limiting factor to height growth. This has received far too little attention in past research.

When mean weekly needle elongation was plotted by sources, all rooms combined, the resulting curves differed in level but only slightly in shape; therefore, they have not been included in this report. Again, significant between-source differences were present (*Table 2*), but they exhibited no consistent relation to geographic origin of the seed. Neither were there significant interactions between sources and temperature. Although transpositions between sources from room to room were more prevalent than in the case of height growth, these were most generally confined to sources of similar needle vigor.

In the low-temperature Room 2 an abnormal type of needle development occurred on several seedlings of three sources, 739, 752, and 755. Numerous basal needles on the internodes failed to break through the fascicle sheath, and during subsequent elongation growth the affected needles resembled tightly coiled springs. The symptoms were very similar in all respects to those described by LaCroix (1962) for "curly needle" disease. Whatever the underlying cause of this abnormality, it is evident that low-temperature conditions stimulated its appearance.

Needle Weight

Ovendry weights of the current-year (1962) needles were significantly higher in the intermediate-temperature Room 1 than the other 3 rooms (*Table 2*). The level of significance

Table 4. — Length of apical needles as percentage of basal needles on current-year internode during period of most active growth.

Room No.	Week Number 5	6	7	8	9	10	11	12	13
				Percent					
2[1])				95	92	87	86	82	80
3	100	108	100	100	102	98			
4	100	100	96	94	90	87			

[1]) Initiation of needle growth in Room 2 was delayed; see *Figure 3.*

was not high, however, and it may indicate a chance relationship rather than a real difference. If real, this difference could be due to several factors, such as more favorable conditions for storage of reserve foods during the experiment or greater needle size; however, the correlation between 1962 needle weight and needle length was not significant over all sources and growth rooms combined *(Table 3)*. Because of the randomization procedure, there was no reason to believe that differences in needle number could contribute to this variation among rooms.

Significant between-source variations in 1962 needle weight were found, and the array of sources by needle weight closely corresponded to the array by total height *(Table 2)*. The correlation between 1962 needle weight and height growth was also highly significant *(Table 3)*. This relationship was not unexpected. Sources exhibiting vigorous height growth during the experiment were also more vigorous the preceding season, and therefore produced a greater number of needle primordia in the developing buds, needle number in red pine is predetermined in the bud formed the previous season. The greater number of needles more than compensated for the shorter needle length on the long internodes of vigorous sources.

Ovendry weights of the previous year's (1961) needles showed no significant difference among rooms *(Table 2)*. Apparently no marked differences occurred in the amount of stored foods in these older needles. Non-significance therefore reflects the pre-experiment randomization among growth rooms.

The array of 1961 needle weights according to source was similar to arrays of both the 1962 needle weights and height growth. The correlations between these latter characteristics and 1961 needle weight were highly significant and positive. The correlation between 1962 needle length and 1961 needle weight, however, was highly significant and negative *(Table 3)*. These analyses are rather difficult to evaluate since the differences reflect not only the responses of the trees to the environment during the season of treatment, but also to the previous two seasons during which the 1961 needles were formed and matured.

Wood Growth and Anatomy

In general, trees in the intermediate-temperature Rooms 1 and 4, which differed only in night temperature, were consistently greater in all measures of wood growth than those in the high- and low-temperature rooms *(Table 2)*.

The only environmental factor varying between Rooms 1 and 2 was day temperature. It is therefore reasonable to assume that the reduced wood growth of trees in Room 2 may have been caused by a decrease in the photosynthetic contribution resulting from the lower day temperature. This difference is also reflected in the anatomical measures of wood growth. Total growth ring width of the 1962 internode in trees of Room 2 was significantly less than that of trees in all other rooms; this was in spite of the fact that trees in Room 2 grew most in height. The narrow growth rings were due primarily to a reduction in the amount of latewood rather than earlywood, as also evidenced by the smaller latewood percentage and specific gravity values. Reduction in the amount of latewood may have been caused, in part, by the delayed cessation of height growth in Room 2 and the consequent delayed initiation of latewood development.

The decreased wood growth of trees in Room 3, on the contrary, could very probably be traced to a pronounced increase in respiration during the high day temperatures; the conditions in Rooms 3 and 4 differed only in day temperature. Total ring width in trees of Room 3 was also significantly less than in trees from the intermediate-temperature rooms. Again, the difference was primarily attributable to reduced width of the latewood zone. However, the significantly lower wood specific gravity of trees from Room 3 was partly traceable to the thinner latewood cell walls. Increased respiration undoubtedly contributed in a major way to this reduction in wall thickness by consuming photosynthates that otherwise would have been utilized in wall development.

From these results, day temperature appears to be more critical than night temperature for wood growth of young red pines within the temperature ranges studied. Wood growth is presumably reduced by limiting photosynthesis at low day temperatures and by increasing respiration at high day temperatures. As in vegetative growth, however, the effect of temperature on wood growth cannot be viewed simply as a balance between photosynthesis and respiration, since other temperature-induced processes are most certainly involved.

The emphasis on day temperature by no means rules out a possible night temperature influence on wood growth in this study. Rooms 1 and 4, for example, differed only in night temperature. Although most of the measured growth characteristics did not differ significantly between these two rooms, the trees in Room 1 were consistently superior to those in Room 4 in all vegetative and most wood growth characteristics. These results suggest that either the lower night temperature or the greater day-night temperature differential in Room 1 promoted growth. Somewhat different results probably could have been obtained by extending the range of night temperatures. Nevertheless, it is believed that the temperature conditions of Rooms 1 and 4 are quite realistic and closely approximate those prevailing over a large part of the natural red pine range during the period of most active growth.

The array of sources remains fairly constant from one wood growth characteristic to another *(Table 2)*. This consistency stems from the facts that not only are all the wood growth variables inter-related, but they are also dependent in various ways on terminal height growth. Thus, as in height growth, sources may differ significantly with regard to a particular wood growth characteristic, but these variations appear to bear no consistent relationship with patterns of geographic origin.

In *Table 2*, the data represent source means for all rooms combined. The differences due to temperature are therefore theoretically uniform over all sources. The correlations between a number of the more important variables contributing to the differences among sources were analyzed *(Table 3)*.

Basal area increment for 1962, determined at 1 cm. above the ground line, and wood volume increment for 1962 are measures of the total wood produced during treatment. The correlation between total volume increment and height growth was highly significant because of the large contribution of the current-year internode to volume increment in 3-year-old trees. The correlations between total volume increment and weights of the 1961 and 1962 needles were also highly significant because volume growth depends on both the reserve food storage and photosynthetic contribution of the needles in red pine. A positive relation between needle weight and stem increment has also been reported in *Picea abies* by SCHMIDT (1953) and SCHÖPFER (1961).

The current-year internode not only contributes a large part of the volume, but it is also representative of the growth response of a young tree. An examination of the wood anatomy of this internode should reveal information regarding the source of volume variation. For example, total width of the growth ring in the current-year internode was not significantly correlated with height growth, but the correlations between total ring width and both 1961 and 1962 needle weights were significant. Statistical significance in these two correlations was due entirely to the earlywood part of the growth ring, for similar analyses involving latewood width were non-significant in every case.

Previous work with red pine (LARSON, 1964 a) has shown that earlywood is produced during the period of active terminal growth. Earlywood continues to form, particularly in the upper stem parts, during the period of active needle elongation following terminal extension growth. Earlywood development is believed to be regulated by a hormonal stimulus emanating from the developing shoot and elongating needles. Consequently, it cannot necessarily be quantitatively defined by arbitrary measures of growth. This is indicated by the lack of significance between needle length and earlywood width *(Table 3)*. Needle weight, on the other hand, exerts a more direct influence on earlywood formation through the utilization of reserve foods from the previous year's needles (1961) and the current photosynthetic contribution of both complements of needles. The larger r-value for the correlation between earlywood width and 1962 needle weight is larger than the correlation with 1961 needle weight. New needles probably contribute more than older needles to diameter growth of the current-year internode (LARSON, 1964 b).

The conclusion that earlywood and latewood are relatively independent in their physiological development (LARSON, 1964 a) is borne out by a number of correlations. Latewood width was non-significantly related to height growth, to 1961 and 1962 needle weights, to 1962 needle elongation, and to earlywood width in the same growth ring. Since latewood development in red pine, as in Scots pine (MIKOLA, 1962), is almost exclusively dependent on current assimilates rather than reserve foods, it appears to be much more sensitive than earlywood to fluctuations and changes in environmental conditions. Partial confirmation of this point may be obtained from the response of trees to temperature among growth rooms *(Table 2)*. Total variation in partial ring widths and the F-value testing significance among rooms were far greater for latewood than for earlywood.

Differences in the physiology of development between earlywood and latewood also govern the correlations involving latewood percentage and specific gravity. The latter two variables were negatively related to needle weight because of the contribution of earlywood width in these calculations. Latewood percentage, averaging more than 45 percent, was considerably higher than normal for young red pine. This high latewood content was due to the extended growing period (about 6 months); conditions permitted latewood development to continue much longer than in nature. Nevertheless, the latewood was still a juvenile type, and this juvenility undoubtedly weakened the relationship between latewood percentage and specific gravity. Cell wall thickness of the latewood was more closely related to specific gravity, agreeing with the findings of VAN BUIJTENEN (1964) for *Pinus elliottii*.

Conclusion

The 10 red pine sources included in this study exhibited a relatively wide range of variability in both vegetative and wood growth characteristics. No meaningful relationship could be established between any of these growth characteristics and geographic origin of the seed source. Results do indicate that there may be appreciable differences between red pine populations. However, in this study variability appeared to express itself in the rate rather than in the duration of growth. For example, within a given growth room (temperature condition) the dates of initiation and cessation of height growth were the same for all sources, but the rates of height growth varied widely. Similarly, the duration of needle elongation was approximately the same for all sources, but the different rates of elongation resulted in a rather wide range of final needle lengths.

Although the individual sources differed quite widely in the growth characteristics tested, the array by sources remained fairly constant from one temperature regime to another. Transpositions of sources did occur between growth rooms, but such transpositions were almost always among sources that did not differ significantly in the particular growth characteristic being tested. This uniformity of response to temperature may be typical of red pine as a species and would tend to confirm, in some respects, the general conclusions of FOWLER (1964). However, the possibility must also be considered that a greater range of sources might reveal a more variable temperature response.

Correlative growth phenomena should be taken into consideration when evaluating both growth room and seed source experiments. This precaution becomes particularly important when plants older than one year are used. Current growth is greatly influenced by previous growth conditions, by plant size, and by availability of reserve foods. In the present study, the correlative growth relationship between height growth and needle elongation was quite striking. Height growth decreased and needle growth increased under high temperature conditions. The reverse held true under low temperature conditions. It is not known to what extent this relationship will be revealed either in natural plantings where numerous variable factors influence both height and needle growth, or in species with different growth requirements. Nevertheless, such a correlative relationship could be of practical importance in evaluating certain seed sources planted under widely varying climatic conditions.

Other growth correlations can be equally important when numerous characteristics are being evaluated. The measurable components of volume and wood growth are highly dependent on many factors: previous plant size and photosynthetic surface, availability of reserve foods, current growth conditions, and inherent efficiency of growth processes. In young trees, growth correlations can assume major importance, particularly when the trees are grown under controlled environments. Trees apparently respond to different environments not only by the total amount and duration of growth but also by changes in the distribution of available assimilates to different growth centers. The criteria used for evaluating growth room and seed source studies in young material should allow for the variability contributed by these growth interactions.

Summary

Three-year-old *Pinus resinosa* seedlings, representing seed collections from 10 widely separated natural stands,

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 reduced 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 physiological 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 stressed 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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