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EFFECTS OF TEMPERATURE, PHOTOPERIOD AND PROVENANCE ON THE GROWTH AND DEVELOPMENT OF SCOTCH PINE SEEDLINGS

by

Keith Frank Jensen

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Heads of Major Departments

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Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1963

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INTRODUCTION

Scotch pine (*Pinus sylvestris* L.) has shown promise as a forest tree in species adaptation studies in Iowa. Total yields at age 40 of approximately 4,600 cubic feet per acre were considerably greater than those of native upland hardwoods, 1,600 cubic feet; and comparable to the yields of eastern white pine (*P. strobus* L.), 5,500 cubic feet; of red pine (*P. resinosa* Ait.), 4,500 cubic feet; and of jack pine (*P. banksiana* Lamb.), 4,300 cubic feet on the same site and soil type.[1] Moreover, Scotch pine's tolerance of calcareous soils and resistance to drought make its use desirable on many sites and soil types in Iowa. Conversely, poor bole form and early-winter yellowing of foliage of most of the seed sources of Scotch pine previously planted in Iowa have reduced appreciably the value of this species as a timber and Christmas tree.

Wide variation in vigor, growth rate, tree form and foliage color throughout the natural range of Scotch pine has been well documented (Baldwin 1954, 1956, Schreiner *et al.* 1962, Wood 1949, Wright and Baldwin 1956, 1957 and Wright and Santamour 1959). Consequently, field and greenhouse provenance tests have been established in Iowa to aid in the selection of suitable seed sources, races and individuals

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[1]Gatherum, G. E., Ames, Iowa. 1963. Data from species adaptation studies. Private communication.

within sources and races.

The objectives of these field and greenhouse studies were to: (1) aid in the selection of variants within Scotch pine for planting in northeast Iowa for different uses, (2) obtain a relative measure of the magnitude of variation among the sources of Scotch pine studied, (3) identify further those environmental factors which effect such variation through natural selection and (4) perhaps provide criteria for future, early selection of suitable seed sources.

The field study was established at the Yellow River State Forest in northeast Iowa to determine the variation in growth and development among 10 seed sources of Scotch pine. The greenhouse experiments, conducted on the Iowa State University campus to determine the independent and interrelated effects of temperature, photoperiod, pre-chilling and provenance on the growth and development of Scotch pine seedlings, were established to aid in the evaluation of the variation among and within seed sources planted in the field.

REVIEW OF LITERATURE

Provenance

The primary objectives of forest tree provenance studies have been to: (1) determine the magnitude of genetic differences among populations, (2) detect the distribution of definite properties over the natural range of the species and (3) find suitable provenances for specific sites and uses (Langner 1961 and Veen 1954).

Variation in growth and development

Variation in growth and development of Scotch pine has been reported by many investigators (Baldwin 1954, 1956, Lines and Aldhous 1957, Schreiner *et al*. 1962, Wood 1949 and Wright and Baldwin 1956, 1957). Height growth variation was obtained by Baldwin (1954), Lines and Aldhous (1957), Schreiner *et al*. (1962), Wood (1949) and Wright and Baldwin (1956, 1957). Wright and Baldwin (1956, 1957) found large differences in height growth among 55 seed sources of Scotch pine planted in New Hampshire in 1938. Similar differences were noted by Wood (1949) and later by Lines and Aldhous (1957) among 22 seed sources planted in England.

Baldwin (1954), Schreiner *et al*. (1962), Wood (1949) and Wright and Baldwin (1956, 1957) observed variation in form and vigor of Scotch pine. A quality index based on vigor and form factors gave a wide range of values (Wood 1949). Differences among seed sources in basal sweep, number of crooks and lean were reported by Wright and Baldwin (1957).

Foliage-color variation in Scotch pine has been noted by Baldwin (1954, 1956), Schreiner *et al*. (1962) and Wright and Baldwin (1957). Foliage color ranged from a pronounced blue-green to a golden color in a provenance study in New Hampshire (Baldwin 1956). Similarly foliage color, observed in a nursery provenance study in New York, ranged from purple to yellow (Schreiner *et al*. 1962).

Differences in survival among Scotch pine seed sources have been noted (Schreiner *et al*. 1962, Wood 1949 and Wright and Baldwin 1957). A range in survival from 65 to 92 percent among 43 seed sources was obtained by Schreiner *et al*. (1962) in New York. Wood (1949) stated that when a long dry period followed planting, survival tended to be lowest among the sources originating from areas of high rainfall.

Scotch pine seed source needle length differences have been reported by Schreiner *et al*. (1962) and Wright and Baldwin (1957). Schreiner *et al*. (1962) reported a range in needle length from 4.49 to 12.34 cm with 2-year-old needles on 3-year-old seedlings in provenance studies in New York.

Latitudinal variation

Scotch pine is the most widely distributed pine species in Europe and Asia (Wright and Santamour 1959). Its natural range extends from Spain to eastern Siberia and from Turkey to north of the Arctic Circle. Within this wide natural range, great variation among Scotch pine seed sources of different latitudinal origin has been observed (Baldwin 1954, 1956, Lines and Aldhous 1957, Schreiner et al. 1962, Wood 1949 and Wright and Baldwin 1956, 1957).

Variation in height growth, related to differences in latitudinal origin, has been reported by Baldwin (1954), Lines and Aldhous (1957), Schreiner et al. (1962), Wood (1949) and Wright and Baldwin (1956, 1957). Lines and Aldhous (1957) and Wright and Baldwin (1957) observed that the seed sources from central Europe grew fastest while the seed sources from the Scandinavian countries grew slowest.

Baldwin (1954), Schreiner et al. (1962), Wood (1949) and Wright and Baldwin (1957) reported variation in vigor and form among Scotch pine seed sources of different latitudinal origin. In a test with 55 seed sources, Wright and Baldwin (1957) found that the Belgium and Germany-Poland-Czechoslovakia-Hungary sources had the most basal sweep, lean and large crooks while the Scandinavian sources had the least. Using a quality index based on vigor and form factors, Wood (1949) obtained similar results.

Differences in Scotch pine foliage color, related to differences in latitudinal origin, have been observed (Baldwin 1954, 1956, Schreiner et al. 1962 and Wright and Baldwin 1957). Baldwin (1956) correlated yellow-foliage color with high latitudinal origin in a study with 46 seed sources in New Hampshire, but could not find a latitudinal relationship with any other shade of color. The coastal sources from around the Baltic

Sea and Atlantic Coast and the inland mountain sources retained a blue-green color throughout the winter.

Wright and Baldwin (1957) classified 55 sources of Scotch pine into 11 latitudinal groups. They concluded that temperature, photoperiod and other factors that vary from north to south cause genetic differentiation. Conversely, no significant differences were observed among provenances from different altitudes within the same latitudinal group. In a similar manner, Wood (1949) and Lines and Aldhous (1957) classified 22 sources into 5 latitudinal groups.

Photoperiod

The photoperiod effect, caused by the relative length of the light and dark periods in the diurnal cycle, influences the vegetative and reproductive processes in woody species. Some of the processes affected by photoperiod are shoot growth, diameter growth, breaking of dormancy, needle growth, leaf abscission, frost resistance, seed germination and flowering (Kramer and Kozlowski 1960 and Wareing 1956).

Effect on tree growth and development

The effect of photoperiod on height growth of woody species has been observed by Ashby (1962), Bagley and Read (1960), Downs and Borthwick (1956), Garner and Allard (1920), Jester and Kramer (1939), Kramer (1936, 1957, 1958), Nienstaedt and Olson (1961), Nitsch (1957), Olmsted (1951), Pauley (1954), Skok (1961, 1962), Wareing (1948, 1950a, 1950b, 1956) and Wareing and Roberts (1956). The rate and duration of height growth usually was increased by long days and decreased by short days.

Cambial activity of woody species was influenced by day length (Wareing 1951, 1956 and Wareing and Roberts 1956). In some species, where cambium activity was independent of terminal growth, short days hastened the cessation of cambial activity while long days prolonged the duration of cambial activity (Wareing 1951, 1956).

Black (1957), Downs (1958), Downs and Borthwick (1956), Gustafson (1938), Hellmers (1959), Irgens-Moller (1957), Kramer (1936), Olmsted (1951), Veen (1951) and Wareing (1948, 1951, 1954, 1956) reported that the breaking of dormancy of woody species was affected by photoperiod. This response varied, however, depending on the state of dormancy of the buds, the position of the buds and temperature.

The effect of photoperiod on length and number of needles of woody species has been observed by Wareing (1950a, 1950b). Needle length of Scotch pine increased with an increase in photoperiod (Wareing 1950b). Wareing (1950a) found that a short, dark period increased the number of needles of Scotch pine over the number obtained with continuous illumination.

Mechanism

Wareing (1950a) proposed that the photoperiod mechanism in Scotch pine might be composed of two opposing systems operating within the plant during the dark period. A growth promoting system, depending on some substance, presumably auxin which is formed in the light phase, is active during the first hours of darkness. The second, a growth inhibitor system which becomes active after 4 hours of darkness, causes an early cessation of growth.

Evidence supporting this type of a mechanism has been reported by several investigators (La Rue 1936, Leopold 1949, Snow 1935, Thimann and Skoog 1934, Wareing 1950a and Zahner 1955). La Rue (1936), Snow (1935) and Thimann and Skoog (1934) observed that auxin compounds affected plant functions that also were affected by photoperiod. Scotch pine (Wareing 1950a), yellow poplar and loblolly pine (Zahner 1955) made greater growth when subjected to interrupted dark periods than when grown under continuous dark periods. Moreover, Leopold (1949) extracted more auxin from leaves under long-day than under short-day conditions.

Downs (1962) reported that a pigment, phytochrome, which is part of the system that controls growth, dormancy, germination and coloration of woody plants, has been isolated. This pigment exists in two forms, one which absorbs red and one which absorbs far-red radiant energy. This system has red, far-red reversibility, is saturated in either direction by low energy levels and drifts from the far-red to the red-absorbing form of the pigment in the dark. Apparently, the pigment or one of its immediate products has enzyme characteristics that affect growth. This system is compatible with the mechanism suggested by Wareing (1950a).

<u>Photoperiodic ecotypes or clines</u>

An ecotype is a distinct race resulting from the selective action of a particular environment, and a cline is a pattern of genetical variation in which the differences of a character or characters are graded in a definite direction in geographic space (Dorman 1952). Provenance studies have shown that photoperiod is one of the environmental factors important in the selective action leading to the formation of a distinct ecotype or cline (Downs and Piringer 1958, Irgens-Moller 1957, Kramer 1943, Nienstaedt and Olson 1961, Pauley 1954, 1958, Vaartaja 1954, 1957, 1960 and Wettstein-Westersheim and Grull 1954). Wettstein-Westersheim and Grull (1954) and Vaartaja (1954) found that the effect of photoperiod on growth of Scotch pine varied among seed sources of different latitudinal and altitudinal origins.

Langlet (1962) suggested that the variation found within the natural range of Scotch pine is clinal while Wright and Baldwin (1957) concluded that the variation consists of distinct ecotypes.

Temperature

Hellmers (1962) suggested that temperature is a difficult factor to evaluate because it indirectly influences growth through its effect on practically every factor that affects growth directly. Went (1953) stated that the effect of temperature is largely mediated through its influence on chemical reactions. Such physiological processes as photosynthesis, respiration, cell division and elongation, enzymatic activity, chlorophyll synthesis and transpiration are affected by temperature (Kramer and Kozlowski 1960).

The day-night temperature differential has been found to be important in tree growth and development (Hellmers 1962, Hellmers and Sundahl 1959 and Kramer 1957, 1958). Kramer (1957, 1958) found that loblolly pine seedlings made the most shoot growth under the largest day-night temperature differential used. Similar results were obtained in studies on Douglas fir (Hellmers and Sundahl 1959) and in further studies on loblolly pine (Hellmers 1962).

Tree growth has been correlated with day temperature, night temperature and heat sum, which is a measure of total daily heat irrespective of the time of application (Hellmers 1962, 1963, Hellmers and Ashby 1958, Hellmers and Sundahl 1959 and Olson et al. 1959). Day temperature had a marked effect on top growth of redwood (Hellmers and Sundahl 1959), while night temperature had a marked effect on growth of digger pine (Hellmers 1962). Growth of Jeffrey pine (Hellmers 1963), erectcone pine (Hellmers and Ashby 1958) and eastern hemlock (Olson et al. 1959) was related to heat sum.

Under northern conditions where temperature often is the most limiting factor, Mikola (1962) observed that the temperature of the growing season had a decisive effect on radial growth and needle length, and that annual height growth of Scotch pine is determined mainly by the temperature of the preceding season because the number of needles on a shoot is predetermined in a bud which is formed in the preceding summer.

Temperature, Photoperiod and Pre-chilling Interactions

Temperature and photoperiod have interrelated as well as independent effects on the growth and development of woody species. Downs (1962) reported that a low night temperature or an exposure to a period of low temperature may modify the effect of photoperiod on growth.

Ashby (1962), Kriebel and Wang (1962) and Perry and Wang (1960) found that chilling or exposure to a period of low temperature hastened the breaking of dormancy; the greater the amount of chilling a plant received, the shorter the period to bud break after the plant was placed in conditions favorable for growth.

METHODS OF INVESTIGATION

Field Investigation

The field study was established to determine the variation in growth and development among 10 Scotch pine seed sources. The geographic origin of the seed sources ranged from central Spain, 41°N latitude, to southern Finland, 60°N latitude, encompassing a difference of 19° in latitude and 1,500 meters in elevation. Origin of the seed sources is shown in Figure 1. The Turkey sources were not included in the field study.

The study was conducted at the Paint Creek Unit of the Yellow River State Forest, Allamakee County. The study area is located at a latitude of 43° 00'N, a longitude of 91° 15'W and an altitude of 320 meters. A pattern of broad ridges and narrow valleys is typical of the general area. The ridges are up to 61 meters high and are broken by small stream channels or an occasional flood plain. Very little level land is present except on the ridge tops and flood plains. Fayette silt loam, a grey-brown podzol, is the soil type of the area. Its parent material is loess from the Iowa till plain (Simonson *et al*. 1952).

The investigation was established in an open meadow with a N60°E to N60°W aspect and a slope of 12 percent (Figure 2). The major vegetation consists of Kentucky bluegrass (*Poa pratensis* L.), red clover (*Trifolium pratense* L.) and timothy (*Phleum pratense* L.). The meadow is surrounded by a mixed

Figure 1. Geographic origin of Scotch pine seed sources used in the field and greenhouse studies. (N. Austria-450m refers to the seed source from northern Austria at an elevation of 450 meters.)

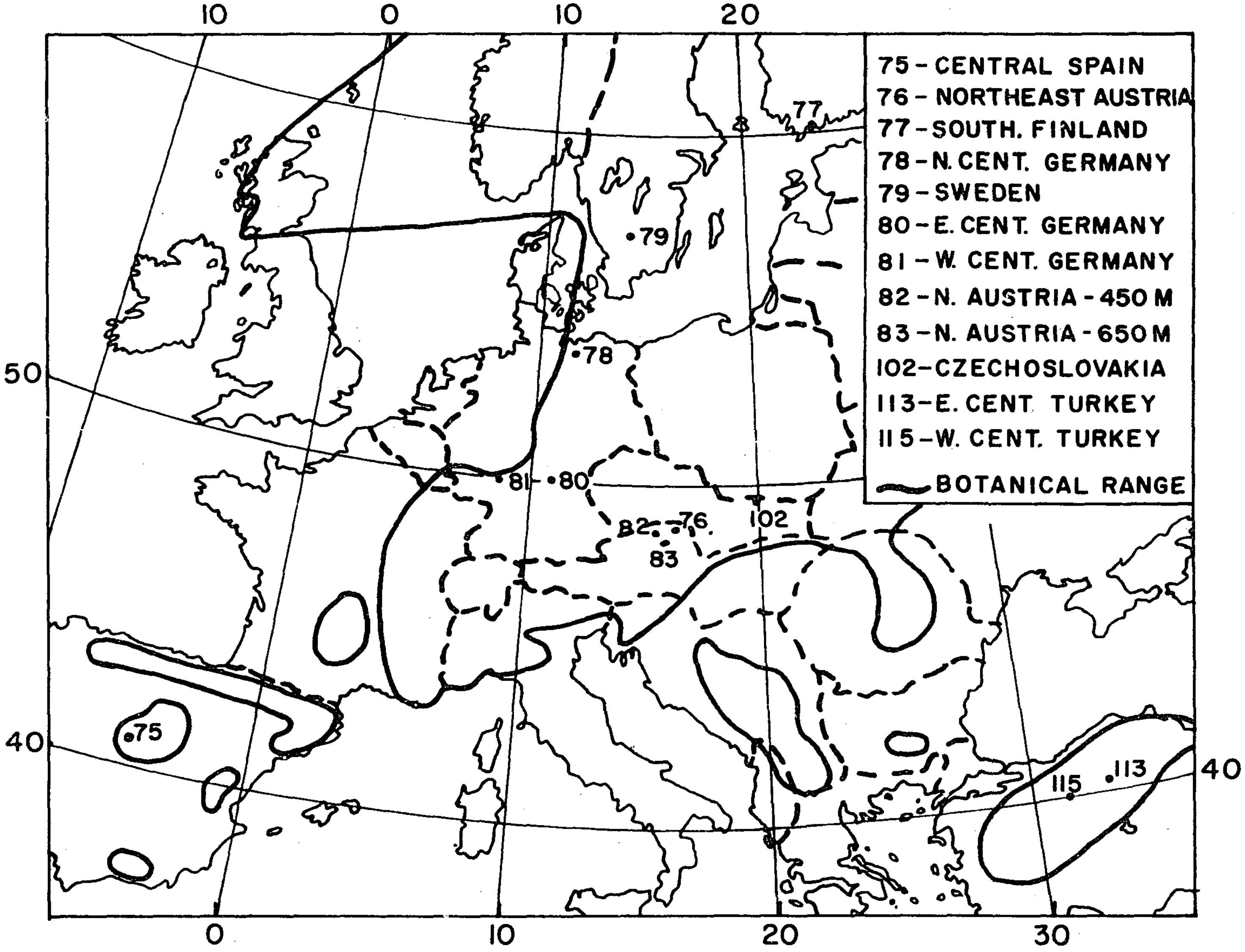
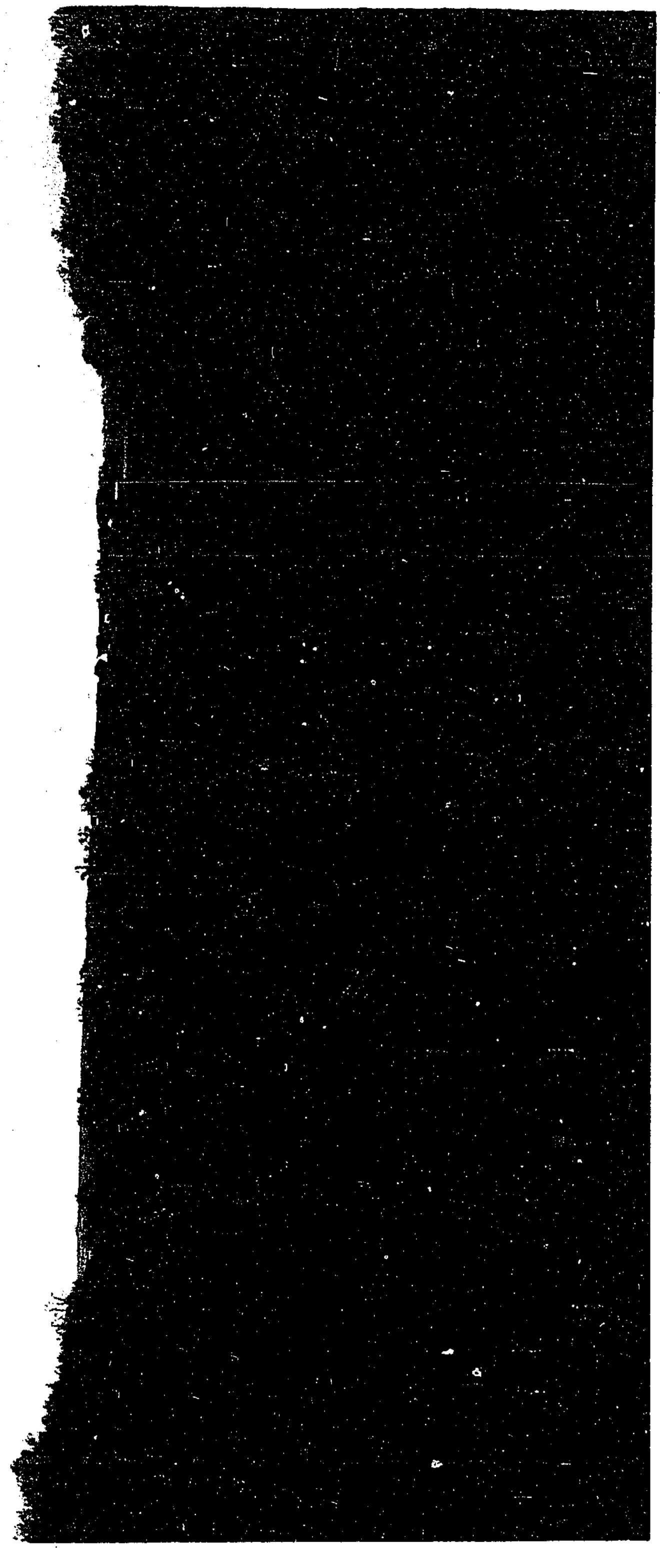

75 - CENTRAL SPAIN
76 - NORTHEAST AUSTRIA
77 - SOUTH. FINLAND
78 - N. CENT. GERMANY
79 - SWEDEN
80 - E. CENT. GERMANY
81 - W. CENT. GERMANY
82 - N. AUSTRIA - 450 M
83 - N. AUSTRIA - 650 M
102 - CZECHOSLOVAKIA
113 - E. CENT. TURKEY
115 - W. CENT. TURKEY
BOTANICAL RANGE
10
0
10
20
50
40
40
0
10
20
30
75
76
77
78
79
80
81
82
83
102
113
115

Figure 2. General view of the study area at northeast Iowa.



hardwood forest type of basswood (*Tilia americana* L.), white ash (*Fraxinus americana* L.), oaks (*Quercus spp.* L.), hickories (*Carya spp.* Nutt.) and elms (*Ulmus spp.* L.).

Climatic conditions are described as moist subhumid to humid, with a moisture index of 30 (Thornthwaite 1948). The long-time average annual precipitation is 33.3 inches. The long-time average yearly maximum, minimum and mean temperatures are 69.7°F, 18.9°F and 48.9°F. The length of the growing season is approximately 140 days. Photoperiod ranges from 15 hours on June 21 to 9 hours on December 21.

This study was established as a randomized block design according to Cochran and Cox (1957). Approximately 100 seedlings of each of 10 seed sources were planted in April 1958 in a 6x6-foot spacing in each of two replications. Mortality loss of all except the central Spain and Sweden seed sources was replaced in April 1959. Lack of additional stock for these sources precluded replacement. Five-year survival and height and diameter growth were obtained in August 1962, and the data were analyzed. Percent survival was converted to arc sin $\sqrt{\text{proportion}}$ to normalize distribution before analysis. Color data were obtained in November 1962.

Greenhouse Investigations

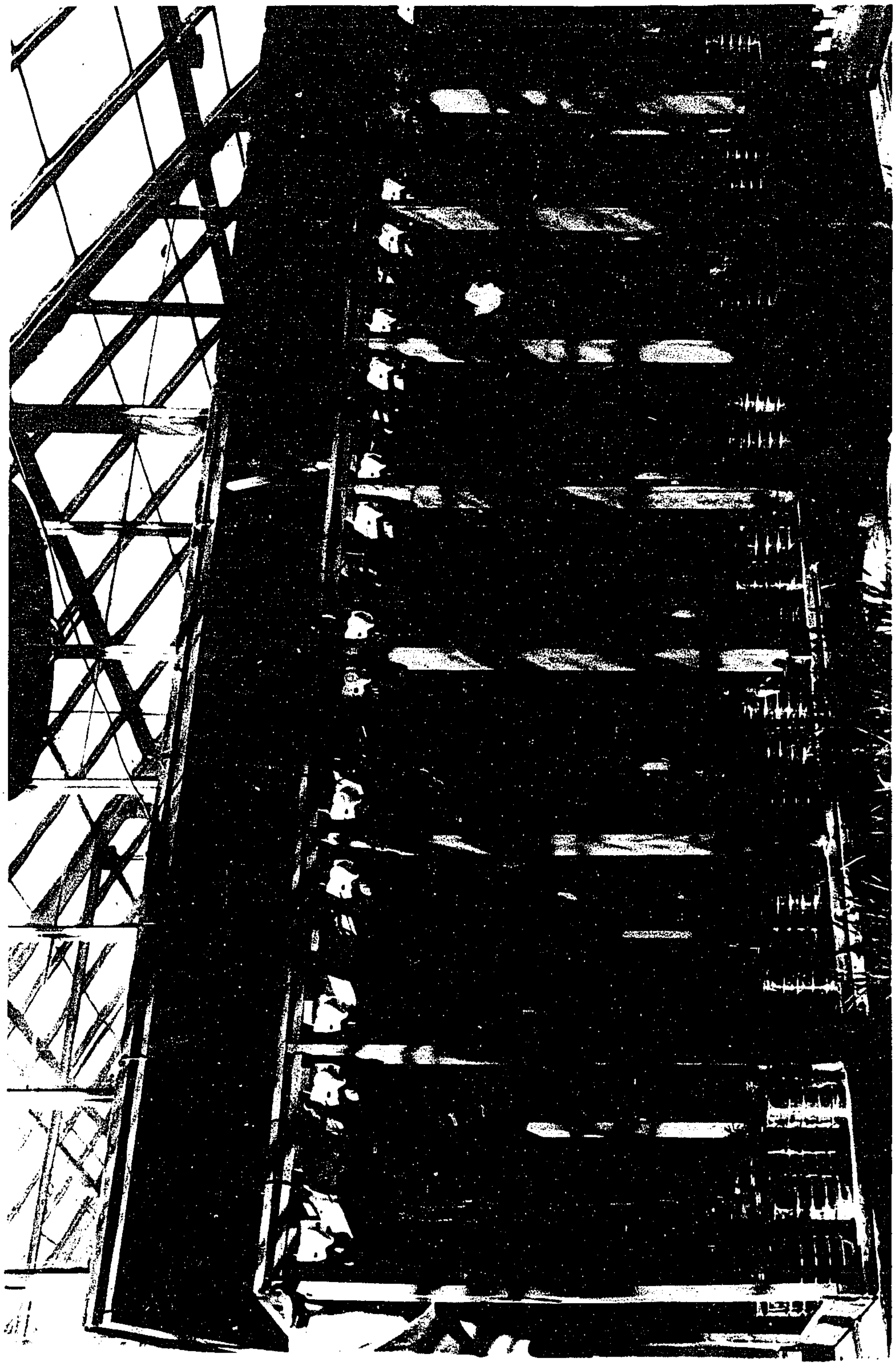
Preliminary investigation

The purpose of the preliminary greenhouse study was to determine the independent and interrelated effects of temperature, photoperiod and provenance on the growth and development of Scotch pine seedlings. The study was established as a split-plot experiment in a randomized block design within unreplicated main-plot temperature treatments. Within each of two mean daily temperatures, 56^{o} and $71^{o}F$, three replications of three photoperiods, 12, 16 and 20 hours, were established. Nine hours of each photoperiod consisted of daylight; a combination of fluorescent and incandescent lights was used to extend day length to the desired interval. Artificial light intensity averaged 40 foot-candles. Two seedlings of each of seven seed sources of Scotch pine were placed within each photoperiod replication. Sources used were east central Germany, west central Germany, northern Austria-450m, northern Austria-650m, Czechoslovakia, east central Turkey and west central Turkey, encompassing a difference of 10^{o} in latitude and 1,200 meters in elevation.

Seedlings, germinated in the nursery beds in spring 1960, were potted and placed in the photoperiod chambers in the greenhouse in October 1960 (Figure 3). A second, smaller group of seedlings was potted in October 1960, and subjected to prolonged chilling under a layer of straw mulch in the nursery. In January 1961, these seedlings were placed in the photoperiod chambers in the $71^{o}F$ greenhouse.

Height growth measurements were taken weekly from bud burst until 90 days after growth initiation. At the end of the study in March 1961, needle length and total green weight

Figure 3. General view of photoperiod chambers in the greenhouse.



of all seedlings were determined.

Final investigations

Photoperiod, temperature and provenance The purpose of this study was to complement the preliminary evaluation of the independent and interrelated effects of photoperiod, temperature and provenance on the growth and development of Scotch pine seedlings through the use of a wider range of temperature and a narrower range of photoperiod treatments. The same experimental design and equipment were used as in the preliminary investigation. The mean daily temperatures were 57°, 65° and 76°F, the photoperiods, 14, 16 and 18 hours and the seed sources, the same as used previously, with the exception of the east central Germany source which was no longer available. The seedlings received the same treatment as in the preliminary study and were placed in the photoperiod chambers in October 1962.

Height growth measurements were taken weekly from bud burst until bud set and bi-weekly from bud set until the end of the study, 130 days after growth initiation. At this time, needle length and total green weight of all seedlings were determined.

Photoperiod, pre-chilling and provenance The purpose of this study was to evaluate further the pre-chilling-photoperiod interaction observed in the preliminary study. This study was a split-plot experiment in a completely randomized design. Three replications of three photoperiods, 12, 16 and 20 hours, were established with equipment similar to that used in the preliminary study. At the end of each pre-chilling interval, 0, 2, 4, 6, 8 or 10 weeks, one seedling of each of three sources was placed within each photoperiod replication. Sources used were west central Germany, northern Austria-650m and east central Turkey.

Seedlings, receiving the same treatment as those in the preliminary study, were placed in an unheated greenhouse in October 1962. At the end of the prescribed pre-chilling interval, each seedling was moved to the photoperiod chamber in a greenhouse with a mean daily temperature of 65°F.

Height growth measurements were taken weekly from bud burst until bud set and bi-weekly after this time. Data collected 84 days after the seedlings were placed in the photoperiod chambers were used in the analysis.

RESULTS

Field Investigation

Survival varied from 40 to 84 percent (Figure 4), and the differences were significant at the 1-percent probability level (Table 1). Survival of the Sweden seed source was lower than survival of the Germany, northern Austria-650m, Czechoslovakia and Finland sources, based on Duncan's multiple range test (Duncan 1955).

Differences in height growth among seed sources ranged from 0.0 to 2.8 feet (Table 2), and were significant at the 1-percent probability level (Table 1). No significant differences were found among the Germany, Austria and Czechoslovakia sources, but this group made more height growth than the Sweden, Finland and Spain sources. Differences among the latter three sources were not significant at the 5-percent level.

Seed source diameter differences at the ground line ranged from 0.0 to 0.7 inch (Table 2), and were significant at the 1-percent probability level (Table 1). Differences among the Germany, Austria and Czechoslovakia sources and among the Spain, Sweden and Finland sources were not significant at the 5-percent level. However, the difference between the two groups was significant at the 1-percent level.

Foliage-color differences ranged from greenish green-yellow, 7.5 GY 5/4, of the Spain source to yellow, 5.0 Y 5/6, of the Finland source (Table 3), based on Munsell color

Figure 4. Average 5-year provenance survival. Smallest significant differences, based on Duncan's multiple range test (Duncan 1955), indicated by arrows: solid line, 1-percent level; dashed line, 5-percent level.

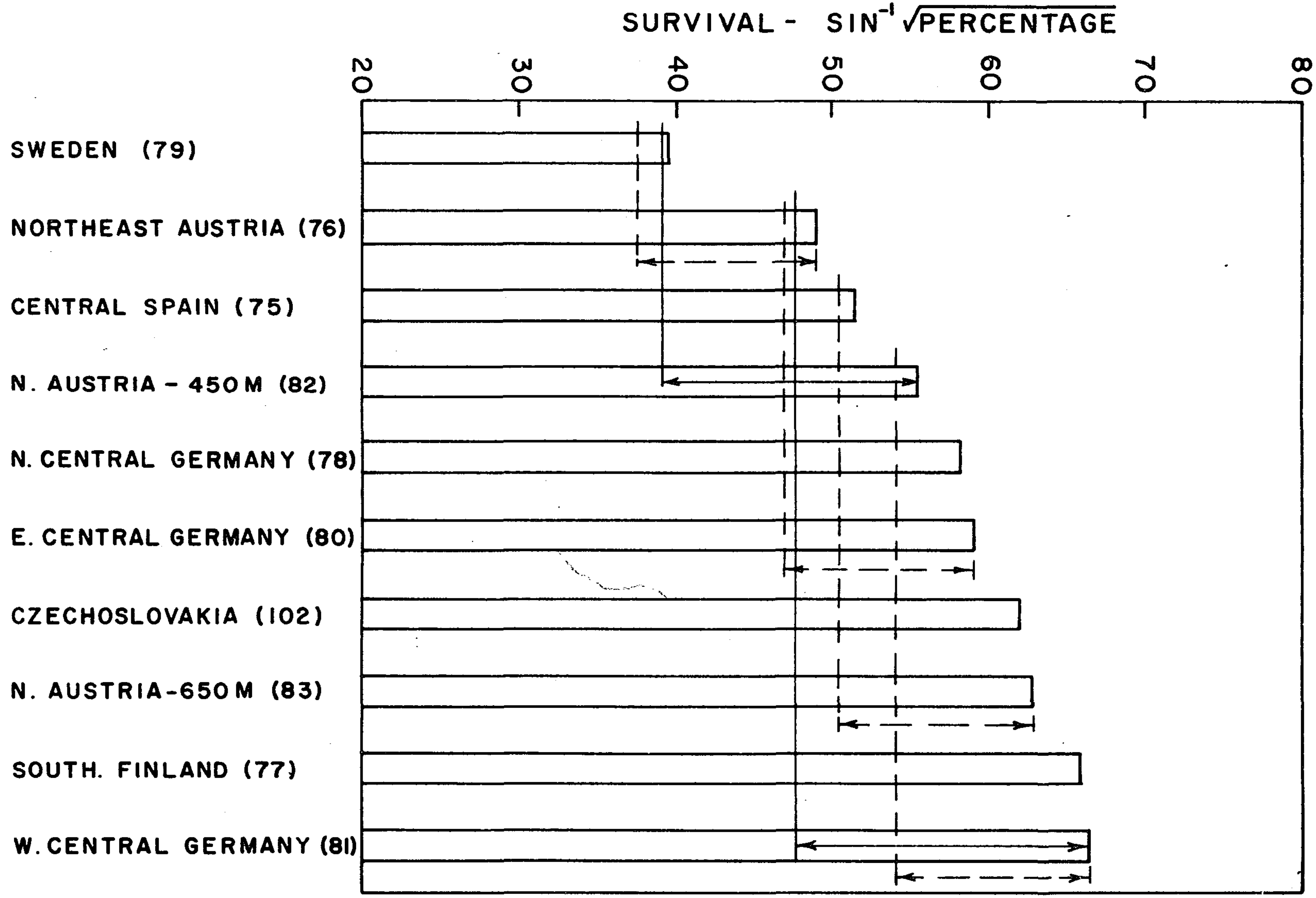

SURVIVAL - SIN^{-1} √PERCENTAGE
20
30
40
50
60
70
80
SWEDEN (79)
NORTHEAST AUSTRIA (76)
CENTRAL SPAIN (75)
N. AUSTRIA - 450 M (82)
N. CENTRAL GERMANY (78)
E. CENTRAL GERMANY (80)
CZECHOSLOVAKIA (102)
N. AUSTRIA-650 M (83)
SOUTH. FINLAND (77)
W. CENTRAL GERMANY (81)

Table 1. Analysis of variance of survival and height and diameter growth

Variation	df	Survival SS	Survival MS	Height growth SS	Height growth MS	Diameter growth SS	Diameter growth MS
Total	19	1,547.41		19.42		1.33	
Replication	1	62.69		0.04		0.00	
Seed source	9	1,266.82	140.76**	18.72	2.08**	1.25	0.14**
Error A	9	217.90	24.21	0.66	0.07	0.08	0.01

**Significant at 1-percent probability level.

Table 2. Average 5-year provenance height growth in feet and diameter growth in inches

Provenance	Number of observations	Height growth[a]	Diameter growth[a]
W. central Germany(81)	224	6.2	2.0
N. central Germany(78)	221	6.0	1.9
N. Austria-450m(82)	220	5.8	2.0
N. Austria-650m(83)	223	5.8	2.0
Czechoslovakia(102)	224	5.8	1.8
E. central Germany(80)	216	5.7	1.9
Northeast Austria(76)	220	5.6	1.8
Sweden(79)	78	4.0	1.5
Southern Finland(77)	224	4.0	1.4
Central Spain(75)	137	3.4	1.3

Grouping lines (height growth): the first seven provenances (6.2–5.6) are grouped at 5%; the last three (4.0–3.4) are grouped; 1% between the groups. Grouping lines (diameter growth): the first seven (2.0–1.8) are grouped and the last three (1.5–1.3) are grouped, at 5%.

[a]Means grouped by a line do not differ at the designated probability level.

Table 3. Relative fall-winter provenance foliage color[a], 5 years after planting

Provenance	Quantitative color	Qualitative color
Central Spain(75)	7.5 GY 5/4	Greenish green-yellow
Northeast Austria(76)	2.5 GY 5/4	Yellowish green-yellow
W. central Germany(81)	2.5 GY 5/4	Yellowish green-yellow
N. central Germany(78)	2.5 GY 5/6	Yellowish green-yellow
E. central Germany(80)	2.5 GY 5/6	Yellowish green-yellow
N. Austria-450m(82)	2.5 GY 5/6	Yellowish green-yellow
N. Austria-650m(83)	2.5 GY 5/6	Yellowish green-yellow
Czechoslovakia(102)	2.5 GY 5/6	Yellowish green-yellow
Sweden(79)	2.5 GY 6/6	Yellowish green-yellow
Southern Finland(77)	5.0 Y 5/6	Yellow

[a]Based on Munsell color charts (1952).

charts (1952).

Greenhouse Investigations

Preliminary investigation

Height growth   Height growth increased with an increase in photoperiod from 12 to 20 hours (Figures 5 and 6). The average increases from 12 to 16 hours and from 16 to 20 hours were significant at the 1-percent probability level (Table 4). Height growth decreased with an increase in temperature from 56° to 71°F. The average decrease was significant at the 1-percent level.

The effect of photoperiod on height growth was greater at 56° than at 71°F. Moreover, height growth increased slightly with increased temperature at the 12-hour photoperiod but decreased with increased temperature at the 16- and 20-hour day lengths. This temperature-photoperiod interaction was significant at the 1-percent level. Possibly, height growth was inhibited by higher temperatures over longer day lengths, or differences in distribution of assimilate, related to higher temperatures, resulted in less leader growth.

Differences among seed sources were significant at the 1-percent probability level. Height growth of the Czechoslovakia and west central Germany seed sources was greater than height growth of all other sources.

Although the increase in height growth with an increase in photoperiod from 12 to 16 hours was significant for all sources, the height growth increase of the northern Austria-650m source was not significant with an increase in photoperiod from 16 to 20 hours. Moreover, variation among sources at the 16- and 20-hour photoperiods was appreciably greater than at the 12-hour day length. This seed source-photoperiod interaction was significant at the 5-percent level.

The seed source-temperature interaction was significant at the 1-percent level. The decrease in height growth with increased temperature from 56° to 71°F ranged from 1 mm for the east central Germany source to approximately 18 mm for the Czechoslovakia source. Additionally, the range in differences among seed sources was appreciably greater at 56° than at 71°F.

Figure 5. Height growth response to photoperiod at the 56°F temperature. The 20-hour photoperiod chamber is shown at the left, the 12-hour chamber at the right.

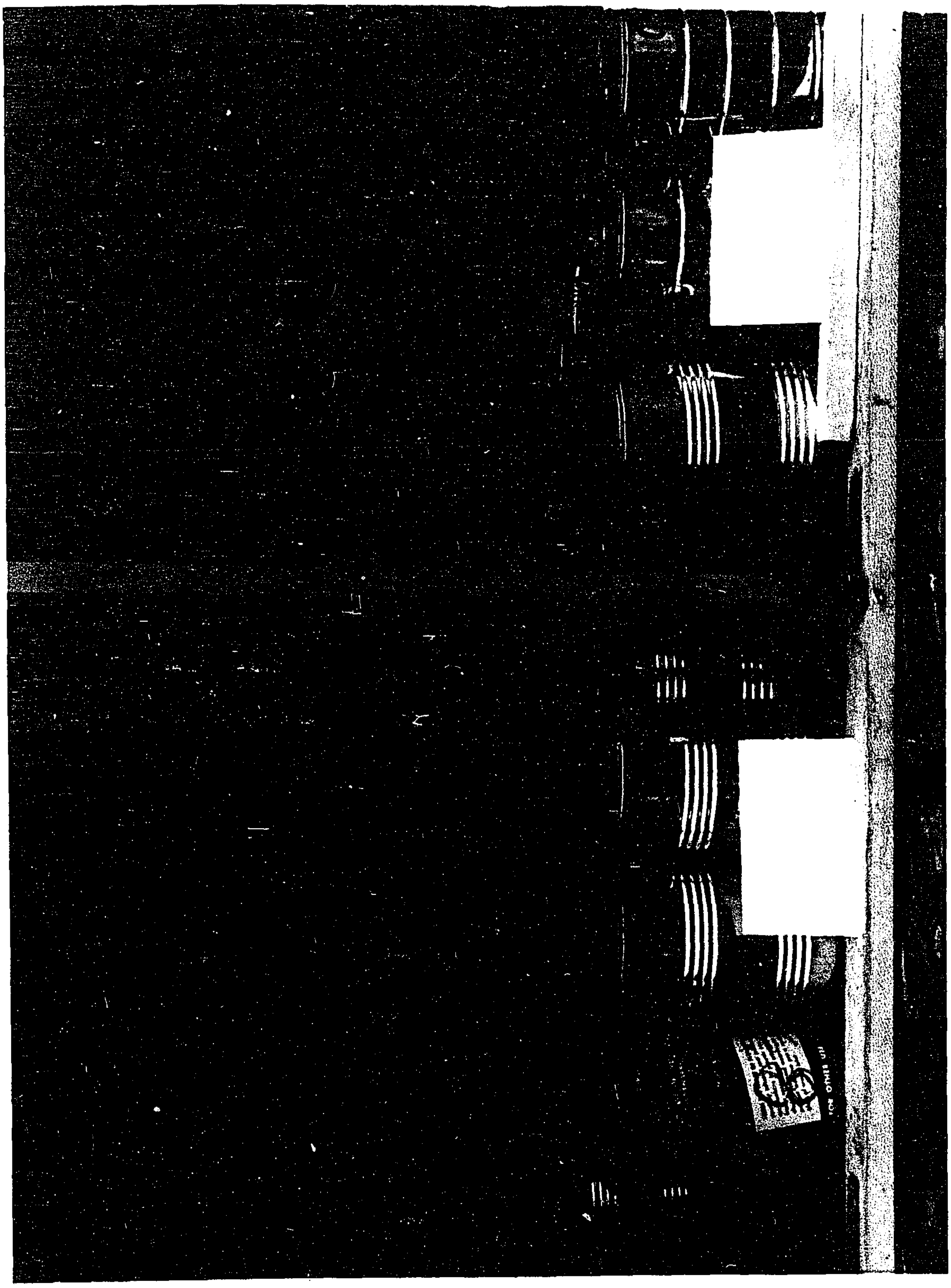


Figure 6. The effects of photoperiod, temperature and seed source on mean height growth of Scotch pine seedlings: A. Seed sources pooled; B. Photoperiods pooled; C. Temperatures pooled.

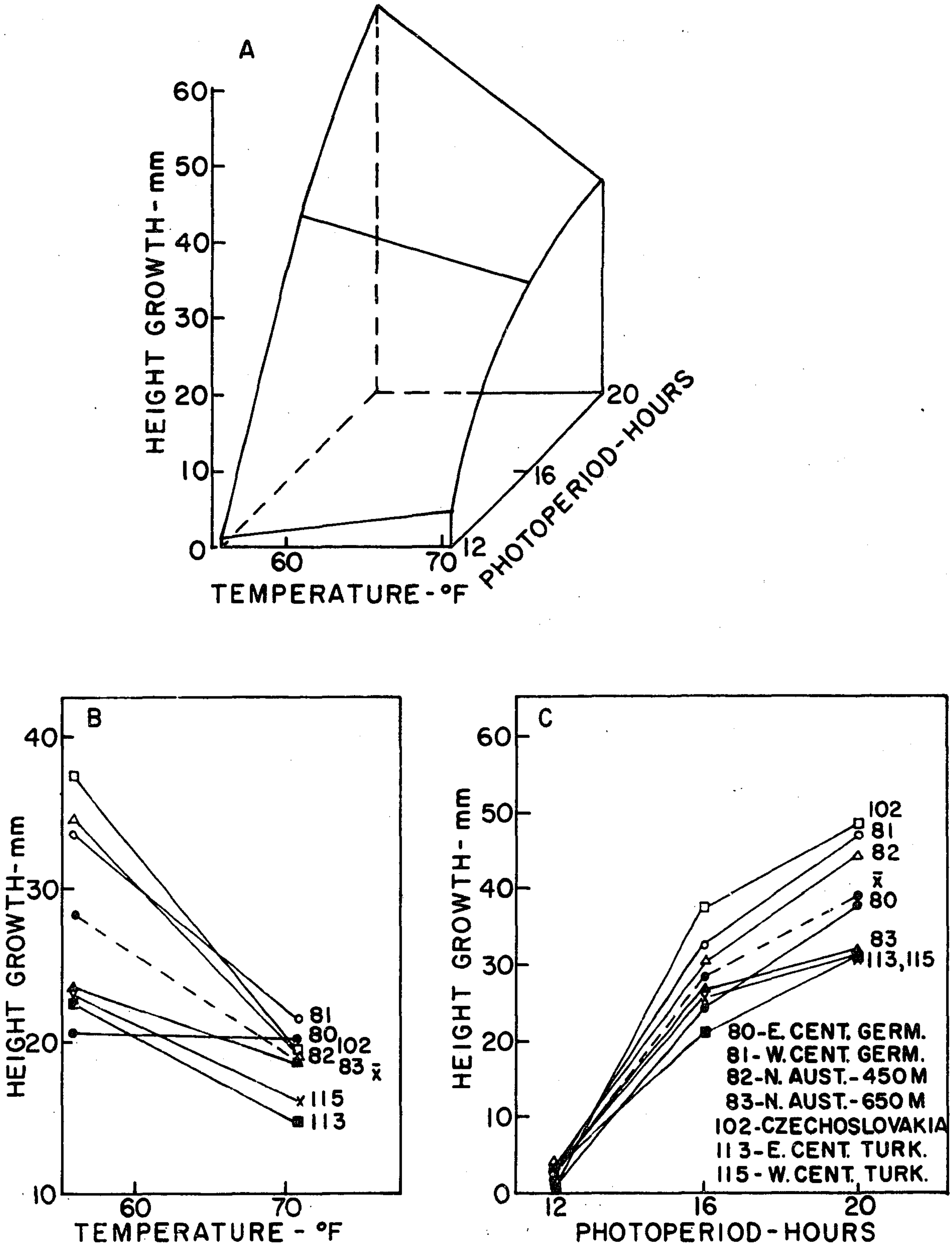

A
HEIGHT GROWTH - mm
0
10
20
30
40
50
60
60
70
TEMPERATURE - °F
12
16
20
PHOTOPERIOD - HOURS
B
HEIGHT GROWTH - mm
10
20
30
40
60
70
TEMPERATURE - °F
81
80
102
82
83
x̄
115
113
C
HEIGHT GROWTH - mm
0
10
20
30
40
50
60
12
16
20
PHOTOPERIOD - HOURS
102
81
82
x̄
80
83
113,115
80-E. CENT. GERM.
81-W. CENT. GERM.
82-N. AUST.-450 M
83-N. AUST.-650 M
102-CZECHOSLOVAKIA
113-E. CENT. TURK.
115-W. CENT. TURK.

Table 4. Analysis of variance of height growth, needle length, total green weight and bud burst of Scotch pine seedlings

Variation	df	Height growth SS	Height growth MS	Needle length SS	Needle length MS
Total	125	45,140.64		90,385.30	
Temperature	1	3,021.34	3,021.34**	47,024.11	47,024.11**
Rep/Temp[a]	4	131.06	32.76	449.46	112.36
Photoperiod	2	29,474.31	14,737.16**	24,986.73	12,493.36**
PxT	2	3,653.82	1,826.91**	2,702.09	1,351.04**
Error A	8	158.68	19.84	388.98	48.62
Seed source	6	1,923.39	320.56**	3,498.27	583.04**
SxT	6	947.19	157.86**	1,874.65	312.44**
SxP	12	1,331.86	110.99*	1,882.50	156.88*
SxPxT	12	789.23	65.77	2,114.24	176.18*
Error B	72	3,709.76	51.52	5,464.27	75.89

[a]This value was used to test the significance of temperature, based on the assumption that it is equal to the value that would have been found if true temperature replicates had been used.

*Significant at 5-percent probability level.

**Significant at 1-percent probability level.

Table 4. (Continued)

Variation	df	Total green weight SS	MS	Bud burst SS	MS
Total	125	162.47		92,417.21	
Temperature	1	0.08	0.08	6,990.34	6,990.34*
Rep/Temp	4	4.31	1.08	3,502.12	875.53
Photoperiod	2	66.22	33.11**	25,065.18	12,332.59**
PxT	2	2.05	1.02	3,234.35	1,617.18
Error A	8	15.56	1.94	3,186.87	398.36
Seed source	6	9.63	1.60*	10,027.36	1,671.23**
SxT	6	6.31	1.05	3,292.08	548.68
SxP	12	5.17	0.43	7,730.60	644.22
SxPxT	12	7.81	0.65	3,536.85	294.74
Error B	72	45.33	0.62	25,851.46	359.05

Needle length Needle length increased with an increase in photoperiod from 12 to 20 hours (Figure 7). The average increase from 12 to 16 hours was significant at the 1-percent probability level (Table 4), but not significant from 16 to 20 hours at the 5-percent level. The mean increase in needle length with increased temperature from 56° to 71°F was significant at the 1-percent level.

Mean needle length increases from 56° to 71°F at the 16- and 20-hour photoperiods were considerably greater than the increase at the 12-hour photoperiod. This photoperiod-temperature interaction was significant at the 1-percent level. However, part of the difference may be attributed to the measurement of needles prior to growth culmination at the shortest photoperiod and cooler temperature.

Differences among seed sources were significant at the 1-percent probability level. Needle length of the Austrian seed sources was greater than needle length of all other sources.

The increase in needle length with increased photoperiod from 12 to 16 hours varied greatly among seed sources, and this seed source-photoperiod interaction was significant at the 5-percent level.

Increased needle length with an increase in temperature from 56° to 71°F also varied appreciably among seed sources. Moreover, the range in differences among seed sources was considerably greater at 71° than at 56°F. The seed source-temperature interaction was significant at the 1-percent level, and the seed source-photoperiod-temperature interaction was significant at the 5-percent level.

<u>Total green weight</u> Total green weight increased with an increase in photoperiod from 12 to 20 hours (Table 5). The average increase from 12 to 16 hours was significant at the 1-percent probability level (Table 4), but not significant from 16 to 20 hours at the 5-percent level. The mean total green weight difference between temperatures was not significant at the 5-percent level.

Green weights of the east central Turkey, Czechoslovakia and northern Austria-650m seed sources were greater than green weights of the other sources, and the differences were

Figure 7. The effects of photoperiod, temperature and seed source on mean needle length of Scotch pine seedlings: A. Seed sources pooled; B. Photoperiods pooled; C. Temperatures pooled.

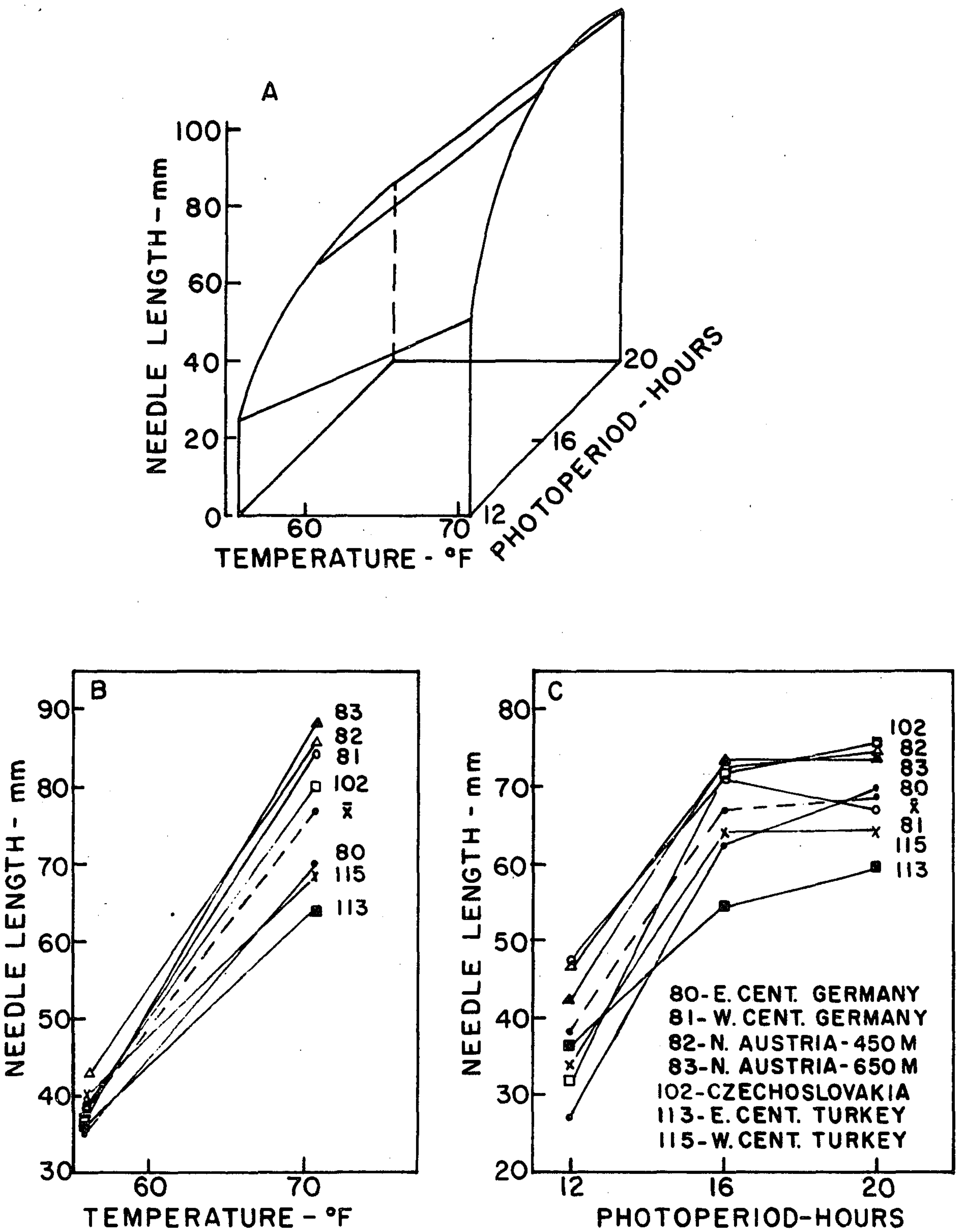

A
NEEDLE LENGTH - mm
TEMPERATURE - °F
PHOTOPERIOD - HOURS
B
NEEDLE LENGTH - mm
TEMPERATURE - °F
83
82
81
102
x̄
80
115
113
C
NEEDLE LENGTH - mm
PHOTOPERIOD-HOURS
102
82
83
80
x̄
81
115
113
80- E. CENT. GERMANY
81- W. CENT. GERMANY
82-N. AUSTRIA-450 M
83-N. AUSTRIA-650 M
102-CZECHOSLOVAKIA
113-E. CENT. TURKEY
115-W. CENT. TURKEY

Table 5. The effects of photoperiod and seed source on mean total green weight of Scotch pine seedlings, temperatures pooled

Provenance	Green weight (grams) at designated photoperiod (hours)			
	12	16	20	Mean
E. central Turkey(113)	1.89	3.12	3.98	3.00
Czechoslovakia(102)	1.62	3.55	3.72	2.96
N. Austria-650m(83)	2.19	2.98	3.51	2.89
N. Austria-450m(82)	1.92	2.59	3.48	2.66
W. central Turkey(115)	1.43	2.57	3.43	2.48
W. central Germany(81)	1.57	2.80	3.00	2.46
E. central Germany(80)	1.16	2.73	2.75	2.21
Mean	1.68	2.91	3.41	

significant at the 5-percent level.

Bud burst The number of days to bud burst decreased with an increase in photoperiod from 12 to 20 hours (Table 6). The mean decrease from 12 to 16 hours was significant at the 1-percent probability level (Table 4), but not significant from 16 to 20 hours at the 5-percent level. The date of mean bud burst was 15 days earlier for the 71° than for the 56°F temperature, and this difference was significant at the 5-percent level.

Bud burst dates of the northern Austria-450m and west central Turkey sources were earlier than bud burst dates of the other sources, and the differences were significant at the 1-percent level.

Table 6. The effects of photoperiod and seed source on the mean number of days to bud burst of Scotch pine seedlings, temperatures pooled

Provenance	Mean number of days to bud burst[a] at designated photoperiod (hours) 12	16	20	Mean
E. central Germany(80)	65.9	26.4	8.4	33.6
Czechoslovakia(102)	57.9	27.8	9.6	31.7
E. central Turkey(113)	57.5	17.6	9.4	28.2
W. central Germany(81)	32.2	18.3	6.3	19.0
N. Austria-650m(83)	39.0	6.5	3.1	16.2
W. central Turkey(115)	19.9	10.4	8.9	13.1
N. Austria-450m(82)	12.8	9.2	5.1	9.0
Mean	40.7	16.6	7.3	

[a]The mean number of days to bud burst was measured as the mean interval from the date that the first seedling started growth in the study until the buds of all seedlings in a treatment had burst.

<u>Height growth patterns</u> Seedling height growth initiation occurred earlier, and the rate of growth was greater with an increase in photoperiod (Figure 8). Differences among photoperiods were considerably greater at 56° than at 71°F. Conversely, differences among photoperiods were not significant when seedlings were pre-chilled. The pre-chilling treatment apparently offset the shorter photoperiod effect.

Height growth patterns varied among seed sources (Figure 9). Growth rates of the Czechoslovakia, northern Austria-450m and west central Germany seed sources were considerably greater than growth rates of the other sources. Additionally, growth

Figure 8. The effects of photoperiod, temperature and pre-chilling on height growth patterns of Scotch pine seedlings, seed sources pooled.

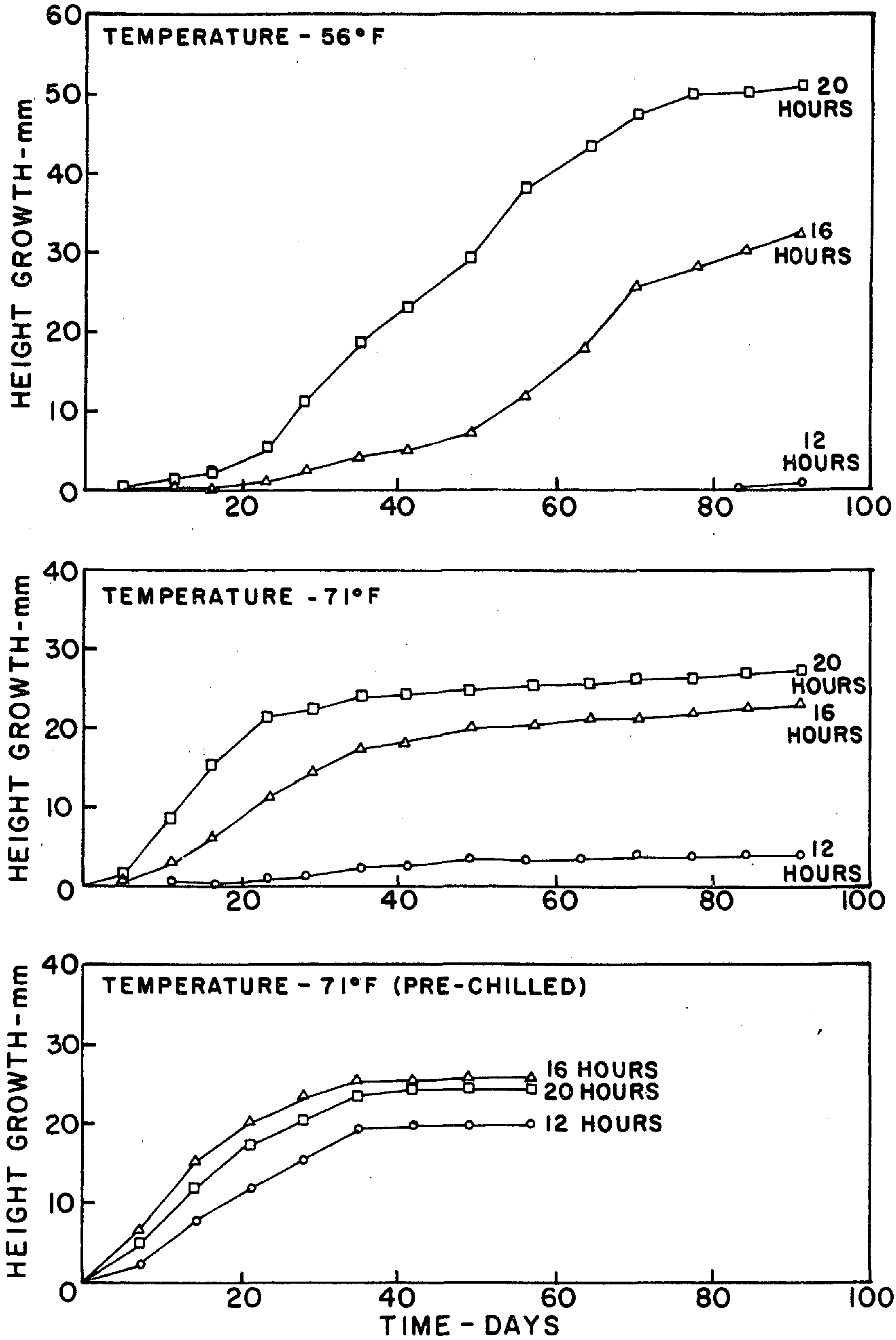
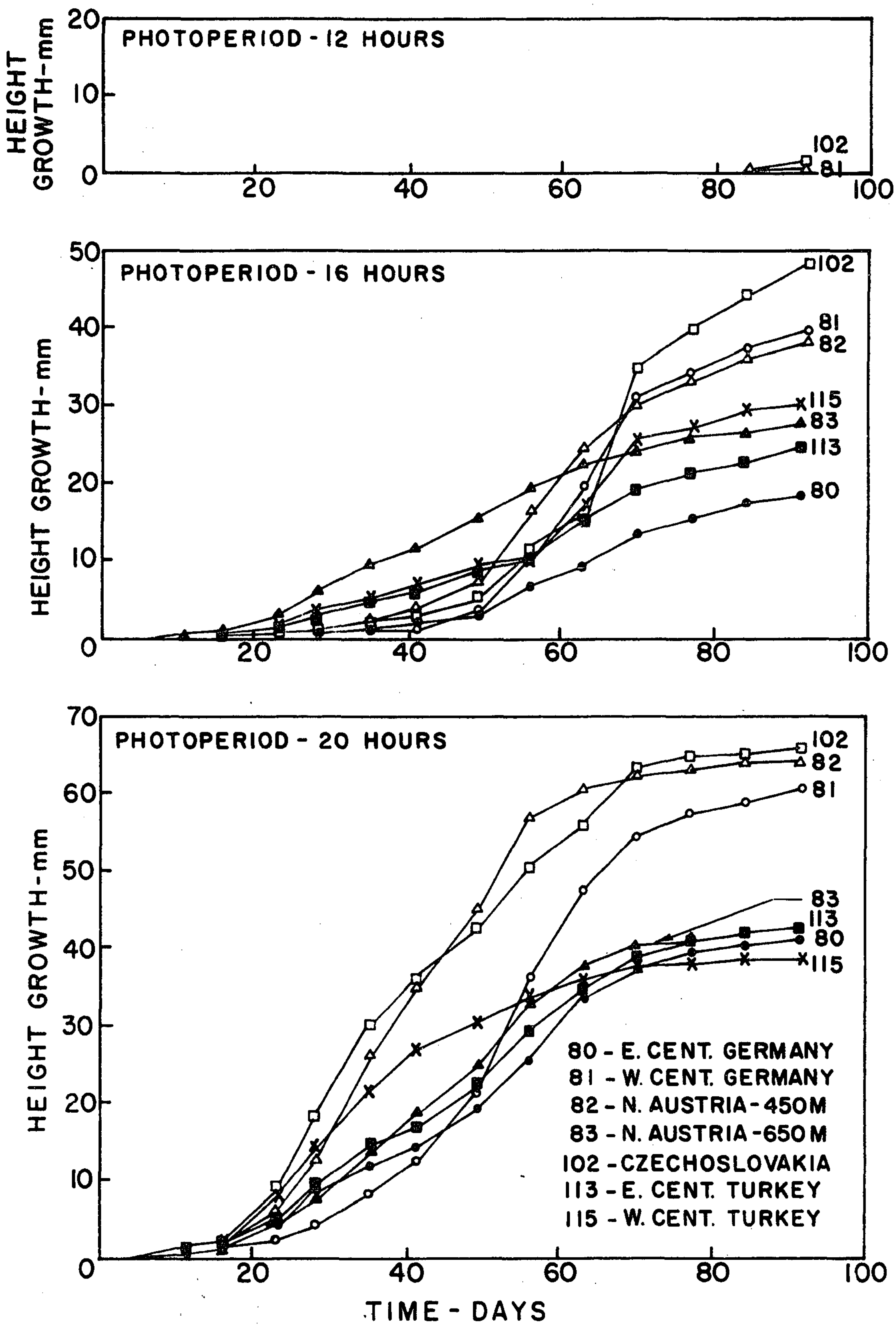

TEMPERATURE - 56° F
HEIGHT GROWTH - mm
20 HOURS
16 HOURS
12 HOURS
TEMPERATURE - 71° F
20 HOURS
16 HOURS
12 HOURS
TEMPERATURE - 71° F (PRE-CHILLED)
16 HOURS
20 HOURS
12 HOURS
TIME - DAYS

Figure 9. The effects of photoperiod and seed source on height growth patterns of Scotch pine seedlings at the 56°F temperature.


PHOTOPERIOD - 12 HOURS
HEIGHT GROWTH-mm
102
81
PHOTOPERIOD - 16 HOURS
HEIGHT GROWTH-mm
102
81
82
115
83
113
80
PHOTOPERIOD - 20 HOURS
HEIGHT GROWTH-mm
102
82
81
83
113
80
115
80 - E. CENT. GERMANY
81 - W. CENT. GERMANY
82 - N. AUSTRIA - 450 M
83 - N. AUSTRIA - 650 M
102 - CZECHOSLOVAKIA
113 - E. CENT. TURKEY
115 - W. CENT. TURKEY
TIME - DAYS

of these three sources at the 56°F temperature began earlier and continued for a longer period of time at the 20-hour than at the 16-hour photoperiod.

Final investigations

Photoperiod, temperature and provenance   This part of the final investigation was conducted to complement the data obtained in the preliminary investigation; consequently, similar and contradictory relationships will become evident. A comparison of these relationships between the two investigations can be obtained from the analyses of variance, Tables 4 and 7. An interpretation of the relationships will be made in the Discussion.

Height growth   Height growth increased with an increase in photoperiod from 14 to 18 hours and with a decrease in temperature from 76° to 57°F (Figure 10). The average increases from 14 to 16 hours and from 16 to 18 hours were significant at the 1-percent probability level (Table 7). The mean decrease from 57° to 65°F was significant at the 1-percent level while the decrease from 65° to 76°F was not significant at the 5-percent level. Moreover, height growth had not culminated at the 57°F temperature treatment when the study was terminated.

The effect of photoperiod on height growth was less at the 57° than at the 65° and 76°F temperatures. Additionally, differences among temperatures were smaller at the 18- than the 14-hour photoperiod. This photoperiod-temperature interaction was significant at the 5-percent probability level.

Differences in height growth among seed sources were significant at the 1-percent level. The Austrian sources made more height growth than all other sources. None of the interactions involving seed source was significant at the 5-percent level.

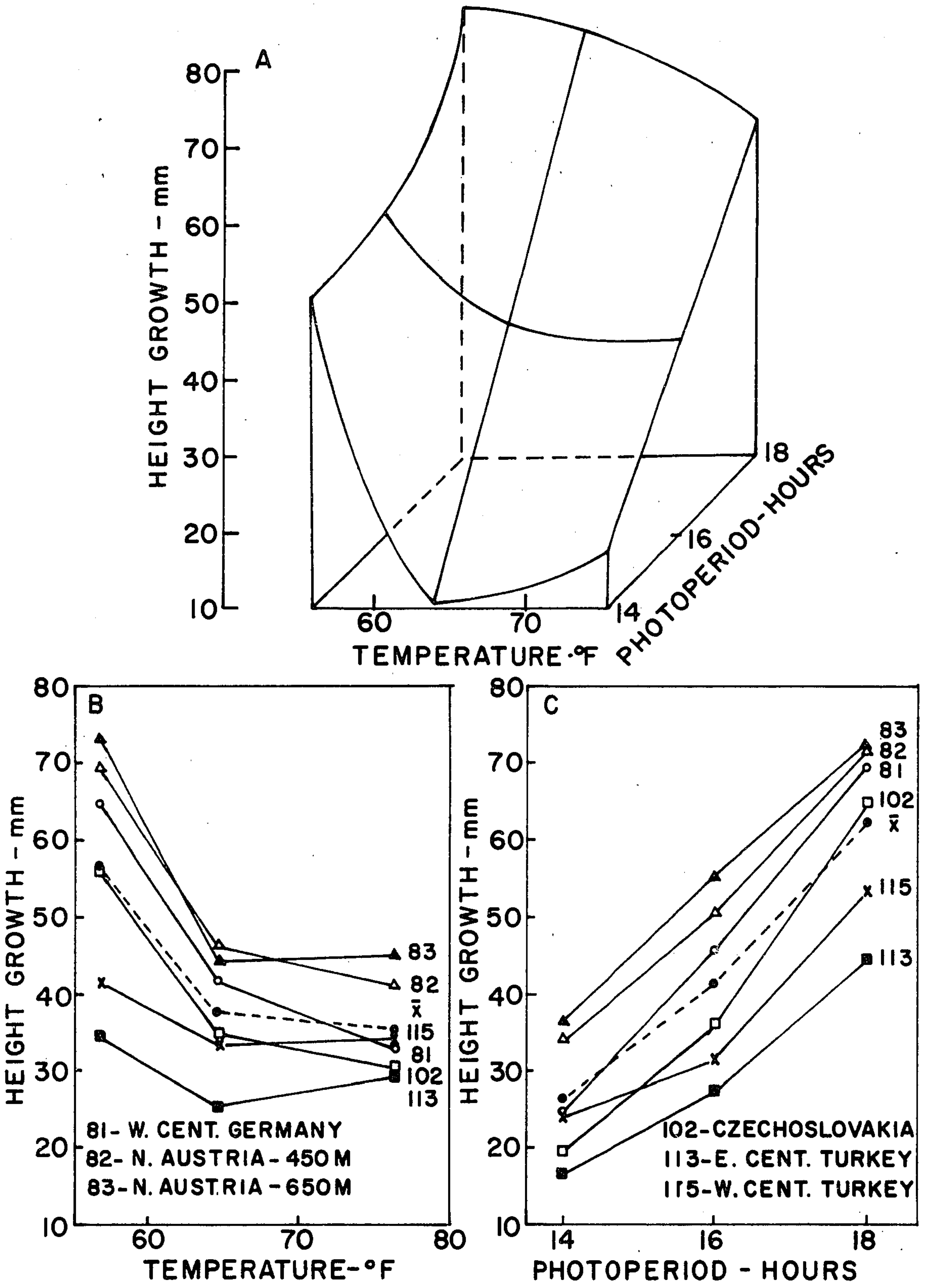
Needle length Needle length increased with an increase in temperature from 57° to 76°F (Figure 11), and both the increases from 57° to 65°F and from 65° to 76°F were significant at the 1-percent probability level (Table 7). However, part of the increase was caused by the measurement of needles prior to growth culmination at the lowest temperature. Differences among photoperiods and the photoperiod-temperature interaction were not significant at the 5-percent level.

Differences among seed sources were significant at the 1-percent probability level. The Czechoslovakia source had the longest needles while the Turkey sources had the shortest needles of all sources.

Needle length of some seed sources increased slightly while others decreased slightly with an increase in photoperiod. This seed source-photoperiod interaction was significant at the 5-percent level.

The seed source-temperature interaction was significant at the 1-percent probability level. Increased needle length with an increase in temperature varied among seed sources. Moreover, the range in differences among seed sources varied

Figure 10. The effects of photoperiod, temperature and seed source on mean height growth of Scotch pine seedlings: **A.** Seed sources pooled; B. Photoperiods pooled; C. Temperatures pooled.



A
HEIGHT GROWTH - mm
80
70
60
50
40
30
20
10
60
70
TEMPERATURE-°F
14
16
18
PHOTOPERIOD-HOURS
B
HEIGHT GROWTH - mm
83
82
x̄
115
81
102
113
81- W. CENT. GERMANY
82- N. AUSTRIA-450 M
83- N. AUSTRIA-650 M
60
70
80
TEMPERATURE-°F
C
HEIGHT GROWTH - mm
83
82
81
102
x̄
115
113
102-CZECHOSLOVAKIA
113-E. CENT. TURKEY
115-W. CENT. TURKEY
14
16
18
PHOTOPERIOD - HOURS

Table 7. Analysis of variance of height growth, needle length, total green weight and bud burst of Scotch pine seedlings

Variation	df	Height growth		Needle length	
		SS	MS	SS	MS
Total	161	102,073.66		112,537.63	
Temperature	2	14,514.68	7,257.34**	86,949.64	43,474.82**
Rep/Temp[a]	6	3,181.30	530.22	1,006.52	167.75
Photoperiod	2	35,953.96	17,976.98**	624.81	312.40
PxT	4	6,439.86	1,606.64*	1,522.53	380.64
Error A	12	4,061.21	338.43	1,846.78	153.90
Seed source	5	12,422.51	2,484.50**	3,690.26	738.05**
SxT	10	3,514.56	351.46	2,883.48	288.35**
SxP	10	1,589.53	158.95	2,223.55	222.36*
SxPxT	20	3,217.70	160.88	3,106.83	155.34
Error B	90	17,178.35	190.87	8,683.23	96.48

[a]This value was used to test the significance of temperature, based on the assumption that it is equal to the value that would have been found if true temperature replicates had been used.

*Significant at 5-percent probability level.

**Significant at 1-percent probability level.

Table 7. (Continued)

Variation	df	Total green weight SS	MS	Bud burst SS	MS
Total	161	916.67		213,750.50	
Temperature	2	243.39	121.70**	139,027.11	69,513.56**
Rep/Temp	6	27.75	4.62	2,661.11	443.52
Photoperiod	2	114.29	57.14**	29,449.00	14,724.50**
PxT	4	55.51	13.88*	1,595.56	398.89
Error A	12	33.82	2.82	3,266.89	272.24
Seed source	5	20.61	4.12	4,600.35	920.07**
SxT	10	66.89	6.69*	5,729.48	572.95**
SxP	10	26.22	2.62	4,399.59	439.96*
SxPxT	20	58.46	2.92	6,363.41	318.17*
Error B	90	269.73	3.00	16,658.00	185.09

among temperatures.

Total green weight Total green weight increased with an increase in photoperiod from 14 to 18 hours and with an increase in temperature from 57^{o} to 76^{o}F (Table 8). The average increase from 14 to 16 hours was significant at the 1-percent probability level (Table 7), while the increase from 16 to 18 hours was significant at the 5-percent level. The mean increase from 57^{o} to 65^{o}F was significant at the 1-percent level while the change from 65^{o} to 76^{o}F was not significant at the 5-percent level. However, growth had not terminated at the lowest temperature when the study was ended.

The photoperiod-temperature interaction was significant at the 5-percent probability level. Mean green weight increase

Figure 11. The effects of photoperiod, temperature and seed source on mean needle length of Scotch pine seedlings: A. Seed sources pooled; B. Photoperiods pooled; C. Temperatures pooled.

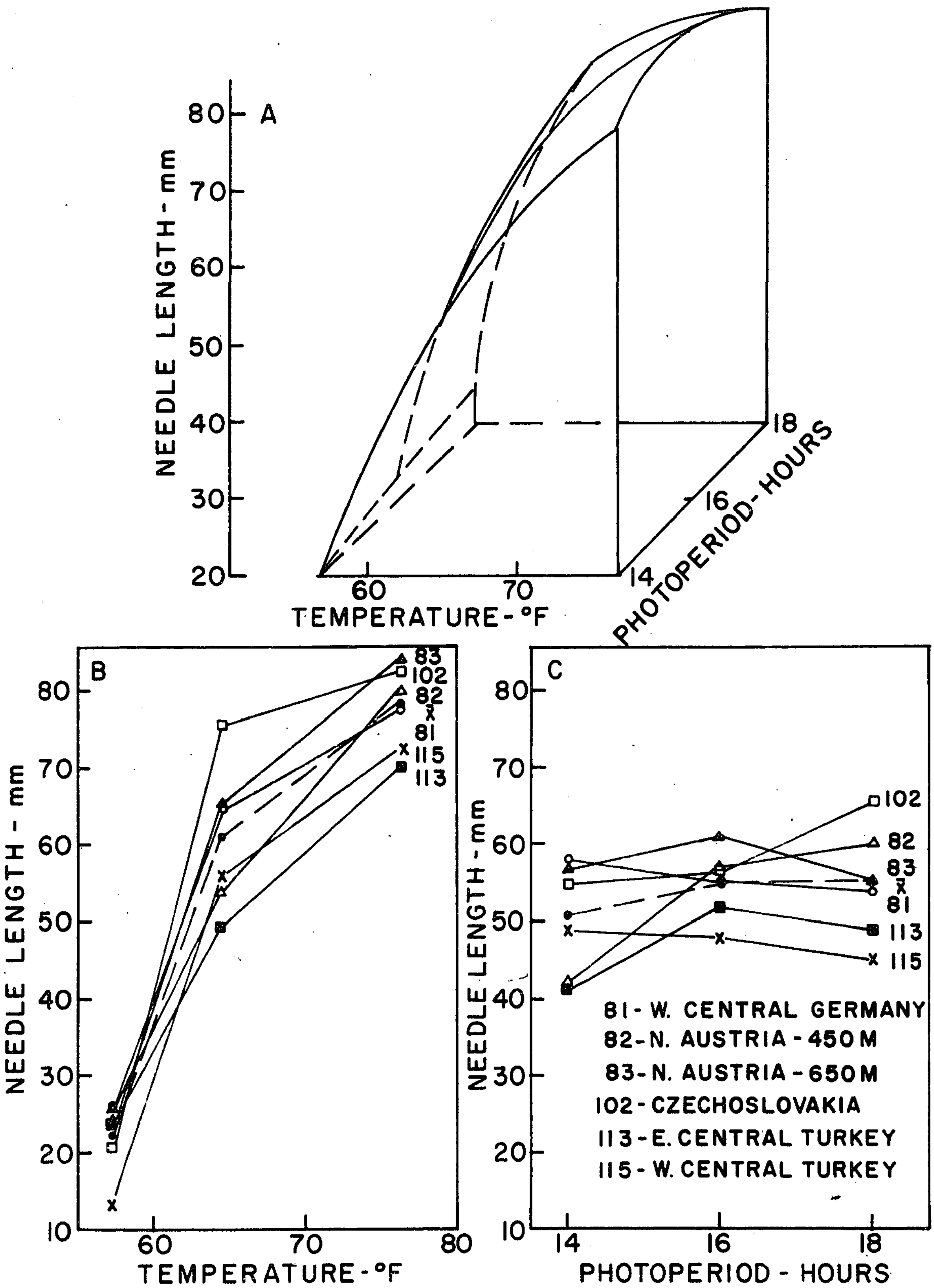

A
NEEDLE LENGTH - mm
80
70
60
50
40
30
20
60
70
TEMPERATURE - °F
14
16
18
PHOTOPERIOD - HOURS
B
NEEDLE LENGTH - mm
TEMPERATURE - °F
83
102
82
81
115
113
C
NEEDLE LENGTH - mm
PHOTOPERIOD - HOURS
102
82
83
81
113
115
81 - W. CENTRAL GERMANY
82 - N. AUSTRIA - 450 M
83 - N. AUSTRIA - 650 M
102 - CZECHOSLOVAKIA
113 - E. CENTRAL TURKEY
115 - W. CENTRAL TURKEY

Table 8. The effects of photoperiod and temperature on mean total green weight of Scotch pine seedlings, seed sources pooled

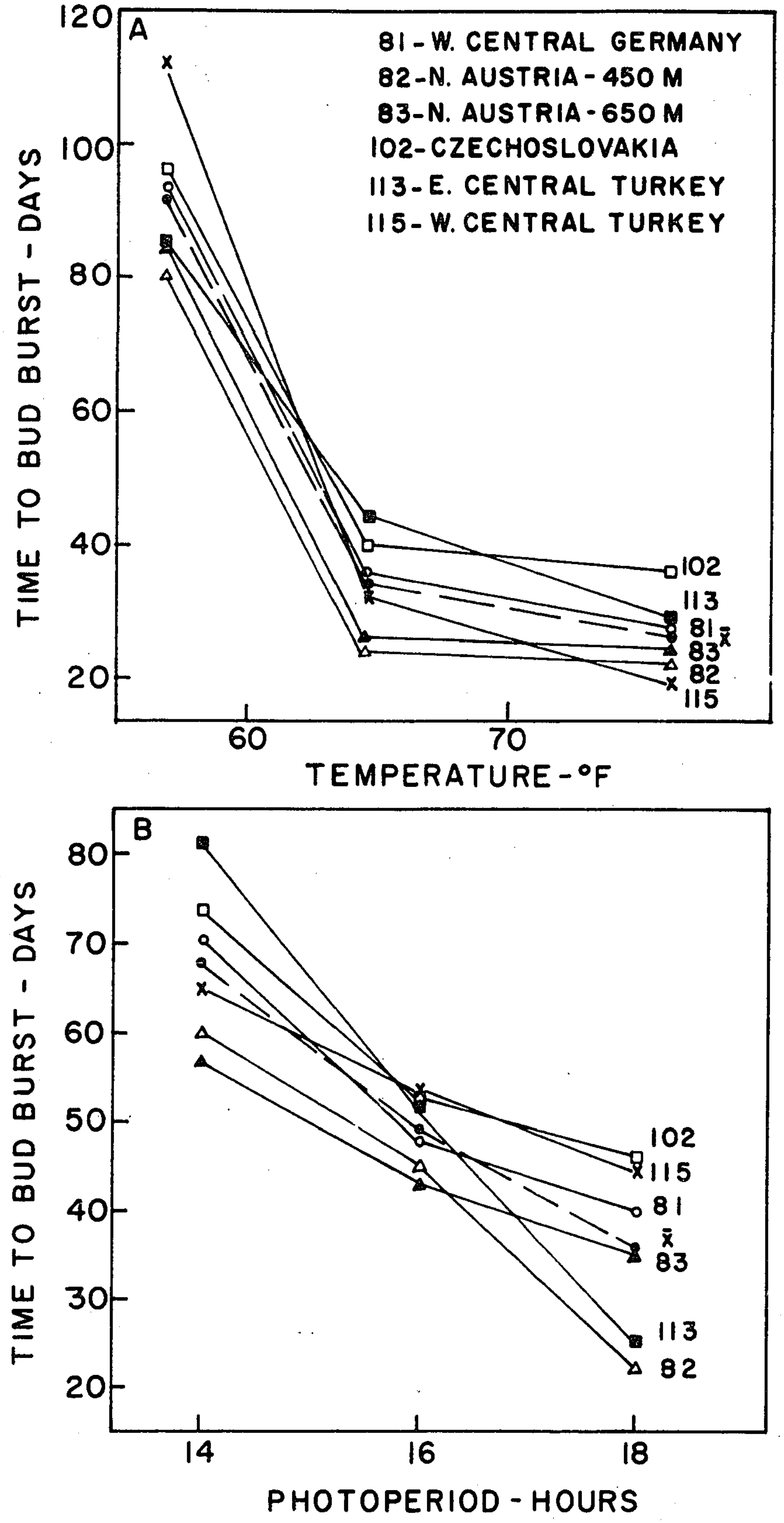
Temperature °F	Green weight (grams) at designated photoperiods (hours) 14	16	18	Mean
57	3.87	4.15	4.16	4.06
65	4.62	6.93	8.37	6.64
76	5.66	6.62	7.75	6.68
Mean	4.71	5.90	6.76	

with an increase in photoperiod at the 65°F temperature was greater than the increase at the 57° and 76°F temperatures.

Differences in total green weight among seed sources were not significant at the 5-percent level. Conversely, the seed source-temperature interaction was significant at the 5-percent level. Total green weight differences among seed sources ranged from 0.80 gm at the 57°F temperature to 3.39 gm at the 76°F temperature. Moreover, the increase with an increase in temperature from 57° to 76°F varied from 1.52 gm for the west central Germany source to 4.67 gm for the west central Turkey source.

<u>Bud burst</u> The number of days to bud burst decreased with an increase in photoperiod from 14 to 18 hours and with an increase in temperature from 57° to 76°F (Figure 12). The average decreases from 14 to 16 hours and from 16 to 18 hours were significant at the 1-percent probability level (Table 7).

Figure 12. The effects of photoperiod, temperature and seed source on mean number of days to bud burst of Scotch pine seedlings: A. Photoperiods pooled; B. Temperatures pooled (The mean number of days to bud burst was measured as the mean interval from the date that the first seedling started growth in the study until the buds of all seedlings in a treatment had burst).


A
81 - W. CENTRAL GERMANY
82 - N. AUSTRIA - 450 M
83 - N. AUSTRIA - 650 M
102 - CZECHOSLOVAKIA
113 - E. CENTRAL TURKEY
115 - W. CENTRAL TURKEY
TIME TO BUD BURST - DAYS
TEMPERATURE - °F
B
TIME TO BUD BURST - DAYS
PHOTOPERIOD - HOURS

The mean decrease from 57° to 65°F was significant at the 1-percent level, but the decrease from 65° to 76°F was not significant at the 5-percent level.

Differences in number of days to bud burst among seed sources were significant at the 1-percent probability level. The west central Turkey and Czechoslovakia sources burst bud later and the Austrian sources burst bud earlier than all other sources.

The seed source-photoperiod interaction was significant at the 5-percent level. The decrease in the number of days to bud burst with an increase in photoperiod ranged from 20 days for the west central Turkey source to 56 days for the east central Turkey source.

The decrease in the number of days to bud burst with an increase in temperature from 57° to 65°F was significant for all sources, while the decrease from 65° to 76°F was significant for only the Turkey sources. This seed source-temperature interaction was significant at the 1-percent level, and the seed source-photoperiod-temperature interaction was significant at the 5-percent level.

Height growth patterns At all temperatures, height growth initiation occurred earlier, and the growth rate was faster with an increase in photoperiod (Figure 13). Moreover, height growth initiation was later and the growth rate faster at the 57°F temperature than at the 65° and 76°F temperatures (Figure 14). At the two higher temperatures,

Figure 13. The effects of photoperiod and temperature on height growth patterns of Scotch pine seedlings, seed sources pooled.

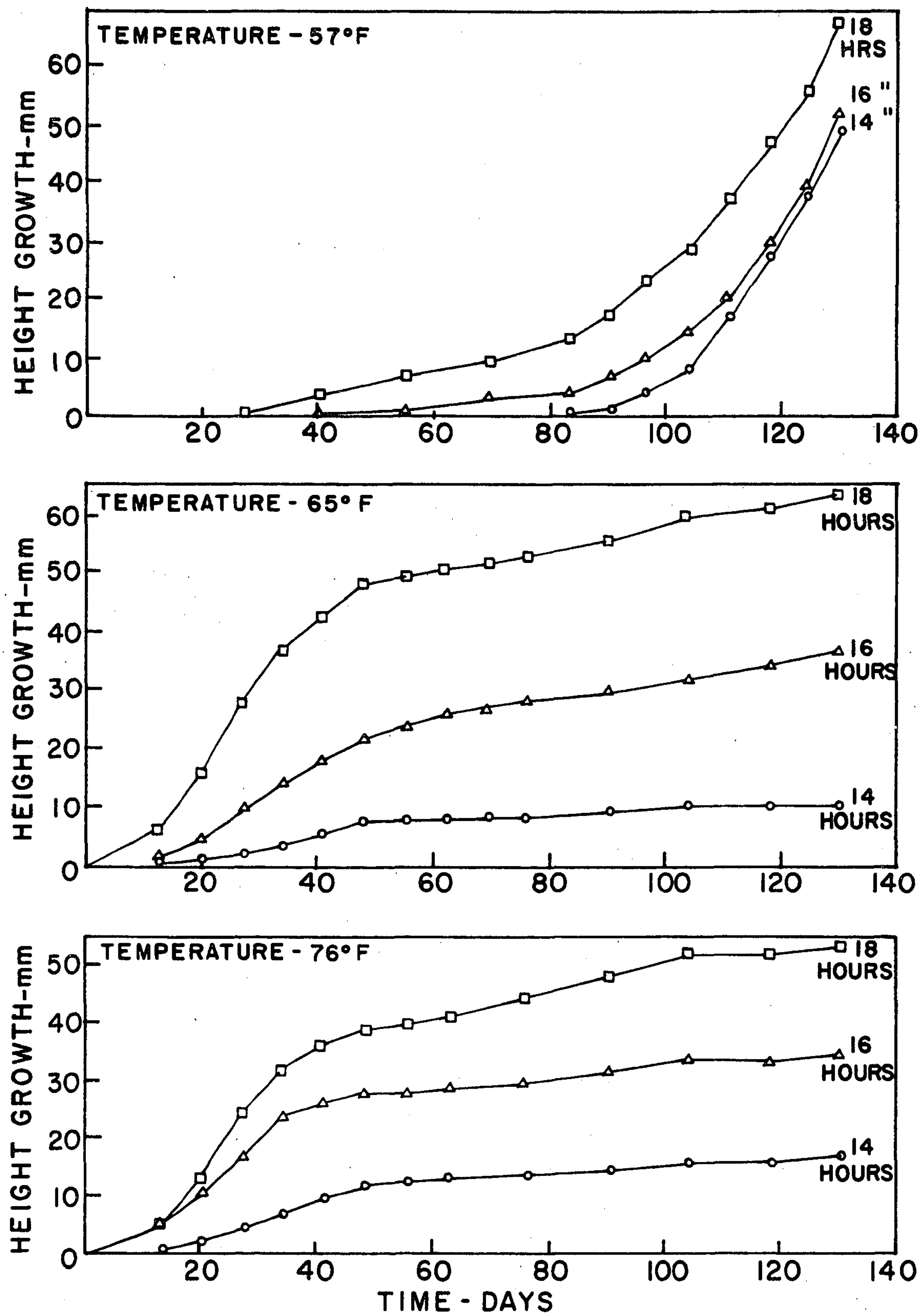
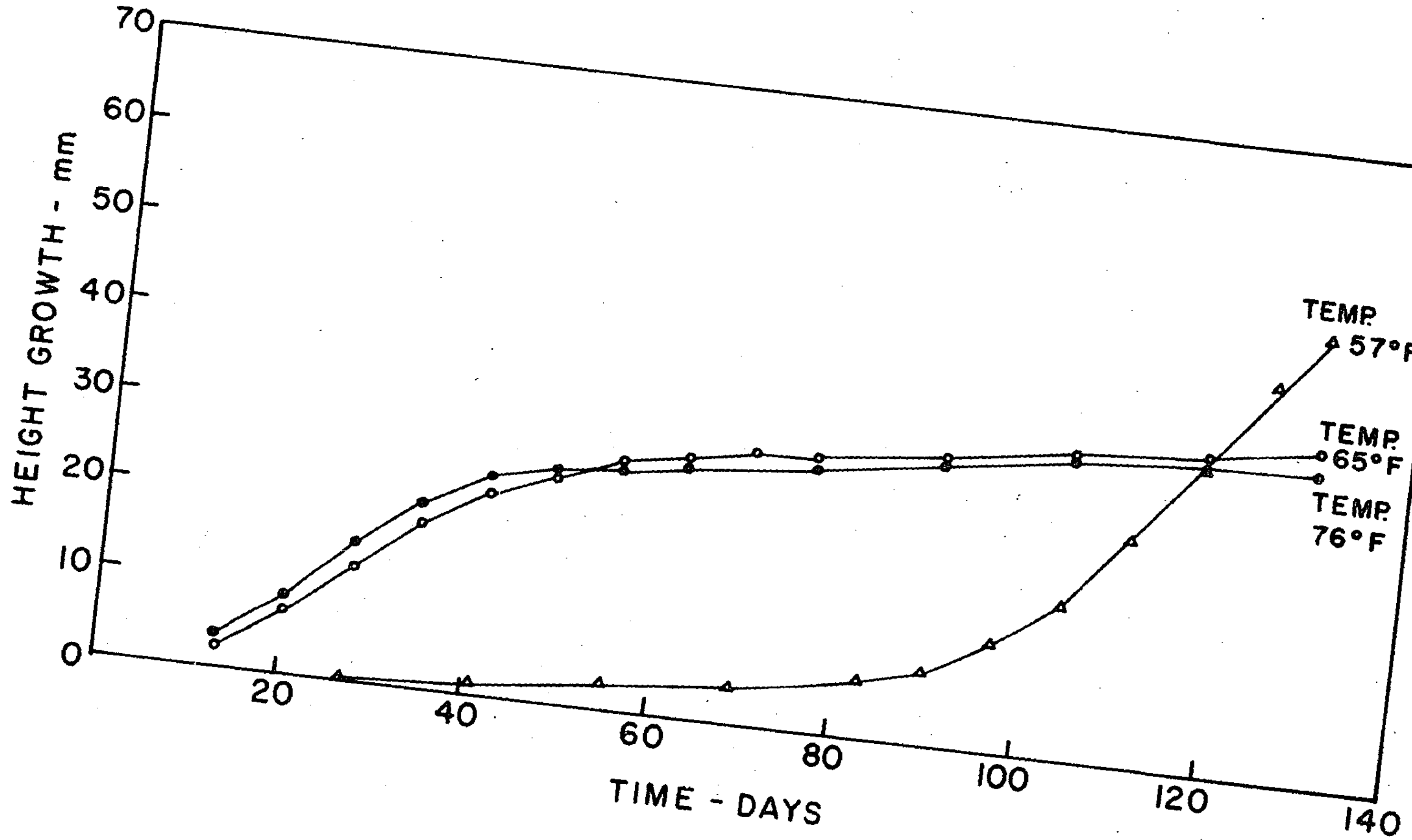

TEMPERATURE - 57°F
18 HRS
16 "
14 "
HEIGHT GROWTH-mm
TEMPERATURE - 65° F
18 HOURS
16 HOURS
14 HOURS
HEIGHT GROWTH-mm
TEMPERATURE - 76° F
18 HOURS
16 HOURS
14 HOURS
HEIGHT GROWTH-mm
TIME - DAYS

Figure 14. The effect of temperature on height growth patterns of Scotch pine seedlings, photoperiods and seed sources pooled.


HEIGHT GROWTH - mm
0
10
20
30
40
50
60
70
20
40
60
80
100
120
140
TIME - DAYS
TEMP. 57°F
TEMP. 65°F
TEMP. 76°F

time of growth initiation, growth rate and total growth were similar.

Height growth patterns varied among seed sources (Figure 15). In general, the growth rates of the Austrian sources were greater than the growth rates of the Turkey sources.

Photoperiod, pre-chilling and provenance

Height growth   Height growth increased with an increase in photoperiod from 12 to 20 hours and with an increase in the length of the pre-chilling period up to 10 weeks (Figure 16). The average increases from 12 to 16 hours and from 16 to 20 hours were significant at the 1-percent probability level (Table 9). Height growth after 8 or 10 weeks of pre-chilling was greater than height growth after 0, 2 or 4 weeks of pre-chilling, and the difference was significant at the 1-percent level.

Differences in height growth among seed sources were significant at the 1-percent probability level. The east central Turkey source made less growth than the west central Germany and northern Austria-650m sources.

The seed source-photoperiod interaction was significant at the 1-percent level. The increase in height growth with an increase in photoperiod ranged from 51 mm for the east central Turkey source to 81 mm for the west central Germany source.

Height growth patterns   Total height growth and the rate of growth increased while the number of days to growth

Figure 15. The effects of photoperiod and seed squrce on height growth patterns of Scotch pine seedlings at the 65°F temperature.

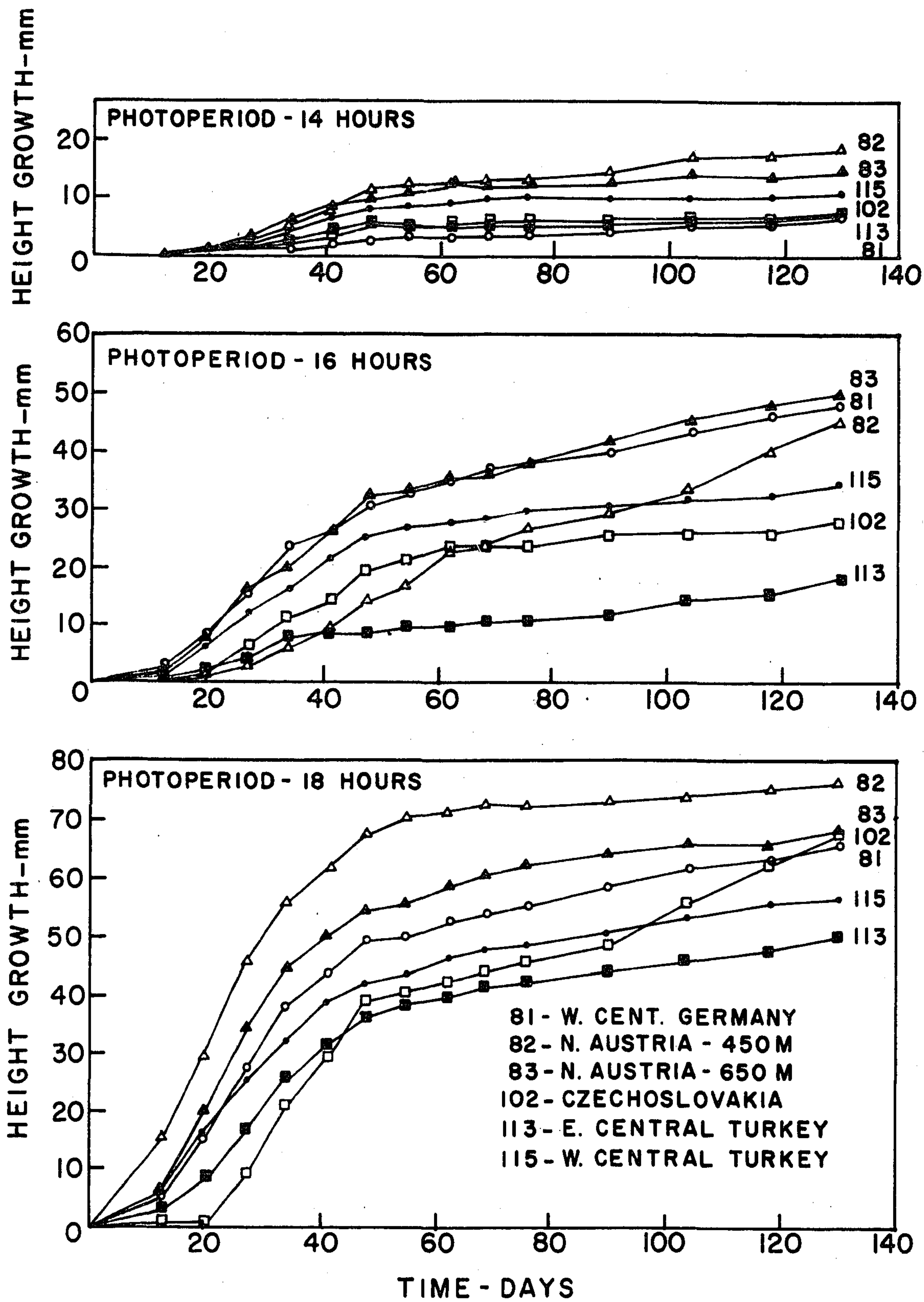

HEIGHT GROWTH-mm
PHOTOPERIOD - 14 HOURS
0
10
20
82
83
115
102
113
81
20
40
60
80
100
120
140
HEIGHT GROWTH-mm
PHOTOPERIOD - 16 HOURS
0
10
20
30
40
50
60
83
81
82
115
102
113
HEIGHT GROWTH-mm
PHOTOPERIOD - 18 HOURS
0
10
20
30
40
50
60
70
80
82
83
102
81
115
113
81 - W. CENT. GERMANY
82 - N. AUSTRIA - 450 M
83 - N. AUSTRIA - 650 M
102 - CZECHOSLOVAKIA
113 - E. CENTRAL TURKEY
115 - W. CENTRAL TURKEY
TIME - DAYS

Figure 16. The effects of photoperiod, pre-chilling and seed source on mean height growth of Scotch pine seedlings: A. Seed sources pooled; B. Photoperiods pooled; C. Pre-chilling periods pooled.

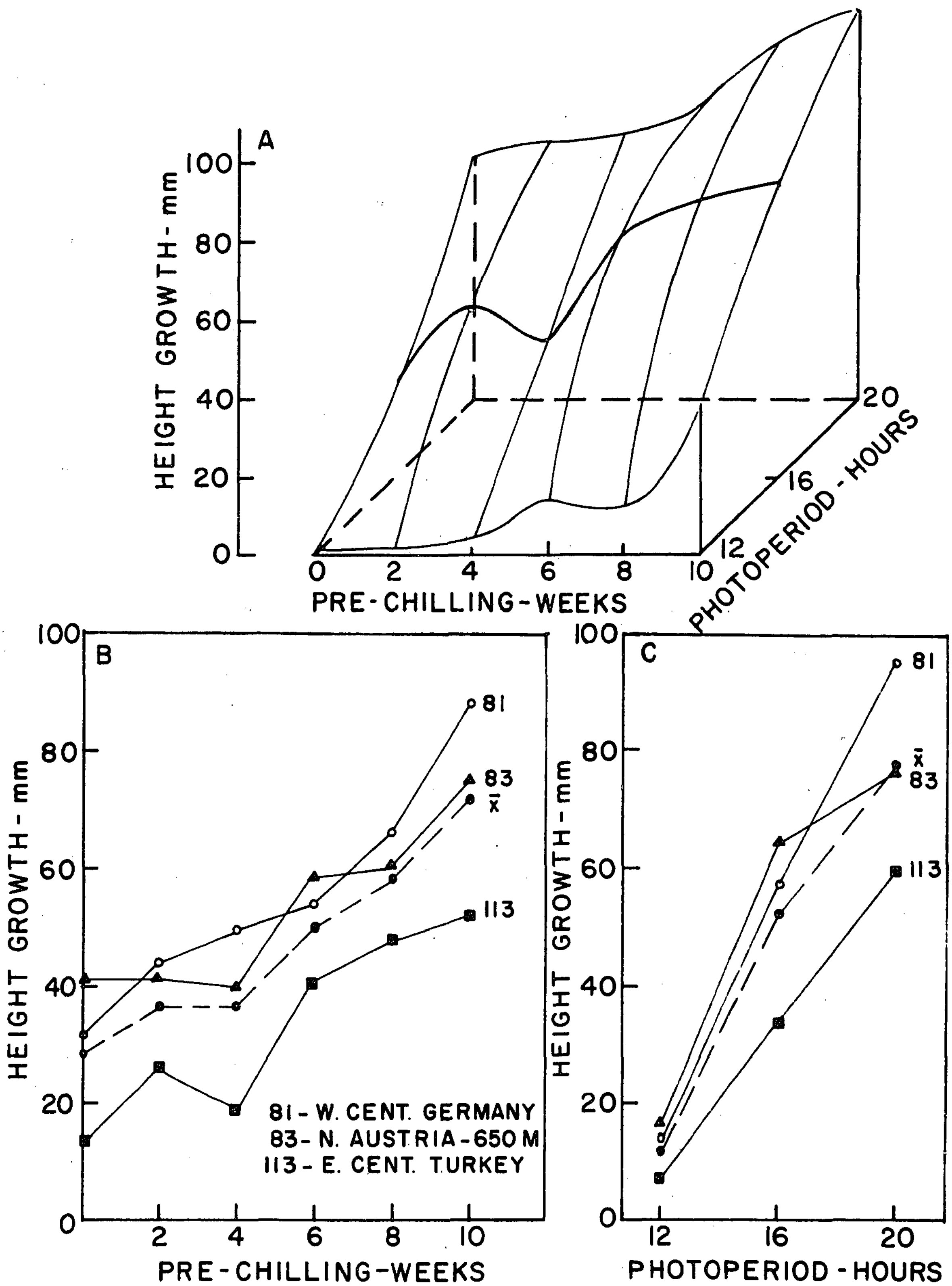

A
HEIGHT GROWTH - mm
0
20
40
60
80
100
0
2
4
6
8
10
PRE-CHILLING-WEEKS
12
16
20
PHOTOPERIOD - HOURS
B
HEIGHT GROWTH - mm
0
20
40
60
80
100
2
4
6
8
10
PRE-CHILLING-WEEKS
81
83
x̄
113
81 - W. CENT. GERMANY
83 - N. AUSTRIA - 650 M
113 - E. CENT. TURKEY
C
HEIGHT GROWTH - mm
0
20
40
60
80
100
12
16
20
PHOTOPERIOD - HOURS
81
x̄
83
113

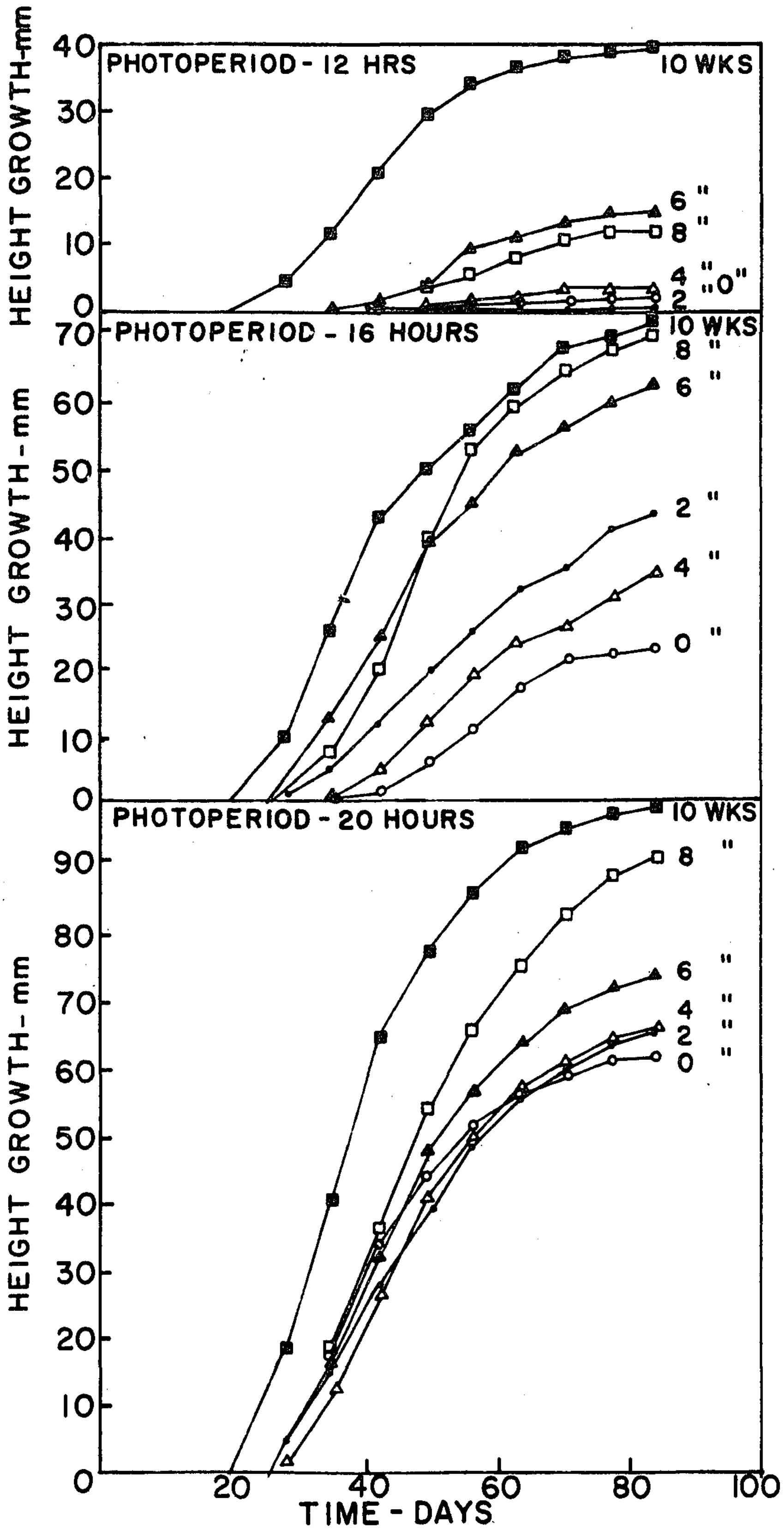
Table 9. Analysis of variance of height growth of Scotch pine seedlings

Variation	df	Height growth SS	MS
Total	161	218,973.23	
Photoperiod(1)	2	114,208.04	57,104.02**
Rep/Photoperiod	6	4,342.08	723.68
Pre-chilling(2)	5	35,231.38	7,046.28**
P(1)xP(2)	10	4,376.25	437.62
Error A	30	12,808.15	426.94
Seed source	2	15,524.79	7,762.40**
SxP(1)	4	6,530.73	1,632.68**
SxP(2)	10	2,566.51	256.65
SxP(1)xP(2)	20	7,048.20	352.41
Error B	72	16,337.10	226.90

**Significant at 1-percent probability level.

initiation possibly decreased with an increase in the length of the pre-chilling period (Figure 17). Six to eight weeks of pre-chilling increased height growth in the 12- and 20-hour photoperiods while only two weeks of pre-chilling increased height growth in the 16-hour photoperiod. Moreover, in the 16-hour photoperiod the effects of the 8- and 10-week pre-chilling were similar, while in the 12- and 20-hour photoperiods the 10-week pre-chilling increased growth more than the 8-week pre-chilling.

Figure 17. The effects of photoperiod and pre-chilling period on height growth patterns of Scotch pine seedlings, seed sources pooled.


PHOTOPERIOD - 12 HRS
10 WKS
6 "
8 "
4 "
"0"
2
PHOTOPERIOD - 16 HOURS
10 WKS
8 "
6 "
2 "
4 "
0 "
PHOTOPERIOD - 20 HOURS
10 WKS
8 "
6 "
4 "
2 "
0 "
HEIGHT GROWTH-mm
HEIGHT GROWTH - mm
HEIGHT GROWTH - mm
TIME - DAYS
0
20
40
60
80
100
10
30
50
70
90

DISCUSSION

Field Investigation

Average 5-year survival of the 10 Scotch pine seed sources ranged from 40 to 84 percent, and differences among sources were significant at the 1-percent probability level. Survival of the west central Germany, southern Finland, northern Austria-650m and the Czechoslovakia sources was highest, but no general trends or relationships between survival and latitudinal origin of seed sources were apparent.

Part of the differences in survival among seed sources was related to establishment problems. Although mortality in the first year was high for most sources, losses in the last 4 years, among the seedlings that survived the first year, were less than 2 percent for all sources. Furthermore, mortality losses on plots in which seedlings were replaced were less than 5 percent during the subsequent 4 years. Hence, the initial adaptability of a source can not be determined definitely until the confounding effect of establishment has been removed.

Average 5-year seed source height and diameter growth differences were significant at the 1-percent probability level. Height and diameter growth of the sources from central Europe was considerably greater than growth of the sources from the Scandinavian countries. These results corroborate the findings of Lines and Aldhous (1957), Schreiner _et al_.

(1962), Wood (1949) and Wright and Baldwin (1956, 1957).

The slow height and diameter growth of the Spain source, comparable to the growth of the sources from the Scandinavian countries, may be related to selection of a genotype with a slow growth rate, to "browning" of needles on young seedlings in late winter, to movement of the source from a high to a low altitude at the same latitude or to any combination of these. "Browning" of the needles in the nursery and the first year in the field may have reduced the photosynthetic efficiency of the source, thus resulting in slower initial growth for the Spain source than for the central European sources. Introduction of a seed source from high to low altitudes at the same latitude effects environmental changes comparable to the changes resulting from the movement of a source from north to south latitudes. Growth of the Spain source, moved from between 1,000 and 1,500 meters altitude to 320 meters at approximately the same latitude, was similar to growth of the Scandinavian sources, moved south approximately 17° latitude and from less than 100 meters altitude to 320 meters. Movement of the central European sources over a narrower latitudinal and altitudinal range apparently had less influence on growth.

Relative fall-winter foliage color ranged from the yellow of the Finland source to the greenish green-yellow of the Spain source (Munsell color charts 1952), thus corroborating the results of Baldwin (1956) who related yellow foliage color to high latitudinal origin.

From this evaluation of 5-year seedling survival and height and diameter growth, the west central Germany, northern Austria-650m and the Czechoslovakia sources appear to be well adapted and will grow rapidly on the Fayette silt loam soil type in northeast Iowa. However, information concerning bole straightness of these sources is necessary before their desirability as timber trees can be determined. Wood (1949) and Wright and Baldwin (1957) observed that the sources of Scotch pine with the poorest bole form came from central Europe.

The Spain source has the most desirable Christmas tree color and form (Figure 18), but the confounding of survival with establishment precludes definite statements concerning adaptability of the Spain source at this time. Hence, additional information regarding the adaptability of the Spain source to environmental conditions in northeast Iowa must be obtained before definite recommendations concerning its use as a Christmas tree can be made.

Greenhouse Investigations

The growth and development of Scotch pine seedlings were affected appreciably by photoperiod, temperature, pre-chilling, seed source and their interactions. The greater height and total green weight growth with increased photoperiod probably is related to earlier bud burst, resulting in a longer growth period, and a faster growth rate (Figures 8 and 13). Needle length also appeared to increase with an increase in photo-

Figure 18. Representative form of a 5-year-old Scotch pine Christmas tree from the Spain seed source.


3
3
2
2

period, but the data are questionable because needle growth had not terminated in all studies when measurements were made.

The decrease in height growth with increased temperature may be related to growth inhibition, changes in the distribution of assimilate, a pre-chilling effect or any combination of these. The shorter growing periods at temperatures over 65°F apparently are related to the inhibition of growth which resulted in a switch from growth to differentiation. The decrease in height growth, increase in needle length and no change in total green weight with increased temperature, observed in the preliminary investigation and at the two higher temperatures in the final investigation where growth had terminated, may indicate a change in the distribution of assimilate. Apparently more of the total assimilate was used in height growth at the lower temperatures and in needle length at the higher temperatures. This relationship tends to corroborate the observation of Kramer (1957) that increased respiration, resulting from increased temperature, does not account solely for the reduction in height growth and that other factors also are involved in the response of tree seedlings to temperature. The greater height growth with increased pre-chilling apparently is related to a faster growth rate and possibly an earlier date of bud burst, resulting in a longer period of growth (Figure 17). The increase in height growth with a decrease in temperature probably is related to this pre-chilling effect. The 56° and 57°F temperature, lowest temperatures used in the preliminary and final investigations, may have been low enough, and the period before growth initiation long enough, that the seedlings were incidently pre-chilled. The mean daily temperature of the unheated greenhouse where the seedlings were pre-chilled in the final greenhouse investigation was only 9°F cooler.

Seed source effected a marked difference in height growth, needle length and number of days to bud burst of Scotch pine seedlings. Within any specific treatment combination, height growth differences among the seed sources appeared to be related to the rate of growth and not to the length of the growth period. Within the range of 40° to 50° latitudinal origin, the magnitude of the differences among seed sources was more meaningful than trends, but a general increase in height growth and needle length with increased latitudinal origin is suggested. Testing seed sources from over the entire natural range of Scotch pine probably would result in greater differences and more definite trends.

The effects of photoperiod, temperature, pre-chilling and seed source on growth and development of Scotch pine seedlings were interrelated. Seedling responses differed from expected responses based on additive influences of independent factors; thus, an intercorrelation of environmental factors and seed source genotype is suggested. The interrelated influence of temperature and photoperiod occurred at high and low temperatures, long and short photoperiods and before and during growth. The decrease in height growth with increased temperature was greatest at the longer photoperiods in the treatments where growth had terminated; the delay in growth initiation at the lower temperatures was greatest at the shorter photoperiods. A period of pre-chilling prior to bud burst effected an increase in height growth in all photoperiods at the 65°F temperature and as great a seedling response at the shortest as at the longest photoperiod at the 71°F temperature. The existence and magnitude of these interactions should be known when variants within species are grown outside their natural range. Variants growing naturally under short growing seasons and long photoperiods will respond differently when grown under long growing seasons and short photoperiods; thus, the relative importance of temperature, photoperiod and their interaction will change from area to area.

Height growth of the northern seed sources of Scotch pine was greater than height growth of the southern sources at the lower temperatures and longer photoperiods, conditions indigenous to the northern latitudes. Height growth of all sources generally was greater at the longer photoperiods and the lower temperatures. Pauley (1958) suggests an increase in stem growth of certain southern ecotypes when moved to more northerly latitudes with lower temperatures and longer photoperiods. However, he warns against the susceptibility of such ecotypes to early-autumn frost damage.

Needle length of all sources generally was greater at the higher temperatures. Needle length of the northern seed sources generally was greater than needle length of the southern sources at the higher temperatures and at all photoperiods.

Variance within a species is related to within-population variation caused by mutations, random assortment, etc., and to between-population variation caused by natural selection, the elimination of existing genotypes by various environmental factors. Apparently, photoperiod and temperature are two of the more important environmental factors involved in the process of natural selection over the natural range of Scotch pine.

Comparison of Field and Greenhouse Investigations

A comparison of the field and greenhouse investigations is difficult at this time because of the limited differences among the seed sources in the field, the absence in the greenhouse of part of the sources used in the field study and the limited number and distribution of the sources used in the greenhouse investigations. However, the seed sources from central Europe generally made the best height growth in both the field investigation under natural environmental conditions and in the greenhouse investigations under artificial conditions. Additionally, the southern European seed sources, represented by the Spain source in the field investigation, and the Turkey sources in the greenhouse investigations, under the photoperiod and temperature conditions indigenous to northeast Iowa, made less height growth than the central European seed sources.

Correlation of field and greenhouse data apparently may provide a means for the early selection of variants within a species for field planting. However, correlations of field responses at later stages in the development of the stand with the present greenhouse responses and future greenhouse, nursery and laboratory responses of additional sources from over the entire natural range of Scotch pine, are needed before a complete appraisal of this approach can be made.

SUMMARY

This experiment consisted of two parts: (1) the field investigation to determine the variation in growth and development among 10 seed sources of Scotch pine growing under natural environmental conditions and (2) the greenhouse investigations to determine the independent and interrelated effects of temperature, photoperiod, pre-chilling and provenance on the growth and development of Scotch pine seedlings.

The field investigation was established in Allamakee County in northeast Iowa. Approximately 100 seedlings of each of 10 seed sources were planted in April 1958, in a 6x6-foot spacing in each of two replications. The results of the field investigation were:

1. Average 5-year survival ranged from 40 to 84 percent, and differences among seed sources were significant at the 1-percent probability level.
2. Average 5-year height growth ranged from 3.4 to 6.2 feet, and differences among seed sources were significant at the 1-percent level.
3. Average 5-year diameter growth ranged from 1.3 to 2.0 inches, and differences among seed sources were significant at the 1-percent level.
4. Relative fall-winter foliage color ranged from yellow, 5.0 Y 5/6, for the Finland source to greenish green-yellow, 7.5 GY 5/4, for the Spain source (Munsell color charts 1952).

The west central Germany, northern Austria-650m and Czechoslovakia seed sources appeared well adapted and grew rapidly on the Fayette silt loam soil type in northeast Iowa, but information, concerning the bole form of these sources, is necessary before their desirability as timber trees can be determined. Moreover, the Spain source has the best Christmas tree color and form, but its use at this time in northeast Iowa is questionable because of inadequate information regarding adaptability.

The greenhouse investigations were conducted on the Iowa State University campus. A preliminary investigation included mean daily temperatures of 56° and 71°F, photoperiods of 12, 16 and 20 hours and seven seed sources, and the first part of a final investigation consisted of mean daily temperatures of 57°, 65° and 76°F, photoperiods of 14, 16 and 18 hours and six seed sources. Three replications were established within each main temperature treatment, and the seed sources ranged from central Turkey to central Germany. Two seedlings of each seed source were placed within each of the treatment replications. In the second part of the final investigation, seedlings of three sources, ranging from central Turkey to central Germany, were pre-chilled for 0, 2, 4, 6, 8 or 10 weeks before they were placed within one of three photoperiods, 12, 16 and 20 hours, replicated three times. The results of the greenhouse investigations were:

1. Height growth increased with an increase in photo-

period and length of pre-chilling period, decreased with an increase in temperature and, in general, increased with increase in latitudinal origin of seed source.

2. Needle length increased with an increase in temperature, apparently increased with an increase in photoperiod and, in general, increased with an increase in latitudinal origin of seed source.
3. Bud burst occurred earlier at the longer photoperiods and higher temperatures. It varied among seed sources, but trends were not evident.
4. Total green weight increased with an increase in photoperiod but did not vary among temperatures where growth had terminated. It varied among seed sources, but trends were not evident.
5. Height growth, needle length, total green weight and bud burst were influenced to varying degrees by the photoperiod-temperature, seed source-photoperiod, seed source-temperature and seed source-photoperiod-temperature interactions. In general, height growth of all sources was greatest at the longer photoperiods and lower temperatures. Moreover, height growth of the northern seed sources was greater than height growth of the southern sources at the lower temperatures and the longer photoperiods. Needle length of all sources appeared to be greatest at the higher

> temperatures. Additionally, needle length of the northern seed sources was greater than needle length of the southern sources at the higher temperatures and at all photoperiods.

Growth and development of Scotch pine seedlings were affected appreciably by photoperiod, temperature, pre-chilling, provenance and their interactions. Photoperiod and temperature appear to be two of the more important environmental factors involved in the process of natural selection over the natural range of Scotch pine.

A comparison of the field and greenhouse investigations is difficult at this time because of the limited differences among the seed sources in the field, the absence in the greenhouse of part of the sources used in the field study and the limited number and distribution of the sources used in the greenhouse investigations. Correlation of field and greenhouse data apparently may provide a means for the early selection of variants within a species for field planting. However, correlations of field responses at later stages in the development of the stand with the present greenhouse responses and future greenhouse, nursery and laboratory responses of additional sources from over the entire natural range of Scotch pine, are needed before a complete appraisal of this approach can be made.

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