Temperature and light effects on seedling performance of Pinus albicaulia
by James Stuart Jacobs

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
Temperature and light effects on the performance of whitebark pine seedlings normally growing at high altitude were studied in laboratory experiments that measured effects of stratification time on germination, temperature on germination, temperature on root growth, and temperature and light effects on photosynthesis. The effects of temperature on stratification, germination, and root growth were compared with those of P. flexilis from low elevation forests and P. contorta from middle elevation forests.

My principal conclusions were: 1) Germination was increased by a one month stratification. Germination rates were unaffected by additional stratification of 2 to 8 months.

2) Germination rates for lodgepole pine (5 mg/seed, 80%) were twice that of whitebark (127 mg/seed, 45%) and timber pines (65 mg/seed, 31%).

3) . Minimum (IO0C), optimum (20°C) and maximum (40°C) temperatures for germination were similar, despite difference in the species and their native environments.

4) Over an eight day period, root growth rates began at 10°C, were optimal near 30°C, and ceased above 45°C; despite differences in provenance P. contorta and P. flexilis performed similarly.

5) Root growth rate was highest during the first 4 days after germination and declined by 50% in P. albicaulis, 50% in P. flexilis, and 75% in P. contorta after 8 days of growth.

6) At the optimum temperature, the growth rates of P. albicaulis (127 mg/seed) and P. flexilis (65 mg/seed) were twice that of P. contorta (5 mg/seed).

7) Net photosynthesis occurred at leaf temperatures of 4°C, was maximum at 19°C, and fell sharply toward 37°C; this was due to the fact that with increasing temperature one records linear increases in gross photosynthesis and exponential increases in respiration.

8) Gross photosynthesis increased with tight, probably through 1600 E/M2*S. Net photosynthesis increased with tight because gross photosynthesis increased far more rapidly than respiration. Saturation occurred near 1000 uE/M2*S and the tight compensation point varied from 100 to 1000 uE/M2*S depending on current leaf temperature and preconditioning temperatures.

9) While tight had no measurable preconditioning effect, net photosynthesis increased significantly with increases in preconditioning temperature. Since respiration was unaffected, gross photosynthesis (estimated as dark respiration plus net photosynthesis) must have also increased with increases in preconditioning temperature.

TEMPERATURE AND LIGHT EFFECTS ON SEEDLING PERFORMANCE OF *PINUS ALBICAULIS*

by

James Stuart Jacobs

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APPROVAL

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

28 July 1989 — Date

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Date July 28, 1989

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ABSTRACT

Temperature and light effects on the performance of whitebark pine seedlings normally growing at high altitude were studied in laboratory experiments that measured effects of stratification time on germination, temperature on germination, temperature on root growth, and temperature and light effects on photosynthesis. The effects of temperature on stratification, germination, and root growth were compared with those of *P. flexilis* from low elevation forests and *P. contorta* from middle elevation forests.

My principal conclusions were:

1) Germination was increased by a one month stratification. Germination rates were unaffected by additional stratification of 2 to 8 months.

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5) Root growth rate was highest during the first 4 days after germination and declined by 50% in *P. albicaulis,* 50% in *P. flexilis,* and 75% in *P. contorta* after 8 days of growth.

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7) Net photosynthesis occurred at leaf temperatures of 4°C, was maximum at 19°C, and fell sharply toward 37°C; this was due to the fact that with increasing temperature one records linear increases in gross photosynthesis and exponential increases in respiration.

8) Gross photosynthesis increased with light, probably through 1600 E/M2*S. Net photosynthesis increased with light because gross photosynthesis increased far more rapidly than respiration. Saturation occurred near 1000 uE/M2*S and the light compensation point varied from 100 to 1000 uE/M2*S depending on current leaf temperature and preconditioning temperatures.

9) While light had no measurable preconditioning effect, net photosynthesis increased significantly with increases in preconditioning temperature. Since respiration was unaffected, gross photosynthesis (estimated as dark respiration plus net photosynthesis) must have also increased with increases in preconditioning temperature.

I

INTRODUCTION

While whitebark pine has been little studied, interest in it has increased with the recognition of its non-timber values: aesthetic value, recreational value, watershed value, and producer of food for bears, squirrels and the clarks nutcracker (McCaughey and Weaver 1989).

To understand the tree's natural distribution and facilitate its management, five processes which affect its establishment were examined.

1) The effects of stratification time on germination of whitebark, lodgepole and limber pines were measured and compared. Incidental observations of the relations between seeds size and germination rate were also made.

2) The effects of temperature on germination of non-dormant (stratified) seeds of the three pine species were measured and compared.

3) The effects of temperature on root growth of the three pine species were measured and compared.

4) The effects of temperature and temperature preconditioning on photosynthesis and respiration of whitebark pine seedlings were measured.

5) The effects of light level and light preconditioning on photosynthesis and respiration of whitebark pine seedlings were measured.

Whitebark pine, lodgepole pine and limber pine populations studied came from upper timberline (2652 m), middle altitude forests (1859 m), and lower timberline (1478 m) near 46° N. latitude. Stratification, germination, and root growth requirements were compared to determine whether distribution differences are correlated with (possibly based on) differences in these characteristics.

II

EFFECTS OF STRATIFICATION TIME AND SEED SIZE ON PINE GERMINATION

Germination of many species is improved by a period of low temperature stratification. Its duration can vary from a brief exposure to near freezing temperature (*e.g. Pinus banksiana,* 0-7 days) through more extended periods (*e.g. Pinus cembra* , 90-270 days, Schopmeyer 1974). Stratification improves germination of fresh seed in 46% of the pines and of stored seed in 19% of the pines (Schopmeyer 1974). In the Northern Rocky Mountains, natural stratification time available for seeds dispersed in the fall can vary with altitude and aspect from five months at low altitudes and south slopes to eight months at high altitudes and north slopes. In addition, pine seeds buried in moist soil in autumn stratify over eight months before snow melts, while seeds that fall from cones during the winter might only have a stratification period of one month in the spring. One wonders therefore whether pines use only a short stratification time to prevent fall germination or whether they require some of the longer stratification time available. I find no published accounts of stratification time on pines of the Northern Rocky Mountains.

Observations are reported here on the effect of stratification time (one to eight months) on the germination of Rocky Mountain pines seed collected from three altitudes: whitebark pine from upper timberline, lodgepole pine from middle altitude forests, and limber pine from lower timberline.

Methods

Seeds of the three pines were collected at three altitudes and locations in western Montana. Seeds of *P. albicaulis* were collected from an *Abies lasiocarpa-Vaccinium scoparium* habitat type near Jardine, Montana. (Palmer Mountain, 2652 m) in the autumn of 1984 and 1987. Seeds collected in 1984 were stored frozen at the Forest Service nursery (Coeur d'Alene, Idaho), in sealed containers. *P. contorta* seeds were collected from an *Abies lasiocarpa-Vaccinium scoparium* habitat type south of Bozeman, Montana (Hyalite Canyon, 1859 m) in January 1988. *P. flexilis* seeds were collected from a *Pinus flexilis-Festuca idahoensis* habitat type near Choteau, Montana (Rocky Mountain Road, 1478 m) in November 1987.

The seeds were sterilized, stratified, and germinated in optimum conditions. To minimize the danger of fungal attack the seeds were surface sterilized prior to stratification by soaking in 40% chlorox for ten minutes and rinsing ten times in distilled water to remove the chlorox (Wenny and Dumroese 1987). To obtain full imbibition, seeds were placed in nylon bags and soaked in clear running tap water for 48 hours. The seeds were then surface dried, lightly dusted with spurgon fungicide (tetrachloro-para-benzoquinone 98%) and placed between two moistened blotter papers in plastic germination boxes (14 x 13 x 3.5 cm), 100 seeds per box. The seeds were stratified in a refrigerator (1.5°C) for 0, 1, 2, 3, 5 and 8 months. When the stratification was complete, the stratification-germination boxes were transferred to a germination chamber (25°C day, 15°C night, and a 10 hour photoperiod). Germination occurred over a period of 1 to 3 months and percent germination was determined after it ceased.

Two irregularities in treatment should be mentioned. First, seeds of whitebark and limber pines used in the 1-8 month runs were stratified within two months after collection.

Whitebark and limber pine seeds used in the unstratified run were stored in a dry lab (5-20% humidity, 20°—25°C) for 12 months. In all cases, lodgepole pine seeds were fresh from unopened cones. Germination rates of unstratified seeds may have been artificially low. Second, while *P. contorta* and *P. flexilis* seeds were tested as collected, empty seeds of *P. albicaulis* were discarded. Germination rates of *P. albicaulis* may have therefore been artificially high.

Results and Discussion

Germination was apparently increased by increasing stratification time from 0 to 1 month. Germination rates of the unstratified seeds may have been increased or decreased by a storage period (12 months at 20°—25°C) which was longer than experienced by stratified seeds (0-2 months). Recommended stratification periods for *P. albicaulis* and *P. flexilis* are the same for stored and fresh seeds. Cold stratification is not recommended for fresh seed, but 30—50 days stratification is recommended for stored *P. contorta* seed (Schopmeyer 1974). My results show increased germination of fresh *P.contorta* seeds with stratification (Figure 1).

While germination rates for peaches (Carlson and Tukey 1945) and apples (Luckwill 1952) increased with increasing stratification time, we saw no increase in germination of pines with stratification times ranging from 1 to 8 months. A more detailed investigation of germination with shorter stratification time (0—50 days) and consistent seed quality would refine stratification procedures and perhaps provide clues as to stratification mechanisms.

Germination response to stratification time did not differ among species (and populations) normally found at upper timberline (whitebark pine) middle forest zone (lodgepole pine) and lower timberline (limber pine). This suggests that once the catastrophe of autumn germination has been prevented, the trees' best strategy is to germinate at the earliest spring soil warming to optimize the use of water available at this time. Such optimization in the spring may be critical to survive the summer dry climate of the northern Rocky Mountains (Weaver 1980).

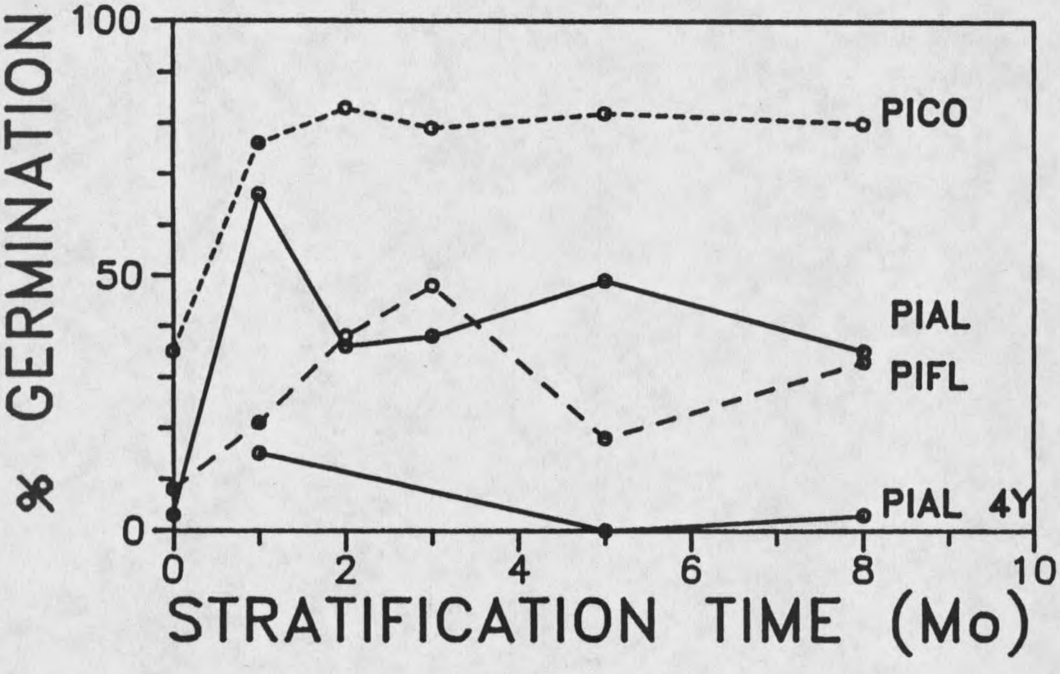

Figure 1. Germination percent of *Pinus albicaulis* (PIAL), *Pinus contorta* (PICO), and *Pinus flexilis* (PIFL) seeds stratified over a period of 8 months. PIAL 4Y represents four year old whitebark pine seeds.

Whitebark pine (45%) and limber pine (31%) had germination rates half those of lodgepole pine (80%). The difference may be attributed to their seed size (126, 65, 5 mg respectively) and their ability to afford the respiratory cost, and lost germination ability in the first season. The difference might also be correlated with the relative genetic loads (= % lethal genes in the population) of those species (Brussard 1989). Competitive selection of lodgepole pine growing in closed stands at middle altitude probably eliminate deleterious genes more effectively than non-competitive survival of whitebark pine and limber pine normally occurring on rare safe sites found at upper or lower timberline.

Germination of four year old *P. albicaulis* seed was only 10% of that observed in seeds gathered in the autumn before the experiment. This could be due to difference in the seed population, or to gradual respiratory consumption of storage reserves. On the basis of seed size, one might expect lower germination rates for limber pine (65 mg/seed) and lodgepole pine (5 mg/seed) than whitebark pine (126 mg/seed) because lodgepole and limber pine seeds are smaller. Ward McCaughey (U.S.D.A. Forest Service Lab, Bozeman Montana, personal communication 1988) has observed the germination in the field of whitebark pine seed more than one year old.

III

TEMPERATURE EFFECTS ON GERMINATION OF THREE ROCKY MOUNTAIN PINES

The germination of a non-dormant seed depends largely on temperature and moisture conditions (Fitter and Hay 1981), and responses vary among species. Non-dormant seeds have minimum temperatures for germination, optimum temperatures at which rapid germination occurs, and a temperature maximum above which seed death is likely to occur. Within (or between) species, the seed source may influence germination temperature. For example, cardinal temperature points (minimum, optimum and maximum) may differ among populations collected at different altitudes (Kramer and Kozlowski 1979).

Temperature effects on the germination response of *P. flexilis* (lower timberline), *P. contorta* (middle altitude), and *P. albicaulis* (upper timberline) from altitudes with different average temperature regimes (Weaver 1980) were compared with respect to species and location.

Methods

Seeds of three Rocky Mountain pines were collected, stratified, and germinated on a temperature gradient bar for determination of temperature effects on germination.

Seeds of the three pines were collected at three altitudes and locations in western Montana. Seeds of *P. albicaulis* were collected from an *Abies lasiocarpa-Vaccinium scoparium* habitat type near Jardine, Montana (Palmer Mountain, 2652 m) in the autumn of 1987. *P. contorta* seeds were collected from an *Abies lasiocarpa-Vaccinium scoparium* habitat type south of Bozeman, Montana (Hyalite Canyon, 1859 m) in January 1988. *P. flexilis* seeds were collected from a *Pinus flexilis-Festuca idahoensis* habitat type near Choteau, Montana (Rocky Mountain Road, 1478 m) in November 1987.

The seeds were sterilized and stratified in optimum conditions. To reduce the danger of fungal attack the seeds were surface sterilized prior to stratification by soaking in 40% chlorox for ten minutes and rinsing ten times in distilled water to remove the chlorox (Wenny and Dumroese 1987). To obtain full imbibition, seeds were placed in nylon bags and soaked in clear running tap water for 48 hours. The seeds were then surface dried, lightly dusted with spurgon fungicide (tetrachloro-para-benzoquinone 98%) and placed between two moistened blotter papers in plastic germination boxes (14 x 13 x 3.5 cm), 100 seeds per box. The seeds were stratified in a refrigerator (1.5°C) for up to 8 months.

Stratified seeds were placed on a temperature gradient with a temperature range of 8 to 48°C and germinating seeds were counted over a period of two weeks. The temperature gradient bar construction was similar to that of Barbour and Racine (1967). Three aluminum plates (one per species) 90 x 14.5 x 0.7 cm lay parallel and connected by tubes with 50°C water passed through at one end, and 4°C isopropyl alcohol at the other. Each bar was coated with lacquer (to minimize Al^{+++} exposure) and a moist blotter. The blotter paper was kept continuously moist by immersing its warm end in a tray of water, and by the condensation of water on its cold end. The bars were covered with plastic wrap and a plexi-glass box top to minimize evaporation and temperature fluctuation. Ten stratified seeds were lined up across the bar at each 5 cm interval on the bar. Treatment temperature was measured by placing the tip of a thermocouple on the blotter paper at each seed line.

Seeds germinating in each temperature treatment were counted every 48 hours for two weeks. The experiment was replicated on three different dates (July 15, 1988, December 2, 1988 and February 27, 1989).

Results

The three species of pine exhibited similar cardinal points for germination with a minimum of 10°C, an optimum range of 15° to 35°C, and a maximum of 40°C (Figure 2). Upper timberline *P. albicaulis* germination seemed to peak at 35°C, while *P. contorta* and *P. flexilis* germination peaked at 20°C (Figure 2). Middle altitude *P. contorta* may be slightly more heat tolerant with some individuals surviving at 40°C. Fungal and bacterial infection were common at temperatures above 40°C. Germination at 1.5°C (up to 25% in whitebark pine) was observed in the stratification chamber but only among seeds stratified for more than 5 months.

Discussion

Temperature cardinal points of *P. albicaulis, P. contorta,* and *P. flexilis* (Figure 2) are similar to those of other western conifers. Optimum temperature for ponderosa pine east of the Rocky Mountains is 24°—30°C (Kramer and Kozlowski 1979). Cardinal points for lodgepole pine and engleman spruce are 12°C, 16° to 25°C, and 35°C (Kaufman and Eckart 1977).

Since seed collections were made at very different altitudes, I also conclude that altitudinal variation of seed source had little or no effect on the cardinal points of pine seed germination (10°, 20°, and 40°C, Figure 2) in spite of the large difference in climate of seed origin (Weaver 1980). *Pinus aristida* from high elevations in California and *Pinus silvestris* from low elevations also have similar temperature responses (Tranquillini 1979). The temperature optimum for upper timberline whitebark pine (30°—35°C range) was apparently higher than that of middle altitude lodgepole pine and lower timberline limber pine (20°C, Figure 2); this observation supports speculation by Tranquillini (1979) that

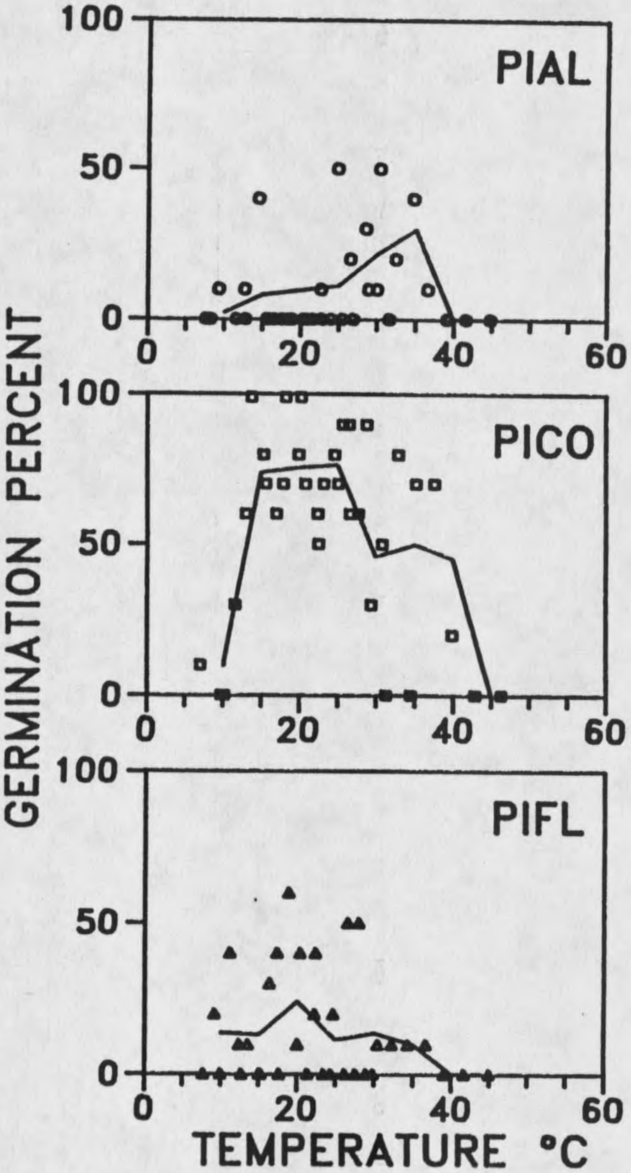

Figure 2. Percent germination of *Pinus albicaulis* (PIAL), *Pinus contorta* (PICO), and *Pinus flexilis* (PIFL) at temperatures ranging from 8° to 48°C. Curves are drawn through the median of points in each five degree interval. Each point represents the percent of 10 seeds tested at that temperature.

higher germination rates above 20°C for *Pinus sylvestris* collected at high altitudes compared to *P. sylvestris* collected at low altitudes is an adaptation to high soil surface temperatures at high altitude.

While Kramer and Kozlowski (1979) observed that diurnal thermoperiodicity increased germination of many tree seeds, this phenomenon was not observed in my limited experiments. Although temperatures in a seed row were constant, germination rate on the gradient bar was identical to that of seeds from the same source germinated in a chamber with 25°/15°C diurnal periods (See Chapter II).

IV

TEMPERATURE EFFECT ON ROOT GROWTH RATES OF THREE ROCKY MOUNTAIN PINES

For most plants, root growth is important for the acquisition of water and nutrient resources. Root growth rate is especially important for seedlings establishing in Rocky Mountain forest habitat types where soil water and nutrient supplies are relatively low (Weaver 1979) and the relatively moist spring is followed by a dry summer (Weaver 1980). One speculates that it is good strategy for a germinant to get its roots into more persistently moist deeper soil layers as quickly as possible and before the surface layers dry out.

Soil temperatures too low to allow root growth might limit the distribution of a tree species to relatively warm sites at low altitude or to warm microsites (*e.g.* south facing) in a higher altitudinal zone. To explore the possibility that the distributions of whitebark pine (upper timberline), lodgepole pine (middle altitude), and limber pine (lower timberline) are controlled by seedling temperature requirements, data was simultaneously sought on the effect of soil temperatures on root growth of the pine species and data indicative of temperatures that might be found in these zones.

Methods

Temperature effects on root growth were compared between *P. albicaulis* from upper timberline, *P. contorta* from middle altitude forests, and *P. flexilis* from lower timberline. *P. albicaulis* and *P. flexilis* are timberline species with large seeds (127 and 65 mg/seed, respectively) dispersed mostly by animals. *P. contorta var. latifolia* is a small seeded pine (5 mg/seed) dispersed mostly by wind. Seeds of the three pines were collected at three altitudes and locations in western Montana. Seeds of *P. albicaulis* were collected from an *Abies lasiocarpa-Vaccinium scoparium* habitat type near Jardine, Montana (Palmer Mountain, 2652 m) in the autumn of 1987. *P. contorta* seeds were collected from an *Abies lasiocarpa-Vaccinium scoparium* habitat type south of Bozeman, Montana (Hyalite Canyon, 1859 m) in January 1988. *P. flexilis* seeds were collected from a *Pinus flexilis-Festuca idahoensis* habitat type near Choteau, Montana (Rocky Mountain Road, 1478m) in November 1987.

Seeds were sterilized, stratified, germinated, and transferred for growth observations to a temperature gradient bar. To reduce the danger of fungal attack the seeds were surface sterilized prior to stratification by soaking in 40% chlorox for ten minutes and rinsing ten times in distilled water to remove the chlorox (Wenny and Dumroese 1987). To obtain full imbibition, seeds were then placed in nylon bags and soaked in clear running tap water for 48 hours. The seeds were then surface dried, lightly dusted with spurgon fungicide (tetrachloro-para-benzoquinone 98%) and placed between two moistened blotter papers in plastic germination boxes (14 x 13 x 3.5 cm), 100 seeds per box. The seeds were stratified in a refrigerator (1.5°C) for 1-3 months. When the stratification was complete, the stratification-germination boxes were transferred to a germination chamber (25°C day, 15°C night, and a 10 hour photoperiod).

The germinated seeds were transferred to a temperature gradient bar to measure root growth rates at temperatures ranging from 4°C to 48°C. Three aluminum plates 90 x 14.5 x 0.7 cm lay parallel and connected by tubes with 50°C water passed through at one end, and -4°C isopropyl alcohol at the other (Barbour and Racine 1968). Each bar was coated with lacquer (to minimize Al^{+++} exposure), a moist blotter, and, 1 mm above the blotter, a glass plate. Each bar was tilted at a 45 degree angle to the temperature gradient so the roots would grow geotropically straight down between the blotter and the glass. The blotter paper was kept continuously moist by immersing its warm end in a tray of water, and by the condensation of water on its cold end. The bars were covered with a plexi-glass box top to minimize evaporation and temperature fluctuation. Initial root length was measured when seeds were placed on the bar and every 48 hours thereafter for 8 days. Bar temperatures at sites where the roots grew were measured by inserting a thermocouple between the glass plate and the blotter paper. The experiment was replicated on four dates (April 26, May 6, June 1, and June 22,1988).

Results

Germination began with the appearance of a radicle which elongated steadily over the course of the experiment. After eight days, roots of *P. albicaulis, P. contorta,* and *P. flexilis* growing within 5°C of the optimum, obtained mean lengths of 81 mm, 34 mm, and 92 mm respectively and diameters of approximately 2 mm, 1 mm, and 2 mm, respectively. While roots of *P. albicaulis* and *P. flexilis* turned brown and ceased growth at temperatures above 33°C, roots of *P. contorta* tolerated temperatures up to 35°C. Regardless of root temperature, shoots grew to a height of approximately 2 cm; shoot growth began within two days of germination in the optimum temperature range but was postponed till as late as the sixth day at the cooler temperatures. At temperatures above 33°C shoots tended to lose turgidity and slump to the blotter paper.

Root growth rate (mm/day) was compared among species (one per bar) at various temperatures (4° to 48°C), and ages (0-2, 2-4, 4-6, 6-8 days). In all three pine species, root growth occurred at all the temperatures tested and showed minimum, optimum, and maximum temperatures of 5°, 30°, and 50°C respectively (Figure 3). Seeds that germinated after 5 -8 months in the stratification chambers grew slowly at 1.5°C. *P. flexilis* had the highest median growth rate at optimum (10 mm/day), *P. albicaulis* was nearly as high (8 mm/day), and *P. contorta* had half the growth rate of the other

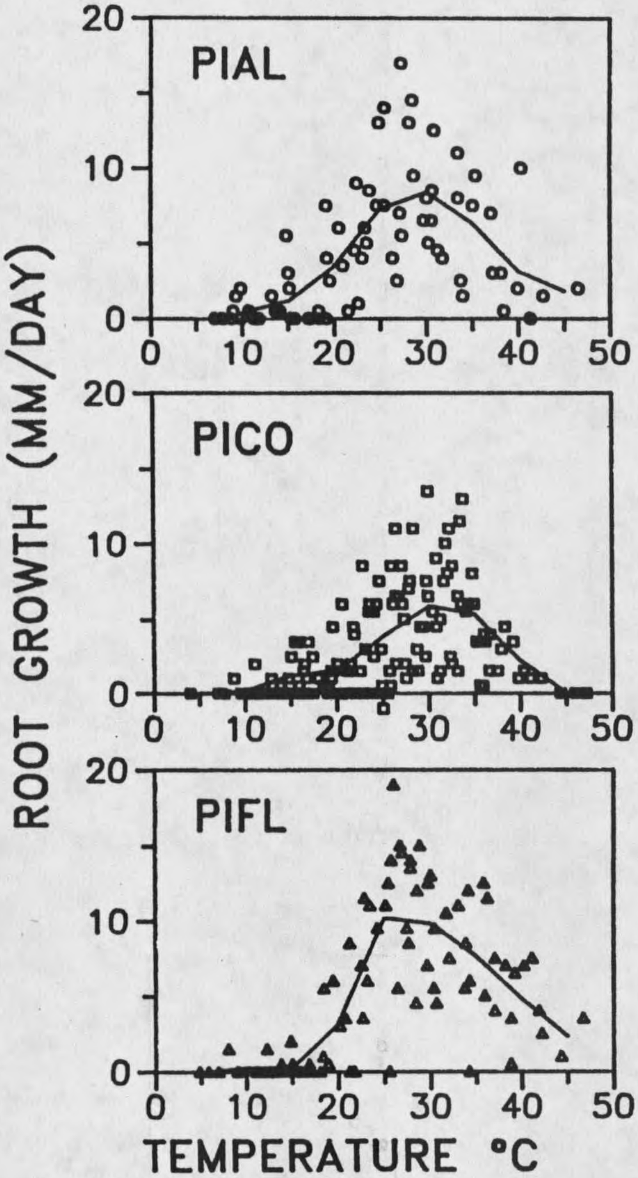

Figure 3. The effect of temperature on root growth rate for *Pinus albicaulis* (PIAL), *Pinus contorta* (PICO), and *Pinus flexilis* (PIFL). The data from four runs were combined and average curves were drawn through it by plotting them through the medians of the points included in five degree intervals.