



Temperature and light effects on seedling performance of *Pinus albicaulis*  
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  
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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.

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 (IOOC), 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 light, probably through 1600 E/M<sup>2</sup>\*S. Net photosynthesis increased with light because gross photosynthesis increased far more rapidly than respiration. Saturation occurred near 1000 uE/M<sup>2</sup>\*S and the light compensation point varied from 100 to 1000 uE/M<sup>2</sup>\*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.

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SEEDLING PERFORMANCE OF *PINUS ALBICAULIS*

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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.

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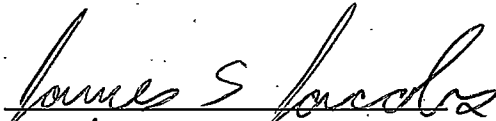
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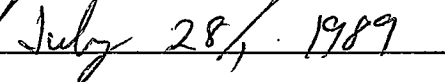
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## ABSTRACT

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.
- 2) Germination rates for lodgepole pine (5 mg/seed, 80%) were twice that of whitebark (127 mg/seed, 45%) and limber pines (65 mg/seed, 31%).
- 3) Minimum (10°C), 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 light, probably through 1600 E/M<sup>2</sup>\*S. Net photosynthesis increased with light because gross photosynthesis increased far more rapidly than respiration. Saturation occurred near 1000 uE/M<sup>2</sup>\*S and the light compensation point varied from 100 to 1000 uE/M<sup>2</sup>\*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.

## 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).

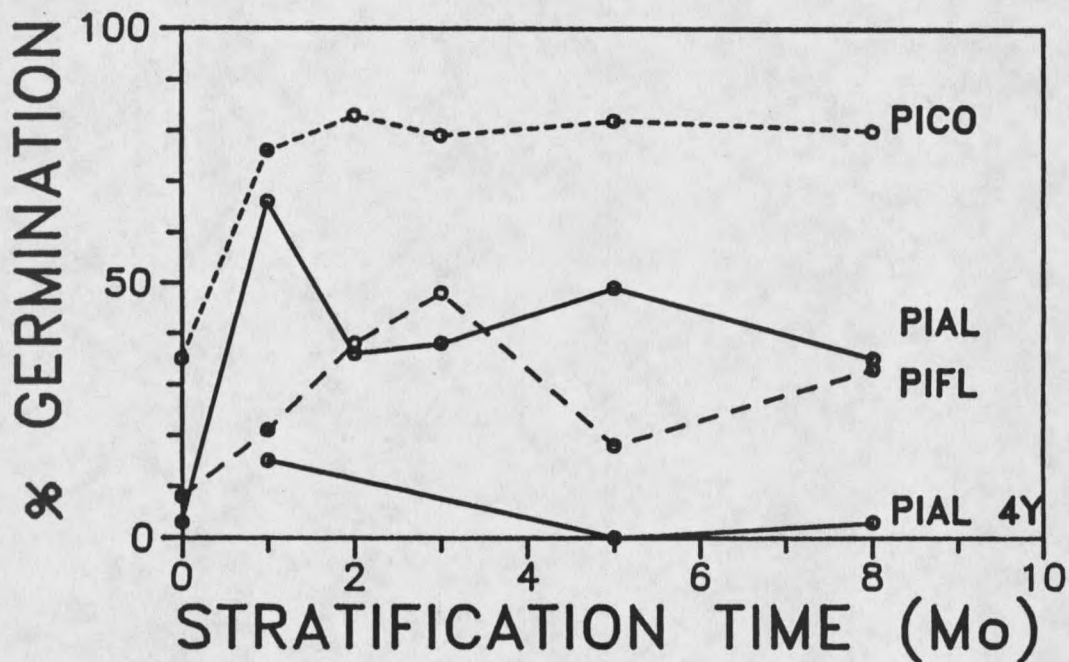


Figure 1. Germination percent of *Pinus albicaulis* (PIAL), *Pinus contorta* (PICO), and *Pinus flexilis* (PIFL) seeds stratified over a period of 8 months. PIAL 4Y represents four year old whitebark pine seeds.

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<sup>+++</sup> 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).

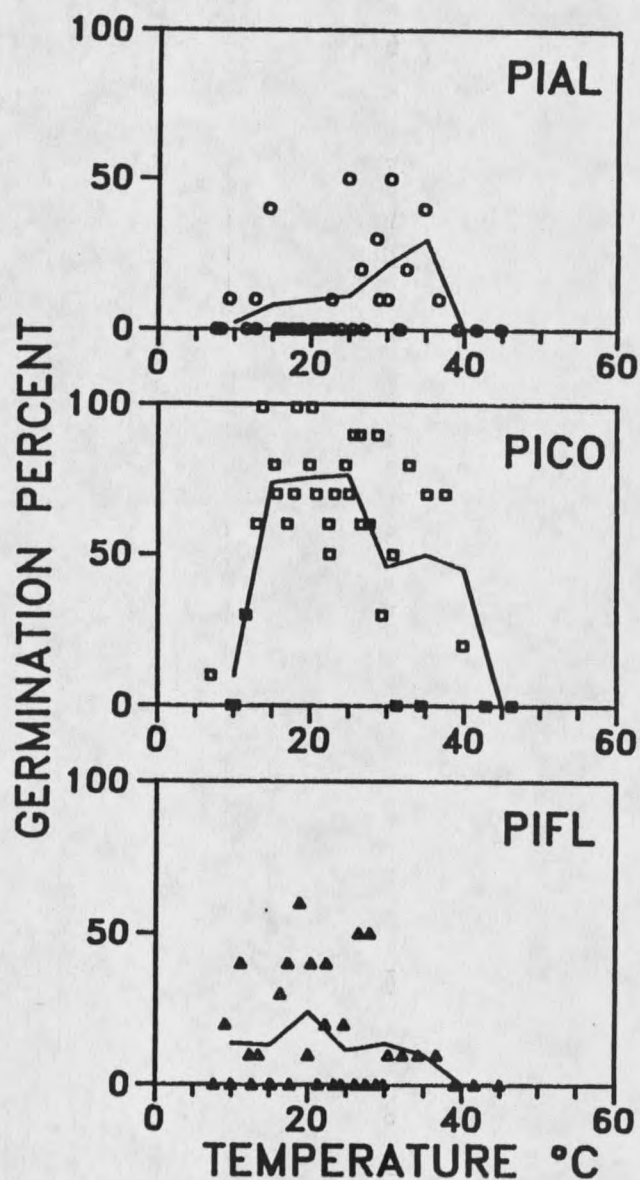
### Results

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 engelman 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 Kozłowski (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<sup>+++</sup> 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

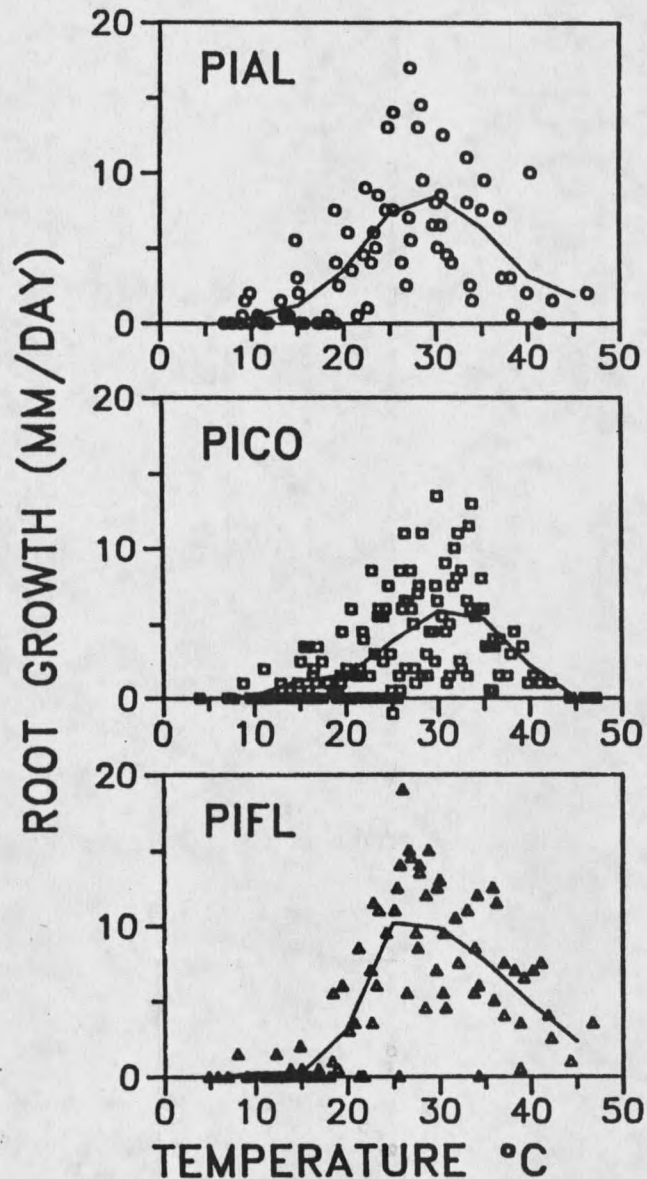
would grow geotropically straight down between the blotter and the glass. The blotter paper was kept continuously moist by immersing its warm end in a tray of water, and by the condensation of water on its cold end. The bars were covered with a plexi-glass box top to minimize evaporation and temperature 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.

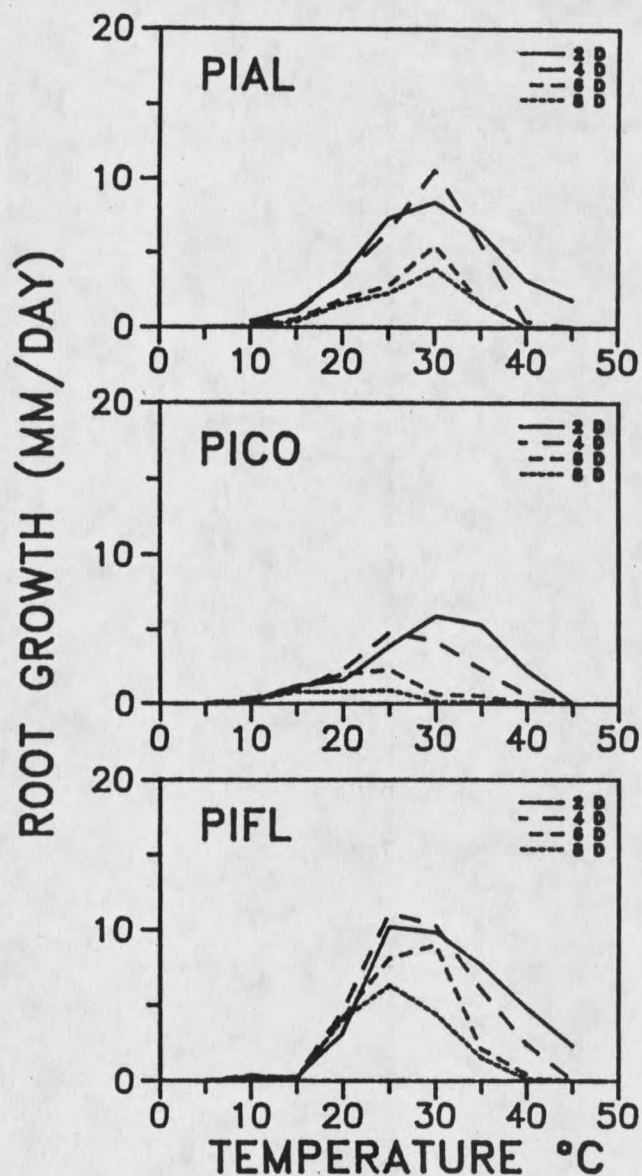
Root growth rate (mm/day) was compared among species (one per bar) at various temperatures (4° to 48°C), and ages (0-2, 2-4, 4-6, 6-8 days). In all three pine species, root growth occurred at all the temperatures tested and showed minimum, optimum, and maximum temperatures of 5°, 30°, and 50°C respectively (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.

two pines (6 mm/day). Growth rate gradually decreased after four days; the decrease was greatest in *P. contorta* which runs out of stored energy sooner (Figure 4).



**Figure 4.** Root growth temperature response curves for *Pinus albicaulis* (PIAL), *Pinus contorta* (PICO), and *Pinus flexilis* (PIFL) measured after 2,4,6, and 8 days. The curves are drawn through medians calculated over 5C intervals.

### Discussion

The cardinal temperatures (5°C min., 30°C opt., and 50°C max.) for root growth rate for the three pines are similar with respect to temperature. The growth curves (Figure 3) are also similar to the temperature response curves for some cool season plants (peas, Leitsch 1916) and warm season plants (corn, Lehenbauer 1914) and are typical of cytoplasmic enzyme response curves (Leopold 1964). While this suggests that temperature-root growth curves may be fairly general, (*i.e.* they probably apply to mature pines and a wide variety of other species), data presented in the following paragraph show that roots of alpine species must be able to grow at lower temperatures.

With an effective growth minimum of 10°C, pine root growth must be limited, at least seasonally, by temperature in soils of high elevation sites. In a grassland environment (1665 m Casper, Wyoming), monthly average soil temperatures at 10 cm exceeded 10°C between May and September and never exceeded 21°C (USDA Climatological Data 1982). In tundra at 3300 m (10500 feet), soil at 15 cm never reached temperatures greater than 10°C (Wardle 1968). Pines may be excluded from tundra environments by sub minimal soil temperatures (less than 10°C); root growth at 10°C is apparently too slow, and growth observed in the stratification chambers after 5 months at 1.5°C is even more certainly too slow for pine establishment.

Roots of pine germinants with large seeds (whitebark and limber pine) have larger energy supplies, the faster root growth rates, and longer periods of rapid growth than those of smaller seeded pines (*P. contorta*) (Figures 3 and 4). While it has been suggested that the large seed size of *P. albicaulis* and *P. flexilis* is a device for encouraging seed dispersal by birds (Hutchinson and Lanner 1982, Lanner 1980) it may also be important for survival of seedlings in the stressful environments to which it is dispersed--that is, sites

where surface soils are subject to frost action in spring, summer drought, frost action in fall and winter, and winter desiccation.

## V

EFFECTS OF LIGHT, TEMPERATURE, AND PRECONDITIONING ON CO<sub>2</sub> EXCHANGE IN *PINUS ALBICAULIS*

The requirements of *P. albicaulis* for light, heat, water, and nutrients (*i.e.* its physiological niche dimensions, Hutchinson 1957) are major determinants of the tree's potential distribution. Environmental control may well be exercised on trees in the seedling stage, that is, before developing their capacity (*e.g.* through storage reserves or "excess" acquisition systems, especially roots) to buffer themselves against acute environmental impacts (Larcher 1980). The control might be exercised through acute environmental stress (*e.g.* frost or drought damage) or through chronic failure of photosynthesis to exceed respiration on an annual basis due to inadequate availability of light, heat, water, or nutrients.

The objective of this sub-project was to gather data useful for modeling the effects of light and temperature conditions on the growth of whitebark pine seedlings. For such a model it is necessary to know:

- 1) the effect of temperature on net photosynthesis, and ideally on gross photosynthesis and respiration as well;
- 2) the effect of season (= temperature and day length preconditions) on the temperature-net photosynthesis relationship;
- 3) the effect of light level on photosynthesis as sun fleck distribution and light intensity vary throughout the day;
- 4) the effect of light preconditioning, *i.e.* likely seedling responses to modification of the light environment by blow down, beetle kill, and thinning.

### Methods

STOCK. Whitebark pine seeds were gathered in a mixed stand of *P. albicaulis* and *P. contorta* in an *Abies lasiocarpa*-*Vaccinium scoparium* habitat type. The site lay at 2652 m. on Palmer Mountain near Jardine, Montana. Seeds were stored, stratified, planted, and grown for two years in the Coeur d'Alene nursery.

Two year old *Pinus albicaulis* seedlings were obtained as bare root stock in October of 1987. The seedlings were placed in 3.8 x 20.3 cm. "Conetainer" tubes in soil composed of equal volumes of Fort Ellis loam, sand, and peat, steam pasteurized at 180°F and maintained in a greenhouse over winter at 15°C, under natural photoperiod. In March 1988, seedlings were transferred to a vernalization room (5°C night/9°C day) to prevent breaking dormancy.

SEEDLING PRECONDITIONING. During the spring of 1987, seedlings were preconditioned for 35 days (19 April — 24 May) at three temperatures and two light levels. Temperatures in the three growth chambers were 25°C day/15°C night (hotter than field conditions), 15°C day/5°C night (similar to July — August), and 5°C day/5°C night (similar to April — May) (Weaver 1980 and Weaver 1989). Using florescent and incandescent light (12 60-watt incandescent, 16 6-foot cool white florescent tubes) each growth chamber provided six seedlings a light level of 800 micro-Einsteins per meter squared per second ( $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ ) (33% of full sun and simulating light levels in an open stand) and, by shading with steel screen, a second six seedlings to a light level of 200  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$  (10% of full sun and simulating understory conditions in a fully-shaded spot, Wellner 1948). The photoperiod was 14 hours, equivalent to the photoperiod one month before bud break (Lat 45, May, *World Almanac* 1969, Schmidt and Lotan 1980). In spite of the short days seedlings in the 25°C day — 15°C night and 15°C day — 5°C night chambers broke bud

dormancy during preconditioning; the resultant growth was clipped off so only year-old needle photosynthesis and respiration was measured. The base of each "conetainer" tube was submerged in 2 cm. of water to prevent water stress.

Light levels were compared with those in a pure mature whitebark woodland (19 April 1989, Lone Mountain south of Bozeman, 2758 m= 9050 ft.). Under a nearly clear sky light levels were  $1600 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  in the open,  $1619 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  in sun spots, and  $230 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  in full shade. Under nearly complete cloud cover light levels fell to 250, 192, and  $140 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  The understory appeared to be either under full sun (50%,  $1600 \mu\text{E}/\text{m}^2 \times \text{Sec.}$ ) or fully shaded (50%,  $200 \mu\text{E}/\text{m}^2 \times \text{Sec.}$ ); with a vertical periscope we estimated the overstory cover to be 52% (cf. Weaver and Dale).

CO<sub>2</sub> EXCHANGE MEASUREMENTS. Photosynthetic rates of seedlings given the six preconditioning treatments were measured, via CO<sub>2</sub> exchange, at four temperatures (0°, 15°, 25° and 35°C) and five light levels (dark, 210, 420, 1050, and  $1580 \mu\text{E}/\text{m}^2 \times \text{Sec.}$ ) from May 24 to June 14. Six 5 cm diameter x 15 cm long plexi-glass chambers, one for a seedling from each preconditioning treatment, were cemented side-by-side in a rectangular water jacket. Chamber air temperatures were maintained by pumping water from a water bath through the water jacket surrounding the chambers. A thin copper-constantan thermocouple was inserted into a *P. albicaulis* needle and placed in the chamber as an index of leaf temperature. The chambers were lighted with a Xenon lamp and light levels were regulated using wire screens: 6 screen = 210, 4 screens = 420, 1 screen = 1050, and 0 screens =  $1580 \mu\text{E}/\text{m}^2 \times \text{Sec.}$ . Plumbers "bolwax" was used to seal the "conetainers" into the chambers and to seal the soil-root systems out of the chambers.

CO<sub>2</sub> flux density was measured with an Analytical Development Co. open system IR gas analyzer. Air from outside the lab was pumped through copper tubing in the water bath to adjust its temperature, through a silica gel desiccant and split for reference and analysis air. The reference air was passed through a flow regulator and to the reference port of the

gas analyzer. The analysis air went to a manifold which directed it to the six chambers with the seedlings. The analysis air was directed through one of the six chambers at a time, to a flow regulator, and then to the analysis port of the gas analyzer. Flow rate for reference and analysis air was maintained at 150 ml/minute. The difference between reference and analysis air was checked with an empty chamber at the beginning and end of each day to be sure the CO<sub>2</sub> concentration was equal.

The experiment was replicated six times. Each run began at 0°C and progressed through four temperature steps to 35°C; the plants were allowed one hour to equilibrate after each adjustment. Within each temperature level net photosynthesis was measured at irradiation levels including dark (for respiration), four light levels up to 1580  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ , and a second end-of-run measurement of dark respiration; the plants were allowed to equilibrate 20 minutes between changes in light levels. Since it took two days to complete one replication (run through the four temperatures and five light levels), the seedlings were returned to their preconditioning chambers for the night.

Whole seedling photosynthetic rates were converted to leaf area rates by dividing whole seedling photosynthesis by the leaf area of the seedling. All the needles were plucked from the seedling and run through a Licor optical planimeter to measure the aggregate projectable area (Kvet and Marshall 1971). In contrast to a plate-like leaf, a needle is a three-sided triangular prism formed by division of a cylindrical needle bundle into five needles. Since the cylinder splits from the tip down, each needle is curved outward from the axis so that the projectable area is roughly equivalent to a radial section (0.5 diameter x height) through the needle bundle cylinder. Assuming this, one sees that total needle area is proportional to projectable area as needle radius is to needle circumference (*i.e.*,  $r$  [for one radial side] +  $r$  [for the second radial side] +  $(2 \times \pi \times r/5)$  =  $1.256r$  for the circumferential side) so total needle area can be calculated by multiplying projected area by 3.256.

Statistical analysis of the data was by analysis of variance across the six replications with a Newman-Kuels comparison of means (Snedecor and Cochran 1980).

### Results

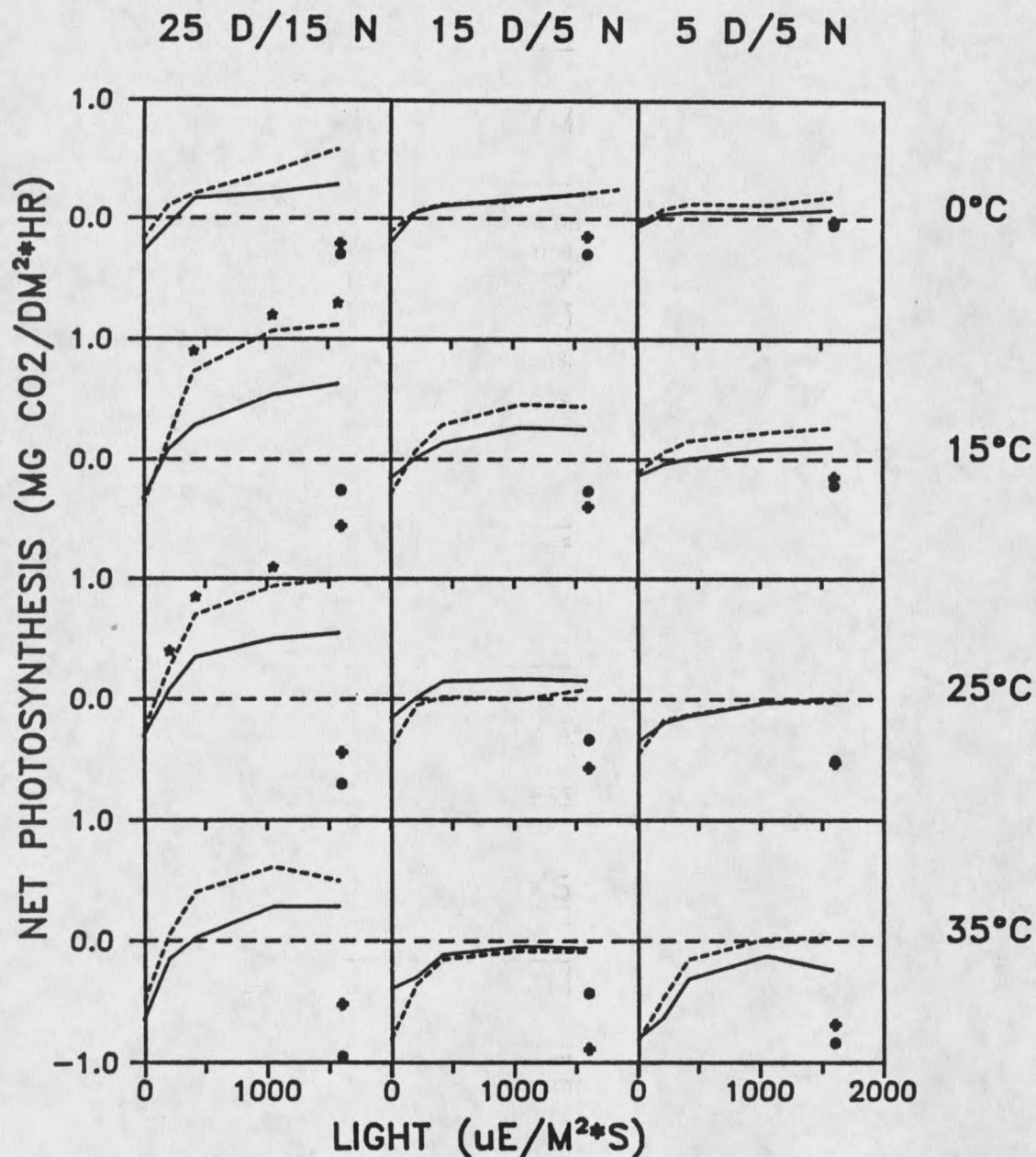
**LIGHT EFFECTS.** Net photosynthesis tended to increase with increasing light due to large increases in photon availability and small increases in temperature (Figure 5).

1) Net photosynthesis increased from low light to a maximum at  $1050 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  for seedlings preconditioned under July — August ( $15^\circ \text{ day}/5^\circ \text{ night}$ ) and April — May ( $5^\circ \text{ day}/5^\circ \text{ night}$ ) conditions, and  $1580 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  for seedlings preconditioned at warmer temperatures ( $25^\circ \text{ day}/15^\circ \text{ night}$ , Figure 5).

2) Due to increases in respiration with temperature, the  $\text{CO}_2$  compensation point tended to increase with increasing temperature (Figure 5). For example, while  $\text{CO}_2$  compensation point was  $200 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  or less at  $0^\circ\text{C}$  and  $15^\circ\text{C}$ , the  $\text{CO}_2$  compensation point was never reached in the  $25^\circ\text{C}$  and  $35^\circ\text{C}$  runs after July — August ( $15^\circ \text{ day}/5^\circ \text{ night}$ ) or April — May ( $5^\circ \text{ day}/5^\circ \text{ night}$ ) preconditioning.

3) In the  $0^\circ\text{C}$  run there was a slight increase in net photosynthesis between 1000 and  $1600 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  (Figure 5); increases in needle temperature probably caused this. The effect of light level on needle temperature increase was greatest in the  $0^\circ\text{C}$  run (a  $5^\circ \text{ C}$  increase) and least in the  $35^\circ\text{C}$  run (a  $2^\circ\text{C}$  increase, Table 1).

Dark respiration was measured at the beginning and end of each temperature run; there were no significant differences (Figure 5). Light preconditioning had no significant effect on dark respiration (Figure 5). While no measure of photorespiration was made, it probably existed and probably increased with increasing temperature (Zelitch 1971).



**Figure 5.** The effect of increasing light on net photosynthesis at 0°, 15°, 25°, and 35°C for seedlings preconditioned at three temperatures (hot = 25°/15°C day/night, July — August = 15°/5°C day/night, and April — May = 5°/5° day/night) and two light levels (200 = dashed lines and 800 = solid lines  $\mu\text{E}/\text{m}^2\cdot\text{Sec}$ .). Respiration rates before and after the run are reported as 0 light and as “high light” points; a solid circle (800  $\mu\text{E}/\text{m}^2\cdot\text{Sec}$ .) and a cross (200  $\mu\text{E}/\text{m}^2\cdot\text{Sec}$ .). Stars indicate responses which differ significantly ( $p$  5%) between light levels.

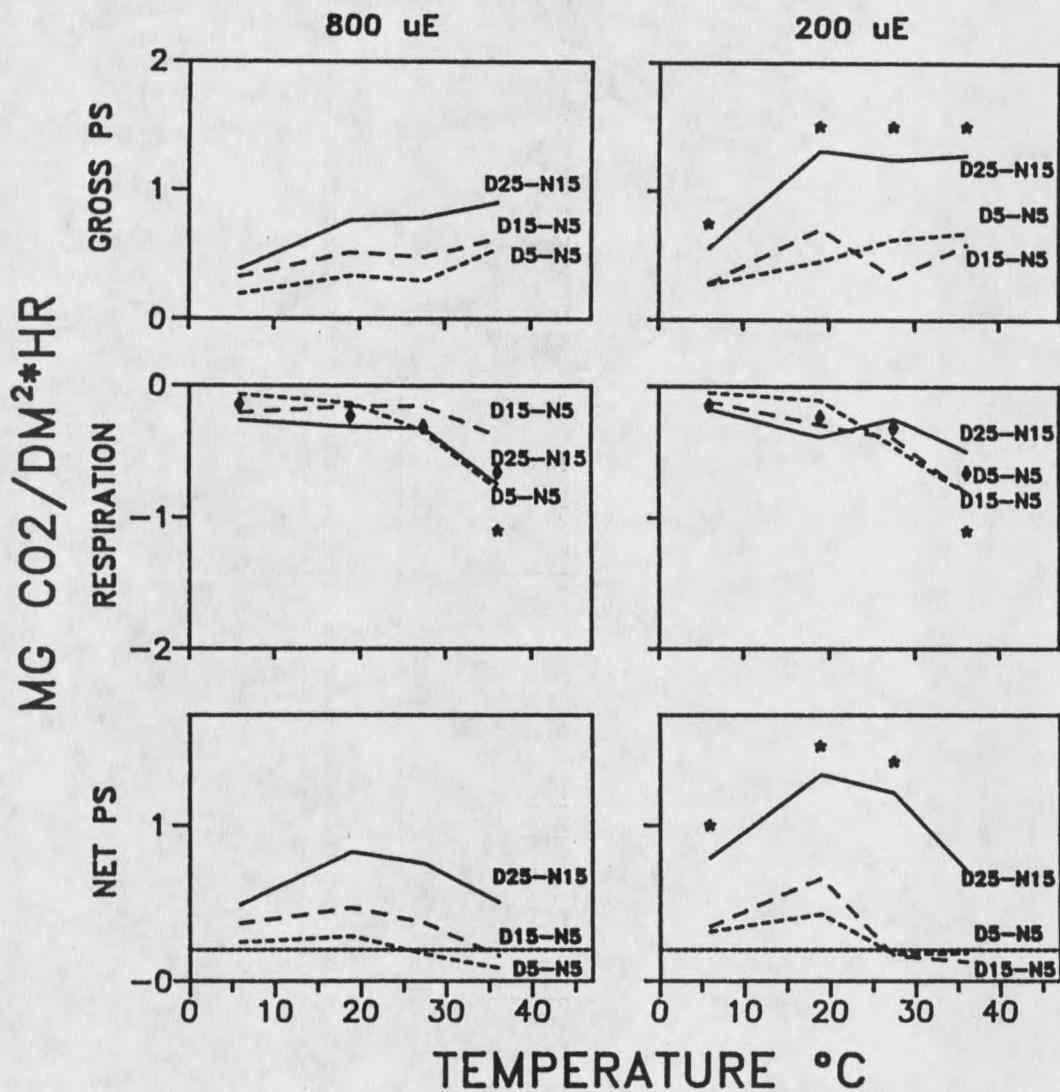
**Table 1.** Mean needle temperatures (C) measured in photosynthesis chambers during runs at four temperature and six light levels (n=6).

Temp (C)	Light ( $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ )				
	0	200	420	1050	1580
0°	2.81	3.75	4.22	5.92	7.05
15°	16.16	16.62	17.41	18.93	19.77
25°	25.41	25.45	25.63	27.46	28.19
35°	34.61	34.90	35.05	36.12	36.89

Gross photosynthesis equals net photosynthesis plus dark respiration plus photorespiration. With increasing photon availability gross photosynthesis surely rose at least through the saturation of net photosynthesis ( $1000 \mu\text{E}/\text{m}^2 \times \text{Sec.}$ ). It may well have continued to rise, hidden by increasing photorespiration, through the  $1500 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  light level (Zelitch 1971).

Seedlings preconditioned at  $200 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  had a higher rate of net photosynthesis than seedlings preconditioned at  $800 \mu\text{E}/\text{m}^2 \times \text{Sec.}$  in many cases, but the increase was significant only on plants given the hot (possibly scorching,  $25^\circ\text{C}$  day —  $15^\circ\text{C}$  night) preconditioning and run at  $15^\circ\text{C}$  and  $25^\circ\text{C}$  (Figure 5).

**TEMPERATURE EFFECTS.** Net photosynthesis rates at light saturation increased from below  $0^\circ\text{C}$  to a maximum at  $19^\circ\text{C}$  in all preconditioning treatments (Figure 6). They decreased slightly at  $25^\circ\text{C}$  and more sharply at  $35^\circ\text{C}$  in most cases (Figure 6). While the temperature optimum was constant, warm preconditioning apparently did increase net photosynthetic rates at optimum temperatures; the difference was significant for hot ( $25^\circ\text{C}$  day —  $15^\circ\text{C}$  night) preconditions.



**Figure 6.** Temperature effects on respiration, net photosynthesis and gross photosynthesis at light saturation (1050  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ ) of whitebark pine for three temperature and two light preconditions. The diamonds mark the mean respiration values of the six precondition treatments and were used to calculate gross photosynthesis. The stars indicate responses which differ significantly ( $p=5\%$ ) among treatments.

Dark respiration ( $\text{CO}_2$  evolution) increased gradually from  $0^\circ\text{C}$  to  $25^\circ\text{C}$  and more sharply from  $25^\circ\text{C}$  to  $35^\circ\text{C}$ ; respiration rates at  $35^\circ\text{C}$  were significantly greater ( $P < 1\%$ ) than rates at lower temperatures for all preconditions (Figure 6). Temperature

preconditions did not significantly affect respiration rates in any temperature run (Figure 6). Photorespiration probably increased with increasing temperature (Zelitch 1971).

Gross photosynthesis, calculated as net photosynthesis plus dark respiration, increased gradually from 0° to 35°C (Figure 6). It was apparently increased by hot (25°—15°C) preconditions and the increase was significant ( $P < 0.05$ ) in seedlings preconditioned at the 200  $\mu\text{E}/\text{m}^2 \times \text{Sec}$ . light level (Figure 6). The failure to add in photorespiration underestimates gross photosynthesis.

### Discussion

**LIGHT EFFECTS.** Whitebark pine seedlings can be found in forest sun flecks and on open sites where light levels may be 200 (shade) to 1600 (sun)  $\mu\text{E}/\text{M}^2 \times \text{S}$ . Seedlings were therefore preconditioned for 35 days at light levels of 200  $\mu\text{E}/\text{M}^2 \times \text{S}$  (like shaded spots in a whitebark pine woodland) and 800  $\mu\text{E}$  (the highest growth chamber irradiance available, but less than the 1600  $\mu\text{E}/\text{M}^2 \times \text{S}$  found in large sun flecks of a whitebark pine woodland or in an opening created by a burn or beetle kill). Due to the high heat and relatively poor circulation in the hot (25°C day/15°C night) growth chamber trees preconditioned at high light probably suffered heat damage which lowered gross photosynthesis below that of trees conditioned under shadier conditions. It is not known whether damage would occur at these temperatures in the field.

Light level effects on total respiration rate were not measured, though some increase, due to photorespiration, is expected (Zelitch 1971). There was no apparent preconditioning effect of light level on dark respiration (Figure 5), and no measures of its preconditioning effect on photorespiration.

Both net and gross photosynthesis increase with photon availability (two exceptions at 35°C, Figure 5); the increase in net photosynthesis is steep at first and tends to peak at

1000  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ ; this continuing rise in net photosynthesis at low temperatures ( $0^\circ$  to  $15^\circ\text{C}$ ) can be attributed to warming of leaves while drops at high temperatures ( $35^\circ\text{C}$ ) may be due to overheating of leaves. Gross photosynthesis may continue to rise through the 1600  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$  level, since the failure to add in photorespiration at these levels results in an underestimate of gross photosynthesis.

There was no apparent effect of light preconditioning on mature needles.

1) While adaptation to low light often involves an especially steep initial response to increasing light (Leopold 1964, Hadley & Smith 1987), no difference was observed in the initial response between plants preconditioned in low and high light (Figure 5).

2) While adaptation to low light often involves a low saturation point (Hadley and Smith 1987) no difference between plants conditioned at low and high light levels was observed (Figure 5). Since initial response and saturation adaptations usually occur in growing leaves only (Leopold 1964), their absence might have been expected. No data was collected relevant to adaptation by new needles forming after a stand opening event.

3) While photosynthesis in high light levels of 200 and 800  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$  preconditioned needles was similar under spring ( $5^\circ\text{C}$  day —  $5^\circ\text{C}$  night) and summer ( $15^\circ\text{C}$  day —  $5^\circ\text{C}$  night) temperatures, photosynthesis of hot ( $25^\circ$  —  $15^\circ$ ) preconditioned plants grown at 800  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$  was less than those grown at 200  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$  (Figure 5). This contrary-to-expected difference can be attributed to destruction of chlorophyll by high temperatures rather than any direct light effect.

**TEMPERATURE EFFECTS.** Dark respiration appears to rise exponentially with rising temperature in the  $0^\circ$  —  $40^\circ\text{C}$  range, and neither trends nor statistically significant effects of preconditioning on it were observed (Figure 6). Respiration rises with increasing temperature in other plants, including pines (Decker 1944). As noted above, the estimate of respiration and conditioning effects on respiration include no consideration of photorespiration.

Gross photosynthesis (calculated as net photosynthesis plus dark respiration) appears to rise linearly with temperature in the 0° — 40° C range (Figure 6). Because the estimate of gross photosynthesis omits photorespiration, it is probably low (as much as 2.8 x dark respiration at high light levels; *Pinus silvestris* (Zelawski 1967).

Because respiration rates rise more rapidly with increasing temperature than gross photosynthesis rates, net photosynthesis is maximum at an intermediate temperature (approximately 19°C); in *P. albicaulis* woodlands 19°C is often reached during July and August, but is rare in June and September (Weaver 1989). Net photosynthesis responded similarly to temperature for other high elevation conifers; lodgepole pine (Dykstra 1974) and engleman spruce (Hadley and Smith 1987). The optimum temperature for photosynthesis in lower altitude pines may be higher (e.g. *Pinus taeda*, 30°C, Decker 1944). One deduces, however, from net photosynthesis, that seedlings will grow at temperatures from below 0° to above 35°C. These data are probably relevant to older trees as well as seedlings, since only mature needles such as those that dominate the canopies of shoots older than two years were studied.

While light preconditioning had no effect on the photosynthesis of mature leaves (except when overheating may have occurred), temperature preconditioning did have the following significant effects:

- 1) High temperature preconditioning increased gross photosynthesis (significantly so under low light conditions where there is no evidence of over heating), probably by increasing the amount or efficiency of Calvin cycle (dark reaction) enzymes (Figure 6). This means that, at the same temperature, photosynthesis will be greater if trees are in summer than in winter condition.
- 2) The light range over which net photosynthesis increased linearly under increasing light also increased with increases in the warmth of the preconditioning treatment (Figure 5).

3) Compensation points measured at low temperatures are lower than those measured at higher temperatures (Figure 5); the differences are greatest under the low temperature pretreatment and not statistically significant.

4) While changes in photosynthetic rate with preconditioning were seen at all temperatures, there was no change in the optimum temperature for net photosynthesis (Figure 6). Warm preconditioning increased net photosynthesis without increasing dark respiration or increasing the temperature optimum for photosynthesis. In lower altitude conifers, seasonal adaptations involving a change in optimum temperature have been reported (*Pinus radiata*, Rook 1968; *Pseudotsuga menziesii*, Sorensen 1964; and *Pinus taeda* Strain *et al* 1976). I have no data to support hypotheses on mechanisms for increase in net photosynthesis without a change in temperature optimum.

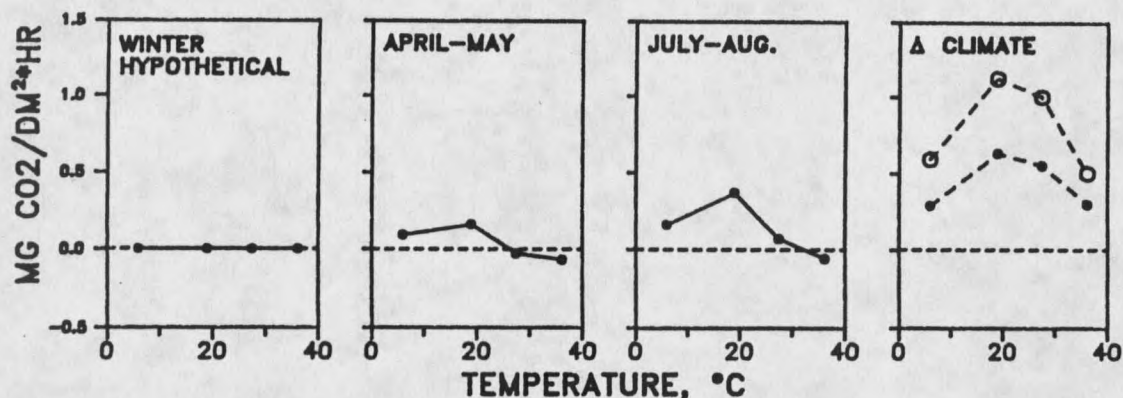
In this study, plants from one seed source only were observed; one expects different performance from ecotypes collected from significantly different environments (Heslop Harrison 1964). Altitudinal ecotypes have been reported by Fryer and Ledig (1972) and Krueger and Ferrell (1965).

### Conclusions and Applications

To describe whitebark pine seedling growth in the field, a modeler would likely determine net photosynthesis for each moment and sum over all moments in a year.

Net photosynthesis occurs at 0°, maximizes near 20°, and drops toward 35°C (Figure 7). The curve is bell shaped because respiration rates rise exponentially while gross photosynthesis rises linearly.

While optima change little with preconditioning temperature, warm pretreatment increases net photosynthesis at all measurement temperatures. As a result, one expects net photosynthesis to be very low in winter, higher in spring, and still higher in summer.



**Figure 7.** Net photosynthesis measured under four temperatures, for whitebark pine seedlings preconditioned under three temperatures regimes and two light levels. Winter data is estimated from Tranquillini (1979). Effects of spring (5° night — 5° day C) and summer (5° night — 15° day C) preconditionings were measured; light preconditionings had no significant effect and data was pooled. Under warm climate change (15° night — 25° day C) precondition net photosynthesis increased less under high (800  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ , solid circles) than low (200  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ , open circles) light level; high temperature stress may be indicated.

Though widely applicable, the winter data quoted (Tranquillini 1979), should be verified for whitebark pine. The conditioning trend continues to temperatures higher than those normally experienced by whitebark pine and suggest that in the absence of competition whitebark pine could grow at lower altitudes. Dark respiration rates increase with temperature, but are apparently unaffected by season. Net photosynthesis increases significantly with increasing light, so seedlings are expected to grow faster in sunlight than in shade. The shady pretreatment apparently had no effect on either gross photosynthesis, net photosynthesis, or respiration rate of mature needles; the literature on deciduous trees suggests that immature leaves might be affected more strongly. It would be desirable in future studies to check for photoperiod effects. Would a day length shorter than 14 hours reduce the photosynthesis of needles in winter and would day lengths longer than 14 hours increase the photosynthesis of needles in summer?

The ideal model would also incorporate data on nutrient and water relations not sought in this project.

## VI

## SUMMARY AND APPLICATIONS

A one month period of stratification improved germination in whitebark, lodgepole and limber pine seeds. Longer periods of stratification had no additional effect. Despite marked differences in provenance, there was no response difference to stratification time among the species; a short stratification time is apparently sufficient to prevent premature germination. Horticulturalists may want to test the efficacy of even shorter stratification treatments.

The small seeds of lodgepole pine had twice the germination rate of whitebark and limber pines with large seeds. Since such low germination rates seem wasteful, a tendency to second year germination in large seeded trees may be indicated; such postponement may be impractical for pines with small seeds and smaller reserves for respiration unavoidable in the intervening time.

The cardinal points for germination of whitebark, lodgepole and limber pine seeds are 10°, 20° — 30°, and 40°C. Altitudinal origin of the three pines had no effect on germination temperature. This may indicate that soil temperature at the time of germination does not vary with altitude.

The cardinal points for root growth are 10°, 30°, and 45°C for whitebark, lodgepole, and limber pines. These are similar to cardinal temperatures for germination, perhaps because both processes depend on cytoplasmic enzymes. Similarities between species of different altitudinal origin indicates that germination and root growth temperature requirements do not determine species distribution. Horticulturalists growing whitebark pine

in greenhouse conditions will want to provide germination and root growth temperatures in these ranges.

The cardinal points for net photosynthesis of whitebark pine seedlings are 0°, 15° — 25°, and 37°C. Temperatures for photosynthesis are significantly lower than those for root growth and germination. Whitebark pine can not be expected to perform well in the field or the lab at temperatures below 0°C or above 25°C. While a temperature preconditioning (winter, spring, or summer conditions) had no influence on cardinal points for photosynthesis, seedlings preconditioned with conditions warmer than occur in the field had high rates of photosynthesis; temperature stress did appear in these seedlings, however, under the higher light level. Since the species already occupies the coolest forest environments in our region, global warming might threaten whitebark pine survival by pushing its habitat above the mountain top environments.

Net photosynthesis of whitebark pine seedlings increased with increasing light from negative (respiration) levels at 0 light, through CO<sub>2</sub> compensation at about 200  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ , to light saturation at about 1000  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$ . This information will be useful to modelers attempting description of energy balance of seedlings occupying variously shaded sites. Although preconditioning of mature leaves at different light levels (200  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$  = dark shade and 800  $\mu\text{E}/\text{m}^2 \times \text{Sec.}$  = light shade) had little or no significant effect on whitebark pine photosynthesis, immature leaves may be more plastic. Expected field conditions may be the most appropriate preconditioning condition.

## VII

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