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EFFECTS OF TEMPERATURE AND TEMPERATURE PRECONDITIONING ON SEEDLING PERFORMANCE OF WHITEBARK PINE

J. Jacobs
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ABSTRACT

Four experiments explored the effects of temperature on the germination and seedling performance of whitebark pine (*Pinus albicaulis*). While 1 month of stratification increased germination from 5 percent to about 40 percent, longer stratification periods (to 8 months) did not improve germination. Germination occurred throughout the 10 to 40 °C range with a broad optimum near 30 °C. Root growth occurred throughout the 10 to 45 °C range with an optimum near 30 °C. Long exposure (5 months) to low temperature (1.5 °C) lowered the temperature threshold for both germination and root growth. The apparent temperature range (perhaps 0 to 35 °C) and optimum (20 °C) for net photosynthesis at light saturation were lower than for germination and growth. While no preconditioning effect of light level (200 to 800 $\mu\text{E}/\text{M}^2\text{S}$) on the photosynthetic capacities of mature leaves was seen, photosynthesis increased progressively from needles preconditioned with winter, spring (5 °C day to 5 °C night), summer (15 °C day to 5 °C night), and abnormally warm (25 °C day to 15 °C night) temperatures.

INTRODUCTION

The establishment of whitebark pine (*Pinus albicaulis* Engelm.) on a site must depend on its response to quantities of energy (light and heat), materials (water and nutrients), and destructive forces (fire, herbivory, and trampling) present at the site (Hutchinson 1957). The trees' response might depend, as well, on preconditioning with respect to water (May and others 1962), temperature (Tranquillini 1979), or even destructive forces (Ryan 1983).

The object of our research was to explore the effects of one environmental phenomenon, temperature, on whitebark pine's readiness to germinate, germination, root growth, and photosynthesis. The magnitude of temperature preconditioning effects was studied on one of these processes, net photosynthesis.

METHODS

Seed Source

Seeds for studies of stratification, germination, root growth, and photosynthesis were collected from an *Abies lasiocarpa*-*Vaccinium scoparium* habitat type near Jardine, MT (Palmer Mountain, 2,652 m) in the autumn of 1987. They were stored under dry 20 °C conditions.

Stratification Time

To determine the effects of stratification time on germination rate, filled seeds were stratified for 0, 1, 2, 3, 5, or 8 months and germination rates were compared (Jacobs 1989). All seeds were x-rayed before stratification and empty seeds were discarded. To minimize the danger of fungal attack during stratification, the seeds were surface sterilized by soaking in 40-percent Clorox for 10 minutes and rinsing 10 times in distilled water to remove the Clorox (Wenny and Dumroese 1987). The seeds were then placed in nylon bags and soaked in clear running tap water for 48 hours. The imbibed seeds were surface dried, lightly dusted with Spurgon fungicide (Tetrachloro-para-benzoquinone 98 percent) and placed between two moistened blotter papers in plastic germination boxes (14 by 13 by 3.5 cm), 100 seeds per box. The seeds were stratified in a refrigerator (1.5 °C) for 0 to 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 photo-period). Germination occurred over a period of 1 to 3 months. After germination ceased, percent germination was calculated.

Germination Rates

To determine the effect of temperature on germination rate, the germination rates of seeds stratified at 1.5 °C for 2 to 3 months were compared at temperatures ranging from 5 to 50 °C (Jacobs 1989). Stratified seeds were placed on a temperature gradient bar with a temperature range of 5 to 50 °C and germinating seeds were counted over a period of 2 weeks. The temperature gradient bar was similar to that of Barbour and Racine (1967): three aluminum plates (one per species) 90 by 14.5 by 0.7 cm lay parallel and connected by tubes with 50 °C water

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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 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 plexiglass box top to minimize evaporation and temperature fluctuation. Stratified seeds were lined up across the bar in columns of 10, and with the columns 5 cm apart. Treatment temperatures were measured by placing the tip of a thermocouple on the blotter paper at each seed column. Seeds germinating in each temperature treatment were counted every 48 hours for 2 weeks. The experiment was replicated on three dates (July 15, 1988; December 2, 1988; and February 27, 1989).

Root Growth Rates

To determine the effects of temperature on root growth rates, the root growth rates of plants growing under cool temperatures were compared with those of plants growing under warmer conditions (Jacobs 1989). The seeds were stratified in a refrigerator (1.5 °C) for 1 to 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). Freshly germinated seeds were transferred to the temperature gradient bar to measure root growth rates at temperatures ranging from 4 to 48 °C. The 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° angle so the roots would grow geotropically straight down between the blotter and the glass and in a region of constant temperature. 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 plexiglass box top to minimize evaporation and temperature fluctuation. Root lengths were 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).

Photosynthetic Rates

Seeds collected in 1984 were stored, stratified, planted, and started in the Coeur d'Alene nursery. We obtained 2-year-old *Pinus albicaulis* seedlings as bare root stock in October of 1987. The seedlings were transferred to 3.8- by 20.3-cm "conetainer" tubes in a soil composed of equal volumes of Fort Ellis loam, sand, and peat; steam pasteurized at 180 °F; and maintained in a greenhouse at 15 °C and natural photoperiod over winter. In March 1988, seedlings were transferred to a vernalization room (5 °C night/9 °C day) to prevent breaking dormancy.

Seedlings were preconditioned for 35 days (April 19 to May 24, 1988) at three day-night temperature combinations 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, this proceedings). In each temperature regime six seedlings received light levels equal to 33 percent of full sun (800 $\mu\text{E}/\text{M}^2\cdot\text{S}$ = micro-Einsteins PAR (= micro moles of photosynthetically active radiation) per meter squared per second and simulating light levels in an open stand) and six seedlings received 10 percent of full sun (200 $\mu\text{E}/\text{M}^2\cdot\text{S}$ and simulating understory conditions in a fully shaded spot, Wellner 1948). Light was provided with fluorescent and incandescent light (twelve 60-watt incandescent, and sixteen 6-ft cool white fluorescent tubes) shaded, in the low-light case, with steel screen. Light levels measured in a mature whitebark pine stand (52 percent cover, Weaver and others, this proceedings) were 250-1,619 $\mu\text{E}/\text{M}^2\cdot\text{S}$ in sun spots and 140-230 $\mu\text{E}/\text{M}^2\cdot\text{S}$ in full shade. The photoperiod was 14 hours, equivalent to the photoperiod 1 month before bud break (lat. 45° N., May, Long 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 were measured. The base of each conetainer tube was submerged in 2 cm of water to prevent water stress.

Photosynthetic rates of seedlings given the six preconditioning treatments were measured, via CO_2 exchange, at four temperatures (0, 15, 25, and 35 °C) and five light levels (dark, 210, 420, 1,050, and 1,580 $\mu\text{E}/\text{M}^2\cdot\text{S}$) between May 24 and June 14. Six 5-cm-diameter by 15-cm-long plexiglass chambers, one for a seedling from each preconditioning treatment, were cemented side-by-side in a rectangular water jacket. The air was mixed by turbulence as it flowed from top to bottom of the tubular chamber. Chamber air temperatures were maintained by pumping water from a water bath through the water jacket surrounding the chambers. The roots were outside the chambers and therefore near room temperature (21 °C). A thin copper-constantan thermocouple was inserted into a *Pinus 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. Plumbers' "bolwax" was used to seal the conetainers into the chambers and to seal the soil-root systems out of the chambers.

CO_2 flux density was measured with an Analytical Development Company open system IR gas analyzer. Air from the ceiling of a hallway was pumped through copper tubing in the water bath to adjust its temperature, through a silica gel to dry it, and split for reference and analysis air. Both reference and analysis air were, thus, very dry. 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 that 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 verify that the CO₂ concentrations were 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 1 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 1,580 $\mu\text{E}/\text{M}^2\cdot\text{s}$, 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 2 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 total leaf area of the seedling. All the needles were plucked from the seedling and run through a Licor optical planimeter to measure the projected area (Kvet and Marshall 1971). In contrast to a platelike leaf—whose total area is calculated by doubling projection areas—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 by ht) 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 [that is, r (for one radial side) + r (for the second radial side) + $2\pi r/5 = 1.256r$ (for the circumferential side)] so total needle area can be calculated by multiplying projected area by 3.256. We recognize that total leaf area overestimates functioning leaf area and therefore underestimates absolute photosynthetic rates (Carter and Smith 1985), but believe the units are adequate for comparisons designed to determine the effects of light and temperature levels.

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 AND DISCUSSION

Stratification

Exposure to moist cold is a dormancy-breaking requirement for many species including almost half of the pines (Schopmeyer 1974). Since whitebark pine usually exhibits low germination rates in standard tests, we tested the hypothesis that the 1-month stratification time usually applied is less effective than a stratification time approximating the 5 to 8 months received naturally (Weaver 1980). Germination rates were 4 percent, 68 percent, 38 percent, 41 percent, 52 percent, and 38 percent for seeds stratified for 0, 1, 2, 3, 5, and 8 months, respectively. We conclude that stratification beyond 1 month does little to increase germination and speculate that a short stratification time has been naturally selected, because it prevents fall germination without any chance of delaying spring germination. This conclusion is bolstered

by parallel tests (Jacobs 1989) that show 1-month stratification times were required for species from high (long-winter) altitudes (whitebark pine), middle altitudes (lodgepole pine), and low (short-winter) altitudes (limber pine). We speculate that the low germination rates observed are due in part to seed defect and in part to other dormancy mechanisms that reserve live seed for succeeding years (McCaughey 1989 [whitebark pine]; Perry 1989 [lodgepole pine]).

Temperature and Germination

Our tests show that, newly stratified whitebark pine seeds, germinate at temperatures ranging from 10 to 40 °C and that, while germination rates of specific lots of 10 seeds vary from 0 to 50 percent at most temperatures in this range, germination rates tend to be slightly higher in the 25 to 35 °C range than at cooler or warmer temperatures (fig. 1A). Germination of middle-altitude lodgepole pine and low-altitude limber pine occurred in the same 10 to 40 °C range as the high-altitude whitebark pine. During our stratification studies we saw that, if seeds are kept under cold conditions (1.5 °C) for longer periods of time (over 5 months), most dormancy-broken seeds will germinate. Since stratification is probably completed in the early winter, germination in moist forest soils is likely under temperature and/or endogenous control for most of the winter. If so, germination is expected in the spring near the time of snow melt.

Temperature optima may drop slightly with decreases in altitude from 25 to 35 °C for whitebark, 15 to 35 °C for lodgepole, and 15 to 25 °C for limber pine (Jacobs 1989). We speculate that, because lower temperatures precede the warmer temperatures of late spring, seeds with a lower optimum probably germinate first and are deeper rooted at the onset of any summer drought. If so, natural selection at lower, drier altitudes, where limber pine was collected, probably favors a lower temperature optimum than that favored at higher moister altitudes where whitebark pine predominates.

Temperature and Root Growth

Our tests show that, in newly stratified whitebark pine seeds, root growth can occur at temperatures between 10 and 45 °C and that, at the temperature optimum (25 to 35 °C), root extension of new germinants is 5 to 15 mm per day (fig. 1B). Root growth of high-altitude whitebark pine, middle-altitude lodgepole pine, and low-altitude limber pine has similar ranges (10 to 45 °C) and optima (30 °C) (Jacobs 1989). During our stratification experiments we also saw that, if seeds germinate after long (5 months) cold (1.5 °C) storage, root growth will occur at temperatures below the range reported. We conclude that in nature, germination must produce roots near snow melt, most growth occurs at suboptimal temperatures, and high-temperature stress is rare or nonexistent for most roots. This assertion is supported by soil temperature data at 5 cm depth from level grasslands just below the conifer zone at Bozeman, MT, and Casper, WY (NOAA 1985). Of the 6 months with average maximum

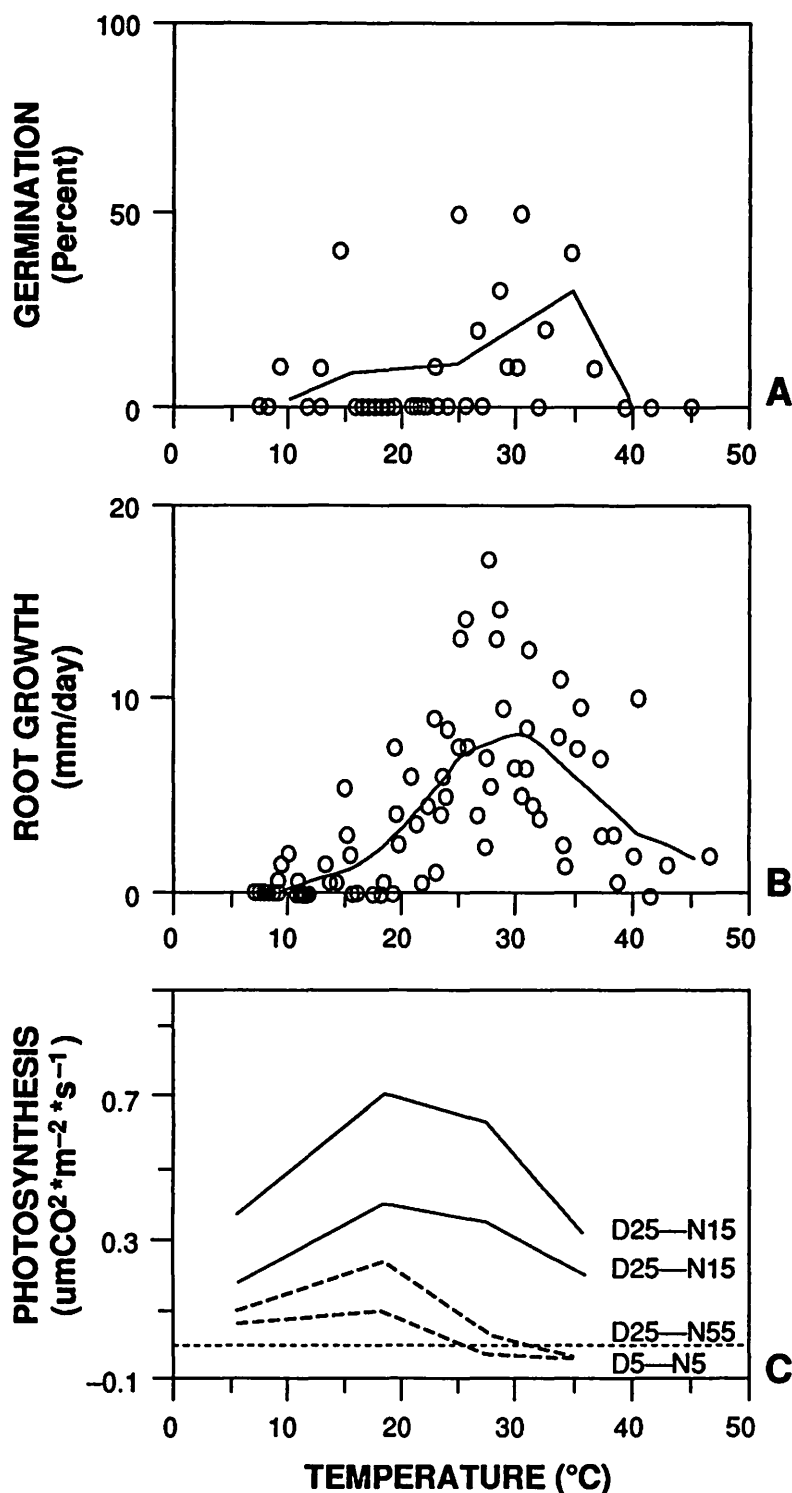


Figure 1—Effect of temperature on seed germination, root growth, and net photosynthesis: (A) Percent germination in 33 lots of 10 seeds tested at temperatures between 5 and 45 °C. The line passes through the median of non-zero values. (B) Initial growth rates (mm/day) of 71 roots grown at temperatures between 5 and 50 °C; the line passes through the median of non-zero values. (C) Photosynthetic rates at saturation for plants preconditioned at spring (5 °C day to 5 °C night), summer (15 °C day to 5 °C night), and warmer than natural (25 °C day to 5 °C night) conditions. Plants preconditioned under the hot conditions (solid lines) and low light (200 $\mu\text{E}/\text{M}^2\cdot\text{S}$) had higher photosynthetic rates (upper solid line) than the chlorotic plants preconditioned under high light (800 $\mu\text{E}/\text{M}^2\cdot\text{S}$).

temperature above 10 °C, only 3 have average maximum temperatures above 20 °C and maximum temperatures of 30 °C are reached rarely, if at all. If maximum temperatures almost never exceed 30 °C at 5 cm, the inhibition of root growth observed there (Weaver 1981) is more likely due to drought than high temperature; both factors may be important in more superficial layers.

Photosynthetic rates for ecologically and genetically related *Pinus cembra* increase fourfold as average soil temperatures rise from 0 to 8 °C (Tranquillini 1979); the increase in photosynthesis with increases in average soil temperature may indicate the daily duration of root activity; that is, hours above a root growth minimum of 10 °C.

Temperature and Photosynthesis

Net photosynthesis rises with increasing light from 0 to a maximum near 1,050 $\mu\text{E}/\text{M}^2\cdot\text{S}$ for seedlings preconditioned under naturally occurring conditions. *Pinus contorta* (Dykstra 1974) and *Picea engelmannii* (Hadley and Smith 1987) were also light saturated at about 50 percent of full sun. While we saw no consistent difference in photosynthetic rates of mature leaves preconditioned for 1 month at 200 or 800 $\mu\text{E}/\text{M}^2\cdot\text{S}$, shade leaves might have been formed if branches had been shaded during needle initiation (Jacobs 1989).

Net photosynthesis at light saturation probably occurs at all above-freezing temperatures. It occurs at -4 °C in *Pinus cembra*, a close ecologic, taxonomic, and genetic relative (Tranquillini 1979), and in whitebark pine was shown to occur at 5 °C, was maximum near 20 °C, and declined significantly above 20 °C (fig. 1C). The temperature optimum for photosynthesis of *Pinus contorta* is also near 20 °C (Dykstra 1974). Dark respiration increased slightly from 5 °C ($0.13 \mu\text{mole m}^{-2}\text{sec}^{-1}$) to 30 °C ($0.19 \mu\text{mole m}^{-2}\text{sec}^{-1}$) and rose significantly as 35 °C ($0.32 \mu\text{mole m}^{-2}\text{sec}^{-1}$) was approached (Jacobs 1989). Despite the fact that both germination and root growth occur in the soil at temperatures lower than air temperature, both apparently have higher temperature cardinal points (minimum 10-optimum 30-maximum 40 °C) than does photosynthesis (0 min, 25 opt, and 35-40 °C, fig. 1)—a process proceeding at air temperature.

Net photosynthetic rates of whitebark pine are affected by temperature preconditioning (reviewed for other timberline species by Tranquillini 1979). Studies of photosynthesis of *Pinus cembra* (Tranquillini 1979) showed no photosynthesis during the winter months and *Pinus albicaulis* probably behaves similarly. Warming from winter to simulated spring (day 5 °C-night 5 °C) and summer (day 15 °C-night 5 °C) temperatures increased photosynthetic rates from 0.00 to 0.06 and $0.19 \mu\text{mole m}^{-2}\text{sec}^{-1}$, respectively (fig. 1C). Further warming, to temperatures of 25 °C day-5 °C night, not even experienced in dry grasslands below, increased photosynthetic rates to 0.38-0.69 $\mu\text{mole m}^{-2}\text{sec}^{-1}$ (fig. 1C). The increase in net photosynthetic rates with higher temperature preconditioning must be primarily due to increases in gross photosynthesis or decreases in photorespiration—because differences in preconditioning temperature caused no difference in dark respiration rates. Light preconditioning had no

effect on photosynthetic rate under spring or summer conditions; under warmer than natural preconditions, however, net photosynthesis of plants preconditioned with low light (200 $\mu\text{E}/\text{M}^2\cdot\text{S}$) was significantly higher than that of plants preconditioned with higher light levels (800 $\mu\text{E}/\text{M}^2\cdot\text{S}$).

Acclimatization (preconditioning) results suggest that—with adequate water and with competitor reduction, perhaps by fire or management—whitebark pine might survive under the warmest temperature conditions in our region. The trees may have used this capability in surviving the hypsithermal, a warm dry postglacial period, that deforested some of the highest sites in our region (for example, the Bighorn and Beartooth Mountains). This possibility is supported by the vigorous growth of trees transplanted from high forests to lawns in the valley below where their success surely depends on both heavy watering and the elimination of less cold-tolerant competitors such as *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Abies lasiocarpa* (Arno and Weaver, this proceedings).

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Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from P. Kolb)—Do shaded seedlings have lower compensation points than sun-grown seedlings?

A.—Our growth chamber lights were not as bright as sunlight (1,600 uE/M²*S) so different light levels really refer to a light shade (800 uE/M²*S)—rare in the field—and a deep shade (200 uE/M²*S). Plants preconditioned in deeper shade usually had slightly lower compensation points (Jacobs 1989), but I doubt that the differences were statistically significant. It would be interesting to compare compensation points of sun and shade seedlings in the field.

Q. (from P. Kolb)—Why are photosynthetic rates of your shade-conditioned seedlings higher than those of your sun-conditioned seedlings?

A.—Light preconditioning had no differential effect on plants grown under normal spring (5 °C day-5 °C night) or summer (15 °C day-5 °C night) conditions. Plants grown at high temperature (25 °C day-15 °C night) with relatively high light levels (800 uE/M²*S) were chlorotic and therefore demonstrated lower photosynthetic rates than plants preconditioned at lower light levels (200 uE/M²*S).

Q. (from D. Mattson)—How does photosynthetic performance of whitebark pine under different light and temperature conditions compare with that of associated conifers (*Abies lasiocarpa*, *Picea engelmannii*, or *Pinus contorta*)?

A.—Lodgepole (Dykstra 1974) and Engelmann spruce (Hadley and Smith 1987) are similar to whitebark in light saturation levels (50 percent of full sun) and temperature optima (20 °C). Your question would be answered best with one experiment comparing all four species with uniform methods. Even these data would provide only a partial explanation of shade and temperature tolerance, as information on photosynthesis should be integrated with information on other processes (such as, respiration rates) to understand the carbon balance (growth) of the tree. Models integrating a variety of environmental factors will be required to predict the distribution and growth of whitebark pine; the models of Tranquillini (1979) and Keene (this proceedings) are relevant.