

High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings

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Summary We studied the effects of high temperature and drought on the survival, growth and water relations of seedlings of *Pinus ponderosa* (Dougl.) Lawson, one of few coniferous tree species that can successfully colonize drought-prone sites with high soil surface temperatures. Temperature profiles were measured with 0.07-mm thermocouples in a sparse ponderosa pine forest in northern Idaho. The soil surface and the adjacent 5 mm of air reached maximum temperatures exceeding 75 °C, well above the lethal temperature threshold for most plants. Air temperatures 50 mm above the soil surface (seedling needle height) rarely exceeded 45 °C. *Pinus ponderosa* seedlings that survived maintained basal stem temperatures as much as 15 °C lower than the surrounding air. The apparent threshold temperature at the seedling stem surface resulting in death was approximately 63 °C for less than 1 min. No correlation between seedling mortality and needle temperature was found, although some needles reached temperatures as high as 60 °C for periods of ≤ 1 min. Surviving seedlings had significantly higher stomatal conductance than seedlings that did not survive until fall. Transpiration rates, calculated from measured needle temperatures, stomatal conductance and evaporative demand, were high (up to 16.7 mmol m⁻² s⁻¹), indicating that water transport through seedling stems may have acted as a heat transfer mechanism, cooling the stem below the lethal threshold temperature. Heat exchange calculations showed that rapid water flow through seedling stems can absorb sufficient energy to reduce stem temperature by 30 °C during peak sunlight hours.

Keywords: heat tolerance, lethal temperature threshold, stomatal conductance, transpirational cooling.

Introduction

High soil surface temperatures are correlated with low seedling survival in many environments, including boreal forests and northern European forests (Levitt 1980, Gauslaa 1984, Koppelaar et al. 1991), and hot deserts (Shreve 1931, Turner et al. 1966, Nobel 1984, 1988a, 1988b). It has been assumed that high temperatures affect seedlings, first, by increasing

evaporative demand, and second, by direct tissue damage where seedlings are in contact with hot surfaces (Baker 1929, Kramer 1980, Levitt 1980, Gauslaa 1984, Hålgren et al. 1991). The onset of heat-induced tissue damage is between 50 and 55 °C for most plant species (Daubenmire 1943, Lange and Lange 1963, Levitt 1980, Kappen 1981, Larcher 1983, Seidel 1986, Weis and Berry 1987, Colombo and Timmer 1992). Although the deleterious effect of high soil surface temperatures on coniferous tree seedlings in temperate climates has been documented (Baker 1929, Seidel 1986, Colombo and Timmer 1992), few studies have examined the mechanisms by which seedlings of some species are able to survive under these circumstances. Physiological adjustment through the formation of heat shock proteins (HSPs) and cell dehydration as well as heat avoidance by reducing the heat load are some of the adaptations found in plants growing in hot environments (Kappen 1981, Gutschick 1987).

High temperature may act as a single stress; however, lack of water is usually an interacting factor. In the Sonoran Desert, significant mortality of *Carnegiea gigantea* (Engelm.) Britt. and Rose seedlings resulted from transpirational water loss induced by high soil surface temperatures (Turner et al. 1966, Nobel 1988a, 1988b). Because the combined effects of drought, high temperature and evaporative demand are major causes of tree seedling mortality on exposed sites in the northwestern USA (Harrington and Kelsey 1979, Vance and Running 1985), it has generally been assumed that drought tolerance is responsible for tree species zonation and distribution in this region (Bates 1932, Daubenmire 1939, 1943).

Pinus ponderosa (Dougl.) Lawson is considered to be one of the most drought tolerant native tree species in the northwestern USA, surviving on hot and dry sites where other tree species fail to establish (Daubenmire 1968). Characteristics of mature *P. ponderosa* trees and older seedlings that contribute to increased survival on these sites are maintenance of high water-use efficiencies, osmotic adjustment of cell water, and an extensive root system capable of utilizing deep soil water resources (Daubenmire 1968, Jackson and Spomer 1979, DeLucia et al. 1988, DeLucia and Heckathorn 1989, DeLucia and Schlesinger 1991). But even *P. ponderosa* seedlings sus-

tain high mortality from the combined effects of drought, high temperature and evaporative demand (Harrington and Kelsey 1979, Vance and Running 1985). How some of these seedlings survive whereas others perish is not understood. For example, surface temperatures of 55 °C caused seedling mortality in *P. ponderosa* on some sites in western Montana, but on other sites seedlings survived temperatures up to 66 °C (Harrington and Kelsey 1979).

We have investigated possible mechanisms that allow *P. ponderosa* seedlings to tolerate high temperatures. The objectives of the study were to determine (1) the soil and air temperature profiles experienced by *P. ponderosa* seedlings, (2) the lethal temperature threshold for seedlings, and (3) the effects of soil water availability on stomatal conductance, transpiration rates, heat tolerance, and survival of *P. ponderosa* seedlings.

Materials and methods

Field study

The study was conducted at the University of Idaho Experimental Forest (46°52' N, 116°47' W), 52 km northeast of Moscow, Idaho, in a seral *Pinus ponderosa*–*Agropyron spicatum* community. A mature *P. ponderosa* overstory of approximately 50 trees per hectare dominated a bunchgrass understorey interspersed with shrubs and herbs. The soil was a Uvi-Spokane association (Barker 1981) silt loam approximately 0.5 m in depth overlying decomposing granite. Each spring, 30 newly germinated ponderosa pine seedlings were randomly chosen for study over two growing seasons in a homogeneous 1-ha area on a south-facing 15° slope.

Root exclusion tubes (Cook and Ratcliff 1984, Snaydon and Howe 1986, Reichenberger and Pyke 1990) were used to exclude bunchgrass roots to three soil depths and thereby modify the water availability for *P. ponderosa* seedlings. The root treatments, each of which was applied to ten seedlings, consisted of a control with no belowground manipulation (the full-root competition treatment), a partial-root competition treatment with a 0.15-m long by 0.1-m diameter stainless steel cylinder inserted around the seedlings, and a no-root competition treatment with a 0.30-m long by 0.1-m diameter tube inserted around the seedlings so that the cylinder rim was flush with the soil surface.

Seedling height, needle area, and mortality were monitored weekly over two growing seasons. Soil surface temperatures, air temperatures at 5 and 50 mm aboveground, seedling stem temperatures at 5 mm above the soil surface, and seedling needle temperatures were continuously measured with 0.07-mm copper-constantan (Type T) thermocouples connected to Campbell Scientific CR-21X and CR-10 microloggers. Thermocouples that measured air temperature were shaded with aluminum foil to avoid the effects of incident radiation. To measure seedling temperatures, thermocouples were hooked around seedling stems and needles and attached with a minute drop of contact cement. Soil surface temperatures were measured with thermocouples buried so that the junction was flush with the soil surface. Temperatures were

recorded at 2-s intervals and stored as 5-min maximum, minimum and average values from the end of June until mid-September. Three newly germinated seedlings from each root exclusion treatment were monitored each season; each seedling had one thermocouple attached to the stem 5 mm above the soil surface and three thermocouples (wired in parallel arrangement) attached to the needles. Soil water potential, temperature, and soil water content were monitored weekly on three sample sites at depths of 0.05, 0.3 and 0.5 m with soil psychrometers (Wescor Corp. PCT-55), which were installed in the soil at the beginning of the study, and by gravimetric analysis. Air temperature and relative humidity at 0.2 m above the ground were measured throughout the summer with a hygrothermograph (Bendix 594), which was periodically calibrated with an Assmann psychrometer. Stomatal conductance was measured monthly by enclosing the aboveground portion of a seedling in a cylindrical cuvette attached to an LI-1600 steady-state porometer (Li-Cor, Inc., Lincoln, NE). The Bonferroni *t*-procedure ($\alpha \leq 0.05$) was used to determine significant differences among root exclusion treatment means.

Greenhouse study

Shortly after germination, 25 *P. ponderosa* seedlings were planted in polystyrene cylinders (0.06 m in diameter by 1.0 m in length) filled with washed sand. Seedlings were exposed to a 12-h photoperiod provided by metal halide lamps that produced a combined lamp and sun irradiance of at least 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$. All containers were initially watered to saturation with a 500 ppm solution of N,P,K (20,20,20; w/w) fertilizer. Seedlings were monitored for root growth by randomly choosing one seedling every week and excavating the root system. After three weeks, when it was determined that seedling roots had penetrated the entire 1-m length of the container, 21 seedlings were each randomly assigned to one of three treatments, consisting of a surface water supply only (top one-third of the container), 0.25-m water supply only (middle-third), or 0.9-m water supply only (bottom-third). Rewatering occurred when stomatal conductance for the majority of seedlings declined to less than 30 $\text{mmol m}^{-2} \text{s}^{-1}$, a value that, as we had previously determined, was indicative of imminent seedling death. Stomatal conductance was measured twice each week through four drying cycles to determine the effects of age, drought stress, and depth to water source on seedlings. Hourly conductance measurements were made on 13 separate occasions during the drying cycles to determine the effects of drought stress on diurnal conductance. Differences between treatment means and diurnal fluctuations of seedling stomatal conductance were compared by the Bonferroni *t*-procedure ($\alpha \leq 0.05$) and linear regression analysis.

Calculations

Transpiration (E) was determined from the relationship:

$$E = g_{\text{wv}}(\rho_{\text{vs}} - \rho_{\text{va}}), \quad (1)$$

where g_{wv} is stomatal conductance to water vapor, ρ_{vs} is water vapor density at the leaf surface, and ρ_{va} is the water vapor

density of air (Larcher 1983, Campbell 1986, Nobel 1991). Vapor density was calculated according to Pearcy et al. (1989). The convective heat flux (q_s) in W m^{-2} to the seedling stem from the air was calculated from:

$$q_s = \rho_a c_p (T_s - T_a) (r_H)^{-1}, \quad (2)$$

where ρ_a is air density in kg m^{-3} , c_p is the specific heat of the air in $\text{kJ m}^{-3} \text{ }^\circ\text{K}^{-1}$, T_s is the seedling stem temperature in $^\circ\text{K}$, T_a is air temperature in $^\circ\text{K}$, and r_H is the resistance to heat exchange through free laminar convection. Resistance was calculated from:

$$(r_H) = d(0.54D_H(G_r(P_r)^{1/4}))^{-1}, \quad (3)$$

where d is stem diameter, 0.54 is a constant value for laminar free heat convection to cylinders, D_H is heat diffusivity of air in $\text{mm}^2 \text{ s}^{-1}$, G_r is the Grashof number, and P_r is the Prandtl number (Campbell 1986). Convective heat exchange to a seedling stem, which is essentially a cylinder with fluids moving through it, is not a linear function. Therefore, the logarithmic mean temperature of seedling stems was used to calculate q_s (Incropera and DeWitt 1985). Stem temperatures were calculated from:

$$T_x = T_i + (q_s'' dx) (mc_p)^{-1}, \quad (4)$$

where x is stem length, q_s'' is the logarithmic mean heat flux, d is the stem diameter, m is the flow rate of water through the stem (where $m = E(\text{total leaf area})$), c_p is the specific heat of water, T_i is the temperature of water entering the seedling stem (and was assumed to be equal to the soil temperature at a depth of 50 mm) and T_x is the temperature of xylem water at some point (x) along the seedling stem (Incropera and DeWitt 1985).

Results

Field study

Seedling shoots developed within 2 to 4 weeks of germination and had a mean of 5 ± 1 cotyledons, 33.5 ± 1.1 single juvenile needles, and a height of 0.08 ± 0.03 m. After this initial growth, and with the exception of an increase in stem diameter from 1 to 3 mm, seedling shoots showed no significant subsequent growth during the first growing season. Mean needle area during this period declined from $920 \pm 105 \text{ mm}^2$ to $530 \pm 75 \text{ mm}^2$ because cotyledons and needles closest to the soil surface senesced.

Aboveground temperatures at the site were highest between 1000 and 1600 h, with the greatest air temperature extremes being recorded 5 mm above the soil surface (Figure 1). Temperatures in excess of 75°C at this height were significantly greater than the maxima of 60°C at the soil surface, 45°C at a height of 0.05 m, and 39°C at a height 0.2 m aboveground. There were no significant differences in air temperature before 1000 h or after 1800 h. Air temperatures close to the soil surface fluctuated by as much as 15°C every 5 min during the periods of highest insolation, compared to variations of less

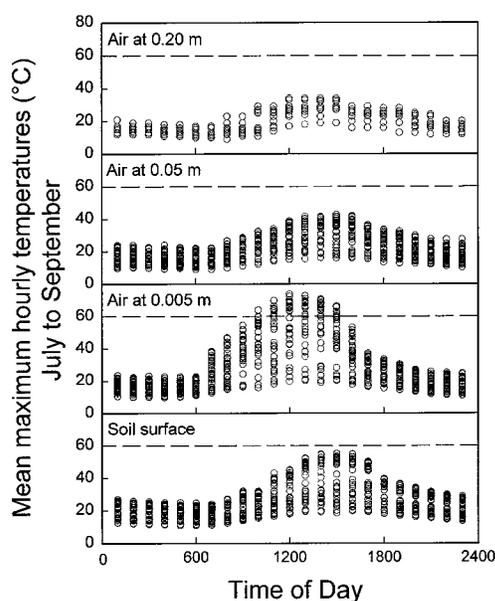


Figure 1. Maximum air temperature at different heights aboveground recorded hourly from mid-July until mid-September at the study site. Each point represents an hourly mean of 12 measurements for each day. Comparisons of daily temperature regimes among heights showed all were significantly different between 1000 and 1800 h during periods of high insolation. The air temperature at 5 mm aboveground was significantly higher than at other heights from 0700 until 1600 h, whereas the soil surface remained warmer until 1800 h. During periods with low solar radiation (cloudy days or evenings) no significant ($\alpha \leq 0.05$) differences among temperatures were found. The dashed line represents the temperature near the 1-min lethal threshold for *P. ponderosa* tissue (Seidel 1986).

than 5°C when solar radiation was lower. Belowground temperatures from July until September were less variable than aboveground temperatures, with means of $18.9 \pm 1.65^\circ\text{C}$ at a soil depth of 0.05 m, $17.8 \pm 0.9^\circ\text{C}$ at 0.25 m, and $17.6 \pm 0.8^\circ\text{C}$ at 0.5 m. Temperatures at these soil depths ranged from 16 to 32°C , 15 to 24°C , and 15 to 22°C , respectively.

Stem temperature trends for *P. ponderosa* seedlings were similar to those of the surrounding air, although significant differences ($\alpha \leq 0.05$) in maximum stem temperatures were observed among the root competition treatments (Figure 2). Seedlings in the no-root competition treatment had, on average, significantly lower stem temperatures than seedlings exposed to root competition. Similarly, seedlings in the partial-root competition treatment had, on average, lower stem temperatures than seedlings in the full-root competition treatment. During periods of maximum soil and air temperatures ($> 60^\circ\text{C}$), seedlings in the no-root competition treatment maintained stem temperatures as much as 20°C lower than the surrounding air. Although a few seedlings from the other two root competition treatments exhibited stem temperatures lower than the surrounding air, most seedlings did not. In all treatments, the only seedlings that survived had maximum stem temperatures of less than 63°C , which was the stem temperature observed to coincide with seedling death. Episodes of high temperature were correlated with mortality of seedlings not

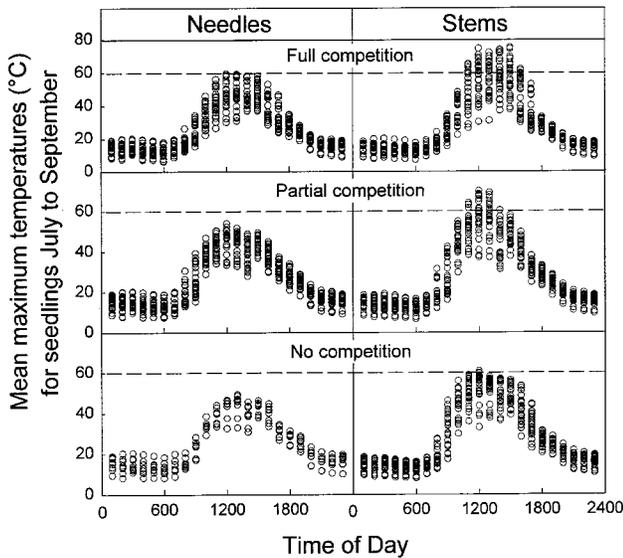


Figure 2. Maximum temperatures recorded hourly on stems and needles of six *P. ponderosa* seedlings for each treatment from mid-July until mid-September. Each point represents an hourly mean of 36 measurements for each day. No significant differences ($\alpha \leq 0.05$) in daily temperature regimes for needles among the three treatments were found. Stem temperatures differed significantly ($\alpha \leq 0.05$) among treatments between 1000 and 1600 h on days with high insolation. The dashed line represents the temperature near the 1-min lethal threshold for *P. ponderosa* tissue (Seidel 1986).

protected from root competition (Figure 3). All seedlings that died had low stomatal conductance and 80% of them had necrotic lesions on the first 10 mm of stem above the soil surface. Other visible indications of stress, such as needle browning, occurred after the appearance of stem lesions. However, seedlings that died with no visible stem lesions exhibited at least 30% needle senescence before death.

Needle temperatures were not significantly different among treatments ($\alpha \leq 0.05$), although means were higher for seedlings in the full-root competition treatment than for seedlings in the other root treatments. In contrast to stem temperatures, needle temperatures were usually higher than the surrounding air. For example, when air temperature reached a maximum of 45 °C during midday, maximum needle temperatures reached 60, 55 and 50 °C for seedlings in the full-root, partial-root and no-root competition treatments, respectively.

During periods of high insolation, stem and needle temperature fluctuations were similar to the air temperature fluctuations (Figure 4). Needle temperatures varied by as much as ± 20 °C every 5 min, whereas stem temperatures varied by ± 10 °C every 5 min. Diel fluctuations of the air temperature during the growing season averaged ± 30 °C at 50 mm and ± 45 °C at 5 mm aboveground.

Seedlings that survived the summer had higher stomatal conductances throughout the growing season than seedlings that died. Mean stomatal conductance of seedlings in the no-root competition treatment was 50% higher than that of seedlings exposed to full-root competition (Figure 5); however, the mean stomatal conductance of surviving seedlings

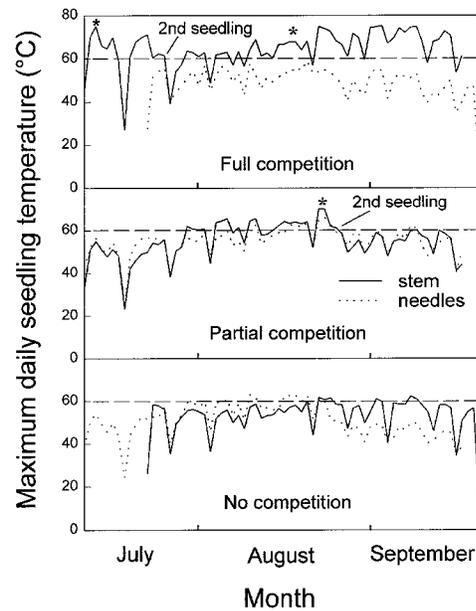


Figure 3. Maximum daily temperatures for a representative seedling from each treatment. The asterisk indicates when the seedling died. Thermocouples on seedlings that died were transferred to a live seedling in the same treatment as indicated. After the second seedling exposed to full-root competition died, no additional transfer was made. The seedling not exposed to competition remained alive throughout the growing season. The dashed line represents the temperature near the 1-min lethal threshold for *P. ponderosa* seedlings (Seidel 1986).

exposed to root competition was not significantly different from that of seedlings in the no-root competition treatment. The absolute water vapor density of the air remained relatively stable at 7.35 ± 1.17 g m⁻³ from July to September, resulting

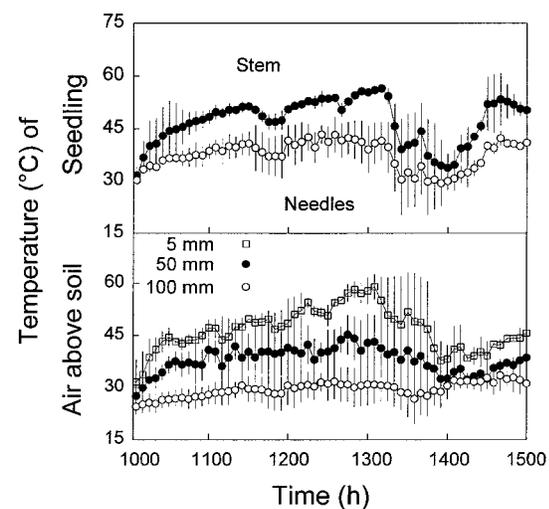


Figure 4. Temperature fluctuations for one mid-August day were typical of the temperatures observed during the summer at the University of Idaho Experimental Forest study site. Mean (symbol), maximum, and minimum (bars) temperatures recorded for one *P. ponderosa* seedling compared to the temperature profile of the air.

in water vapor density deficits that varied with diurnal temperature fluctuations from 3 g m^{-3} during the coolest daily periods to 65 g m^{-3} during the hottest periods. Transpiration rates, calculated from measured stomatal conductance and needle temperatures, reached a maximum of $16.7 \text{ mmol m}^{-2} \text{ s}^{-1}$ when needle temperature was $60 \text{ }^\circ\text{C}$, compared with $6.7 \text{ mmol m}^{-2} \text{ s}^{-1}$ when needle temperature was $35 \text{ }^\circ\text{C}$ (see Figure 5).

Greenhouse study

Maximum and minimum stomatal conductances of greenhouse-grown seedlings were similar to stomatal conductances for naturally established seedlings. Increasing seedling age and drought stress coincided with significantly decreased stomatal conductance (Figure 6). Stomatal conductance values below $20 \text{ mmol m}^{-2} \text{ s}^{-1}$ preceded seedling mortality. The addition of water to drought-stressed seedlings resulted in an increase in stomatal conductance within 24 h. Stomatal conductance and its rate of increase after drought stress was not significantly affected by the depth of the soil water source. Hourly measurements of stomatal conductance from 0600 until 2000 h showed a significant linear decrease of 20% with no significant midday fluctuations. Drought stress had no observed effect on the diurnal pattern of stomatal conductance, although the daily mean for each seedling decreased significantly (Figure 7).

Modeled results

Our calculations showed that xylem water flow through seedling stems is an effective heat transfer mechanism for seedlings with high transpiration rates and narrow stem diameters. As predicted by the heat exchange equation (Equation 4), increased water flow, m , which occurred when transpiration

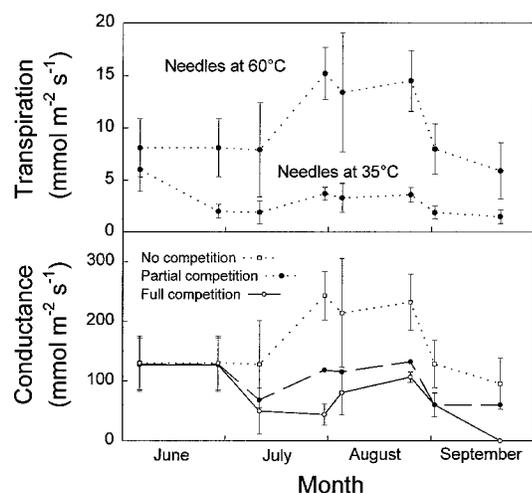


Figure 5. Mean stomatal conductance for seedlings exposed to three intensities of root competition (bottom graph). The effect of elevated needle temperatures on transpirational water loss is shown in the top graph of calculated transpiration for seedlings with no root competition. Each point represents the mean of 20 samples. Vertical bars represent ± 1 SE of the mean.

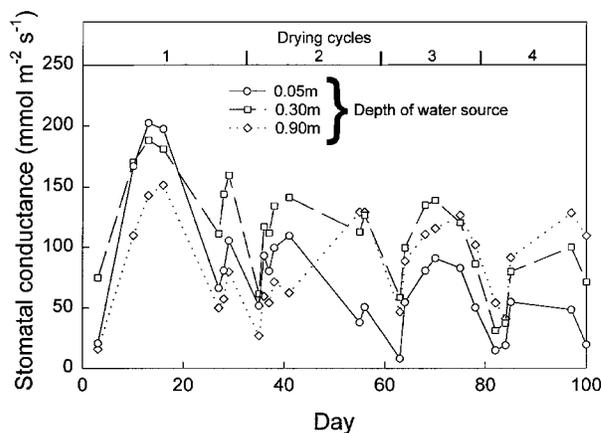


Figure 6. Mean stomatal conductance for each of three treatments watered at three distinct depths within the containers. Watering occurred when the majority of seedlings reached stomatal conductances $\leq 30 \text{ mmol m}^{-2} \text{ s}^{-1}$. Stomatal conductance did not differ significantly ($\alpha \leq 0.05$) among the three treatments. Each point represents the mean of seven samples, with ± 1 SE of between 20 and 50 $\text{mmol m}^{-2} \text{ s}^{-1}$ of the mean.

increased, caused temperature along the stem, T_x , to decrease (Figure 8). In addition, a lower initial water temperature, T_i , which in this case was assumed to be equivalent to the soil temperature, resulted in more energy absorbed before $T_i = T_x$. Stem diameter also determined the heat exchange efficiency of the seedling stem (see Figure 8). We assumed that the xylem water flow rate was not influenced significantly by stem diameter: the predominant driving mechanism for water flow in the model is transpiration from the seedling needles. Calculated water flow through the stem of a seedling (0.324 g h^{-1} for a transpiration rate of $6.7 \text{ mmol s}^{-1} \text{ m}^{-2}$) did not exceed the volume of water expressed between 0 and -2 MPa from seedlings used in pressure-volume analysis (Kolb and Robberecht

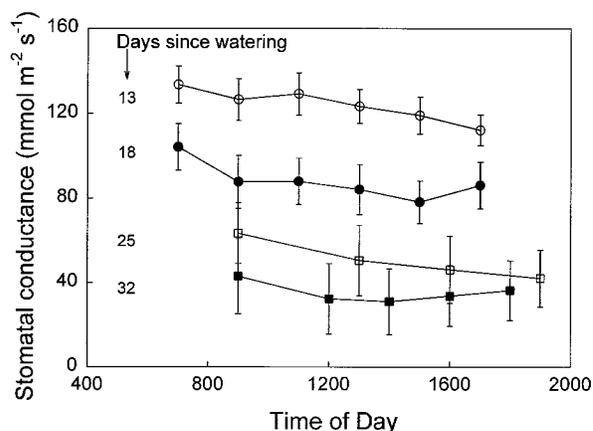


Figure 7. Effect of drought on diurnal variation in stomatal conductance for greenhouse-grown seedlings measured over four weeks of increasing drought. Each symbol represents the mean of 21 seedlings and different symbols correspond to measurements from different days. For clarity, only four out of the 12 days measured are represented on the graph. Vertical bars represent ± 1 SE of the mean.

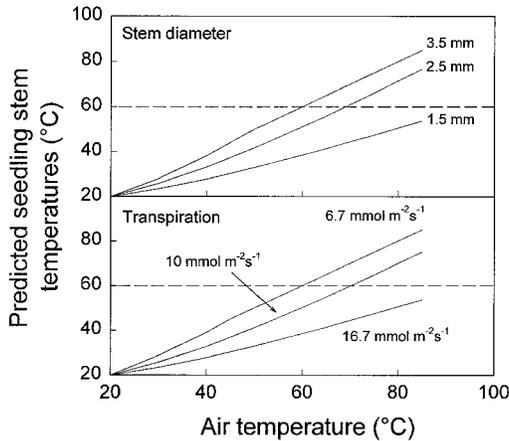


Figure 8. Models of seedling stem temperature based on free-convective heat exchange with the surrounding air, and changes in transpiration rate or seedling stem diameter. The upper graph assumes a constant transpiration rate of $16.7 \text{ mmol m}^{-2} \text{ s}^{-1}$. The lower graph assumes a constant stem diameter of 1.5 mm. Both graphs assume a seedling needle area of 750 mm^2 . The dashed line on each graph represents the temperature near the 1-min lethal threshold for *P. ponderosa* seedlings (Seidel 1986).

unpublished data). The model predicts that increased stem diameter and the proportionate increase in surface area result in increased energy absorption for the same flow rate and heat absorption capacity. Large stem diameters are therefore predicted to be less efficient at heat exchange than small stem diameters, unless the flow rate also increases. Seedlings in the field exhibited diameter growth during the summer without an increase in needle area. Modeled results showed that a seedling with a stem diameter of 1.5 mm needs a minimum transpiration rate of $6.7 \text{ mmol m}^{-2} \text{ s}^{-1}$ to maintain a stem temperature lower than the surrounding air, assuming free convection and a T_i equivalent to a soil temperature of 20°C . At the maximum transpiration rate of $16.7 \text{ mmol m}^{-2} \text{ s}^{-1}$ calculated for seedlings under field conditions, a seedling would be able to maintain a stem temperature 30°C less than the temperature of the surrounding air in the first 10 mm stem segment above the soil surface. Similarly, assuming a maximum transpiration rate, an increase in stem diameter will reduce this cooling capacity to 10°C per 10 mm stem segment at a diameter of 2.5 mm and to 2°C per 10 mm at a diameter of 3.5 mm.

Discussion

Temperatures in excess of 55°C for short durations can cause irreversible tissue damage to plants (Baker 1929, Daubenmire 1943, Raschke 1960, Lange and Lange 1963, Levitt 1980, Kappen 1981, Larcher 1983, Seidel 1986, Weis and Berry 1987, Colombo and Timmer 1992). We recorded soil surface temperatures near 75°C during August at the study site. Similar temperatures have been recorded in many temperate locations and correlated with low seedling survival in a variety of plant species (Lange 1959, Lange and Lange 1963, Kappen 1981, Hålgren et al. 1991). On sites exposed to high insolation,

tree seedling mortality has been observed to occur from heat lesions to the narrow strip of bark around the stem base and to the cotyledons (Baker 1929, Levitt 1980, Hålgren et al. 1991). In our study, *P. ponderosa* seedlings exposed to drought stress in the full-root competition treatment showed similar stem damage and rapid senescence of the cotyledons, whereas seedlings protected from root competition did not develop stem lesions, suggesting that increased water availability may be associated with either increased tolerance to or avoidance of heat stress or both.

Mechanisms for avoidance of high temperatures include those that reduce the amount of solar radiation absorbed by the plant and processes that consume or dissipate energy to lower the heat load (Kappen 1981). High stomatal conductance, which allows for more rapid transpiration, may be the primary mechanism for avoiding heat damage in *P. ponderosa* seedlings. Transpiration can dissipate up to one-quarter of the heat absorbed by plant leaves (Raschke 1960, Lange and Lange 1963, Gates 1965, Thofelt 1975, Gates 1980, Levitt 1980, Kappen 1981, Larcher 1983). Although mean needle temperatures did not differ significantly among the three treatments, needles of seedlings that had higher stomatal conductance were slightly cooler. Because the narrow needles of *P. ponderosa* have a relatively thin boundary layer and a low heat storage capacity, the effectiveness of convective energy exchange with the surrounding air may have reduced the effect of cooling from latent heat exchange. A high transpiration rate indirectly cooled seedling stems, however, by increasing the rate of water flow through the stem xylem. Because the majority of the seedlings appeared to die from temperature-induced lesions to the lower stem, we suggest that heat transfer is the primary mechanism by which *P. ponderosa* seedlings avoid heat stress.

The temperature of the soil water absorbed by seedling roots averaged about 50°C less than the temperature of the soil surface at midday. Thus, the soil water had a large capacity for energy absorption before reaching temperatures lethal to seedling tissue. In addition, increased water flow through seedling stems at midday would have significantly increased the amount of energy that stems could absorb without increasing stem temperatures to beyond the lethal threshold. This conclusion is supported by the calculated and measured energy exchange rates for seedlings with high stomatal conductance. Increases in needle area and stem diameter also affected cooling efficiency. Naturally occurring *P. ponderosa* seedlings had narrow stem diameters (1 to 3 mm) in relation to their total needle area of approximately 750 mm^2 , a characteristic that is necessary for maintaining low stem temperatures. Differences in the ratio of needle area to stem diameter may have accounted for the 5°C difference in stem temperatures measured in the field between seedlings that survived and those that died.

Realization of the theoretical maximum cooling of 30°C would depend on the ability of seedlings to extract sufficient soil water to permit high transpiration rates and to keep stomatal conductance high at high temperatures. Under both greenhouse and field conditions, *P. ponderosa* seedlings develop an extensive root system and low water potentials (Kolb and Robberecht, unpublished data) and thus have access to a large proportion of the water in a large volume of soil extend-

ing to a depth of at least 1 m. Because stomatal conductance generally decreases with increasing evaporative demand (Kramer 1969, Jarvis 1980, Ludlow 1980, Larcher 1983, Nobel 1991), *P. ponderosa* seedlings should have reduced stomatal conductance during midday periods when temperatures and evaporative demand are highest (Running 1984). However, we were unable to detect significant daytime variation in stomatal conductance, regardless of the degree of drought stress or the depth to a water source. High midday temperatures and the associated increase in evaporative demand allowed high transpiration rates to occur. Seedlings in which transpiration was restricted by low soil water availability would have had only a limited capacity for stem cooling and so would have been more susceptible to heat stress.

Although increased transpiration in response to increased temperature and the associated high vapor density deficit is contrary to the concept that stomata regulate plant water loss (Jarvis 1980, Ludlow 1980), the phenomenon has been observed in other plant species. Leaves subjected to high temperatures exhibit rapid increases in transpiration once a threshold temperature is reached, regardless of other environmental stimuli that normally affect stomatal aperture (Gates 1965, Brunner and Eller 1974, Thofelt 1975, Levitt 1980, Kappen 1981). Increases in transpiration rate of up to 400% for a 10 °C increase in temperature have been measured (Gates 1965). The high temperatures associated with forest fires have also been shown to increase the rate of xylem water transport by as much as 500 times the normal rate (Cohen et al. 1990, Cohen and Omi 1991). Based on infrared photography, Thofelt (1975) found that injured portions of leaves were cooler than surrounding leaf tissue and concluded that water transport through the leaf vascular system was a significant means of heat dissipation and transfer.

We conclude that the survival of *P. ponderosa* seedlings on hot dry sites depends primarily on their capacity for heat dissipation through rapid transpiration (Bates 1923, Daubenmire 1943, Daubenmire 1968, Harrington and Kelsey 1979, Jackson and Spomer 1979, Vance and Running 1985, Shainsky and Radosevich 1986, DeLucia et al. 1988, DeLucia and Heckathorn 1989, DeLucia and Schlesinger 1991). Both rapid development of a deep taproot, and the capacity for low plant osmotic potentials facilitate the acquisition of water under dry conditions. The ability to maintain a high stomatal conductance at high temperatures promotes transpirational heat dissipation when the danger of heat stress is greatest. A high leaf area to stem diameter ratio allows effective stem cooling through heat flow in the transpiration stream. It is by virtue of this combination of morphological and physiological characteristics that *P. ponderosa* is able to colonize hot and dry forest sites.

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