Plant Physiol. (1980) 65, 635–640
0032-0889/80/65/0635/06/$00.50/0

Soil Temperature Influences on Root Resistance of *Pinus contorta* Seedlings[1]

Received for publication June 8, 1979 and in revised form October 31, 1979

STEVEN W. RUNNING AND C. PATRICK REID
Department of Forest and Wood Sciences, Colorado State University, Fort Collins, Colorado 80523

ABSTRACT

The influence of low temperature in the root zone on water uptake in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) was studied under laboratory conditions. To remove soil hydraulic influences, two-year-old seedlings were transferred to solution cultures and maintained in temperature controlled water baths. Short term measurements of leaf conductance, leaf water potential and tritiated water movement were taken at root temperatures from 22 C down to 0 C. Root resistance was calculated to be 67% of total plant resistance at 7 C and 93% at 0 C. In addition an Arrhenius break was found in a plant resistance *versus* temperature plot, suggesting a significant change with temperature in the membrane pathway in the root water uptake system.

There has been wide documentation of the influence of Ψ_l[2] on stomatal or k_l. Water-limited western conifers exhibit significant stomatal control triggered by Ψ_l (8). Consequently, recent efforts to model water movement and transpiration in trees have spent considerable effort in developing functions relating Ψ_l to k_l (14, 23).

However, a useful process model of tree water movement cannot rely on collected Ψ_l data, but must be able to predict Ψ_l over a wide range of conditions. Equations such as

$$\Psi_l = \Psi_s - qR - \rho gh \quad (1)$$

where Ψ_l and Ψ_s are leaf and soil water potential, q is total water flow through the plant, R is total plant resistance, and ρgh is the hydrostatic gradient, are useful for dealing with small plants with very little capacitance. They are inadequate for larger trees, because it is not possible to measure q, and prediction of q requires k_l which in a process model requires Ψ_l. Also, sapwood capacitance produces hysteresis in the Ψ_l *versus* q relation (24). Predictions of Ψ_l must be accomplished by defining the individual factors that produce it, and coupling these in the process model. In equation 1, R, total plant resistance, is one factor that must be separated. Much work has been done measuring stomatal resistance (8). Considerably less work has been reported on resistance to flow in the xylem, or hydraulic conductivity (7, 24). Study of root resistance has progressed at two levels of resolution, cellular level work (6, 17) and inferences of root resistance from whole plant studies (5, 9, 10). Root resistance changes are normally a function of soil water potential (Ψ_s) and/or soil temperature, disregarding morphological development such as degree of suberization, and factors such as aeration and root disease. This paper will concentrate on the effect of temperature on root resistance to water transport in the context of whole plant water relations.

The primary objective was to develop a functional relation between soil temperature and root resistance for *Pinus contorta* that was compatible with process modeling efforts of tree water movement (23). To isolate root resistance as the component of plant resistance responding to soil temperature, these water uptake experiments were performed on seedlings in aerated solution culture so there could be no complications caused by soil hydraulic conductivity. In addition, underwater root excision was used to determine the proportion of total water potential drop generated at the root surface. Finally, by comparing seedlings from a greenhouse and a 2 C cold room, influences of preconditioning on root resistance were examined.

MATERIALS AND METHODS

Two-year-old lodgepole pine (*P. contorta*) seedlings from the Colorado State Forest Service nursery at Fort Collins were individually transplanted into 2-liter cans and placed in a greenhouse in September 1977. In January 1978, 12 seedlings were moved to an illuminated cold room at 2 C for 3 months. Although shoots remained dormant under both treatments, roots grew and occupied the increased soil volume. Root uptake studies began in March.

Because an important part of this study required following root water uptake and HTO entry into the seedling precisely, seedlings were removed from the cans and all soil was carefully rinsed away from the root systems. Seedlings were then placed in blackened 2-liter jars in aerated 0.25× Hoagland nutrient solution. Pulses of HTO were administered by transferring the seedling to an identical jar with an aerated nutrient solution of 10 mCi HTO (5 μCi/ml) for the specified period, then rinsing and returning to the original jar. The jars were maintained in a water bath with an immersed cooling coil system allowing water bath temperature control (±0.5 C) from ambient to 0 C. Root temperature was controlled by changing the rate of coolant flow through coils in the water bath.

The above assembly was maintained in a growth chamber with temperature, humidity, and photoperiod control. Unless otherwise stated, growth conditions were: air temperature, 19 ± 0.5 C day, 10 C night; RH, 25 ± 5%; PAR, 85 wm^{-2}; and a photoperiod of 16 h. IR thermometer measurements showed leaf temperature to vary less than ± 0.5 C from air temperature. All tests were performed on a given seedling within 1 week of entry into the growth chamber.

A null balance diffusion porometer (1) was used to measure k_l, transpiration rate, and as a collection apparatus for the transpired HTO vapor. A 70-cm long tube connected the cuvette to the 250-ml volume ionization chamber attached to a Cary model 32 vibrating reed electrometer.

[1] This work was funded by McIntire-Stennis Project No. 5333 through Colorado State University, National Science Foundation Grant DEB 78-05311 to Dr. Dennis Knight at the University of Wyoming, and the Forest and Mountain Meteorology Project of the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

[2] Abbreviations: Ψ_l: leaf water potential; k_l: leaf conductance; TFD: transpiration flux density

In conjunction with HTO measurements, sample twigs were allowed to transpire into the sealed cuvette for 1 min before water vapor was drawn into the evacuated ionization chamber. Relative transpiration rates were recorded by noting the increase in humidity, ΔRH, within the cuvette during the first 20 s. A regression of the ΔRH on measured leaf conductances ($R^2 = 0.86$) provided a k_l estimate at every sampling period. TFD was obtained by:

$$TFD = ABSHD \times k_l \quad (2)$$

where TFD is in $\mu g\ cm^{-2}\ s^{-1}$, ABSHD is absolute humidity deficit in $\mu g\ cm^{-3}$, and k_l is in $cm\ s^{-1}$. Leaf samples in the cuvette, whose transpiration rates were directly measured, averaged 27% of the total leaf area of each seedling.

An HTO sample was obtained by evacuating the ionization chamber to 0.03 MPa atmospheric pressure, then drawing a gaseous sample from the cuvette. Radioactivity in the sample was measured by the "rate of charge" electrometer output on a strip chart. Because radioactivity is a direct function of charge increase in the "rate of charge" method, relative radioactivity was measured by computing slope changes on the output graph. This system gave a completely nondestructive measure of soft beta HTO radioactivity, and monitored radioactivity from transpiration of an entire twig.

Ψ_l was estimated from single fascicles measured in a Scholander pressure chamber under a dissecting microscope.

Leaf area of the cuvette samples for k_l and transpiration measurements were determined by measuring length and diameter of each fascicle and calculating the area geometrically. Upon completion of tests, each seedling was separated into leaf, stem, and root biomass, dried at 70 C, and weighed. In addition, the diameter and length of the stem was measured to aid in estimating internal water storage volume.

The testing schedule typically involved transplanting two seedlings into jars in early afternoon and setting the water bath control. The following morning, the HTO pulse was administered beginning at 0800, 3 h into the photoperiod. The seedlings were monitored all day, with transpiration and radioactivity samples taken every 15 min for the first 2–3 h, then at 0.5- to 1.0-h intervals for the rest of the day. At the end of the photoperiod (2100), the water bath temperature was set to the next lower temperature and the routine repeated the following day. Null balance k_l measurements were taken approximately every 2 h during the day. Pressure chamber data were taken two to three times per day because the seedlings were too small to withstand more frequent loss of fascicles.

On some seedlings, the root system, stem, then branch were sequentially excised under water to determine the distribution of water flow resistances in the seedlings. After each excision, the remainder of the seedling was monitored for 1 h recovery of Ψ_l and k_l.

RESULTS

Study of water movement through seedlings required analysis of both biomass distribution and exchangeable water storage in each sample. Complete water relations tests were run on six *P. contorta* seedlings, four from the greenhouse and two from the cold room. Table I presents oven dry weights of the roots, stem, and leaves of the six seedlings, expressed as total biomass, and per cent of total in roots, shoots, and leaves. Note that over 50% of the biomass in these seedlings was in leaves, with the rest evenly divided between stems and roots.

Of greater utility were calculations of exchangeable water in each seedling. Fresh volume, V_f, was calculated from stem diameter and length measurements. Once dried and weighed, the specific gravity of the stem was calculated. Then using the equation

$$V_{H_2O} = V_f(1 - SG/1.53)\ (0.8) \quad (3)$$

Table I. *Biomass and Water Storage of Lodgepole Pine Seedlings Studied*

Seedling	Biomass		Total Leaf Area	Available Water	
	Total	Root/Stem/Leaf		Total	Root/Stem/Leaf
	g		*cm²*	*g*	
1G[a]	5.18	0.16/0.30/0.44	360	13.8	0.36/0.38/0.26
2G	6.54	0.30/0.17/0.53	597	17.3	0.42/0.26/0.32
3G	7.60	0.38/0.15/0.46	540	21.2	0.50/0.24/0.26
4G	6.39	0.23/0.24/0.53	714	16.5	0.33/0.35/0.32
5C	6.58	0.15/0.16/0.69	764	13.9	0.26/0.23/0.51
6C[b]	7.33	0.30/0.15/0.55	784	18.6	0.43/0.32/0.35
% of total		27/ 20/ 53			40/ 27/ 33

[a] G: greenhouse pretreatment.
[b] C: cold room pretreatment.

where V_{H_2O} is the volume of available water in cm^3 of the fresh tissue whose volume is V_f in cm^3, SG is the specific gravity of the sample, 1.53 is a general density of cellulose and lignin (20, 22), and 0.8 is the coefficient of available water (24), the volume of water in the stem was obtained. Oven dry weights were measured for the root systems of each seedling. We assumed the roots to have a similar specific gravity to that measured for the stems (0.2 ± 0.03 SD). Fresh volume of the root system was calculated as dry weight divided by this specific gravity. Use of equation 3 provided exchangeable root water. Air-drying curves of needle water content *versus* Ψ_l suggested that 60% of total needle water was extractable from 0 to −0.4 MPa (1a). Therefore, exchangeable leaf water was calculated as (fresh weight − dry weight) × 0.6. Table I shows that total exchangeable water averaged 16.9 g, distributed 40% in roots, 27% in stems, and 33% in leaves. Although some of these measurements and calculations, particularly those defining exchangeable water, are imprecise, these values should represent a probable maximum for seedling water volume.

Continuous estimates of seedling transpiration were required to interpret HTO movements and plant resistance changes. Figure 1 shows the diurnal pattern of leaf conductance in a seedling at three different root temperatures. In general, k_l between root temperatures of 10–20 C differed only slightly, however, Ψ_l changed markedly as will be discussed later. The k_l at 2 C root temperature was 65% lower than k_l at 20 C.

Also of interest was the continual drop in k_l throughout the day despite constant evaporative demand. This most likely resulted from the low humidity (25%) affecting guard cell turgor (12). The general slope of reduction was similar regardless of initial k_l or Ψ_l, suggesting that the control mechanism was not tightly coupled to the normal xylem leaf mesophyll water pathway. Also in data not shown from seedlings studied at a lower absolute humidity deficit the slope of k_l reduction was more gradual, again regardless of initial k_l or Ψ_l.

The time course of radioactivity in a seedling is shown in Figure 2. Traces are shown for a 0.5-h pulse at 19 C root temperature, a 1.0-h pulse at 9 C root temperature, and a 1.5-h pulse at 2 C root temperature. The plotted points are from the ionization chamber vibrating reed electrometer, calculated as the difference between slopes of the background and test accumulated charge rates.

The most interesting properties of the HTO pulse were the rate of movement, best measured by the first arrival of HTO after the pulse, and total residence time. Above root temperatures of 9 C, the HTO arrival time was directly correlated with seedling transpiration rate and total available water. Typically, the arrival time was 2.5–3.0 h as shown in Figure 2 at both 19 and 9 C root temperatures. As root temperature approached 0 C, the HTO arrival time lagged farther behind the expected arrival time. This can be explained if transpiration was being satisfied in part by internal plant storage, a likely possibility if xylem water potentials decreased. However, at the levels of Ψ_l attained, −1.0 to −1.2

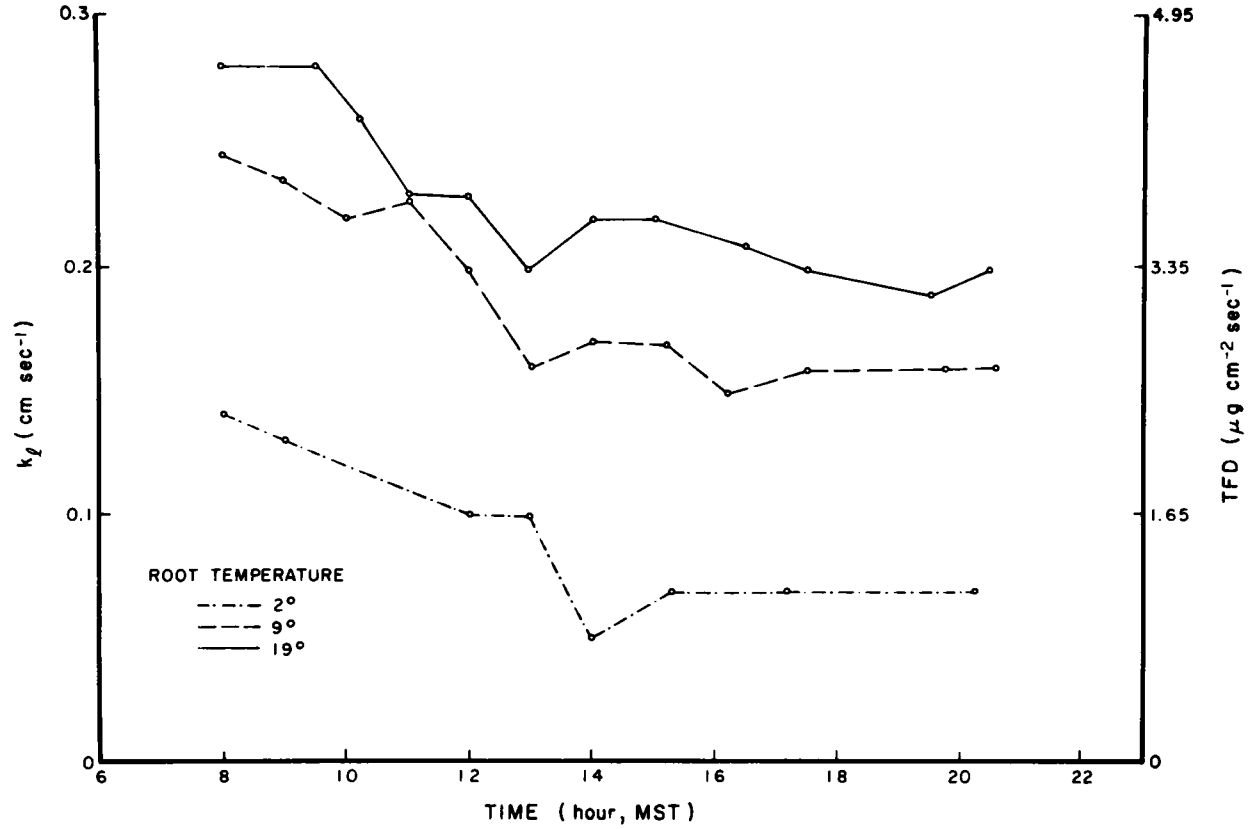

FIG. 1. Diurnal course of leaf conductance, k_l, and TFD of a lodgepole pine seedling at three root temperatures. Daylength = 0500-2100, air temperature = 24 C, RH = 25%.

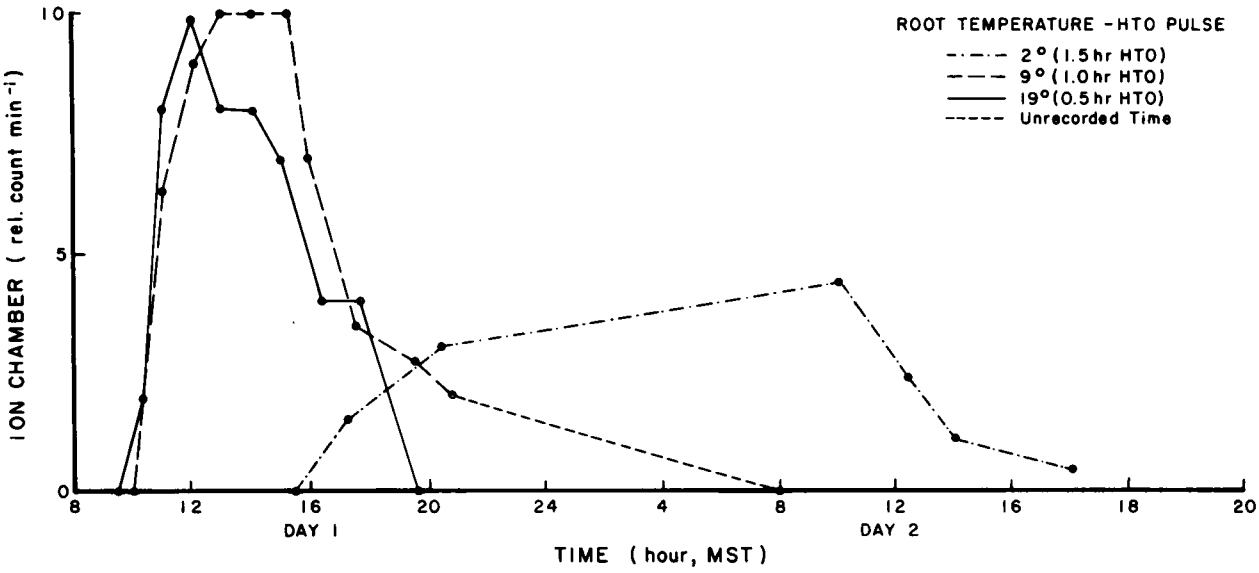

FIG. 2. The diurnal course of HTO radioactivity in a lodgepole pine seedling at three root temperatures, measured by an ionization chamber-vibrating reed electrometer. 10 mCi HTO (5 μCi ml^{-1}) was added at 0800, 3 h after onset of photoperiod, for designated period.

MPa, only a maximum of 0.5 h transpiration was possible from this source, as demonstrated by removing the seedling from water and monitoring transpiration and Ψ_l reduction. Of equal or greater possible importance was the slow movement of the HTO through the plant allowing additional mixing and causing a concentration drop in the front of the HTO pulse, therefore, requiring more time until detectable levels were reached.

The total residence time of the HTO pulse was also variable. In Figure 2 the 0.5-h HTO pulse at 19 C root temperature took 9.5 h to pass through the plant. During this time the equivalent of five and one-half times the total exchangeable water in the plant was transpired. The 1.0-h pulse at 9 C was in residence for 11 h during which time transpiration was four and nine-tenths times total plant water. Pulse residence times below 10 C root temper-

atures were much longer and were often difficult to delineate because of the lower HTO concentrations. However, for all seedlings at any root temperature, transpiration between three and six times total exchangeable plant water was required to reduce HTO to background levels. Data of Kline *et al.* (11) showed that injected HTO pulses in 20-m tall *Pseudotsuga menziesii* required similar turnovers to flush HTO from their transpiring streams. This demonstrates high exchange of water in the seedling water transport system.

Regardless of root temperature, Ψ_l recovered to −0.2 MPa within 2 h after the growth chamber lights went off each night, with the rooting solution near 0.0 MPa. Conversely, each morning, Ψ_l dropped to a constant level within 2 h and remained constant throughout the day primarily because of the constant evaporative demand in the growth chamber. However, as root temperature dropped, Ψ_l dropped, even while producing progressively lower transpiration rates. The slope of $\Delta\Psi_l$/TFD became progressively more negative as root temperature decreased (Fig. 3). Transpiration rates did not decline significantly until root temperature dropped below 10 C. However, even above 10 C, $\Delta\Psi_l$ changed with root temperature.

After monitoring Ψ_l and TFD for one day at 0 C root temperature the roots were excised under water to determine their contribution to the total plant-water relations. Within 10 min, Ψ_l recovered from −1.05 to −0.27 MPa (Fig. 3), representative of other seedlings tested. In all seedlings, k_l also recovered dramatically. Recovery of k_l would be from one and one-half to five times the original k_l before excision but never returned to levels attained at 20 C root temperatures under "no" stress. However, excised seedlings were only measured for 2–3 h after cutting and it is well documented that although Ψ_l of stressed trees can recover rapidly, k_l responds much more slowly. This has been attributed to residual ABA activity (2, 13).

To assess the apparent changes in root resistance shown in Figure 3, total plant resistance was calculated and plotted against root temperatures (Fig. 4) using the equation:

$$R = \frac{\Psi_l - \Psi_s}{TFD} \quad (4)$$

where R is total plant resistance in MPa g^{-1} cm^{-2} s^{-1}, Ψ_l and Ψ_s are leaf and substrate water potentials, the TFD is transpiration flux density in g cm^{-2} s^{-1}. Use of this equation assumed: (*a*) substrate Ψ to equal 0; (*b*) TFD to be representative of whole foliage transpiration rates, and (*c*) an inelastic system with no capacitance. Assumption *a* is reasonable with roots in a solution culture, and *b* is reasonable because one-quarter of the foliage was measured in the cuvette. Assumption *c* becomes more inaccurate as Ψ_l decreases, but should be no more than 20% in error at the lowest root temperature under these conditions with small seedlings (19).

Within the scatter of the points, R_{plant} was virtually constant above 7 C root temperature. Below 7 C, R_{plant} increased exponentially, considerably beyond water viscosity increases. To analyze

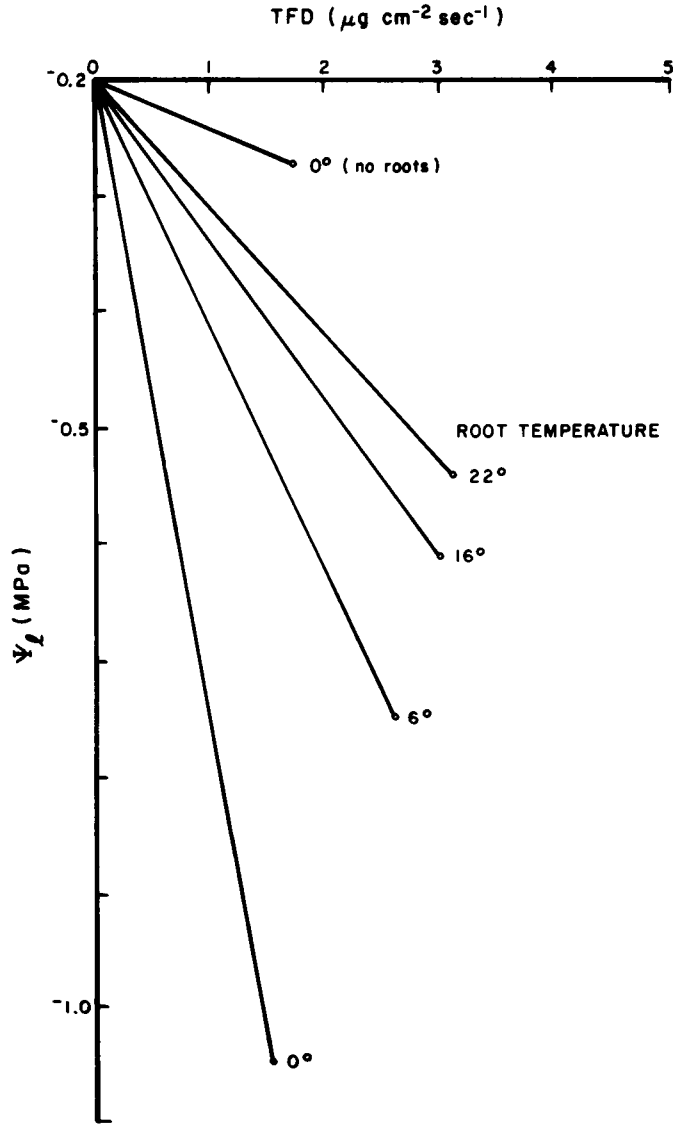

FIG. 3. Plot of TFD *versus* leaf water potential, Ψ_l, at four root temperatures, and at 0 C with the roots excised, for a lodgepole pine seedling.

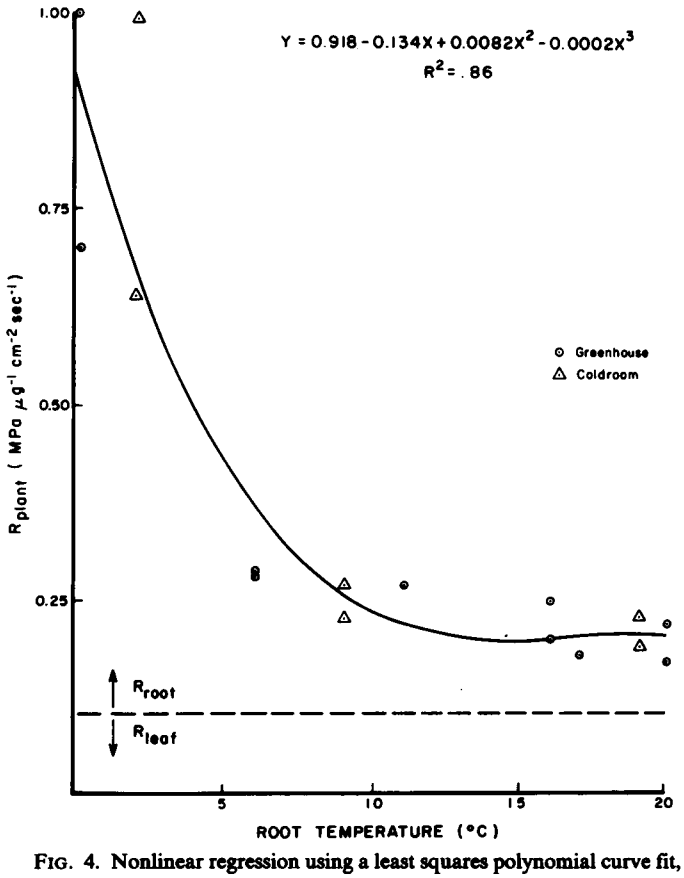

FIG. 4. Nonlinear regression using a least squares polynomial curve fit, of total plant resistance, R_{plant}, on root temperature for all seedlings tested. Area above dashed line represents root resistance. Seedlings were preconditioned in a greenhouse environment (⊙) or at 2 C (△).

the contribution of the root system to R_{plant}, total R was calculated for a number of seedlings with excised roots. Above 7 C root temperature, R of the whole plant minus the root system averaged 33% of the intact R_{plant}. We would argue that at root temperatures below 7 C, k_l and transpiration would remain constant if leaves could obtain water from the roots. If this is true, the entire area above the dotted line in Figure 4 represents the contribution of root resistances for these small seedlings under constant evaporative demand. At 0 C, root resistance would be 93% of total R_{plant} using the regression shown.

By progressively excising the root, stem, and twig, and monitoring Ψ_l of the remaining tissue, Ψ development progressed as shown in Figure 5.

DISCUSSION

The abrupt change in root resistance suggested in Figure 4 below about 6 C may be the result of phase transition of lipids in the root membranes associated with water transport (15, 21). An Arrhenius plot of the data in Figure 4 (Fig. 6) shows a marked similarity to Arrhenius plots of other studies. Clarkson (3) found a similar abrupt break in the Arrhenius plot of sap exudation in detached roots of rye at 10 C. When preconditioned at lower temperatures for 3 days, the break point was at 5 C. Similarly, Markhart *et al.* (16) found an Arrhenius break at 14.7 C in soybean roots that shifted to 8 C when preconditioned at a lower temperature. They also found no break in broccoli, a chilling resistant species. In this study there appeared to be no preconditioned response. In Figure 6, the points from seedlings grown for 3 months in a 2 C cold room and in a greenhouse are shown. Data for plants from the cold room appear well within the scatter of points from seedlings from the greenhouse.

Given that broccoli shows no Arrhenius break, it is surprising that a high elevation conifer like lodgepole pine shows chilling sensitivity. Data for Engelmann spruce (5, 9) also show an abrupt change in R_{plant} beginning around 7–8 C soil temperature. All these studies suggest the importance of a membrane barrier in water movement from the root epidermis to the xylem (17). Corroborative evidence is suggested in that intact dead roots show no Arrhenius break (16). It was not clear how rapidly reversible this membrane phase transition was. When root temperatures were allowed to rise from 0 to 10 C overnight, Ψ_l recovered by at least 0.3 MPa by the next morning. It is difficult to determine without detailed biochemical analysis whether this continued stress effect is the result of residual ABA inhibiting stomatal opening (2) or unreversed membrane solidification in the root system due to the previous chilling. Models of root water uptake have been developed from the general equation:

$$J = L(\Delta P - \sigma\Delta\pi) \quad (5)$$

where J equals water flow in $cm^3\ cm^{-2}\ s^{-1}$, L is hydraulic conductivity in $cm^3\ cm^{-2}\ s^{-1}\ bar^{-1}$, ΔP is the pressure gradient in bars, σ is the dimensionless reflection coefficient, and $\Delta\pi$ is the osmotic driving force in bars (4, 6). In these theoretical models, L, the membrane filtration coefficient is often related only to water viscosity. To be generally applicable these models must also take into account the abrupt changes in L suggested by the data in this paper if used under these conditions for chilling susceptible species.

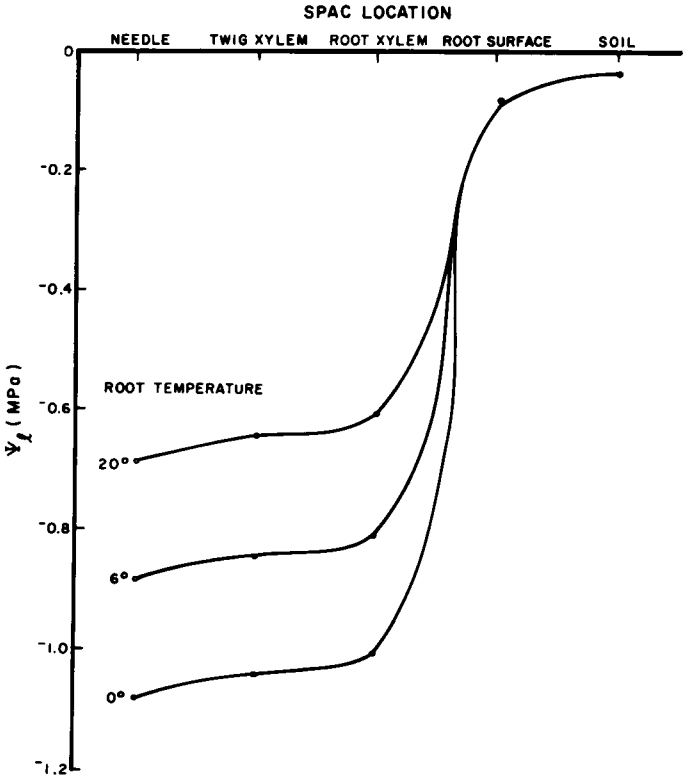

FIG. 5. Composite diagram of the sources of development of leaf water potential in these lodgepole pine seedlings. Produced by progressively removing the roots, stem, and twig and measuring Ψ_l recovery at each stage.

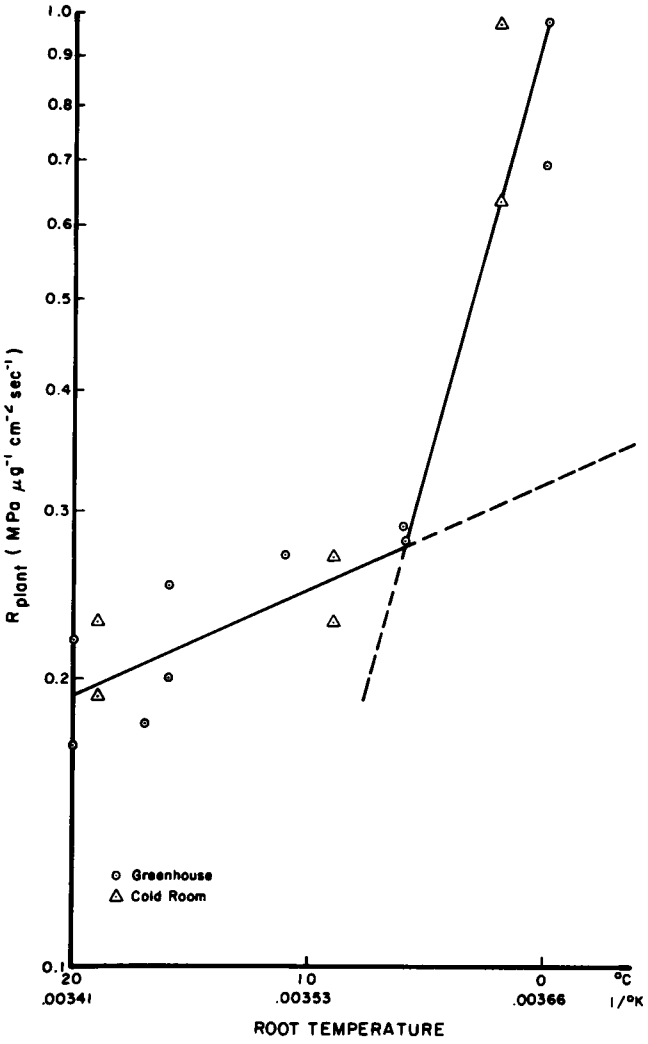

FIG. 6. Arrhenius plot of total plant resistance as affected by root temperature for all seedlings tested. Seedlings were preconditioned under a greenhouse environment (⊙) or at 2 C (△).

Of primary importance to tree water modeling is whether or not the function in Figure 4 represents a general physiological response to soil temperature in *P. contorta*. Can that same function be used to predict root water uptake in larger lodgepole pine in the field? Because of continually changing evaporative demand, spatially inconsistent soil temperatures, appreciable stem water storage relative to transpiration, and the difficulty of working with intact buried root systems, this experiment could not be duplicated in the field with present instrumentation. Instruments that could monitor water potential and tissue water content *in situ*, nondestructively, would allow construction of a mass balance of sections of a tree. Root water uptake could then be measured volumetrically under any conditions.

Even if one can assume that these data reflect the root membrane physiology of larger field trees, there is ample evidence that the proportion of R_{plant} generated at the root surface is not similar to these data. Nnyamah *et al.* (18) showed a gradient from −1.2 MPa in the root xylem to −2.2 MPa at the leaf in 8-m tall *P. menziesii*. Hinckley *et al.* (8) cited numerous other studies where stem Ψ gradients greatly exceed the hydrostatic gradient, and with a nonlinear dependence of Ψ_l on transpiration rate. Waring and Running (24) have calculated significant diurnal changes in xylem hydraulic conductivity and sapwood capacitance in large Douglas fir.

In conclusion, the total plant resistance, R, in equation 1 is controlled by a variety of often unrelated factors. Stomatal R is controlled by radiation, air temperature, and humidity in addition to Ψ_l. Stem resistance can be changed by temperature and water content. Root resistance is a function of soil water content, and as shown here, root temperature. Finally, soil resistance is controlled by soil water content, temperature, and solute concentration. It will never be possible to establish constant ratios of these various resistances to total R_{plant}. At present, only computer models are capable of organizing a holistic view of water flow in the soil-plant-atmosphere continuum.

Acknowledgments—The authors would like to thank Drs. Michael Burke and Merrill Kaufmann for critical review of this manuscript.

LITERATURE CITED

1. Beardsell MF, PG Jarvis, B Davidson 1972 A null-balance diffusion porometer suitable for use with leaves of many shapes. J Appl Ecol 9: 677–690
2. Blake J, WK Ferrell 1977 The association between soil and xylem water potential, leaf resistance, and abscisic acid content in droughted seedlings of Douglas-fir (*Pseudotsuga menziesii*). Physiol Plant 39: 106–109
3. Clarkson DT 1976 The influence of temperature on the exudation of xylem sap from detached root systems of rye (*Secale cereale*) and barley (*Hordeum vulgare*). Planta 132: 297–304
4. Dalton FN, WR Gardner 1978 Temperature dependence of water uptake by plant roots. Agron J 70: 404–406
5. Evans AK 1975 Water relations of Engelmann spruce during snowmelt. Unpublished PhD diss. Colorado State University, Fort Collins
6. Fiscus EL 1975 The interaction between osmotic and pressure-induced water flow in plant roots. Plant Physiol 55: 917–922.
7. Heine RW 1971 Hydraulic conductivity in trees. J Exp Bot 22: 503–511
8. Hinckley TM, JP Lassoie, SW Running 1978 Temporal and spatial variations in the water status of forest trees. For Sci Mono No 20, 72 p.
9. Kaufmann MR 1975 Leaf water stress in Engelmann spruce. Influence of the root and shoot environments. Plant Physiol 56: 841–844
10. Kaufmann MR 1977 Soil temperature and drying cycle effects on water relations of *Pinus radiata*. Can J Bot 55: 2413–2418
11. Kline JR, KL Reed, RH Waring, ML Stewart 1976 Field measurement of transpiration in Douglas-fir. J Appl Ecol 13: 273–282
12. Lange OL, R Losch, ED Schulze, L Kappen 1971 Responses of stomata to changes in humidity. Planta 100: 76–86
13. Little CHA 1975 Inhibition of cambial activity in *Abies balsamea* by internal water stress: role of abscisic acid. Can J Bot 53: 3041–3050
14. Luxmore RJ, DD Huff, RK McConathy, BE Dinger 1978 Some measured and simulated plant water relations of yellow-poplar. For Sci 24: 327–341
15. Lyons JM 1973 Chilling injury in plants. Annu Rev Plant Physiol 24: 445–466
16. Markhart AH, EL Fiscus, AW Naylor, PJ Kramer 1979 The effect of temperature on water and ion transport in soybean and broccoli root systems. Plant Physiol 64: 83–87
17. Newman EI 1976 Water movement through root systems. Phil Trans R Soc Lond B 273: 463–478
18. Nnyamah JU, TA Black, CS Tan 1978 Resistance to water uptake in a Douglas-fir forest. Soil Sci 126: 63–76
19. Running, SW 1980 Relating plant capacitance to the water relations of *Pinus contorta*. For Ecol Man. In press
20. Siau JF 1971 Flow in wood. Syracuse Wood Science Series No 1, Syracuse Univ Press, Syracuse, NY
21. Simon EW 1974 Phospholipids and plant membrane permeability. New Phytol 73: 377–420
22. Skaar C 1972 Water in wood. Syracuse Wood Science Series No 4. Syracuse Univ Press, Syracuse
23. Waring RH, SW Running 1976 Water uptake, storage and transpiration by conifers: a physiological model. *In* OL Lange, ED Schulze, L Kappen, eds, Water and Plant Life, Problems and Modern Approaches. Ecol Studies, Vol 19, Springer-Verlag, Berlin pp 189–202
24. Waring RH, SW Running 1978 Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old growth Douglas-fir. Plant Cell Environ 1: 131–140