Tree Physiology 11, 289–303

Leaf water status and root system water flux of shortleaf pine (*Pinus echinata* Mill.) seedlings in relation to new root growth after transplanting

JOHN C. BRISSETTE[1] and JIM L. CHAMBERS[2]

[1] *USDA Forest Service, Southern Forest Experiment Station, 2500 Shreveport Highway, Pineville, LA 71360, USA*

[2] *School of Forestry, Wildlife, and Fisheries, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, USA*

Received August 21, 1991

Summary

Water relations and root growth of shortleaf pine (*Pinus echinata* Mill.) were studied four weeks after seedlings from a half-sib family had been transplanted to one of three regimes of soil water availability at a root zone temperature of either 15 or 20 °C. About one-third of the variation in new root growth was explained by the root zone environment. The interaction between root zone temperature and soil water availability accounted for 10% of the variation in new root growth. In the most favorable root environment, new roots averaged 620 mm^2 of projected surface area. Leaf water potential increased exponentially with new root projected surface area, becoming constant at about 300 mm^2. Leaf conductance and root system water flux increased linearly with new root growth.

Introduction

After transplanting, the survival and initial growth of bare-root seedlings are often reduced because physiological processes are impaired by lifting, handling, and storage—a condition called transplant shock or planting stress. An important contributor to planting stress is the unavoidable loss of fine roots during lifting (Wakeley 1954, Nambiar 1980). Consequently, transplanted seedlings develop some degree of water stress because they have a reduced absorbing capacity and poorer root–soil contact than seedlings that have not been transplanted (Sands 1984, Grossnickle 1988). Water uptake by transplanted stock depends initially on the old, woody roots that are transplanted (Kramer 1946, Chung and Kramer 1975, Sands et al. 1982, Carlson 1986, MacFall et al. 1990). However, to survive and grow, transplanted seedlings must extend their root systems by the addition of new roots. Growth of new, unsuberized roots greatly increases a seedling's ability to absorb water (Chung and Kramer 1975, Carlson 1986, Colombo and Asselstine 1989, Grossnickle and Russell 1990), but it is not known how much new root development is required to make a substantial improvement in the water relations of a plant.

Root growth results from an interaction among seedling morphology, physiology, and the whole-plant environment. Two key elements of the plant environment are root zone temperature and availability of soil water. In pine seedlings, root zone temperature affects both initiation of new roots and elongation of existing roots

(Nambiar et al. 1979, Andersen et al. 1986). Six weeks after transplanting red oak (*Quercus rubra* L.) seedlings, there was five times as much root growth at a soil water potential of −0.03 MPa as at a soil water potential of −0.4 MPa (Larson and Whitmore 1970). Ritchie and Dunlap (1980), citing unpublished data, reported root growth of loblolly pine (*Pinus taeda* L.) seedlings at soil water potentials as low as −1.3 MPa. However, at low water potentials roots become less permeable, probably because of increased suberization (Kaufmann 1968, Ramos and Kaufmann 1979), and increased resistance to water movement at the soil–root interface (Faiz and Weatherley 1978, Orlander and Due 1986).

Root system absorptive capacity is often evaluated under positive pressure by forcing water through detopped plants and collecting the exudate over a measured period of time (Mees and Weatherley 1957, Ramos and Kaufmann 1979, Sands et al. 1982, Carlson 1986, Johnsen et al. 1988, Smit and Stachowiak 1988, Carlson and Miller 1990, Grossnickle and Russell 1990).

Capacity for water uptake can also be evaluated indirectly. Nambiar et al. (1979) found a significant, positive relationship between midday leaf water potential and new root elongation. The relationship between transpiration and the water potential gradient that drives water transport through the soil–plant system has also been used to monitor seedling establishment after transplanting (Orlander and Rosvall-Ahnebrink 1987, Grossnickle 1988). Leaf conductance and the recovery rate of plant water potential as it returns to its predawn level after stomatal closure may also provide measures of new root growth. Assessing root function using indirect, nondestructive methods is valuable because such measures avoid the experimental problems associated with the positive pressure method of measuring the absorptive capacity of excised roots (Passioura 1988). In addition, indirect measurements can be made with commercially available instruments.

This research had two objectives. The first objective was to describe effects of root zone temperature and water availability on new root growth of bare-root shortleaf pine (*Pinus echinata* Mill.) seedlings four weeks after transplanting. The second objective was to estimate to what extent the amount of new root tissue affected leaf water relations, and to estimate the relative importance of old and new roots to the capacity of a root system to absorb water.

Materials and methods

Plant material

Seeds from several half-sib families of shortleaf pine from the Ouachita and Ozark Mountains were collected at the USDA Forest Service's seed orchard near Mount Ida, Arkansas. Seedlings from four families were grown during the 1988 crop year at Weyerhaeuser Company's Fort Towson Forest Regeneration Center in southeastern Oklahoma. Family 322, from Pope County, Arkansas, appeared most uniform in December and was selected for this research. Seedlings were carefully hand lifted in mid-January and late-February 1989. Accumulated chilling hours (0 to 8 °C at

200 mm above the soil) by the morning of lifting were 715 and 1077 h, respectively. Roots were thoroughly wetted, packed in seedling storage bags, and cold stored (at about 3 °C) for either 7 or 9 days. Seedlings from the January lift were used in a preliminary investigation to determine the soil water availability regimes for the main experiment, and to establish procedures for measuring the response variables.

On the day seedlings were put into an experiment, their roots were pruned to a maximum length of 150 mm and the root system projected surface area was measured with a photoelectronic image analyzer (Decagon Devices, Inc., Pullman, WA). A seedling was selected only if its root system projected surface area was within 1.0 standard deviation of the mean of 100 randomly selected seedlings. The root system projected surface area of each seedling was calculated as the mean of three images; this procedure minimized error caused by overlapping lateral roots. In the main experiment, there were 126 seedlings that averaged 309 mm in height, had a mean root collar diameter of 5.1 mm, and mean root system projected surface area of 3010 mm^2.

Environmental controls

The experiment was conducted in a growth chamber that provided a constant air temperature of 20 °C and a 14-h photoperiod. When the growth chamber lights were on, photosynthetically active radiation was greater than 750 $\mu mol\ m^{-2}\ s^{-1}$ at the top of the seedling crowns. Relative humidity was not controlled, but the chamber floor was kept flooded and relative humidity averaged about 75%.

Two water baths were constructed to control root zone temperatures at 15 ± 0.5 and 20 ± 0.5 °C. The 20 °C bath was maintained by the ambient conditions in the growth chamber. The 15 °C bath was maintained by circulating water between the bath and a reservoir where it was chilled. In each water bath, soil water availability was controlled by means of 63 root-environment chambers. Water availability was regulated by maintaining the growing medium at a constant height above water in a conductive column. Each root-environment chamber was similar to an apparatus described by Snow and Tingey (1985) except that several root-environment chambers were connected to an irrigation reservoir, and the seedlings were potted in masonry sand (Figure 1).

Three soil water availability regimes were compared. A well-watered treatment was considered the control. The other regimes, designated Level 1 and Level 2, were considered water-stress treatments; more water was available at Level 1 than at Level 2. In the preliminary experiment, distances were established between water in the conductive columns and the root systems so that significant differences in leaf water potential (Ψ) and amount of new root development were ensured in the main experiment. In the control, roots were 80 mm above the level of water in the column. Roots in both the Level 1 and Level 2 water-stress treatments were 160 mm above the water; however, the columns for the Level 2 water-stress treatment included a ceramic disk that reduced conductivity, making water less available (Snow and Tingey 1985). There was no quantification of water availability in this study; the necessity of avoiding damage to root systems precluded measuring the water content

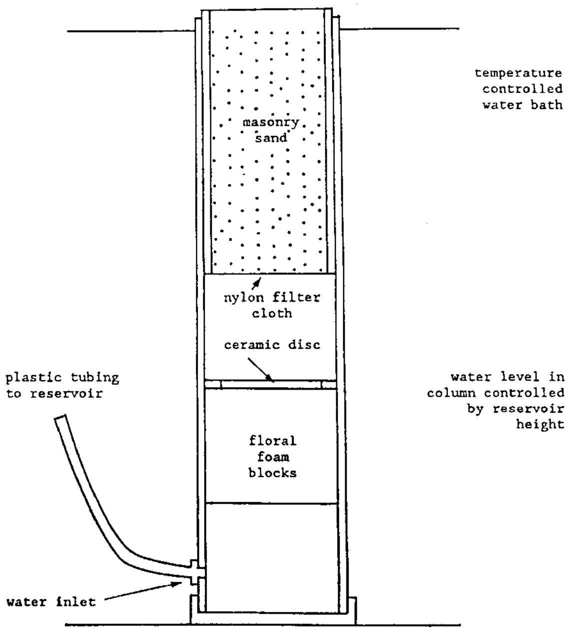

Figure 1. Chamber used to control root zone temperature and soil water availability of individual seedlings.

or water potential of the sand.

There was some mortality among the Level 2 water-stress seedlings. Based on evidence presented by Brix (1960), needle water content was used to define mortality. If the water content of a 36-needle sample was ≤75% (oven-dry weight basis), results for that seedling were not analyzed.

Measurements of water relations

A subsample of eight seedlings in each treatment combination was chosen at random for evaluation of Ψ and leaf conductance (g_s) 28 days after planting. The first Ψ measurement was made near the end of the dark period (i.e., predawn) (Ψ_{pd}), with subsequent measurements made approximately 2.5 and 5.0 h after the lights came on. Measurements of g_s were paired with Ψ measurements taken in the light; the order in which seedlings were evaluated was random and was followed for all subsequent measurements.

The Ψ of two or three fascicles was measured in a pressure chamber (PMS Instrument Co., Corvallis, OR), and the mean was used in analysis. In many cases, high chamber pressure caused needles to break in the stopper that sealed them in the pressure chamber. Therefore, to minimize needle loss, if water was not forced from the xylem by a pressure of 4.0 MPa, Ψ was recorded as −4.0 MPa. After measurements in the light, the growth chamber lights were turned off and a final Ψ measurement was taken approximately 2 h later. This measurement was used to estimate Ψ recovery rate ($\Delta\Psi_{recov}$).

A steady-state porometer (Model LI-1600M; Li-Cor, Inc., Lincoln, NE) was used to measure g_s. Conductance measurements were made in the upper half of the crown with unshaded needles from two, 3-needle fascicles. The mean total needle surface area sampled in the porometer leaf chamber was 504 mm^2.

Measurement of root system water flux

The day following measurement of Ψ and g_s, a maximum of 16 living seedlings from each treatment combination were carefully washed from the sand. Root system water flux (L_R) was measured by a hydrostatic pressure method similar to one described by Carlson and Miller (1990). The shoot of each seedling to be evaluated was severed about 25 mm above the topmost lateral root. The stem above the root system was inserted through a rubber stopper, which was then seated in the removable top of a vessel with the cut stem protruding and the roots suspended in the base of the container. With the top secured to the base to form a pressure vessel, tap water at 20 ± 0.5 °C was pumped through the apparatus at about 0.13 l s^{-1} and 300 ± 0.5 kPa. The vessel held eight seedling root systems.

Water could escape the vessel only by passing through the root systems and out of the cut stems. After a 15-min equilibration period, L_R was measured as water exuded from the root systems. The exuded water was collected in wicks made of plastic tubes about 6.4 mm in diameter and 60 mm long filled with absorbent tissue paper. Wicks were pre-weighed within 15 min of use. Four samples were taken from each seedling at approximately 5-min intervals; actual time was recorded to the nearest second. The weight of the wick and collected water was measured to the nearest mg.

Several precautions were taken to reduce the impact of experimental artifacts associated with forcing water through roots under pressure (Passioura 1988). Longitudinal flow through the root cortex was minimized by using a pressure analogous to relatively slow transpiration, but much greater than would have been possible with a vacuum-driven water collection system. To reduce effects of carbohydrate starvation, seedlings were decapitated immediately before being placed in the vessel, and the length of time roots were under pressure was limited to 40 min. Finally, hydrostatic pressure rather than gaseous pressure was used to avoid cell damage.

Measurement of root surface area

After measurement of L_R, new roots were excised from the root systems and their projected surface area measured on an image analyzer. New roots were distinguished from old roots by color and surface texture. However, because new roots were somewhat translucent, they were stained for image analysis. Old roots were separated into laterals and taproot, and their total projected surface area was measured without the error caused by overlapping roots. Projected surface area is only an index of actual root surface area. Accordingly, projected surface area of new roots was termed new root area index (NRAI), and projected surface area of old roots, old root area index (ORAI). Both NRAI and ORAI were measured to the nearest 10 mm^2.

Statistical Analysis

Analysis of variance (ANOVA) was used to determine the effects of root zone temperature and soil water availability on NRAI. There was a factorial arrangement of the two temperatures and three levels of soil water. Each soil water level was replicated 21 times at each temperature; however, temperatures were not replicated. Consequently, the experimental design was completely random. From the 21 seedlings in each treatment combination, 16 were chosen for measurement of L_R and NRAI. Selection was random with the restriction that seedlings on which water relations had been measured were included. Because there were not 16 living seedlings in all treatments, least squares means were used to compare factor levels.

With NRAI as a covariate, analysis of covariance (ANCOVA) was used to examine effects of root zone temperature and water availability on Ψ_{pd}, $\Delta\Psi_{recov}$, and g_s. Both ORAI and NRAI were covariates in an ANCOVA for L_R. Regression analysis was used to describe relationships between the response variables and those independent variables in the ANCOVA models that were significant at $P = 0.10$.

Both Ψ_{pd} and $\Delta\Psi_{recov}$ increased exponentially with NRAI so a logarithmic transformation of NRAI was used to linearize the function for regression analysis. Approximately half of the seedlings had no new roots; therefore, because the logarithm of zero is undefined, 1 was added to NRAI before its natural logarithm was taken.

Results and discussion

Seedling survival was 96%; five seedlings in the Level 2 water-stress treatments died, four at 20 °C and one at 15 °C (Table 1). At all four measurement times, the mean Ψ of seedlings with any NRAI was at least 1 MPa higher than the mean of

Table 1. New root area index (NRAI, mm^2) 4 weeks after planting in different root zone environments.[1]

Water stress level	Root zone temperature		Least squares mean
	15 °C	20 °C	
Control	40 (16)[2]	620 (16)	330 (32)
Level 1	10 (16)	260 (16)	140 (32)
Level 2	<10 (15)	20 (11)	10 (26)
Least squares mean	20 (47)	300 (43)	

[1] M.S.E. = 84011, for the interaction $F_{(2;84)} = 6.90$, for temperature $F_{(1;84)} = 21.18$, and for water stress $F_{(2;84)} = 8.95$.

[2] Numbers in parentheses are the numbers of surviving seedlings contributing to the adjacent mean.

seedlings without new roots (Figure 2). After the growth chamber lights came on, Ψ of seedlings with new roots declined, presumably because of water loss by transpiration. After a 5-h light period, Ψ of seedlings with new roots recovered to predawn values within 2 h of the lights being turned off, whereas Ψ of seedlings without new roots was essentially unchanged throughout the measurement cycle.

Similar results were observed when g_s was compared for seedlings with and without new roots (Figure 3). Among seedlings with NRAI, g_s declined with increasing exposure to light, whereas among seedlings with no new roots there was very little stomatal activity.

Some new root growth occurred in all treatments, although NRAI in the 15 °C, Level 2 water-stress treatment averaged less than 10 mm^2 (Table 1). The maximum NRAI observed, 1730 mm^2, was in a seedling in the 20 °C control treatment. It was also the only seedling to show new taproot development, accounting for 90 mm^2 of its NRAI. The finding that almost all new root growth originated from lateral roots is consistent with the findings of DeWald and Feret (1988) in loblolly pine seedlings.

Root zone temperature and water availability interacted to affect NRAI (P = 0.002). There was always less root growth at 15 than at 20 °C, but as soil water became less available, root growth declined more rapidly at 20 than at 15 °C (Table 1). Seedlings in the Level 2 water-stress treatment did not exhibit much root growth at either temperature indicating that both root zone temperature and water availability had to be favorable for new roots to grow. The temperature × water stress interaction explained 10% of the total variation in NRAI, and the temperature and

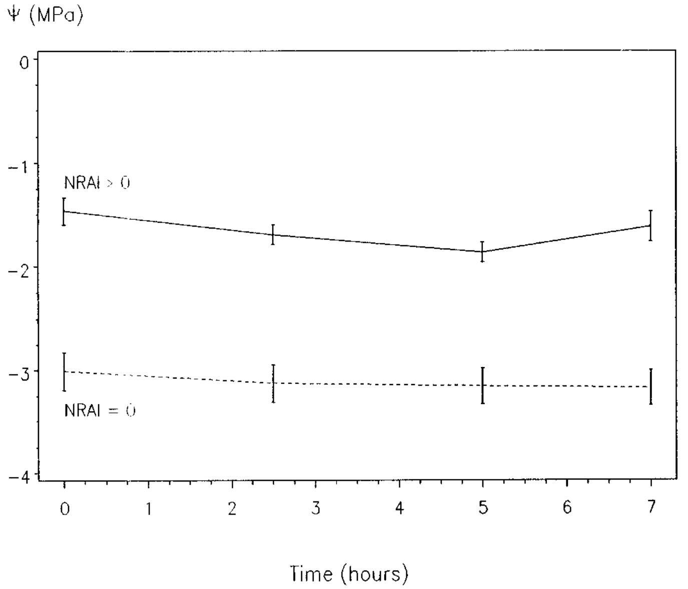

Figure 2. Mean needle water potential (Ψ) of seedlings with new root area index (NRAI) either 0 or greater than 0 measured at predawn (time = 0), after 2.5 and 5 h in the light, and after a 2-h dark period. Vertical lines are ± 1 standard error.

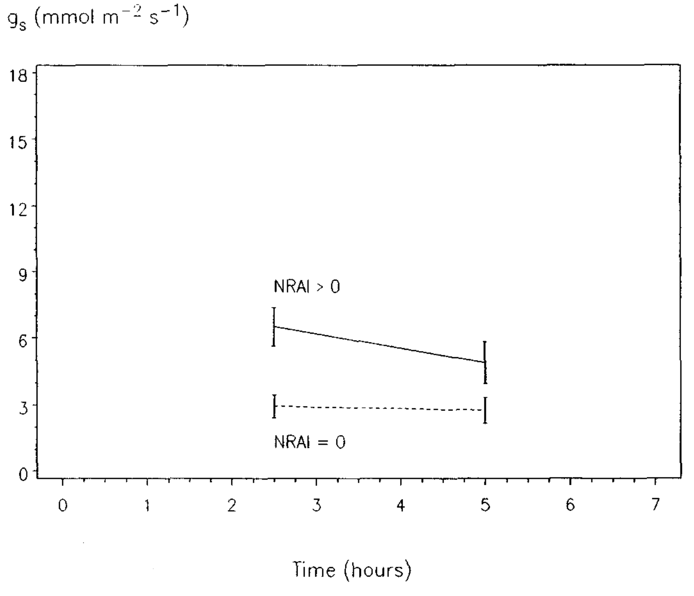

Figure 3. Mean stomatal conductance (g_s) of seedlings with new root area index (NRAI) either 0 or greater than 0 measured after 2.5 and 5 h in the light. Vertical lines are ± 1 standard error.

water stress main effects explained 11 and 10% of the variation, respectively. Although seedlings of only one half-sib family were compared in this study, Hallgren and Tauer (1989) showed differences among shortleaf pine half-sib families in the ability to initiate and elongate new roots. Furthermore, an interaction between family and root zone temperature has been shown to affect new root growth in loblolly pine (*P. taeda* L.) (Carlson 1986) and radiata pine (*P. radiata* D. Don) (Nambiar et al. 1979).

Among seedlings in the Level 2 water-stress treatments, NRAI was negligible (Table 1). Consequently, only seedlings in the control and Level 1 water-stress treatments were used to examine the effects of NRAI on leaf water relations and L_R.

Leaf water potential

The Ψ_{pd} of 32 seedlings was compared and ANCOVA explained 76% of the total variation. Significant independent variables were temperature, water availability, and NRAI (Table 2). The simple linear regression that best described how the root zone environment and NRAI affected Ψ_{pd} was

$$\Psi_{pd} = -1.88 + 0.195\,X_1 - 0.596\,X_2 - 1.046\,X_3 + 0.175\,X_1X_3, \qquad (1)$$

where $X_1 = \ln(\text{NRAI} + 1)$, $X_2 = 0$ if water stress = control and 1 if water stress = Level 1, and $X_3 = 0$ if temperature = 15 °C and 1 if temperature = 20 °C.

Within each temperature, the two water-stress treatments had different intercepts but the same slope (Figure 4). The more negative intercepts for the 20 °C treatments

Table 2. Significance of the effects of experimental factors and seedling attributes on water relations and root system water flux as determined by analysis of covariance

Response	n	Factor			Covariate	
		Temperature	Water stress	Temp × Stress	NRAI[1]	ORAI
Ψ_{pd}	32	0.02	0.003	0.62	0.0001	–
$\Delta\Psi_{recov}$	29	0.27	0.46	0.31	0.0001	–
g_s	31	0.73	0.004	0.48	0.0007	–
L_R	64	0.66	0.07	0.81	0.0001	0.99

[1] For Ψ_{pd} and $\Delta\Psi_{recov}$, values of NRAI were transformed to ln(NRAI + 1).

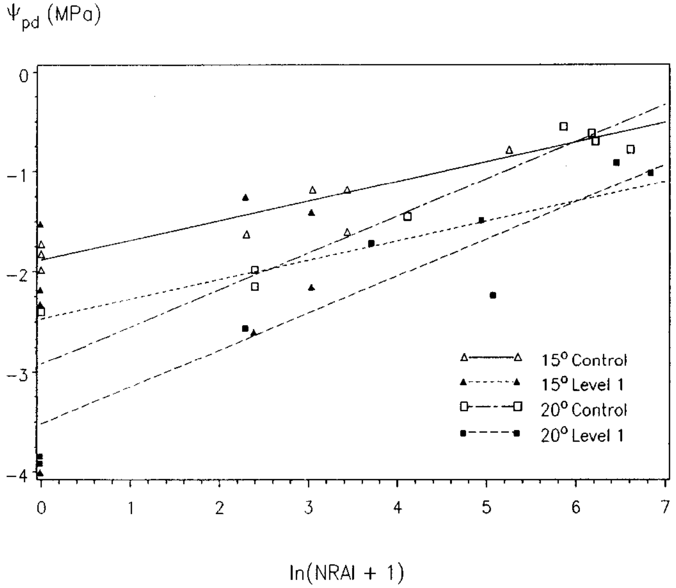

Figure 4. The relationship between predawn needle water potential (Ψ_{pd}) and new root area index (NRAI) 28 days after planting.

reflected a lower water availability, probably because of greater evaporation from the surface of the warmer pots. The steeper slope for the 20 °C treatments may have resulted from both greater root permeability and reduced viscosity of water at the higher temperature.

Because the seedlings were irrigated from below, there was a water content gradient in the seedling pot, with the greatest water content at the bottom. New root growth enabled seedlings to reach sand at a higher water potential than the sand near the planted roots. Therefore, the seedlings with the most root growth had the highest values of Ψ_{pd}, about −0.8 MPa (Figure 4). To achieve a Ψ_{pd} of −0.8 MPa, the regression model predicted that the 15 °C control seedlings needed approximately 250 mm^2 of NRAI and the 20 °C control seedlings needed about 310 mm^2, which represents an increase in total root surface area of about 10%. Thus, a relatively small amount of new root growth resulted in a marked improvement in Ψ_{pd}.

Water potential recovery rate

For the 29 seedlings analyzed, only NRAI affected $\Delta\Psi_{recov}$ (Table 2), and a simple linear regression explained 61% of the total variation:

$$\Delta\Psi_{recov} = -0.055 + 0.051 \ln(\mathrm{NRAI} + 1). \quad (2)$$

The negative intercept indicates that, without new root development, Ψ continued to decline for at least 2 h after the lights in the growth chamber were turned off. However, for seedlings with new roots, $\Delta\Psi_{recov}$ was positive and increased exponentially with NRAI (Figure 5).

About 300 mm^2 of NRAI resulted in the highest values of Ψ_{pd} in this experiment (Figure 4). When applied to the $\Delta\Psi_{recov}$ model, an NRAI of 300 mm^2 resulted in a mean $\Delta\Psi_{recov}$ of 0.24 MPa h^{-1}. Thus, if Ψ increased by about 0.5 MPa after 2 h in the dark, a seedling had enough new root growth to alleviate the water stress induced by transplanting.

The faster Ψ recovers to its predawn value, the longer the period favorable for cell division and elongation, and the more quickly transplanted seedlings become established. The time required for $\Delta\Psi_{recov}$ to become positive depends on resistances to water movement in the soil, at the soil–root interface, and in the roots. Using magnetic resonance imaging, MacFall et al. (1990) observed a water-depletion zone

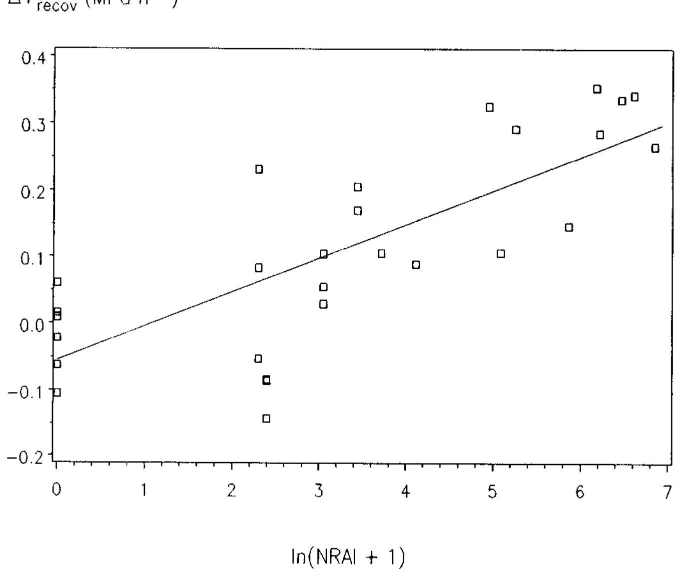

Figure 5. The relationship between needle water potential recovery rate ($\Delta\Psi_{recov}$) after 2 h of darkness and new root area index (NRAI) 28 days after planting.

around woody roots of loblolly pine seedlings. Resistance to water movement through that zone would be greater than in soil at a higher water potential (Brady 1974). Also, resistance at the soil–root interface is greater for transplanted roots than for roots that grow without disturbance (Sands 1984, Grossnickle 1988). Furthermore, as the unsuberized proportion of a root system increases, resistance to water uptake decreases (Chung and Kramer 1975). Thus, new roots increase $\Delta\Psi_{recov}$ because they increase the root system surface area and, compared to old roots, they occupy wetter soil with less resistance to water movement, have better contact with the soil, and are more permeable.

Leaf conductance

Because there were no significant interactions or main effects of time when g_s was measured after 2.5 and 5 h, the mean g_s was used in the analyses. Because the mean g_s of one seedling was about twice that of the rest of the seedlings, it was excluded from the data set. Among the other 31 seedlings, mean g_s was affected by NRAI and water availability (Table 2). A simple linear regression accounted for 70% of the variation

$$g_s = 5.78 + 0.010\,X_1 - 3.52\,X_2, \tag{3}$$

where X_1 = NRAI, and X_2 = 0 if water stress = control and 1 if water stress = Level 1.

The water stress imposed by the Level 1 treatment was reflected in an intercept less than that for control seedlings (Figure 6). Among the control seedlings, each

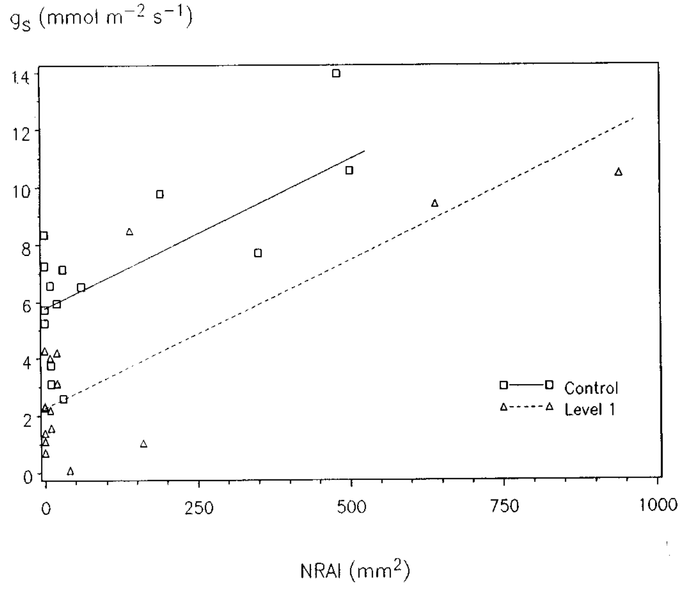

Figure 6. The relationship between leaf conductance (g_s) and new root area index (NRAI) 28 days after planting.

additional 10 mm^2 of NRAI increased g_s by 7%. Because the intercept was less in the Level 1 water-stress treated seedlings, each additional 10 mm^2 of NRAI increased the mean g_s of those seedlings by 13%.

Leaf conductance of well-established trees is often higher than that observed in the seedlings used in this study. Carlson et al. (1988) observed a maximum g_s of 150 to 200 mmol m^{-2} s^{-1} in 6-year-old loblolly pines in the field. On three of their five measurement days, mean g_s was less than 20 mmol m^{-2} s^{-1}, and on the other days the means were about 40 and 60 mmol m^{-2} s^{-1}. One reason for the relatively low conductances in our study was the low irradiance used in the growth chamber. For loblolly pine seedlings, Teskey et al. (1986) showed an increase in g_s with increasing irradiance up to the maximum tested, 1450 μmol m^{-2} s^{-1}. Assuming a similar response for shortleaf pine, interpolation from their data suggests that the 750 to 800 μmol m^{-2} s^{-1} irradiance used in this research resulted in an expected mean g_s about 75% of that at 1450 μmol m^{-2} s^{-1}.

Root system water flux

Water flux was measured on 64 root systems in the control and Level 1 water-stress treatments. Because there were no significant interactions or main effects of time for the four samples of L_R taken at 5-min intervals, mean L_R was used in the analyses. The ANCOVA accounted for 45% of the total variation in mean L_R, and the only significant independent variables were NRAI and water stress. The simplest regression model predicting mean L_R from NRAI and water stress was

$$L_R = 2.562 + 0.00453\,X_1 - 1.187\,X_2, \tag{4}$$

where X_1 = NRAI and X_2 = 0 if water stress = control and 1 if water stress = Level 1.

As with mean g_s, seedlings from the two water-stress treatments had different intercepts but the same slope (Figure 7). Evidently, old roots were affected by water stress but new roots were not. Water stress has been shown to make woody roots less permeable (Ramos and Kaufmann 1979).

Carlson (1986) found a significant, positive relationship between L_R and the volume of old roots of loblolly pine seedlings. However, in this study, ORAI did not affect L_R, probably because the seedlings had been selected for uniformity of root system size.

The regression model predicted that each additional 10 mm^2 of NRAI increased L_R about 2% in the control treatments (Figure 7). For seedlings in the Level 1 water-stress treatment, the predicted increase was 3%, because of the lower intercept of these seedlings. For example, a control seedling with 1000 mm^2 of NRAI would be expected to have an L_R that was 177% greater than that of a seedling with no new root growth. However, a seedling in the Level 1 water-stress treatment with only half as much NRAI should have an increase in L_R of about the same magnitude.

The results suggest that the effect of new roots on L_R was less than it was on g_s. However, L_R was measured at a relatively moderate driving force of 0.3 MPa. The difference between Ψ_{pd} and Ψ when g_s is measured represents the driving force for

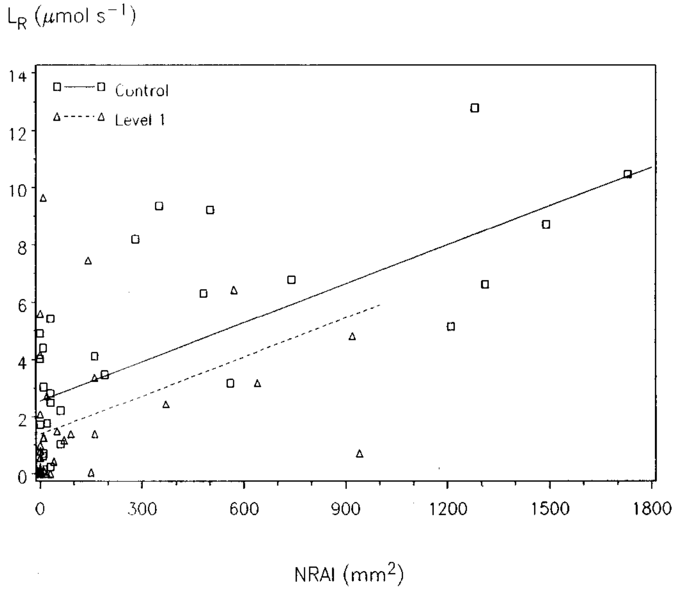

Figure 7. The relationship between root system water flux (L_R) at 0.3 MPa hydrostatic pressure and new root area index (NRAI) 29 days after planting.

transpiration at the time of measurement. In this study, the maximum transpirational driving force was 0.9 MPa, and driving forces ≥ 0.5 MPa were not uncommon. Therefore, in rapidly transpiring seedlings, NRAI should have a greater impact on L_R than under the conditions of this experiment.

We conclude that the interaction between root zone temperature and water availability has a significant impact on new root development after transplanting. Regardless of how favorable soil temperature or water availability may be for root growth, one factor cannot offset a limiting effect of the other. That is, root zone temperature must be favorable and soil water must be readily available for root growth to occur. Relatively little new root growth is needed to increase the capability of root systems to absorb water. In turn, increased uptake reduces water stress and improves leaf water relations after transplanting.

Acknowledgments

We thank John M. McGilvray for designing the systems described to control root zone environment and measure root system water flux, and Curtis D. Andries and Charles M. Stangle for helping with the construction of those systems.

References

Andersen, C.P., E.I. Sucoff and R.K. Dixon. 1986. Effects of root zone temperature on root initiation and elongation in red pine seedlings. Can. J. For. Res. 16:696–700.

Brady, N.C. 1974. The nature and properties of soils. 8th Edn. MacMillan Publ., New York. 639 p.

Brix, H. 1960. Determination of viability of loblolly pine seedlings after wilting. Bot. Gaz. 121:220–223.

Carlson, W.C. 1986. Root system considerations in the quality of loblolly pine seedlings. South. J. Appl. For. 10:87–92.

Carlson, W.C., C.A. Harrington, P. Farnum and S.W. Hallgren. 1988. Effects of root severing treatments on loblolly pine. Can. J. For. Res. 18:1376–1385.

Carlson, W.C. and D.E. Miller. 1990. Target seedling root system size, hydraulic conductivity and water use during seedling establishment. *In* Proc. Combined Meeting of Western Forest Nursery Assoc. Ed. T.D. Landis. USDA Forest Service Gen. Tech. Rep. RM-200, pp 53–66.

Chung, H.-H. and P.J. Kramer. 1975. Absorption of water and ^{32}P through suberized and unsuberized roots of loblolly pine. Can. J. For. Res. 5:229–235.

Colombo, S.J. and M.F. Asselstine. 1989. Root hydraulic conductivity and root growth capacity of black spruce (*Picea mariana*) seedlings. Tree Physiol. 5:73–81.

DeWald, L.E. and P.P. Feret. 1988. Changes in loblolly pine seedling root growth potential, dry weight, and dormancy during cold storage. For. Sci. 34:41–54.

Faiz, S.M.A. and P.E. Weatherley. 1978. Further investigations into the location and magnitude of the hydraulic resistances in the soil:plant system. New Phytol. 81:19–28.

Grossnickle, S.C. 1988. Planting stress in newly planted jack pine and white spruce. 1 Factors influencing water uptake. Tree Physiol. 4:71–83.

Grossnickle, S.C. and J.H. Russell. 1990. Water movement in yellow-cedar seedlings and rooted cuttings: comparison of whole plant and root system pressurization methods. Tree Physiol. 6:57–68.

Hallgren, S.W. and C.G. Tauer. 1989. Root growth potential, first-year survival, and growth of shortleaf pine seedlings show effects of lift date, storage, and family. South. J. Appl. For. 13:163–169.

Johnsen, K.H., S.P. McConnell, J.C. Regelbrugge and J.R. Seiler. 1988. Hydraulic conductance of roots present at the time of lifting and newly regenerated roots of 2+0 eastern white pine seedlings. USDA Forest Service Tree Planters' Notes 39(3):5–8.

Kaufmann, M.R. 1968. Water relations of pine seedlings in relation to root and shoot growth. Plant Physiol. 43:281–288.

Kramer, P.J. 1946. Absorption of water through suberized roots of trees. Plant Physiol. 21:37–41.

Larson, M.M. and F.W. Whitmore. 1970. Moisture stress affects root regeneration and early growth of red oak seedlings. For. Sci. 16:495–498.

MacFall, J.S., G.A. Johnson and P.J. Kramer. 1990. Observation of a water-depletion region surrounding loblolly pine roots by magnetic resonance imaging. Proc. Natl. Acad. Sci. 87:1203–1207.

Mees, G.C. and P.E. Weatherley. 1957. The mechanism of water absorption by roots. I. Preliminary studies on the effects of hydrostatic pressure gradients. Proc. Roy. Soc. Lond. (B) 147:367–380.

Nambiar, E.K.S. 1980. Root configuration and root regeneration in *Pinus radiata* seedlings. N.Z. J. For. Sci. 10:249–263.

Nambiar, E.K.S., G.D. Bowen and R. Sands. 1979. Root regeneration and plant water stress of *Pinus radiata* D. Don seedlings transplanted to different soil temperatures. J. Exp. Bot. 30:1119–1131.

Orlander, G. and K. Due. 1986. Location of hydraulic resistance in the soil-plant pathway in seedlings of *Pinus sylvestris* L. grown in peat. Can. J. For. Res. 16:115–123.

Orlander, G. and G. Rosvall-Ahnebrink. 1987. Evaluating seedling quality by determining their water status. Scand. J. For. Res. 2:167–177.

Passioura, J.B. 1988. Water transport in and to roots. Ann. Rev. Plant Physiol. Plant Mol. Biol. 39:245–265.

Ramos, C. and M.R. Kaufmann. 1979. Hydraulic resistance of rough lemon roots. Physiol. Plant. 45:311–314.

Ritchie, G.A. and J.R. Dunlap. 1980. Root growth potential: its development and expression in forest tree seedlings. N.Z. J. For. Sci. 10:218–248.

Sands, R. 1984. Transplanting stress in radiata pine. Austr. For. Res. 14:67–72.

Sands, R., E.L. Fiscus and C.P.P. Reid. 1982. Hydraulic properties of pine and bean roots with varying degrees of suberization, vascular differentiation and mycorrhizal infection. Austr. J. Plant Physiol. 9:559–569.

Smit, B. and M. Stachowiak. 1988. Effects of hypoxia and elevated carbon dioxide concentration on water flux through *Populus* roots. Tree Physiol. 4:153–165.

Snow, M.D. and D.T. Tingey. 1985. Evaluation of a system for the imposition of plant water stress. Plant Physiol. 77:602–607.

Teskey, R.O., J.A. Fites, L.J. Samuelson and B.C. Bongarten. 1986. Stomatal and nonstomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. Tree Physiol. 2:131–142.

Wakeley, P.C. 1954. Planting the southern pines. USDA Monograph No. 18, 233 p.