Target Seedling Symposium

Chapter 5
Target Seedling Root System Size, Hydraulic Conductivity, and Water Use During Seedling Establishment

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ABSTRACT

Basic survival requires that a seedling root system be large enough to supply water in amounts that cover transpirational loss. Because transpiration is an interactive phenomenon influenced by the planting environment as well as the shoot and root morphology of the tree, what might be sufficient seedling morphology for one geographic region could be inadequate for another region or another species within the same region. A target seedling morphology that has worked well for loblolly pine in the South can be described as 10-12 inches tall, 4 mm in diameter, and having 6 or more lateral roots. The net result is a seedling that has a high probability of survival. The focus of this paper is how hydraulic conductivity and seedling water use can be used to quantify relationships between morphology and function.

ACKNOWLEDGEMENTS

5.1 Introduction
Morphological characteristics of target seedlings should be defined to a large degree by foresters observing success and failure of plantations. These characteristics are imposed by practical limitations of the planting job. These include the size of the root system that can be properly planted and the weight and size of seedlings that can be carried by a planter or placed on a planting machine. One of the factors heavily affected by the morphology of the seedling is the balance between the capacity for water uptake and water loss due to transpiration. The purpose of this paper is to discuss some of the factors affecting the capacity of the root system for taking up water immediately after planting and during the process of establishment and to relate these factors to target seedling design.

5.2 Root Tissues and Water Uptake in Seedlings
Seedlings in a bareroot nursery bed have root system development to a depth of about 15 inches in the first few months (Huberman 1940). Undercutting, root wrenching, and lateral pruning are used to promote development of the root system (Rook 1969, Tanaka et al. 1976) within the depth and lateral width that can be easily planted properly. The resulting root system is mostly woody, with some suberized and unsuberized root tips (depending on month of lifting and prevailing soil temperature), and mycorrhizal fine roots.

Kramer and coworkers have shown that suberized roots and woody root tissues can and indeed must be the location of a major proportion of water uptake in tree root systems (Kramer 1946, Kramer and Bullock 1966, Chung and Kramer 1975, MacFall et al. 1990). This uptake apparently is facilitated by the presence of lenticels on the surface of the root, and by discontinuities in the periderm (bark) plates. Magnetic resonance images of water depletion around loblolly pine seedling roots indicate that soil water depletion is uniform around the tap root rather than just around points where lateral roots disrupt the continuity of the vascular cambium (MacFall et al. 1990). These studies also showed depletion around the tap root prior to depletion around the laterals. It is clear that woody roots are areas of importance in water uptake.

Unsuberized (white) root tips that occur on growing roots are the region of highest uptake per unit of surface area (Sands et al. 1982). Suberized roots also conduct water but at a lower rate per unit area (Chung and Kramer 1975). Sands and coworkers (1982) reported the water uptake rate to be 1.95×10^{-6} cm/s/0.1 MPa pressure differential for unsuberized white root tips, compared with 7.55×10^{-7} cm/s/0.1 MPa in suberized brown root tips. Thus unsuberized roots have the potential to conduct about 2.6 times the volume of water in a given time period at a given water potential gradient than do suberized roots. The root system capacity for water uptake when water is readily available results from relatively lower permeability through the large surface areas of woody and suberized roots and higher permeability through the smaller surface area of unsuberized root tips.

5.3 Effects of Planting on Subsequent Water Relations
It is well known that seedlings should be planted into soil that is moist to the touch. The quality of the planting job determines the availability of soil moisture to the seedling. Seedling roots should be planted with tight soil contact; that is, air pockets should be forced out as the hole is closed. Most of us are familiar with the method described in Figure 5.1 but failure to follow it is still a frequent cause of plantation failures. Site preparation methods such as ripping make it easier to consistently plant seedlings correctly. Even when seedlings are well planted the relative reduction in root-soil contact due to transplanting can be a cause of reduced water uptake and transplanting stress (Sands 1984).

5.4 Hydraulic Conductivity of the Newly Planted Root System
Most planting operations take place in the dormant season when soil temperatures are cool. These cool temperatures decrease the permeability of root membranes and increase the viscosity of water (Kramer 1934, Kramer 1940, 1942, Kaufman 1975, L.opushinsky and Kaufman 1984). Rate of water uptake (hydraulic conductivity) in a loblolly pine seedling after lifting and cold storage is a function of the temperature of water surrounding the roots (Figure 5.2). Root growth is limited by low soil temperatures (Bilan 1961, Stone and Schubert 1959, Andersen et al. 1986) and the magnitude of the effect of temperature on root growth varies by genetic family (Carlson 1986, Nambiar et al. 1979). Temperature affects both the rate of uptake of available water and the rate of metabolism, and thereby influences the length of time that a newly planted seedling will remain with little or no new root growth.

It follows that there is a time period from planting until new root growth occurs when a seedling is dependent on its nursery cultured root system for water uptake. During this period the size of the planted root system determines the rate at which water will be taken up at a given water potential and temperature (Figure 5.3, Carlson 1986). As new root growth occurs, water uptake under pressure (Figure 5.4) becomes a function of the number of new roots (Carlson 1986).

5.5 Water Transport Through Seedlings
Water transport through the seedling is driven by transpiration. Water is lost through the stomatal pores in the leaf
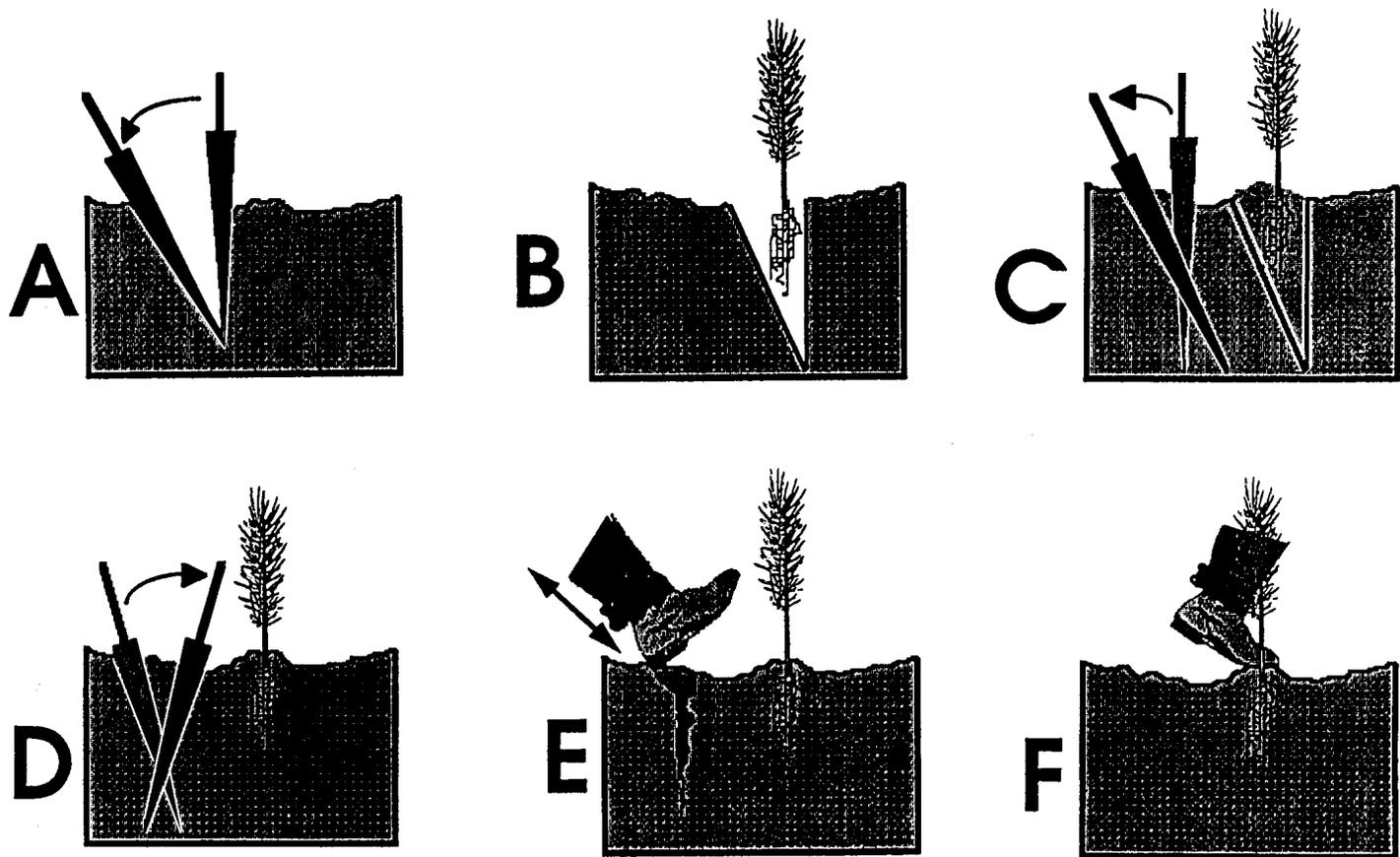
Figure 5.1—*Planting method for ensuring tight root-soil contact. A. Open the hole deeper than the tree will be planted; B. Place tree initially deeper than it will be planted, and pull upward to correct depth (3-6 cm below root collar) to straighten roots; C. Close bottom of hole avoiding air pockets; D. Close top of hole avoiding air pockets; E. Close dibble extraction hole; and F. Firm soil at base of seedling. Seedling should be firmly in the soil.*

surface and to a lesser extent through the leaf cuticle. As water is lost from the leaves, a water potential gradient builds from the leaves, down the stem, into the root system and root-soil interface causing water to move into the plant (Kramer 1939). When transpiration is severely reduced by stomatal closure, flow continues until the within-plant gradient is reduced to the point that the water potential in the root is at equilibrium with that in the soil. Figure 5.5 shows the relationship between water loss by transpiration (measured as weight loss, g/hr) and water uptake (measured as flow through the stem, ml/hr) in a loblolly pine sapling. Kramer (1937) showed similar relationships for seedlings of several species. Note that considerable water is lost by transpiration prior to the beginning of flow. This is because a water potential gradient must form to initiate flow. Such gradients have been documented in large trees (Schulze et al. 1985). As soils
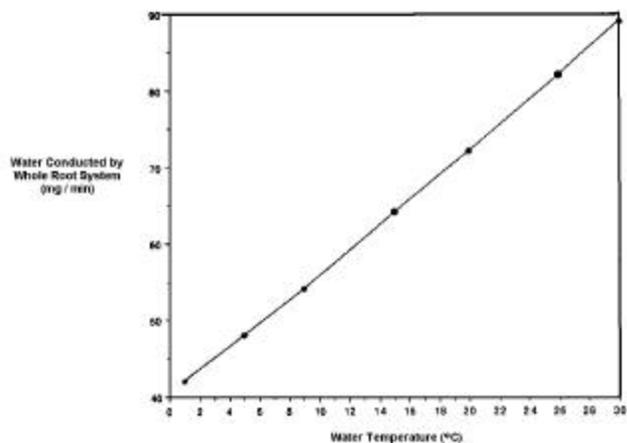

Figure 5.2--*The relationship between water uptake of a loblolly pine root system and water temperature. The apparatus used in obtaining these data is shown in Figure 5.4. Pressure was set at a constant 0.3 MPa. The seedling had a root volume of 4.5 ml and had been potted in sand in a greenhouse at 20°C for 28 days prior to measuring hydraulic conductivity.*

dry and soil and predawn plant water potentials become more negative, the maximum transpiration for the day, estimated in Figure 5.6 by leaf conductance, decreases (Teskey et al. 1986, Carlson et al. 1988). Decreased transpiration, if uptake continues, decreases the hydraulic gradient (increasing water potential) thus reducing stress (Kramer 1937, Grossnickle and Russell 1990).

Soils usually dry from the surface downward therefore it is important that roots grow downward at a rate that will keep a portion of the seedling root system in moist soil. Seedlings that have even a few roots in moist soil are able to recover from midday water stress by the following morning (Farnum 1977, Brissette 1990).

5.6 Target Seedling Morphology and Water Use
Seedling height and needle area are interrelated (Figure 5.7A). Taller seedlings have a greater surface available for both photosynthesis and for water loss by transpiration. Similarly, seedlings with large root volumes have a greater surface area available for water uptake (Figure 5.7B). When whole plant water use is monitored, it can be seen that in fact taller seedlings tend to use more water (Figure 5.8A) as do those with larger root systems (Figure 5.8B). Note the separation of data points around the regression in Figure 5.8B. This is due to some interactions between the morphological and physiological factors that we have been discussing. Specifically some seedlings form new roots sooner than others, and those that form roots more quickly have higher hydraulic conductivity (and therefore lower stress)97and as a result97greater leaf conductance and higher water use. Since trees with larger root volumes also have greater root growth potential (Carlson 1986), the effect is magnified.

Water use as related to seedling morphological balance should be considered on a whole tree basis. Transpiration measurements taken by porometer are point samples recorded on small samples of leaf area. If one multiplies transpiration per unit area by total leaf area and by the photoperiod (the maximum time period stomates are
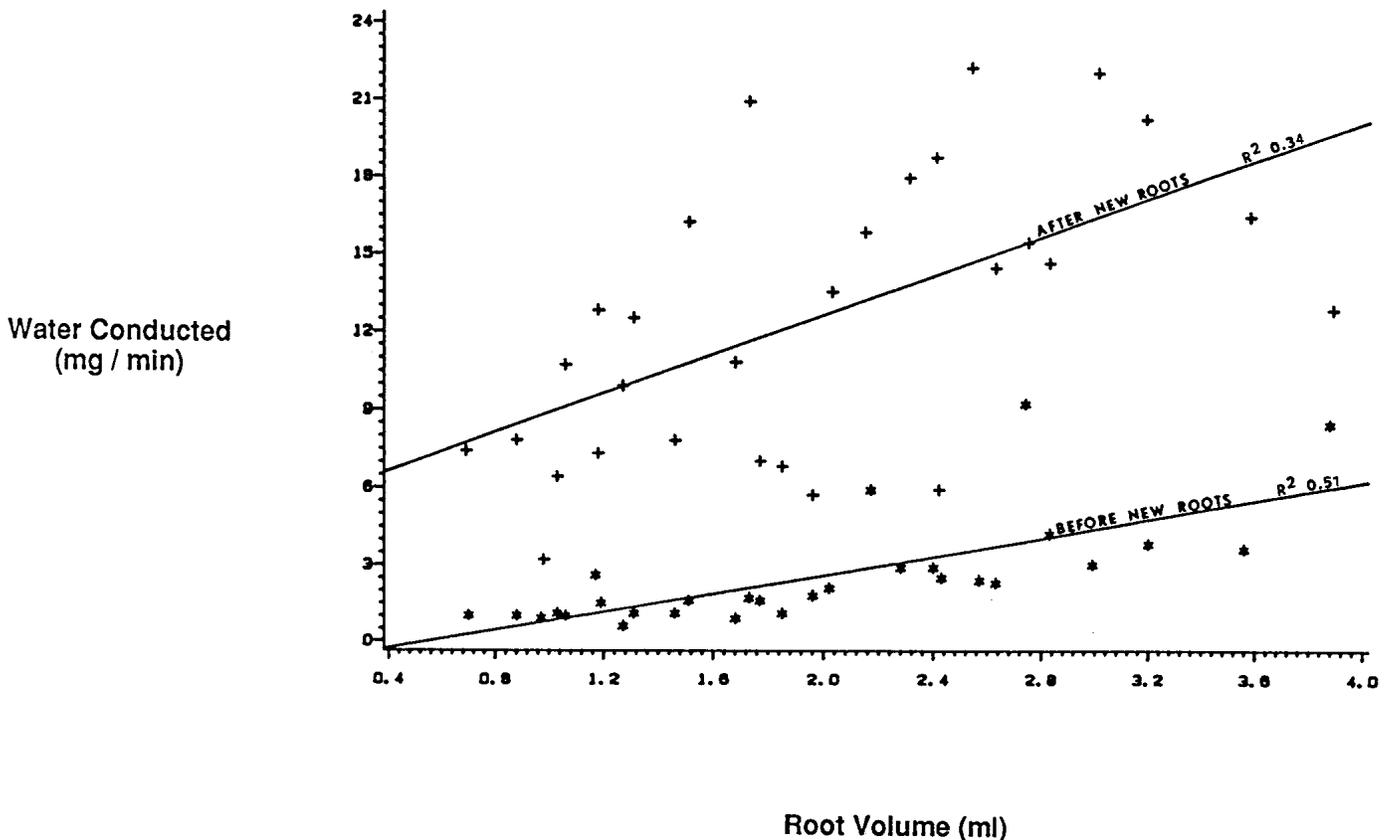

Figure 5.3—*Water conducted by whole root systems of loblolly pine as a function of their root system volume and root growth status. (Hydraulic conductivity was measured at a pressure of 0.2 MPa and a temperature of 20°C in an apparatus similar to that shown in Figure 5.4.) Seedlings in the "before-new-root-growth" group were matched in pairs for root volume to those in the "after-new-root-growth" group. The before new root growth group was tested immediately after cold storage, whereas the other group was potted in sand and held in the greenhouse for 28 days at 20°C prior to testing.*
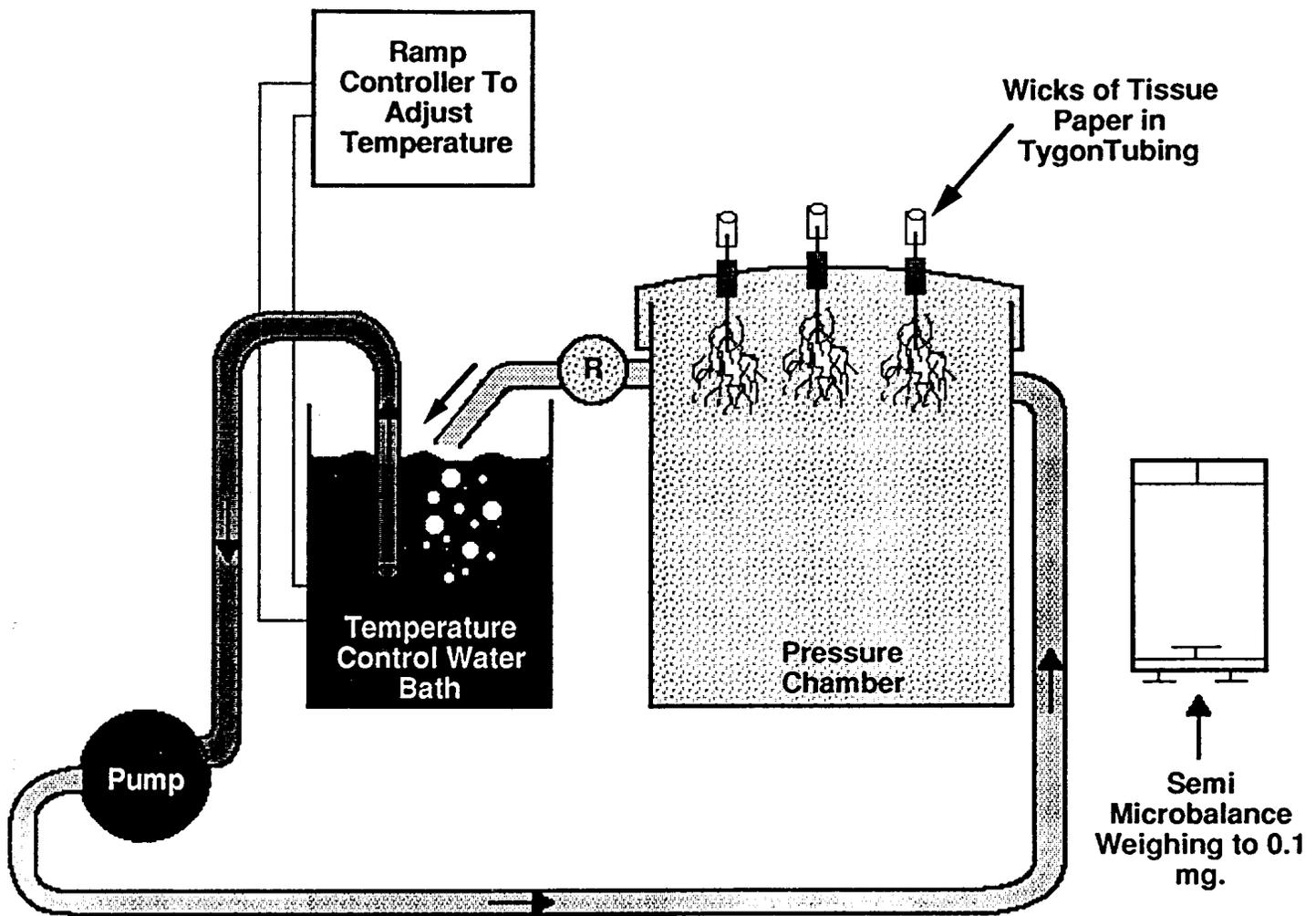
Figure 5.4--*An apparatus for assessing the hydraulic conductivity of seedling root systems. Seedling roots are washed free of soil and detopped about 5 cm above the root collar. The lower shoot is placed through a screw type pressure fitting in the lid of the pressure chamber that includes a custom made silicone rubber washer under a metal washer and cap. As the cap fitting is tightened the metal washer compresses the silicone rubber washer facilitating a water-tight seal. The pressure chamber lid is then placed in the chamber which is full of water. The pressure of the water around the roots is set at the regulator (R) on the outflow side of the chamber and is caused by pumping aerated water from a controlled temperature bath into the closed chamber. A ramp type programmable controller is used to control the temperature of the water bath, which is either cooled by refrigerant circulated through immersion coils or warmed by immersion heaters. The root is allowed to equilibrate for 15 minutes. Then the stump is wiped dry, and a preweighed wick is placed on the stump. At five minute intervals the wicks are replaced, and the wet wicks are weighed to 0. 1 mg. Conducted water is determined by subtracting dry wick weight from wet wick weight. The pressure chamber used was modified from a common pressure cooker.*

open), then one can account for 68 percent of the variation in water use (Figure 5.9A). In addition, there is an important interaction with root development. Figure 5.9B shows a regression of needle area/new root area against water use. Note that on the left-hand side of the figure, where ratios favor new root area, there is maximal water usage. On the rest of the graph, water use is limited by low conductance of poorly balanced seedlings (ratio of needle area to new root area too high). Further interactions occur when reduced conductance limits currently available photosynthates and thereby new root growth.

The nature of the various morphological and physiological interactions discussed above can cause estimates of the effect of root size on the rate of water uptake under pressure (Figure 5.4) to differ from the estimate of the effect of root size on water use by intact seedlings. Thus to estimate effects of root parameters alone, studying the rate of water uptake under low pressures in an apparatus such as that shown in Figure 5.4 is appropriate. For studying interactions between transpiration and uptake, studies on intact seedlings where water use is quantified by weight loss of potted seedlings and transpiration mea-

sured by diffusion porometer (e.g., Figures 5.8-5.9) are preferable. Water flow sensors such as the Dynamax sensor used in Figure 5.5 can also be used to characterize water use in intact trees.

5.7 Seedling Carbohydrate Management During Establishment

When a seedling is under moisture stress, both leaf conductance and rate of photosynthesis are reduced. This leads to a reduction in reserve carbohydrates and currently available photosynthate, the latter of which is considered to be the primary energy source for root growth in some species (van den Driessche 1987, Phillipson 1988). This was discussed clearly in a recent review of seedling establishment by Reitveld (1989). The take home messages for purposes of this discussion are twofold: 1) the period of seedling establishment can be lengthened by moisture stress and depletion of carbohydrate reserves which limit root growth (Kaufman 1968); and 2) the peri-

od of establishment characterized by altered water and carbohydrate status can last more than one year (Baldwin and Barney 1976, Orlander 1986).

5.8 Water Availability in Drying Soils During Establishment

Without precipitation, the soil water potential around the roots will continue to decrease causing the plant's equilibrium water potential (measured predawn) to likewise become more negative. In this scenario, progressively lower root water potentials are necessary to initiate flow (Faiz and Weatherly 1978). Increasingly negative water potentials can cause roots to shrink away from the soil, causing even higher resistance to water uptake.

5.9 New Root Growth and Root System Hydraulic Conductivity

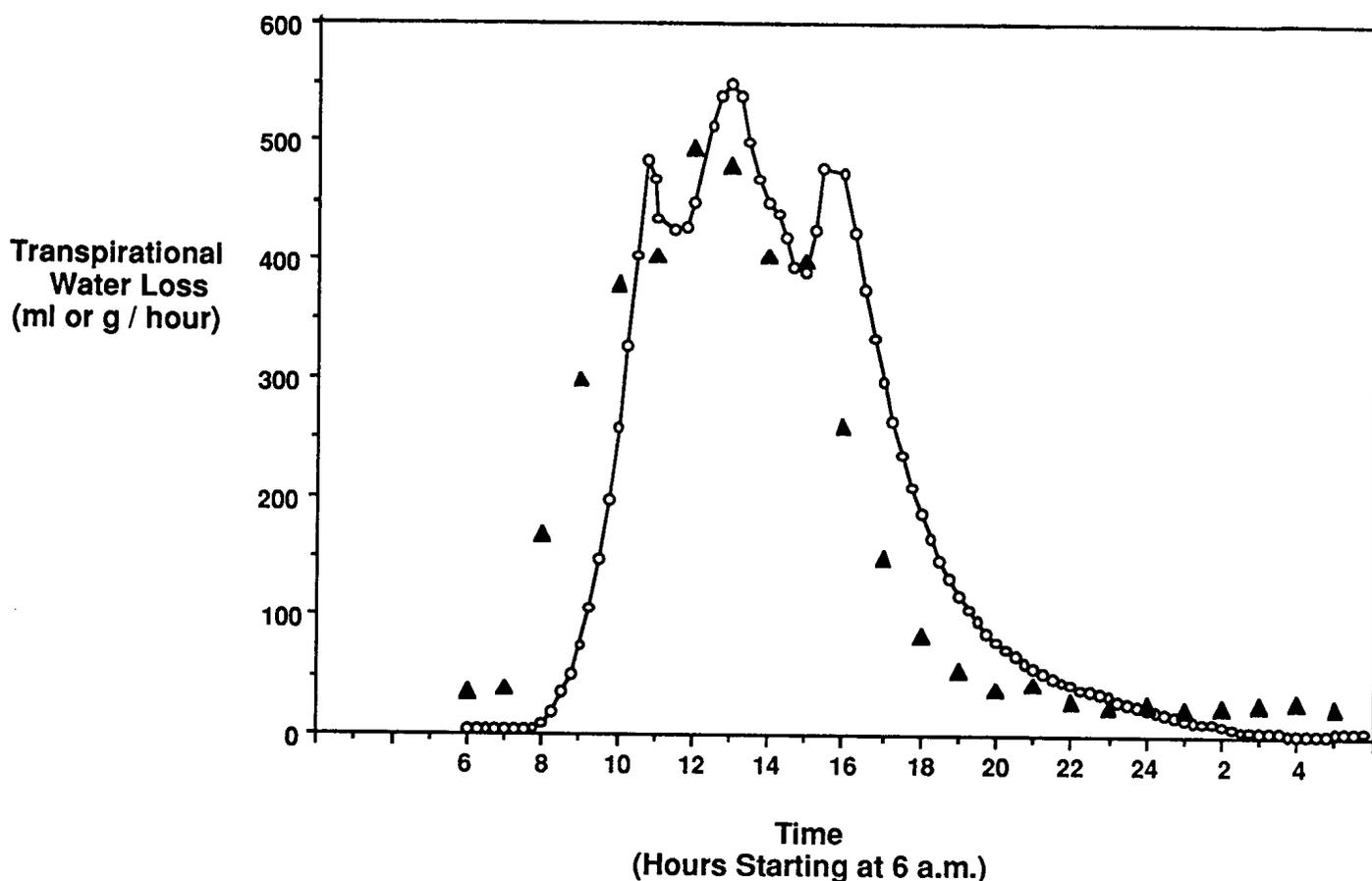Root growth after planting improves water uptake in sev-

Figure 5.5—Transpirational water (?) measured as weight loss and water uptake (O) measured as flow through the main stem of a 6.0 cm dbh loblolly pine sapling. Flow through the stem was measured with a Dynamax sensor (Dynamax Inc., Houston, Texas). For this day, the sensor overestimated flow by 0.7%. In order to attain this low error level, insulating foam on the sensor was cleaned and dried weekly. The two curves are out-of-phase by approximately 2 hours; this effect is caused by transpiration building a negative hydraulic pressure gradient in the stem prior to the beginning of flow. Conversely, that gradient caused flow to continue until water potentials came to equilibrium many hours after stomatal closure.
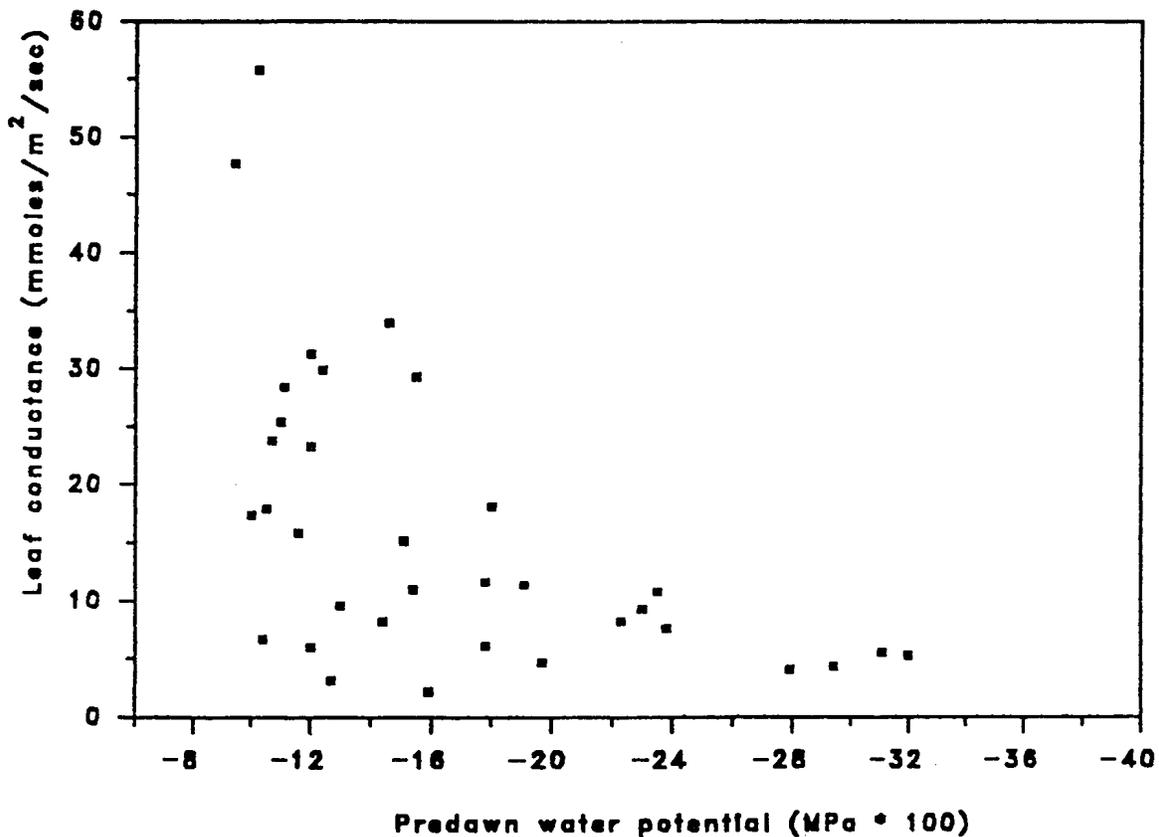
Figure 5.6—*Relationship between leaf conductance and predawn seedling water potential. In order to create a variation in stress levels, a group of seedlings was irrigated with tap water, another group with an aqueous solution of polyethylene glycol (molecular wt. 6000) at an osmotic potential of 0.3 MPa, and another group with aqueous PEG at 0.6 MPa. Seedlings were brought to field capacity, placed with their pots in plastic bags, with a rubber septum on each bag. Each day at the same time, a pot was weighed, water use calculated, and that amount of tap water added to the surface of the soil in the pot by inserting a syringe needle through the septum. Water potential was measured predawn with a pressure chamber (PMS Instruments, Corvallis, Oregon). Leaf conductance was measured midday with a LICOR 1600 diffusion porometer (LICOR Instruments, Lincoln, Nebraska).*

eral ways: 1) new root tips are unsuberized and highly conductive to water, 2) new root tissues are in tight contact with the soil, and 3) extension of the root system will increase the soil volume from which water can be extracted. Increased conductivity after root growth is demonstrated in Figure 5.3, indicating that after new root growth, whole root system conductivity is proportional to the number of new root tips (Carlson 1986). Thus for rapid establishment it is desirable to plant a seedling having a large root surface area to increase the availability of water prior to root growth, and to increase the number of growing root tips when the soil warms enough to promote such growth.

5.10 Considerations for Target Seedling Design, Culture and Use

Ensuring good hydraulic conduction by the root system involves almost all of the factors that lead to rapid seedling establishment (Figure 5.10). Many of these factors are discussed in detail because they must be integrated to obtain consistently good seedling survival and

growth. In the South, Weyerhaeuser Company foresters designed a target seedling 8-10 inches (20-25 cm) tall, 4-5 mm groundline diameter, with a minimum of 6 first-order lateral roots, a well developed terminal bud, and having mostly mature secondary needles. This seedling morphology was designated after close inspection of success and failure of individual seedlings on reforestation sites over a period of a few years. Since soils and climate play major roles in seedling establishment, other land owners should determine the target seedling morphology that works best on their sites and with their species. The role of research is to create nursery cultural practices that will increase the proportion of target seedlings in the crop. Research should also clarify morphology-function relationships such as root system parameters that foresters cannot easily observe when scoring plantation success. Foresters and researchers should work with nursery managers to provide the best quality results.
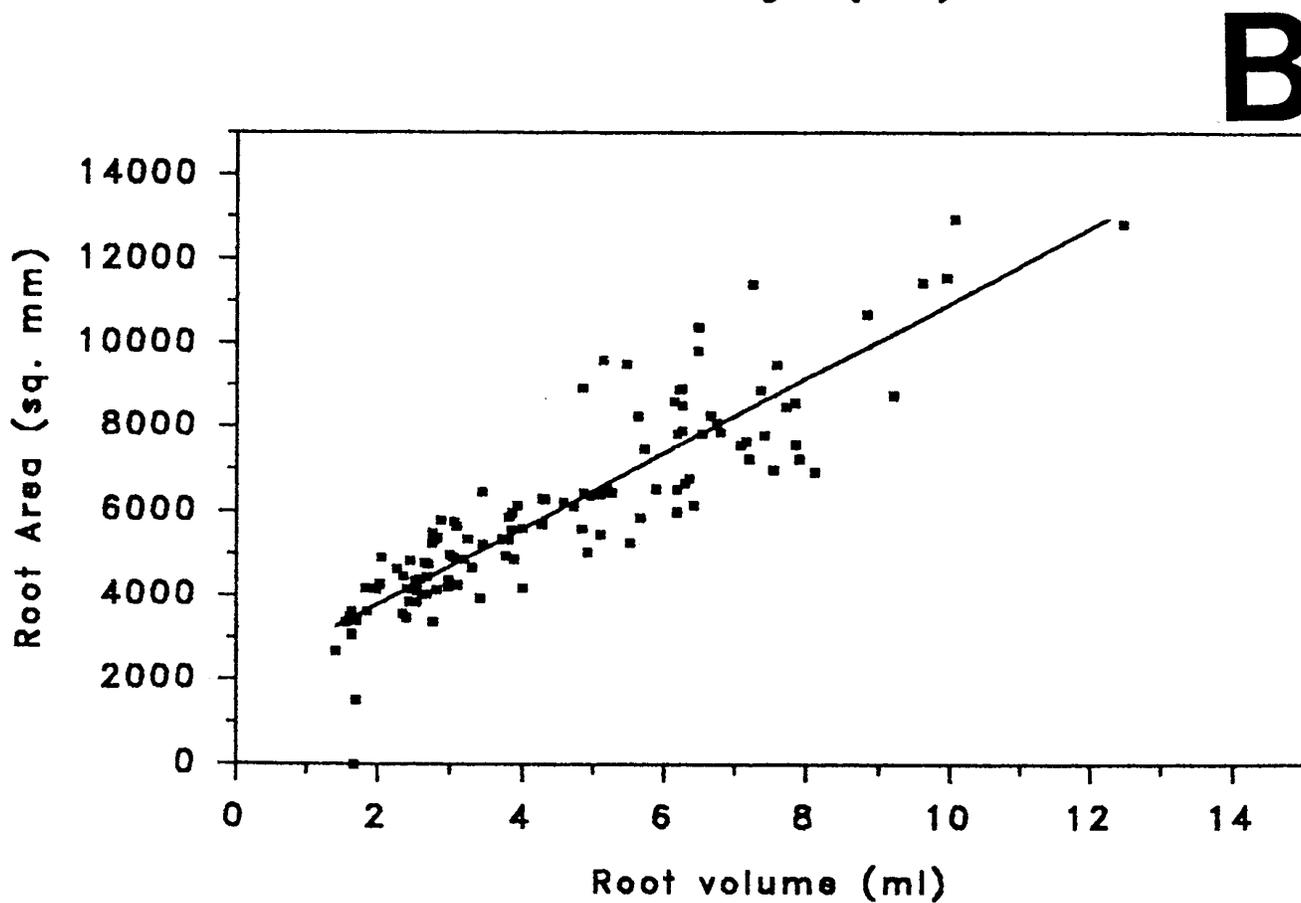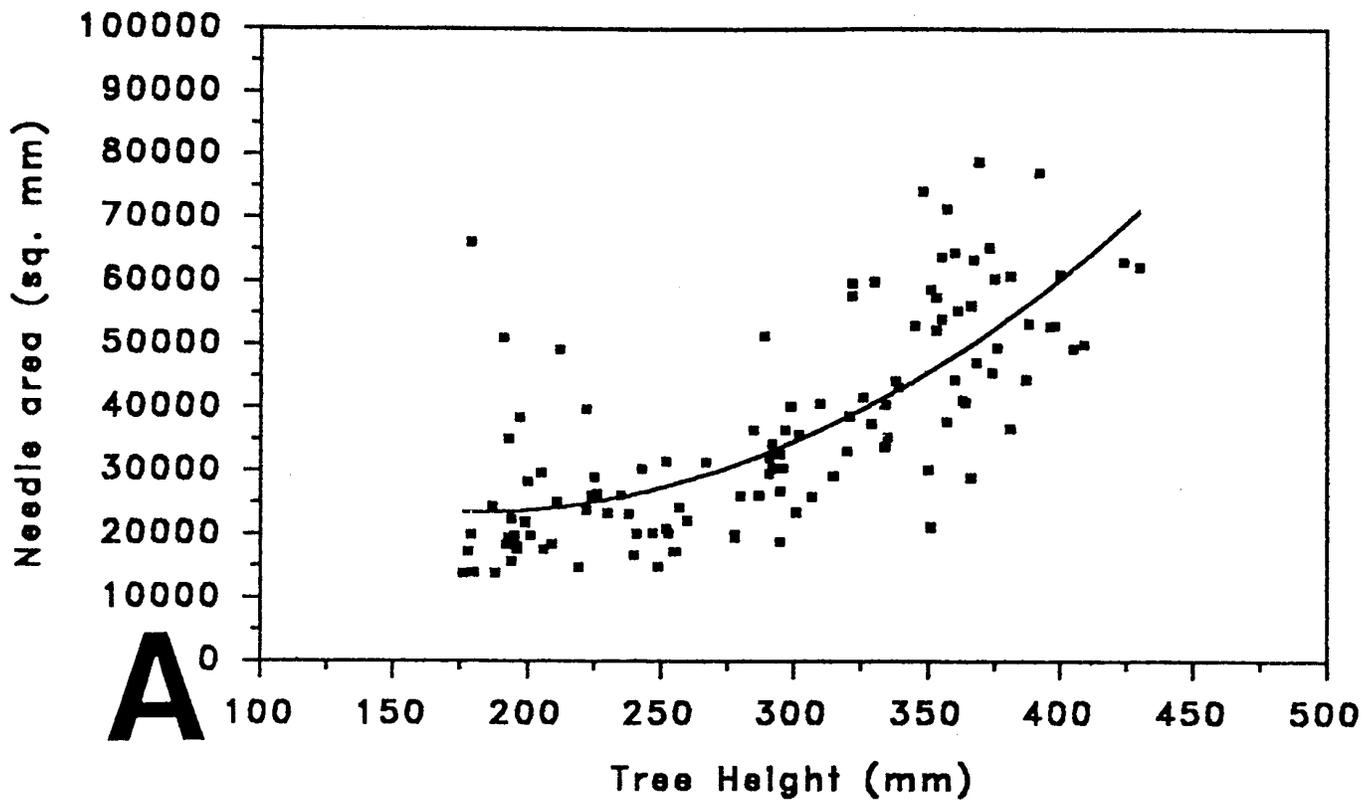
Figure 5.7—*Height was a moderately good estimator of needle surface area (R^2 = 0.71) (A) and root volume was a reasonably good estimator of root surface area (R^2 = 0.79) (B). These seedlings are from the same study as those in Figure 5.6.*
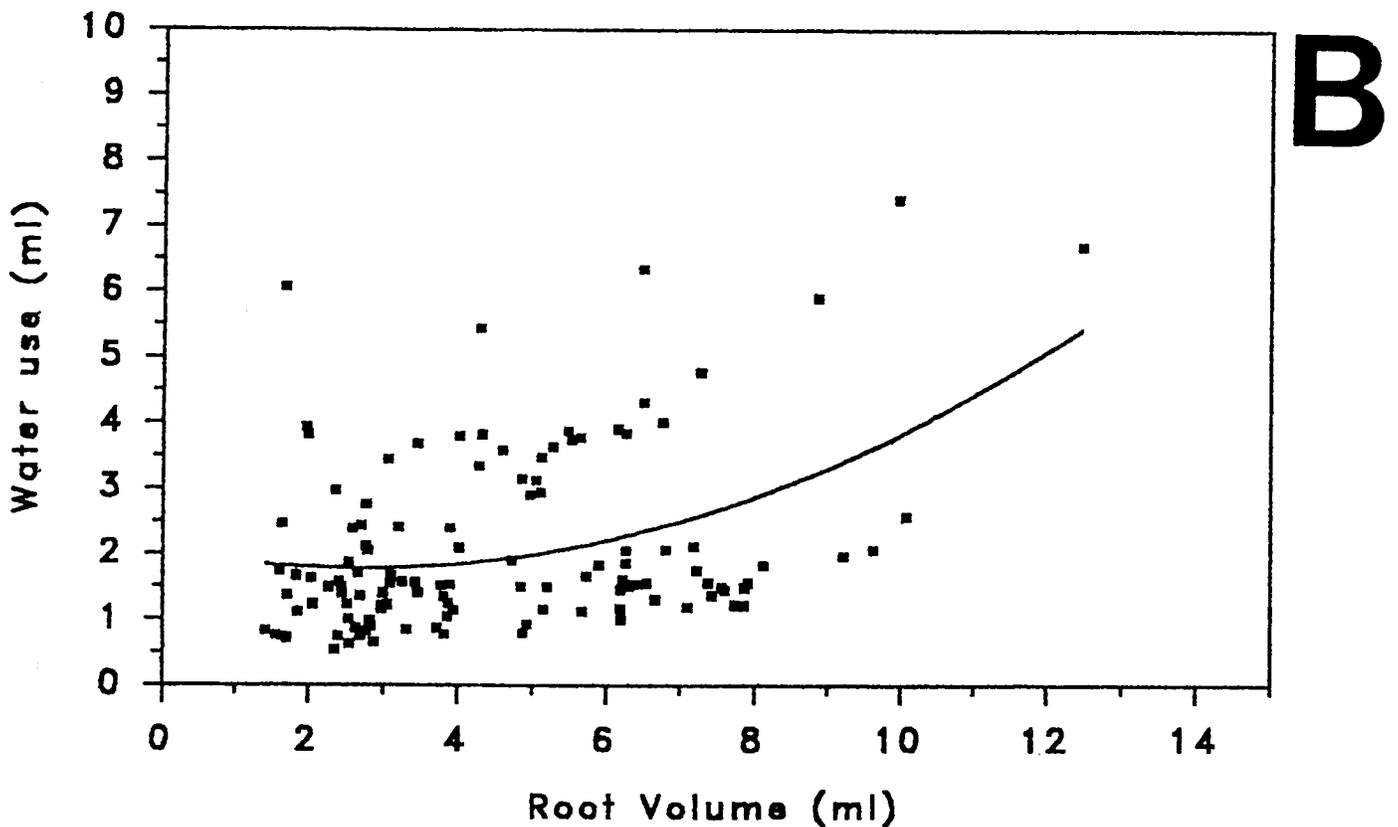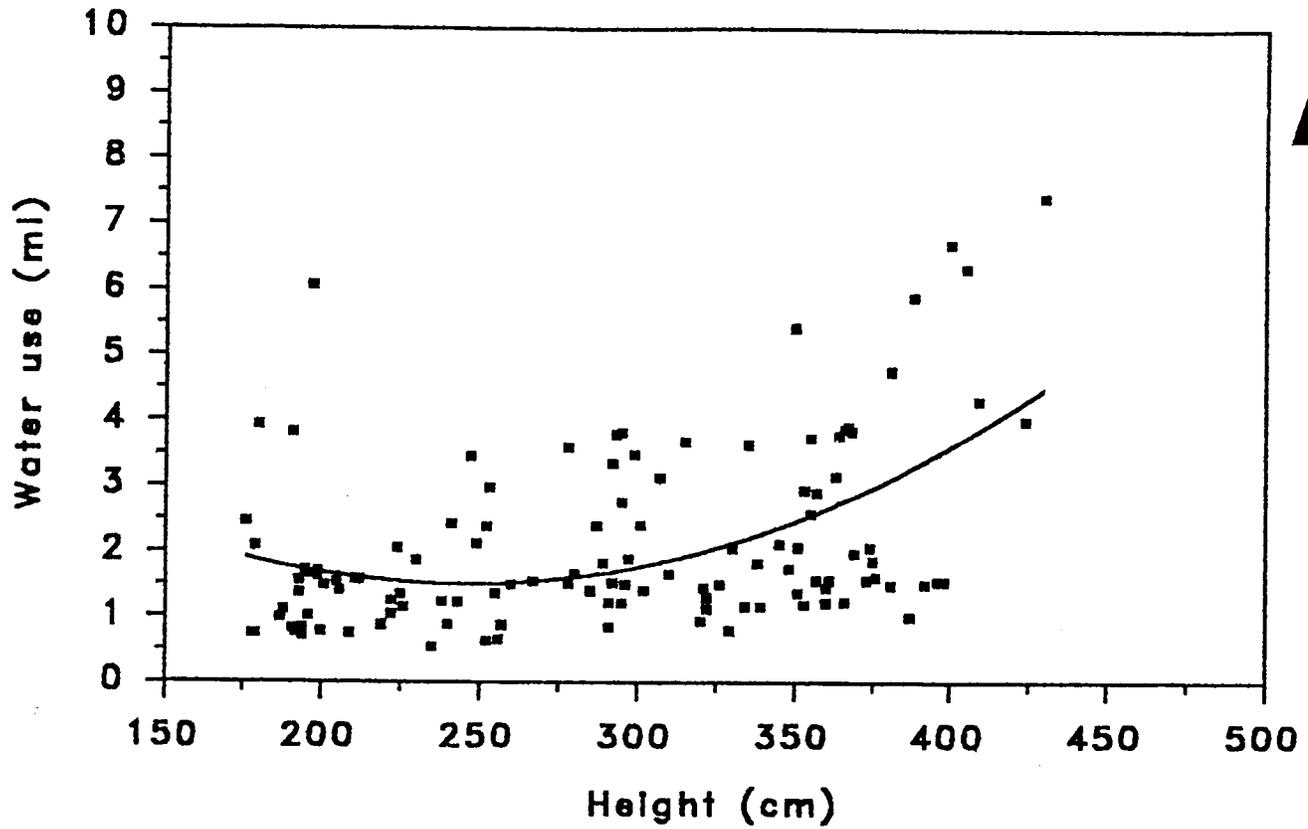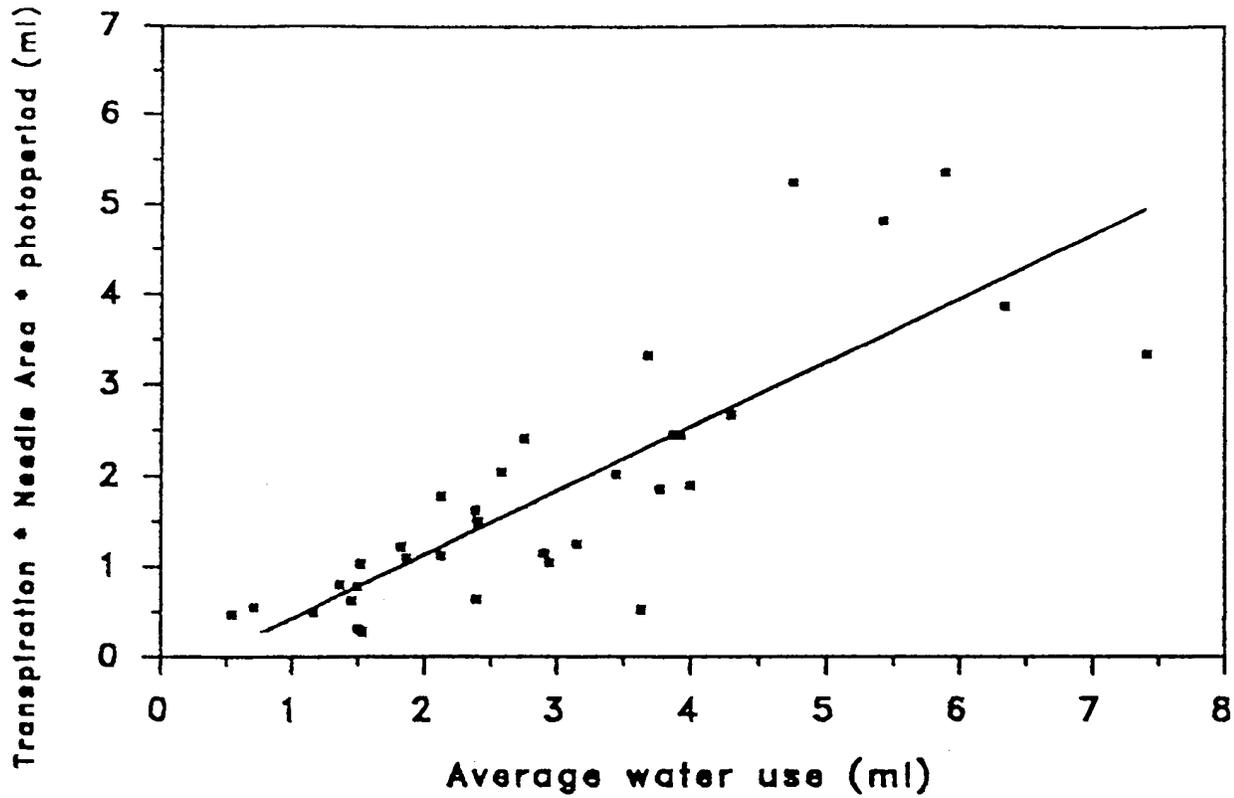
Figure 5.8—*Water use by loblolly pine seedlings kept at a field capacity: (A) Effect of seedling height on water usage ($R^2 = 0.80$), and (B) Effect of root volume on water usage ($R^2 = 0.15$). Reasons for the separation of points around the regression line and thus the low R^2 are discussed in the text. Seedlings were from the study described in Figure 5.6 and were in the group irrigated with tap water only (i.e., no artificial stress was created with PEG).*

Figure 5.9—*Interactive effects of morphological and physiological factors on seedling water use per day: (A) Water use per day Versus transpiration per unit area * needle area per seedling * photoperiod ($R^2 = 0.69$); (B) Water use per day versus needle area/new root area after 28 days. Seedlings are the same as in Figure 5.8.*
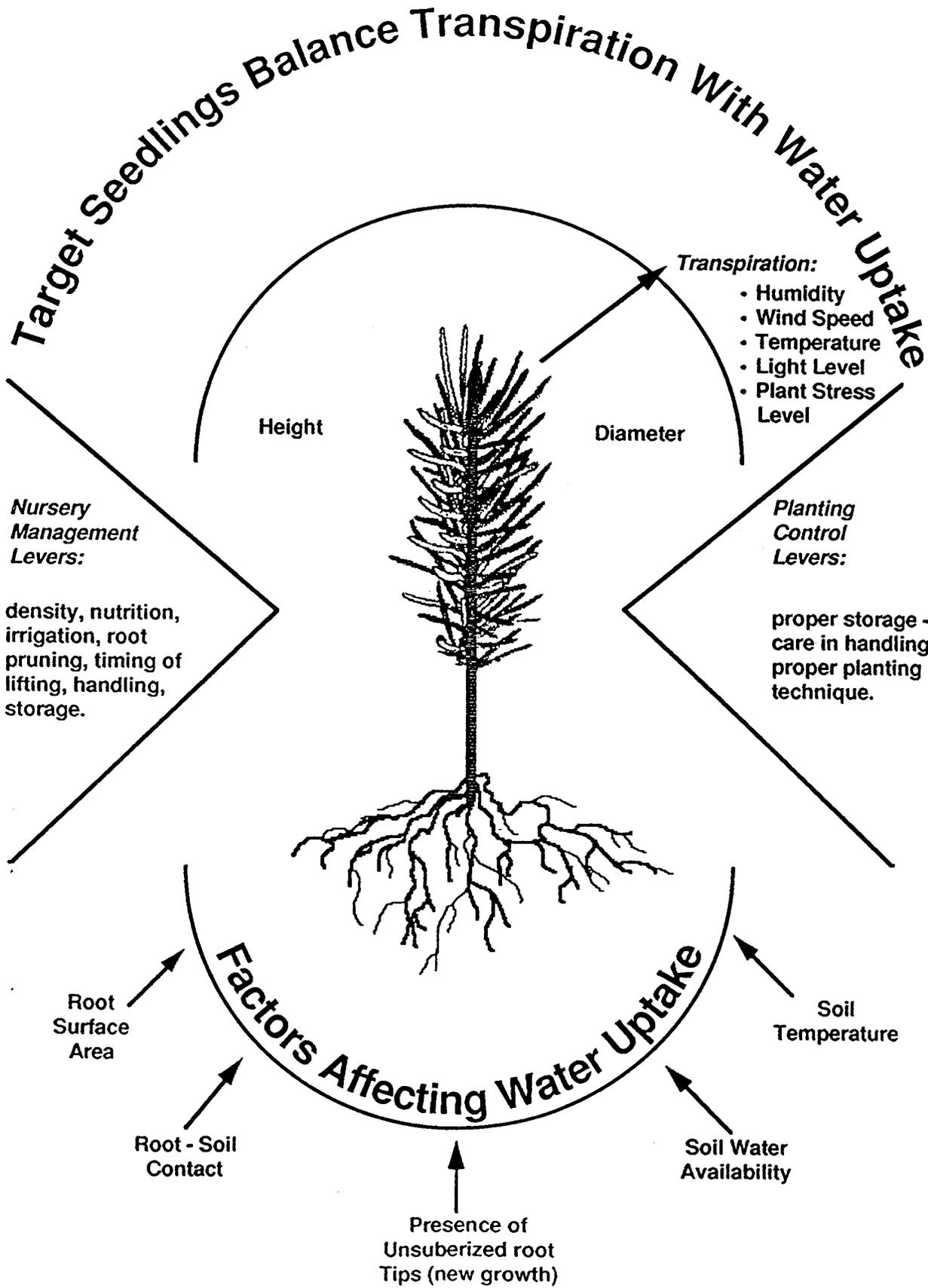
Figure 5.10—*Interactions in the Target Seedling during establishment as described in text.*

Seedling root system surface area should be maximized within the basic dimensions that can be properly planted. This can be done by management of growing density, supplying uniform irrigation and nutrition to well aerated soils, and by root pruning. It is also important that nurseries maintain adequate mycorrhizal populations to ensure well developed mycorrhizal fine roots. Target seedling specifications usually include a description of the root system supplied from the experience of the field forester and/or research done to support reforestation efforts. Displacement of the root system in water (root volume) is a rapid method of estimating root surface area ($R^2 = 0.79$) . This can be done on an individually tagged population of seedlings that can then be outplanted on various sites for survival determinations. Such information can be used to develop cultural practices that induce the development of good quality root systems. Seedling culling in the packing room should include estimates of root system quality. Root surface area and root volume are not used operationally since their measurement is too labor intensive. Presence of a minimum number of first order lateral roots (six seems to be common in both loblolly and radiata pine) and an inspection for root damage are two criteria that can be estimated quickly and can be used to determine if cultural practices and lifting machinery have been applied properly.

Height is reasonably correlated ($R^2 = 0.71$) with needle surface area and therefore can be used to predict potential for water loss by transpiration. Seedling height and diameter should be managed to fit the observed best performance guidelines supplied by the regeneration forester to fit their environment, soil, and site preparation conditions. This means that there should be a continual dialogue between field foresters and nursery staff to set goals and to measure success in achieving these goals.

it is important that seedlings be lifted at a stage of development when carbohydrate reserves are high and when storage will promote new root growth (Carlson 1985). It is also important that seedling root systems not be physically damaged or dried out during lifting, packing, storage, transport, or planting. Storage temperature and duration should minimize respiratory loss of reserves (1-3°C for species that cannot be frozen) and should minimize impairment of photosynthetic processes (McCracken 1978).

Site preparation methods should provide an even distribution of planting spots that are free from competing vegetation, have access to mineral soil, and are easily penetrable with a planting tool. Planting should provide tight contact of the root with the soil over the full length of the root system and should avoid bending the tap root into a J or L configuration (Harrington et al. 1986).

The Target Seedling approach to nursery management and reforestation provides an opportunity to integrate the forester's data on plantation success, the nursery management practices necessary to produce the desired product, and supporting research. We believe that maintaining an ongoing interaction between these parts of the reforestation system is critical to ensure production of the highest quality seedlings.

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