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Water Relations of Pine Seedlings in Relation to Root and Shoot Growth[1]

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Abstract. The effects of water stress on growth and water relations of loblolly and white pine seedlings were studied during series of drying cycles. As mean soil water potential decreased, growth of roots, needles, and buds decreased. Growth of roots during successive severe drying cycles was not uniform, however. A study of needle and root extension showed that of the total growth of roots for 3 7-day drying cycles, only 6 % occurred during the third cycle, while needle extension was uniform for the 3 cycles. The difference in response of needles and roots to drying cycles may be attributed primarily to the effect of water stress on the growing region. When subjected to a severe stress, roots matured toward the tip and became dormant, resulting in less growth during subsequent drying cycles. The intercalary growing region of needles, however, was not altered seriously enough by the stress to cause a difference in amount of growth during each drying cycle.

Transpiration of loblolly pine was lower in the second drying cycle than in the first. Needle water potential after rewatering was as high as that of control plants watered daily; root resistance was apparently not important in restricting transpiration during a second drying cycle. Needle diffusion resistance of loblolly pine, measured with a low-resistance diffusion porometer, was slightly higher during the second drying cycle than during the first. In addition, many primary needles were killed during the first period of stress. These factors contributed to the reduction of transpiration during the second drying cycle. Diffusion resistance of *Coleus* increased and transpiration ceased during the first drying cycle while water potential remained relatively high. After rewatering, both leaf resistance and transpiration returned to the control level, presumably because the stress during the first period of drying was not severe. The diffusion resistances observed for well-watered plants were 30 to 50 sec•cm^{-1} for loblolly pine, 3 to 5 sec•cm^{-1} for *Coleus*, and 4 to 6 sec•cm^{-1} for tomato. These values agree closely with those reported by other workers.

This paper reports the results of studies of the effects of variation in water potential on the root and shoot growth of pine seedlings and of the water relations of plants during successive drying cycles. Although many studies have been made of factors affecting root growth (7), few attempts have been made to study the quantitative relationships between soil water potential and root elongation. Newman (13) found that flax roots at various depths in the soil responded to the soil water potential at those depths. Parmar and Moore (18) studied germination and seedling development of corn grown on paper towels moistened with carbowax solutions of different osmotic potentials. After 4 days primary roots at −3 bars were about 80 % as long, and at −10 bars about 20 % as long as control roots grown on towels moistened with water. Root growth of corn was also reduced in soils having matric potentials of −0.3 to −0.7 bars (4). There are many reports indicating that shoot growth is reduced during periods of water stress, and several relate quantity of growth to water potential (5, 12). However, little attention has been paid to the amount of root or shoot growth or to changes in water relations during successive drying cycles. This is important because most crop plants are subjected to alternate periods of moist and drying soil.

Several studies indicate that plants behave differently subsequent to water stress from those not subjected to stress. Several investigators have shown that transpiration is lower when stressed plants are rewatered than in unstressed controls (8, 16), and many other biochemical and physiological changes occur. Miller (12) found that growth of loblolly pine was increased above the control rate when stressed plants were rewatered.

Methods and Materials

Root Cultural Techniques and Experimental Conditions. One-year old loblolly pine (*Pinus taeda* L.) and 2-year old white pine (*P. strobus* L.) seed-

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lings were used for most experiments. Seedlings were grown in containers which allowed roots to grow out from the soil mass into humid air. Each container consisted of 2 foam plastic drinking cups nested together, with the bottom removed from the inner cup. Several months after planting, root systems were developed well enough to hold the soil together, and the outer cups were removed. The exposed root systems were placed in holes in the tops of darkened, sealed, and insulated enclosures on greenhouse benches. Water in the bottom of the root enclosures was controlled to 25 ± 0.5° to keep the air surrounding the root systems essentially saturated.

Under these conditions, new roots grew out from the soil mass into the humid air while root growth within the soil mass was negligible. Loblolly pine had distinct terminal roots; lateral roots were smaller in diameter, shorter in length, but greater in number. White pine roots were similer to the terminal roots of loblolly pine. Root growth into humid air was rapid when plants were well-watered, even when the growing tip was 25 cm or more from the soil.

This technique for growing seedlings was used because it allowed easy sampling of roots for measurement of root water potential and it also allowed direct observation of new root growth. Another technique for distinguishing new and old roots was examined and is mentioned here for its possible use in other studies of root growth. New and old roots can be separated visually by staining the initial root system with a dye. To determine which dyes might be useful, bare root systems of 1-year old shortleaf pine (*P. echinata* Mill.) were dipped for 15 seconds in 1 % (wt/vol) solutions of 5 dyes. The roots were placed between wet paper towels for 15 minutes, rinsed with running water for 1 minute, and then planted in soil. After 34 days root systems were removed from the soil and examined. Two of the dyes tested, safranin-O and methyl violet, permitted excellent distinction between new and old root growth; neutral red, orange II, and India black ink were of little or no value. Although there were no apparent toxicity problems using any of the dyes, the possibility of adverse effects should be evaluated before making large-scale use of this technique.

During studies of root and shoot growth, temperature was 24 ± 2° during the day and 20 to 24° at night. Relative humidity was generally 60 to 65 %. Normal sunlight was supplemented during some studies with incandescent lights to maintain a 15-hour day-length.

Water Potential Treatments. The technique for studying root growth described above permits subjecting the plants to water stress by allowing the soil to dry out. Although a nearly constant water potential can be maintained in the soil (15) or in nutrient solutions, it is difficult to extrapolate results of growth studies using constant levels of water potential to include the more natural situation where water potential continually fluctuates.

In studying root and shoot growth of pine seedlings, drying cycles of different lengths, and therefore of different severity, were used as water potential treatments. Seedlings were subjected to 4 treatments consisting of daily watering, 4 mild drying cycles, 3 moderate cycles, and 2 severe cycles during a treatment period of 20 days. Soil water potential measurements were made daily for each treatment, except that the water potential of soil rewetted daily was measured at several-day intervals. The mean soil water potentials for the treatment period ranged from −1.2 to −6.8 bars. The minimum soil water potentials in the most severe treatment were −16.3 bars for loblolly pine and −15.9 bars for white pine. Growth was related to soil water potential rather than to plant water potential because collection of samples for plant water measurements would have removed too much leaf area. The relationship between plant and soil water potential was determined in other seedlings.

Twenty-four uniform loblolly pine and white pine seedlings were selected for each water stress treatment. Root growth was measured on all seedlings. Half of the loblolly pine seedlings were selected for measurement of needle growth and half for terminal bud extension in addition to measurement of root growth. Needle and bud measurements were made during the second flush of growth. Since no needle or bud growth of white pine occurred during the treatment period, only root growth of this species was observed.

Terminal bud and needle growth was determined by measuring change in length of the bud or 3 selected needles on each seedling during the treatment period. Roots extending from the soil mass at the end of the treatment period were considered to be new root growth. Because of injury from insects or handling, some measurements were discarded. Useful measurements of bud or needle growth were made on 8 to 11 seedlings, while root growth was observed on 17 to 21 seedlings.

Measurement of Water Potential. The Richards and Ogata (20) thermocouple psychrometer technique was used for most measurements of water potential. Corrections of leaf measurements were made for errors caused by heating of respiration and by leaf diffusion resistance (6). Resistance corrections were 7.6 % for loblolly pine, 11.3 % for white pine, 4.8 % for tomato (*Lycopersicon esculentum* Mill. var. Manalucie), and 4.6 % for *Coleus* (*Coleus blumei* Benth.) (6). The correction for *Coleus* was estimated from tomato and sunflower values.

Measurements of root water potential were made in small psychrometer chambers using single root tips about 4 cm long. Errors caused by heating of respiration were low enough to be ignored. Corrections for diffusion resistance were not made; root tips lack the well-developed waxy layer which is found on leaves, and therefore resistance is not likely to be as great. Satisfactory measurements of root water potential could not be obtained on older roots which had only a small white growing tip or were dormant. Soil water potential measurements are free from these errors, since neither heating due to respiration nor diffusion resistances are important. Micro-organisms in the soil can cause only a negligible amount of heating in the chamber.

Measurement of Leaf Diffusion Resistance. To study diffusion resistance of the leaf surface, a modified form of porometer first designed by Wallihan (26) was used to measure rate of evaporation from leaf material. The modifications in design and operation were suggested by R. O. Slatyer (Division of Land Research, CSIRO, Canberra, Australia). These changes included stirring the air inside the porometer with a small fan and use of a desiccant to dry the air after each reading. Stirring reduces air resistance and makes the porometer more sensitive to changes in leaf resistance. Resistance of pine needles was measured by holding 10 needles together with modeling clay and inserting them into the chamber through a small hole. Resistance of the terminal 5 cm of needles was measured. All resistance measurements were made on leaves or needles attached to the plants.

Experiments involving measurements of leaf diffusion resistance were performed in a growth chamber with a 12-hour light period beginning at 9 AM. Day and night temperatures were 24° and 18.5°, and day and night relative humidities were 60 % and 70 %. Transpiration was observed by measuring the decrease in pot weight during the 12-hour day period. Samples for measuring plant water potential were collected at 9:30 AM. Diffusion resistance of loblolly pine was measured between 9:45 and 10:15 AM, tomato between 10:15 and 10:45 AM, and *Coleus* between 10:45 and 11:00 AM. Fifteen pine and tomato plants were subjected to 2 drying cycles, and 10 plants were watered each evening as controls; 6 *Coleus* plants were allowed to dry, with 4 plants as controls.

Results

Comparison of Plant and Soil Water Potential. The relationships between plant and soil water potentials at 11:30 AM and 10:30 PM were determined for loblolly and white pine seedlings (fig 1). This figure is for loblolly pine sampled at 11:30 AM. Shoot water potential was always lower than root water potential, and, except at low soil water potentials, root water potential was also lower than soil water potential. At soil water potentials above −12 bars, shoot potentials were as much as 4 bars lower during the day than during the night. Root values were also lower during the day by about 1 bar. At lower soil water potentials, however, no diurnal shift in shoot or root potential occurred, probably because stomates did not open enough during the day to cause a measurable decrease in water potential. White pine relationships between plant and soil were quite similar to those of loblolly pine.

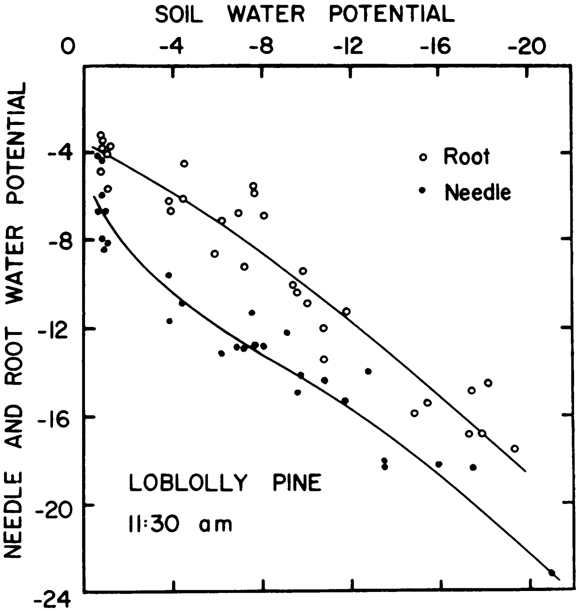

FIG. 1. Relationships between plant and soil water potentials for loblolly pine sampled at 11:30 AM. White pine had relationships which were similar to those shown for loblolly pine.

Effect of Soil Water Potential on Root and Shoot Growth. The influence of soil water potential on growth is shown in figures 2 and 3. The growth in dry weight of roots and in length of roots, needles, and buds was reduced significantly (P = 0.05) by a decrease in mean soil water potential. The dry weight of new white pine roots was more than twice that of loblolly pine in all treatments, although the initial root systems were more similar in weight: loblolly pine root systems weighed 4 to 5 grams, and white pine root systems weighed 6 to 7 grams. The measurements of a reduction in needle and terminal bud extension during water stress confirm those of Miller (12).

Root and Needle Growth During a Series of Drying Cycles. Although no measurements were made during the treatment period, it was observed in the study of root and shoot growth that root growth was not equal in successive drying cycles. Particularly in the more severe treatments more growth of roots occurred during early drying cycles than in the latter cycles.

To confirm this observation, 5 seedlings of each species were subjected to each of 3 watering regimes: daily watering for 21 days, 3 5-day drying cycles, and 3 7-day drying cycles. Lengths of 3 young needles on each seedling were measured at the beginning of the study period. After each drying cycle needles were remeasured, and lengths of selected roots were carefully observed. Plants watered daily were measured at 7-day intervals. After 5 days of drying, needle water potentials were in the range of −10 to −15 bars, and after 7 days between −15 and −20 bars. The growth during each drying cycle or measuring period was then expressed as a percentage of the total growth for the 3 periods.

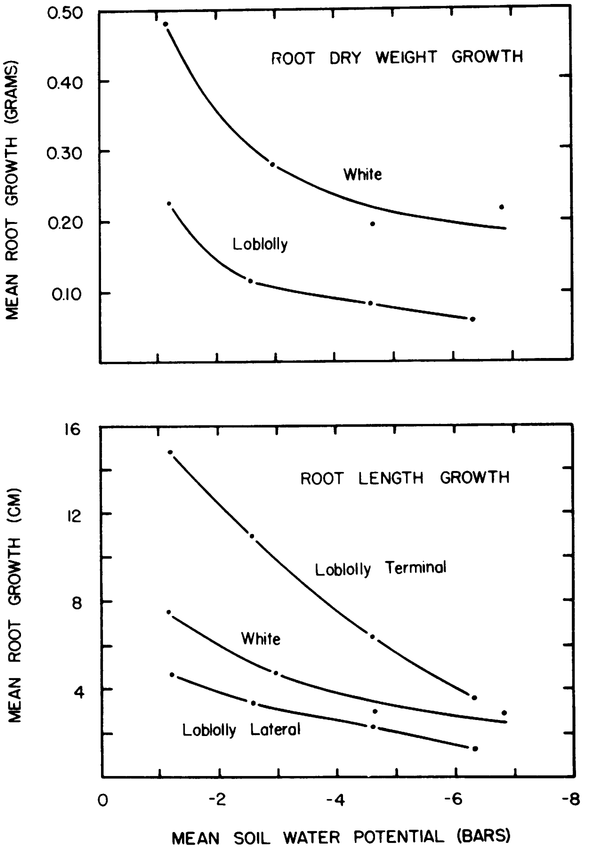

FIG. 2. Effect of mean soil water potential on root dry weight growth (top) and root length growth (bottom). Measurements were made on roots growing from the soil mass into humid air (see text). The treatment period was 20 days.

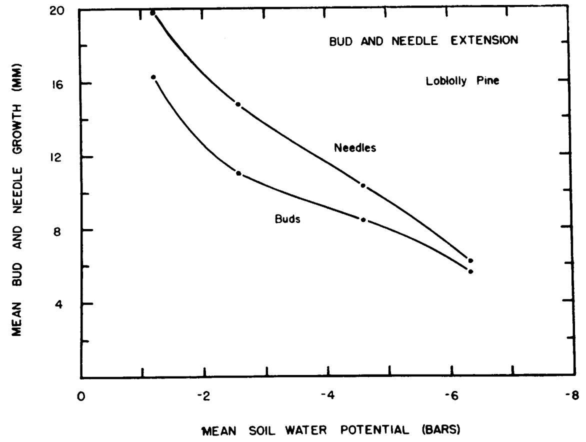

FIG. 3. Effect of mean soil water potential on needle and bud extension of loblolly pine. The treatment period was 20 days.

Figure 4 shows the mean daily growth of needles and the percentage of the total growth during each drying cycle. Growth decreased as the severity of the watering regimes increased, confirming the observations given in figure 3. Needle growth of plants watered daily was reduced during the third measuring period. Since these needles grew rapidly, the reduction in growth reflects a maturation of the needles. In the most severe watering regime (7-day drying cycles), however, growth of needles was uniform for each of the 3 periods.

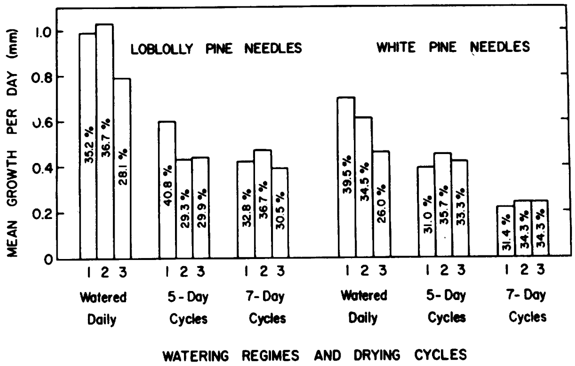

FIG. 4. Mean daily needle growth of loblolly and white pine seedlings during each of 3 drying cycles in 3 watering regimes. Plants watered daily were measured at 7-day intervals. Three needles were measured on each of 4 or 5 seedlings per watering regime. Percentages refer to the amount of growth per drying cycle as a percentage of the total growth during the 3 cycles. These values total to 100 % for each watering regime. Drying cycle differences were significant (P = 0.05) for plants watered daily (both species) and for plants subjected to 5-day drying cycles (loblolly pine only).

Root length growth responded differently to the 3 drying cycles (fig 5). In the more severe watering regimes much less root growth occurred during the second or third drying cycle than during the first. When expressed as a percentage, only 5.9 % of the root growth of loblolly pine and 6.1 % for white pine occurred during the third drying cycle of plants watered every 7 days. Growth also decreased as the severity of drying increased as reported in an earlier experiment (see fig 2, bottom).

Water Potential, Transpiration, and Leaf Diffusion Resistance During Drying Cycles. Preliminary work showed that during an initial drying cycle transpiration of loblolly and white pine decreased at a steady rate, nearly ceasing after a period of

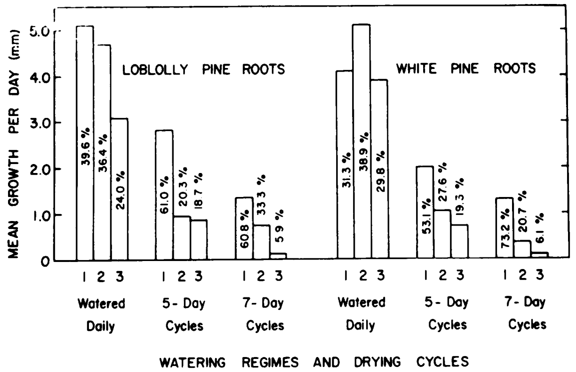

FIG. 5. Mean daily root length growth of loblolly and white pine seedlings during each of 3 drying cycles in 3 watering regimes. Plants watered daily were measured at 7-day intervals. One to 8 terminal roots were measured on each of 2 to 5 seedlings per watering regime. Percentages refer to the amount of growth per drying cycle as a percentage of the total growth during the 3 cycles. These values total to 100 % for each watering regime. Drying cycle differences were significant (P = 0.05) in all watering regimes except white pine seedlings watered daily.

7 or 8 days. After rewatering, however, transpiration increased to only one-third of the rate at the beginning of the first drying cycle and remained at this rate for several days before decreasing. It was suspected that reduced transpiration during the second drying cycle might result from increased stomatal resistance. A study of the effects of 2 drying cycles was made on 3 species: 1-year old loblolly pine grown in foam plastic cups, 3-week old tomato, and 5-week old *Coleus* in clay pots. Measurements included needle or leaf water potential, transpiration (pine and *Coleus* only), and leaf diffusion resistance.

The results for loblolly pine and *Coleus* are shown in figures 6 and 7. Although water potential of loblolly pine had decreased to −20 bars after 7 days, complete recovery to the control level occurred within 24 hours. This recovery supports the conclusions drawn from an experiment in which relative resistances of root systems to uptake of water were measured. Although root resistance of loblolly pine increased after 5 or 7 days of drying, resistance was no greater after 2 or 4 days of rewatering than that of control plants watered daily.

Transpiration of drying plants followed the change in water potential during the first drying cycle. At a water potential of −15 bars, transpiration nearly ceased (sixth day of drying). Transpiration did not recover after rewatering, however. Although water potential of the needles was as high as that of controls, transpiration increased to only about one-third of the control rate, remaining at this level for 5 days. Needle diffusion resistance increased during the initial drying cycle as water potential and transpiration decreased. After rewatering resistance decreased, but the average resistance during the first 5 days after watering was significantly greater than that of controls. Pallas *et al.* (16) also found that stomatal activity was reduced for several days after rewatering. The response of tomato to drying (not shown) was quite similar to that of loblolly pine.

A reduction in transpiring surface also contributed to the reduction in transpiration of pine. Primary needles of some plants were killed as a result of the first drying cycle. To test their importance, primary needles were removed from the control plants at the end of the study period. Mean transpiration on the next 3 days was 5.7, 4.8, and 5.8 gms/plant/12-hour day. Thus the loss of primary needles reduced transpiration about 20 %. There was no difference between treated and control plants in loss of water from the stems.

The response of *Coleus* was nearly the same for the 2 drying cycles (fig 7). Unlike the transpiration of loblolly pine, transpiration of *Coleus* returned to the rate of control plants after watering; resistance also decreased to the control level. An

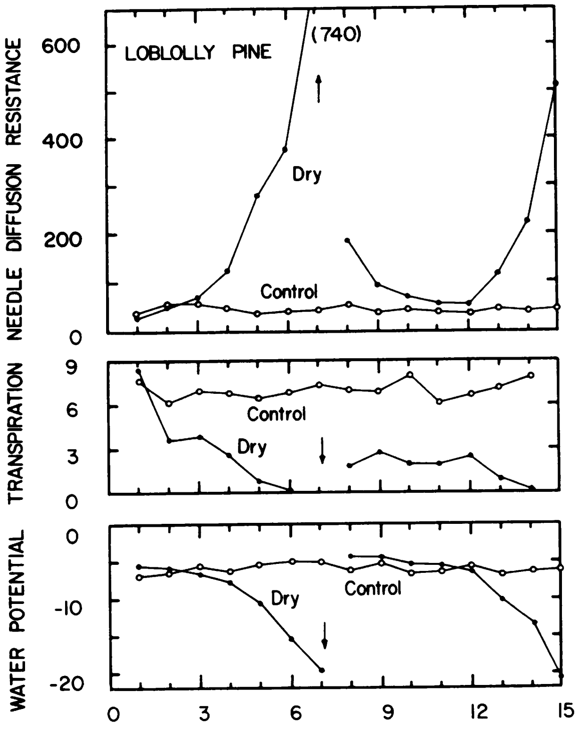

FIG. 6. Water potential, transpiration, and needle diffusion resistance of loblolly pine seedlings. Test plants were watered at the beginning of the study period and after 7 days of drying (arrow). Control plants were watered daily. After the initial drying cycle, water potential of test plants returned to the control level, but transpiration remained lower and needle diffusion resistance remained higher. Water potential is in bars, transpiration in grams per 12-hour day period, and resistance in sec•cm^{-1}.

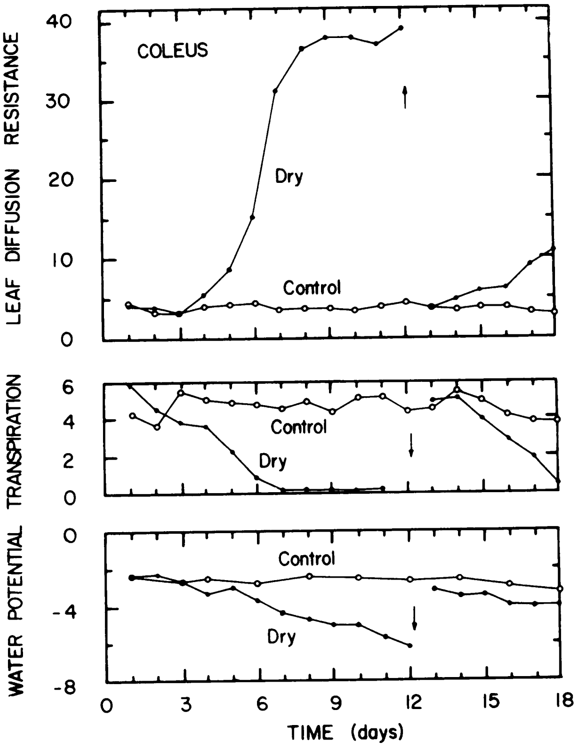

FIG. 7. Water potential, transpiration, and leaf diffusion resistance of *Coleus* plants. Test plants were watered at the beginning of the study period and after 12 days of drying (arrow). Control plants were watered daily. After the initial drying cycle, water potential of test plants remained slightly lower than the control level, but transpiration and leaf diffusion resistance returned to the control level. Water potential is in bars, transpiration in grams per 12-hour day period, and resistance in sec•cm^{-1}.

interesting difference between pine and *Coleus* is that leaf diffusion resistance of *Coleus* reached a plateau at approximately 38 sec•cm^{-1} and transpiration stopped even though the leaf water potential had fallen only to −4 bars. Apparently stomates of *Coleus* closed at a high water potential, preventing further transpiration or a rapid decrease in water potential. The clay pots were partially enclosed in polyethylene film to prevent excessive evaporation. In a preliminary experiment with the pots unprotected, drying was much more rapid and wilting occurred in several days.

Discussion

Figure 1 describes the response of the water potential of pine seedlings to drying of the soil during a single drying cycle. Under natural conditions with all roots of a transpiring plant growing in contact with the soil, water potential decreases from the soil, through the root and shoot of the plant, to the atmosphere. The data shown in figure 1 indicate that when roots were grown from the soil mass into humid air, deviations from this expected gradient were not great. Water potential was measured on roots not directly a part of the pathway for water movement from the soil to the shoot, yet over the upper portion of the range of soil water potentials measured, root water potential was lower than soil water potential. At lower potentials transpiration decreased because of stomatal closure, and therefore the gradient from the soil through the plant is less steep. Under these conditions water may be absorbed from the humid air by the dry roots, causing root water potential to be slightly higher than soil water potential in some cases. The method of growing roots into humid air, however, does not result in serious departures from the plant-soil water relationships occurring in a more natural situation.

It would be desirable to know the relationship between plant and soil water potential during a second or third drying cycle. However, variability resulting from different rates and degrees of drying was too great to permit detection of differences between the first and second cycles. Also, measurements of root water potential during the second drying cycle were unreliable, probably because of death of cortical cells. The layer of collapsed cortical cells may act as a sink for water vapor. Few measurements of root water potential have been reported. Slavikova (22, 23, 24, 25) used changes in refractive index of sugar solutions to measure water potential ("suction force") in roots.

Water stress can decrease growth directly by reducing turgor and by reducing photosynthesis and translocation. It may also have a more indirect effect on growth. Root growth during a series of drying cycles (fig 5) was much less uniform than needle growth. Apparently the initial period of stress, when severe enough, caused a tendency for roots to mature toward the tip and become dormant, and growth during subsequent drying cycles was reduced. Dormancy of roots also occurred after a single period of severe stress, even when watering was resumed on a daily basis. When the stress was not too great, some of the dormant tips became active again after several weeks.

Leshem (11), reporting a similar dormancy in Aleppo pine (*P. halepensis*) roots, found that suberization around the initials in the meristem followed the pattern of Type II described by Plaut (19). Oppenheimer and Kessler (14) also observed suberization of pine root tips as a result of water stress. A brief examination of dormant loblolly and white pine roots suggests that suberization of these species also conforms to Type II of Plaut. Type II suberization consists of a suberized layer of cells in the root cap and in the secondary endodermis, connected by a bridge across the cortex. Cells outside the suberized layer often turn brown, collapse, and die.

A different type of meristem is found in needles.

While root extension is entirely an apical phenomenon almost all growth in length of needles results from meristematic activity in intercalary regions near the base (1). It is not known whether growth of needles during this study resulted from enlargement of pre-existing cells or from continued meristematic supply and expansion of new cells. In either case, the rather uniform growth of needles during successive periods of water stress (fig 4) suggests that no structural modifications resulting from water stress were serious enough to inhibit length growth. Thus in terms of morphological changes, roots of loblolly and white pine seedlings seem to be more sensitive to drying than needles.

Generally, the factors which influence transpiration involve the vapor phase of water movement, and the chief regulatory mechanism in plants is change in stomatal aperture (21). Closure of stomates and a reduction in transpiration could result from a water deficit caused by a high resistance in the root system to uptake of water. However, water potential in loblolly pine needles increased to the control level shortly after rewatering (fig 6) (12). Therefore resistance in the roots to absorption of water is not an important cause for the increased stomatal resistance and reduced rate of transpiration during the second drying cycle. Uniform needle growth in successive drying cycles (fig 4) is further evidence that water absorption is not restricted.

The lack of a reduced transpiration rate after rewatering of *Coleus* plants may be attributed to the lower level of stress to which these plants were subjected. In contrast with pine and tomato, *Coleus* plants had dried to only −6 bars after 12 days. Although *Coleus* is regarded by many as a species which wilts readily, this study indicates that the cause for wilting may be excessive evaporation from the soil rather than high rates of transpiration. When soil evaporation is kept at a minimum, the plants very effectively restrict water loss and maintain a satisfactory water status.

Resistance of pine needles is quite high in comparison with other species. Well-watered loblolly pine needles have resistances of 30 to 50 sec•cm^{-1}, compared with resistances of 4 to 6 and 3 to 5 sec•cm^{-1} in tomato and *Coleus*. Gates (3) recently reported minimum resistances of 20 to 60 sec•cm^{-1} for red pine and 33 to 52 sec•cm^{-1} for white pine. Other conifers had equal or higher minimum resistances. Tomato resistances agree very closely with those of Kuiper (10), who found leaf resistances of 4.1 to 5.8 sec•cm^{-1} for tomato plants with open stomates. Minimum values of leaf resistance of sugar-beet and turnip are 3 to 4 sec•cm^{-1} (2) and of cottonwood, 4 sec•cm^{-1} (17). Thus, the observed resistance of loblolly pine, tomato, and *Coleus* are in the general range of resistances reported by other workers. The high resistance of pine needles to water loss is not surprising because the transpiration rate of pine per unit surface area is quite low (9) in comparison with other species. Low transpiration rates and high diffusion resistance of pine result from a highly cutinized surface and from sunken stomates.

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Literature Cited

1. Esau, K. 1965. Plant Anatomy. John Wiley and Sons, Incorporated, New York. Second Edition. 767 pp.
2. Gaastra, P. 1963. Climatic control of photosynthesis and respiration. In: Environmental Control of Plant Growth. L. T. Evans, ed. Academic Press, New York. p 113–40.
3. Gates, D. M. 1966. Transpiration and energy exchange. Quart. Rev. Biol. 41: 353–64.
4. Grable, A. R. and R. E. Danielson. 1965. Effect of carbon dioxide, oxygen, and soil moisture suction on germination of corn and soybeans. Soil Sci. Soc. Proc. 29: 12–18.
5. Kenworthy, A. L. 1949. Soil moisture and growth of apple trees. Proc. Am. Soc. Hort. Sci. 54: 29–39.
6. Knipling, E. B. 1966. Comparison of the dye method with the thermocouple psychrometer for measuring leaf water potentials. Ph.D. thesis, Duke University, Durham, N. C.
7. Kramer, P. J. 1949. Plant and Soil Water Relationships. McGraw-Hill Book Company, Incorporated, New York. 347 pp.
8. Kramer, P. J. 1950. Effects of wilting on the subsequent intake of water by plants. Am. J. Botany 37: 280–84.
9. Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill Book Company, Incorporated, New York. 642 pp.
10. Kuiper, P. J. C. 1961. The effects of environmental factors on the transpiration of leaves, with special reference to stomatal light response. Mededel. Landbouwhogeschool. Wageningen 61: 1–49.
11. Leshem, B. 1965. The annual activity of intermediary roots of the Aleppo pine. Forest Sci. 11: 291–98.
12. Miller, L. N. 1965. Changes in radiosensitivity of pine seedlings subjected to water stress during chronic gamma irradiation. Health Physics 11: 1653–62.
13. Newman, E. I. 1966. Relationship between root growth of flax (*Linum usitatissimum*) and soil water potential. New Phytologist 65: 273–83.
14. Oppenheimer, H. R. and B. Kessler. 1965. Mechanism of drought resistance in conifers of the Mediterranean Zone and the Arid West of the U.S.A. The Hebrew University of Jerusalem, Faculty of Agriculture, Report No. 8.

15. Painter, L. I. 1966. Method of subjecting growing plants to a continuous soil moisture stress. Agron. J. 58: 459–60.

16. Pallas, J. E., Jr., B. E. Michel, and D. G. Harris. 1967. Photosynthesis, transpiration, leaf temperature, and stomatal activity of cotton plants under varying water potentials. Plant Physiol. 42: 76–88.

17. Parkhurst, D. F. and D. M. Gates. 1966. Transpiration resistance and energy budget of *Populus sargentii* leaves. Nature 210: 172–74.

18. Parmar, M. T. and R. P. Moore. 1966. Effects of simulated drought by polyethylene glycol solutions on corn (*Zea mays* L.) germination and seedling development. Agron. J. 58: 391–92.

19. Plaut, M. 1909. Untersuchungen zur Kenntnis der physiologischen Scheiden bei den Gymnospermen, Equiseten und Bryophyten. Jahrb. Wiss. Bot. 47: 121–85.

20. Richards, L. A. and G. Ogata. 1958. Thermocouple for vapor pressure measurement in biological and soil systems at high humidity. Science 128: 1089–90.

21. Slatyer, R. O. 1967. Plant-Water Relationships. Academic Press, New York. 366 pp.

22. Slavikova, J. 1963. A critical evaluation of the determination of the root-suction force. Acta Univ. Carolinae Biologia 1963: 245–54.

23. Slavikova, J. 1963. Horizontaler Gradient der Saugkraft eines Wurzelastes und sein Zusammenhang mit dem Wassertransport in der Wurzel. Acta Horti. Bot. Pragensis 1963: 73–79.

24. Slavikova, J. 1965. Die maximale Wurzelsaugkraft als ökologischer Factor. Preslia 37: 419–28.

25. Slavikova, J. 1966. Wechselsietige Beziehungen der Wurzelsaugkraft bei einigen Komponenten der Eschenphytozonosen. Preslia 38: 15–22.

26. Wallihan, E. F. 1964. Modification and use of an electric hygrometer for estimating relative stomatal apertures. Plant Physiol. 39: 86–90.