TRANSPIRATION AND PHYSICO-CHEMICAL PROPERTIES OF LEAVES AS RELATED TO DROUGHT RESISTANCE IN LOBLOLLY PINE AND SHORTLEAF PINE[1]

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(WITH TWO FIGURES)

Introduction

In the reforestation program now being carried on by various state and federal agencies, many millions of tree seedlings are planted each year. An extremely large number of these planted seedlings are killed within the first year or two after planting. One of the major causes of the fatalities is the inability of seedlings to resist drought. If the properties involved in drought resistance of seedlings were known, and if those species and age classes of planting stock possessing such properties could be identified or developed, much better survival could be obtained in plantations of tree seedlings.

Drought resistance, the ability of a plant to endure permanent wilting without harm to subsequent development (**11**), has been induced in plants by repeated wilting and also by growing them in soil with a moisture content barely above the wilting percentage (**27, 28**). Observations on permanently wilted herbaceous plants (**27**) show that their transpiration rate may be less than one-fourth of the rate for turgid plants. Most conifers, however, do not show any external evidence of a wilted condition. Hence, in hardening conifers against drought, the wilting percentage of soil moisture must be previously determined to facilitate control of soil moisture conditions.

Although attempts have been made to correlate drought resistance with rate of transpiration, there is much evidence (**1, 2, 4, 21, 24, 32**) to support the statement of MAXIMOV and KRASNOSSELSKY-MAXIMOV (**12**) that the rate of transpiration when soil moisture is abundant cannot be used for judging drought resistance. Transpiration may be greatly reduced when soil moisture approaches the wilting percentage (**15, 19**) and the reduction may vary among plants of different morphological structure, but there appears to be no consistent relationship between drought resistance and rate of transpiration at soil moisture contents near the wilting percentage.

There is evidence of a correlation between drought resistance and bound water content of leaf tissue. KORSTIAN (**9**) found some indication of such a correlation in a preliminary study of southeastern tree species. The work of NEWTON and MARTIN (**17**) is particularly outstanding in that a very definite correlation was obtained in cereal crops and grasses between the degree of drought resistance and the bound water content. NOVIKOV (**18**) also

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found that the amount of bound water present characterized the degree of drought resistance in varieties of wheat when they were in a wilted state but not in a turgid state. He attributed an observed increase in bound water during hardening not to a decrease in total water but to physico-chemical changes in the cell contents.

Information on the relationship of osmotic pressure of cell sap to drought resistance is very conflicting. DRABBLE and DRABBLE (**3**) and LIVINGSTON (**10**) have shown that a high osmotic pressure cannot lower the vapor pressure of cell sap sufficiently to reduce water loss by transpiration to an appreciable extent. KORSTIAN (**8**) obtained evidence indicating that water absorption by plants depends on osmotic pressure, but STODDART (**25**) believes that a high osmotic pressure is a result of drought and not an adaptation to it. NEWTON and MARTIN (**17**) found that osmotic pressure was not a consistently reliable index of drought resistance. In comparing osmotic pressures of two or more species it is difficult to make a proper interpretation because in most cases it is not known whether differences are caused by different water contents or by different solute concentrations.

The primary purpose of this investigation was to ascertain whether the relative drought resistance of seedlings of two species can be determined by physico-chemical means. A secondary purpose was to obtain information on the behavior of seedlings during and after drought by a study of changes in physico-chemical properties. The approach was made by a study of transpiration, bound-water content, total water content, osmotic pressure, and calculated solute concentration in leaves of two species growing in a greenhouse under controlled soil moisture conditions. Loblolly pine (*Pinus taeda* L.) and shortleaf pine (*P. echinata* Mill.) were selected for comparison because both species occur within the same region with loblolly pine on mesic sites, and shortleaf pine on more xeric sites. The apparent adaptations of these species to different sites indicate that shortleaf pine is the more drought resistant of the two species.

Materials and methods

SEEDLINGS AND SOIL

✓ A group of vigorous one-year-old seedlings of loblolly pine and of shortleaf pine were selected at the North Carolina State Nursery and moved to a greenhouse in December, 1935. The seedlings were planted in two-gallon buckets containing Congaree silt loam, the moisture constants of which are presented in table I. A watering tube extended down the side of each bucket into a layer of crushed rock in the bottom. The buckets were covered with a double layer of oilcloth to prevent evaporation of water from the soil. Soil moisture was maintained at 30 per cent. for a month after the completion of planting to permit the seedlings to become established.

TABLE I

MOISTURE CONSTANTS FOR CONGAREE SILT LOAM

ITEM	MOISTURE CONTENT (PERCENTAGE OF DRY WEIGHT)
	%
Moisture equivalent	27.3
Wilting coefficient	14.8
Wilting percentage	7.7
Saturation percentage	53.3

DETERMINATION OF TRANSPIRATION

The gravimetric method for the determination of transpiration was selected for this work. The buckets were weighed daily to determine the weight of water lost by transpiration which was expressed in grams per gram of oven-dried leaf tissue per day.

On April 4 the seedlings of each species were divided into three groups for a study of transpiration under three conditions of soil moisture. In the first group of seedlings, the soil moisture was brought to 30 per cent. at weekly intervals. This moisture content is believed to be approximately an optimum for growth. Between waterings the soil moisture in this group rarely went below 25 per cent. In the second group, the seedlings were left unwatered, and the soil moisture was gradually decreased to the wilting coefficient. Approximately six weeks elapsed before the wilting coefficient was reached. This treatment, according to TUMANOV (**27**), should induce drought hardening. In the third group, the soil moisture was allowed to reach the wilting coefficient, as in the second group, and was then brought back to 30 per cent. moisture. The latter treatment enabled the seedlings to recover from the effects of drought and to resume growth. In the first two groups, transpiration determinations were made at weekly intervals. In addition, daily determinations were made near the end of the experiments for all three groups.

DETERMINATION OF PHYSICO-CHEMICAL PROPERTIES

After completing the transpiration determinations ten samples were collected from each species in each of the three soil moisture categories. Collections were made at 11 P.M. One sample consisted of all the leaves from one seedling. The fresh weight of the sample was obtained after placing it in a closed tin container. Each sample was macerated in a meat grinder and divided into three parts for the determination of bound water, total water, and freezing point, respectively.

The calorimetric method for the determination of bound water (**5, 13, 16, 20, 22, 23, 26**) was selected for this work. In making the determinations, ten samples from each category were run through the procedure together. The samples, each consisting of about 8 grams of the macerated leaf tissue, were placed in tinfoil cups similar to those used by ROBINSON (**20**) and GREATHOUSE (**5**). The cups were placed in glass vials, tightly stoppered, and weighed to ± 0.001 gram. After weighing, the tinfoil cups containing the samples were placed in stoppered freezing tubes with two samples in each tube. The freezing tubes were suspended in a freezing bath at a temperature of – 20° C. ± 2° C. through holes in a cover over the bath. The samples were left in the bath for approximately 12 hours. A pint thermos bottle, containing 250.0 gm. of water was used for a calorimeter. The initial temperature of the water in the calorimeter was determined by using a mercury thermometer which was read to ± 0.005° C. A sample, enclosed in its tinfoil container, was transferred from the freezing bath to the calorimeter. After continuous stirring with a motor-driven stirring rod for approximately 8 minutes, thermal equilibrium was reached and the final temperature was recorded. A correction factor for the heat absorbed by the calorimeter and accessories was obtained by placing 8 ml. of water in the tinfoil cups and following the procedure just outlined. The formulae used in calculating the bound water contents are essentially the same as those used by GREATHOUSE (**5**).

In preparing samples for specific heat determinations on the dry matter in the leaf tissue, leaves were dried for 24 hours at 95° C. and then ground to a fine dust with a mortar and pestle. The ground leaf tissue was placed in tinfoil cups and dried to constant weight ± 0.001 gram at 95° C. The specific heats were determined using the same procedure as for bound water except that benzene was used instead of water in the calorimeter. Benzene, having a lower specific heat, facilitated measurement of the temperature change in the calorimeter. The specific heats of benzene and of tin were obtained by plotting their values as given in the *International Critical Tables* (**31**) and then interpolating for the desired temperature. The specific heats of water and of ice were obtained from the *Handbook of Chemistry and Physics* (**7**). For loblolly pine the mean of 5 specific heat determinations on the dry leaf tissue was 0.213 with a standard error of ± 0.002; the mean of 5 determinations on shortleaf pine was 0.208 with a standard error of ± 0.006.

The total water content of a sample was assumed to be the difference between the fresh weight and the weight after drying the macerated tissue to constant weight ± 0.001 gm. at 95° C. The water content was calculated on a dry weight basis.

Freezing point determinations were made on the leaf tissue using the thermo-electric method (**14**). The apparatus consisted of two thermocouples connected in series to a galvanometer. One junction was maintained at 0° C. The other junction was sealed into the tip of a hypodermic needle and inserted into a 1.5-cm. length of glass tubing containing a portion of the macerated leaf tissue. The junction with the enclosing sample was placed in a freezing tube suspended in a freezing bath. The amount of undercooling and the observed freezing point were recorded. The true freezing point and the osmotic pressure were calculated from the tables of HARRIS and GORTNER (**6**).

Since osmotic pressure of a tissue varies with total water content, the usefulness of osmotic pressure for comparisons of solute concentration in tissues of different water contents is very limited. In an attempt to obtain a more stable factor for such comparisons, the following conversion was devised.

$$\frac{\pi \times [H_2O]}{22.4} = [\text{Solute}]$$

where

π = osmotic pressure
$[H_2O]$ = grams of water per gram of dry leaf tissue
[Solute] = number of gram molecular weights (mols) of solute per kilogram of dry leaf tissue
22.4 = the osmotic pressure of a mol of undissociated solute in 1000 grams of water

This conversion does not give a true measure of solute concentration because the relative amounts of ionized and un-ionized solutes are not known. This formula merely converts osmotic pressure to its equivalent in mols of undissociated solute on a dry weight basis and thus gives a factor which probably does not vary to a great extent with changes in water content. This factor will be designated as *solute concentration* in the following discussion, but

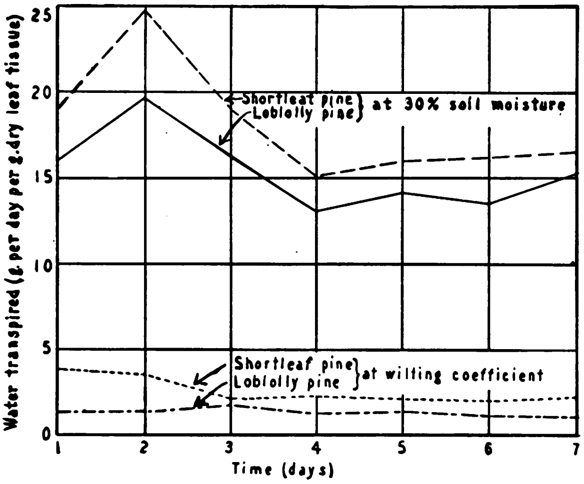

FIG. 1. Daily transpiration of loblolly pine and shortleaf pine at 30 per cent. soil moisture and at the wilting coefficient. Each point is the mean value of 9 determinations.

actually it is just a rough approximation to the true solute concentration because of the unknown degree of dissociation.

Results and discussion

TRANSPIRATION

Shortleaf pine had a higher daily rate of transpiration than loblolly pine with soil moisture at 30 per cent. and also at the wilting coefficient. Mean values of nine trees of each species in the two soil moisture categories on seven successive days are shown in figure 1. The differences between the two species are highly significant at both soil moisture contents as shown by the analysis of variance in table II. Significant also is the variation in transpiration rates resulting from the variation caused by differences in temperature and humidity from day to day. These results indicate that the apparently greater ability of shortleaf pine to resist drought cannot be attributed to an ability to conserve water by retarding transpiration. This conclusion agrees with the statement of MAXIMOV (**11**) that xeric plants are distinguished by a higher rate of transpiration than that of more mesic plants.

TABLE II

ANALYSIS OF VARIANCE IN TRANSPIRATION RATES OF LOBLOLLY PINE AND SHORTLEAF PINE

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	CALCULATED *F* VALUE
Soil moisture at 30 per cent.				
Species	1	222.60	222.60	59.52†
Days	6	915.56	152.59	40.80†
Interaction	6	45.30	7.55	2.02*
Error	112	419.35	3.74	
Total	125	1602.81		
Soil moisture at wilting coefficient (14.8 per cent.)				
Species	1	41.18	41.18	76.26†
Days	6	16.99	2.83	5.24†
Interaction	6	16.06	2.68	4.96†
Error	112	60.27	0.54	
Total	125	134.50		

* Not significant (less than 5 per cent. point).
† Highly significant (greater than 1 per cent. point).

The rate of transpiration of loblolly pine gradually diminished over a period of six weeks as the decreasing soil moisture approached and passed the wilting coefficient (14.8 per cent. moisture). At the end of the six-week period, the rate was only 15.8 per cent. of that at 30 per cent. soil moisture. This gradual reduction is not to be expected according to the results of VIEHMEYER and HENDRICKSON (**30**). They found that extraction of water from soil by peach trees is not affected by soil moisture content until it is reduced to the wilting percentage. Hence transpiration would be expected to remain constant until the wilting percentage is reached. The gradual reduction observed in this work can be explained, however, by assuming that at the beginning of the period of drought, only a portion of the roots were in soil at the wilting coefficient; and as more and more of the roots extracted all of the water available to them, transpiration was gradually reduced. The transpiration rates of the two species at the wilting coefficient, shown in figure 1, are not as low as the negligible amounts of water lost by western conifers as observed by Pearson (**19**). The calculated wilting coefficient for the soil used in this study, however, as shown in table I, is approximately 7 per cent. higher than the true wilting percentage as determined experimentally. Hence there may have been an appreciable amount of available soil moisture at the calculated wilting coefficient.

With soil moisture at 30 per cent. after having been reduced to the wilting coefficient, differences in transpiration rates between the two species were not significant. A comparison of the transpiration rates of loblolly

TABLE III

ANALYSIS OF VARIANCE IN BOUND WATER, TOTAL WATER, OSMOTIC PRESSURE, AND SOLUTE CONCENTRATION IN LEAF SAMPLES OF LOBLOLLY PINE AND SHORTLEAF PINE COLLECTED AT 11 P. M.

ITEM	SOURCE OF VARIATION	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	CALCULATED *F* VALUE
Bound water	Species	1	109.54	109.54	1.65*
	Soil moisture	2	1274.29	637.65	9.61†
	Interaction	2	129.87	64.94	0.98*
	Error	54	3581.43	66.32	
	Total	59	5095.13		
Total water	Species	1	1920.6	1920.6	10.55†
	Soil moisture	2	24202.3	12101.2	66.49†
	Interaction	2	187.1	93.6	0.51*
	Error	54	9827.2	182.0	
	Total	59	36137.2		
Osmotic pressure	Species	1	66.03	66.03	51.19†
	Soil moisture	2	540.34	270.17	209.43†
	Interaction	2	129.06	64.53	50.02†
	Error	54	69.57	1.29	
	Total	59	805.00		
Solute concentration	Species	1	1.3735	1.3735	88.61†
	Soil moisture	2	3.1324	1.5662	101.05†
	Interaction	2	0.6717	0.3358	21.66†
	Error	54	0.8373	0.0155	
	Soil moisture	2	24203.0	12101.0	66.49†
	Total	59	6.0149		

* Not significant.
† Highly significant.

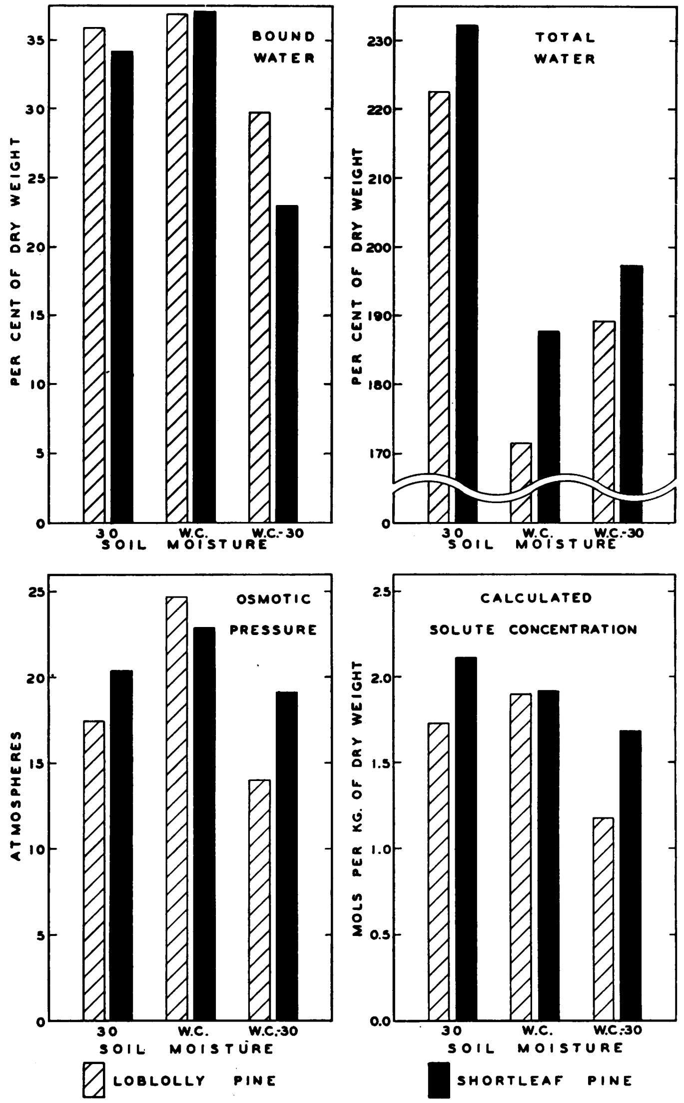

FIG. 2. Mean values of bound water, total water, osmotic pressure, and solute concentration in leaves of loblolly pine and shortleaf pine under various soil moisture conditions. Each value is the mean of 10 determinations.

30 = Soil moisture maintained continuously at 30 per cent.
W.C. = Soil moisture at the wilting coefficient.
W.C.–30 = Soil moisture at 30 per cent. after having been reduced to the wilting coefficient.

TABLE IV

SIGNIFICANCE OF DIFFERENCES BETWEEN MEANS OF PHYSICO-CHEMICAL PROPERTIES OF LEAVES OF LOBLOLLY PINE AND SHORTLEAF PINE

CATEGORIES COMPARED*	BOUND WATER		TOTAL WATER		OSMOTIC PRESSURE		SOLUTE CONCENTRATION	
	DIFFERENCE BETWEEN MEANS	t VALUE†	DIFFERENCE BETWEEN MEANS	t VALUE†	DIFFERENCE BETWEEN MEANS	t VALUE†	DIFFERENCE BETWEEN MEANS	t VALUE†
	%		%		*Atm.*		*Mols.*	
SP:30–LP:30	-1.76	0.5	9.66	1.5	2.98	5.8	0.384	8.3
SP:WC–LP:WC	0.36	0.1	16.23	2.7	-1.85	3.4	0.016	0.3
SP:WC:30–LP:WC:30	-6.71	1.8	8.06	1.3	5.17	10.1	0.512	11.1
LP:30–LP:WC	-1.09	0.3	51.02	8.5	-7.26	14.2	-0.168	3.6
LP:30–LP:WC:30	6.06	1.7	33.37	5.5	3.46	6.8	0.556	12.1
LP:WC–LP:WC:30	7.15	2.0	-17.65	2.9	10.72	21.0	0.724	15.7
SP:30–SP:WC	-3.01	0.8	44.45	7.4	-2.42	4.8	0.200	4.3
SP:30–SP:WC:30	11.16	3.1	34.97	5.8	1.28	2.5	0.428	9.3
SP:WC–SP:WC:30	14.13	3.9	-9.47	1.5	3.70	7.3	0.229	5.0

* SP = shortleaf pine. LP = loblolly pine.
30 = samples from trees in soil at 30 per cent. moisture.
WC = samples from trees in soil with moisture content at the wilting coefficient.
WC:30 = samples from trees in soil at 30 per cent. moisture after having been reduced to the wilting coefficient.

† $t = \frac{\text{difference between means}}{\text{standard error of difference}}$. Values of t greater than 2.0 are considered significant.

pine supplied continuously with 30 per cent. soil moisture and of the same species at 30 per cent. soil moisture after having been reduced to the wilting coefficient showed no significant difference. No comparison was made on the transpiration rates of seedlings of shortleaf pine at these two soil moisture contents.

PHYSICO-CHEMICAL PROPERTIES OF LEAF TISSUES

Analyses of variance were made on all physico-chemical data and are presented in table III. These analyses show that total water, osmotic pressure, and solute concentration in leaves of shortleaf pine and loblolly pine differed significantly between species as well as between soil moisture categories. The analyses also show that soil moisture treatments caused significant differences in bound water contents, and that species did not. The mean values of each physico-chemical property in each category are presented graphically in figure 2. Tests of the significance of differences between individual means are presented in table IV.

The bound water content values may be subject to criticism because of the large variation within categories as indicated by the magnitude of the mean square of error in the analysis of variance in table III. Two factors may contribute to this variation: first, inconsistencies in the technique used in making the determinations; and second, variation in the amount of bound water from tree to tree within categories. No replicated bound water determinations were made on substances known to be homogeneous; hence an absolute check on the reliability of the method is not available. The replications of the specific heat determinations, however, and the calorimeter factor determinations, presented in table V, are very consistent. Since these determinations were made using the same apparatus that was used in making the bound water determinations, the consistency of the specific heat values and the calorimeter factors is an indication of the reliability of the technique.

TABLE V

COMPARISON OF VARIATION IN REPLICATED DETERMINATIONS OF BOUND WATER, SPECIFIC HEAT, AND THE CALORIMETER FACTOR

ITEM	SPECIFIC HEAT OF LOBLOLLY PINE	CALORIMETER FACTOR	BOUND WATER*
Number of replications	5	4	10
Mean	0.213	1.070	35.81
Standard deviation	0.00336	0.00895	7.78
Standard error	0.00151	0.00448	2.46
Standard error expressed as a percentage of the mean	0.7	0.4	6.9

* Determinations were made on leaves of loblolly pine when soil moisture was at 30 per cent.

When soil moisture was at 30 per cent., leaves of shortleaf pine were higher in total water, osmotic pressure, and solute concentration than were leaves of loblolly pine. Bound water contents were not significantly different in leaves of the two species. Consideration of these data alone might lead to the conclusion that the greater drought resistance of shortleaf pine is attributable to osmotic effects. Data on the physico-chemical properties under the other two soil moisture conditions show, however, that osmotic effects have no direct connection with the relative drought resistance of loblolly pine and shortleaf pine.

Changes in the seedlings which occurred when soil moisture was reduced from 30 per cent. to the wilting coefficient furnish some interesting information on the behavior of the two species during drought hardening. Seedlings of both species became dormant as judged by the cessation of growth and the setting of terminal buds. In leaves of both species osmotic pressure increased, and total water decreased considerably. Solute concentration apparently decreased in leaves of shortleaf pine, but increased in leaves of loblolly pine. These changes in solute concentration, although small, are statistically significant. They are not believed to be physiologically significant, however, because of the fact that the changes are in opposite directions in the two species.

No significant change occurred in the bound water content of the leaves of either species when soil moisture was reduced from 30 per cent. to the wilting coefficient. This fact leads to the assumption that no appreciable change took place in the amount of water-binding colloids and crystalloids in leaves of the two species during the drought hardening period. The fact that no consistent change in solute concentration occurred in the two species when soil moisture was reduced may be regarded as evidence partially supporting this assumption.

Physico-chemical differences between species when soil moisture was at the wilting coefficient show which properties cannot be used for determining the relative drought resistance of the two species and also show which factors might be indicative of the relative drought resistance. With soil moisture at the wilting coefficient, leaves of shortleaf pine had a higher total water content and a lower osmotic pressure than leaves of loblolly pine. Solute concentration and bound water contents were practically the same in both species.

Since solute concentration on a dry weight basis was the same in the two species when soil moisture was at the wilting coefficient, it follows that the observed difference in osmotic pressure was the result of the difference in total water content. Since osmotic pressure was influenced in this way, it cannot be used as an indicator of the relative drought resistance of the two species.

The simultaneous occurrence of a higher total water content and a higher transpiration rate in leaves of shortleaf pine when soil moisture was at the wilting coefficient, indicates that this species had a faster rate of absorption of water from soil than loblolly pine when soil moisture was limited. This ability of shortleaf pine might be attributed to a lower ratio of evaporating leaf surface to absorbing root surface. A superficial examination of the root systems of the seedlings used in this work indicated that shortleaf pine seedlings had a lower top-root ratio than loblolly pine. More exact measurements are necessary, however, to prove the point.

The ability of a seedling to maintain a higher total water content in its leaves when soil moisture is limited may be an aid to survival during periods of drought in that it might prolong the period of permanent wilting and thus delay the occurrence of a water content in the leaves below the minimum necessary for life. Such a prolongation of the period of permanent wilting, however, would enable a seedling to survive periods of drought only as long as the soil moisture content did not go below the wilting percentage for a prolonged period.

The fact that shortleaf pine, the more drought resistant of the two species studied, had the greater total water content in its leaves when soil moisture was at the wilting coefficient, leads to the conclusion that the magnitude of the total water content may be used as an indicator of the relative drought resistance of the two species under the conditions of this experiment.

In view of the correlation obtained by other workers between bound water contents and relative drought resistance, an explanation of the lack of such correlation in this study, when soil moisture was at the wilting coefficient, is pertinent. NEWTON and MARTIN (**17**) who obtained a good correlation between drought resistance and bound water contents of cereal crops and grasses, used the cryoscopic method for the determination of bound water in expressed sap. With this method, only the amount of bound water held by the colloids, ions, and molecules expressed in the sap is determined. MEYER (**13**) stated that a considerable amount of water may be bound in cell walls of plant tissues. Since leaves of many species of the genus Pinus, including loblolly pine and shortleaf pine, are characterized by a hypodermal layer of cells with thick walls, the amount of water bound by dispersed substances within the cells may be negligible compared to the amount of water bound in the cell walls. In this investigation, bound water determinations were made on macerated leaf tissue which included both cell walls and cell contents. The amount of water-binding surface in cell walls per unit weight of dry leaf tissue may have been sufficiently uniform in the two species to prevent the detection of small differences in the amount of bound water in the cell sap. Since no data are available on the relative amounts of bound water in cell walls and in cell sap, any interpretation of the bound water contents of the leaf tissue must be based on their face value. Hence, the magnitude of the bound water content of the leaf tissue as determined in this investigation, is not a factor which makes shortleaf pine more drought resistant than loblolly pine.

Striking changes occurred in the leaves of the two species after soil moisture was increased from the wilting coefficient to 30 per cent. The physico-chemical properties were determined one week after the soil moisture had been brought back to 30 per cent. During that week dormancy was broken and growth was resumed. Total water contents of leaves were greater than when soil moisture was at the wilting coefficient, but less than when seedlings were first supplied with 30 per cent. soil moisture. Large decreases in bound water, osmotic pressure, and solute concentration occurred in leaves of both species. Each of these three properties were lower in magnitude than in either of the other two soil moisture categories. These results agree with those of Vassiliev and Vassiliev (**29**) who found that wheat plants grown in soil with insufficient water and then watered abundantly were lower in water content as well as in monosaccharides and sucrose than check plants grown continuously with abundant soil moisture.

Total water, osmotic pressure, and solute concentration were higher in leaves of shortleaf pine than in leaves of loblolly pine after 30 per cent. soil moisture was restored. No significant difference in the bound water contents of the two species was observed in this soil moisture category.

The decreased solute concentration and the decreased bound water contents in the leaves of the two species indicate a rapid depletion of food reserves, including water-binding colloids, in the leaves when dormancy resulting from drought is broken by the restoration of abundant soil moisture. The fact that the decrease in solute concentration was not as great in shortleaf pine as in loblolly pine indicates that the former species may have maintained a better balance between utilization and synthesis of soluble food reserves. This closer balance may enable shortleaf pine to recover more rapidly from the effects of drought, and hence it may be a factor contributing to the ability of this species to survive on drier sites than those on which loblolly pine occurs.

Summary

Determinations of transpiration, bound water, total water, and osmotic pressure were made on seedlings of loblolly pine and shortleaf pine to obtain information on the behavior of these species during and after drought and to ascertain whether any of these factors can be used as indicators of relative drought resistance. Solute concentration, calculated from data on osmotic pressure and total water content, was a valuable aid in interpreting the osmotic pressure differences.

With soil moisture at 30 per cent., shortleaf pine had a higher transpiration rate, more total water, a higher osmotic pressure, and a greater solute concentration than loblolly pine. Bound water contents were not significantly different in the two species.

With soil moisture at the wilting coefficient, shortleaf pine had a higher transpiration rate, more total water, and a lower osmotic pressure than loblolly pine. Solute concentration and bound water contents were practically the same in both species.

When soil moisture was restored to 30 per cent. after having been reduced to the wilting coefficient, leaves of shortleaf pine had more total water, a greater osmotic pressure and a higher solute concentration than leaves of loblolly pine. Transpiration rates and bound water contents were practically the same in both species.

Bound water contents decreased in both species when soil moisture was restored to 30 per cent. after having been reduced to the wilting coefficient.

Points observed in this study which may contribute to the greater drought resistance of shortleaf pine compared to that of loblolly pine are as follows:

1. Shortleaf pine absorbed more water from the soil and at the same time maintained a higher total water content in its leaves even when soil moisture was limited.
2. Shortleaf pine maintained a higher solute concentration when recovering from the effects of drought; that is, when 30 per cent. soil moisture was restored.

The data also show that the greater drought resistance of shortleaf pine cannot be attributed to an ability to conserve water either by retarding transpiration or by forming bound water. Further, the greater drought resistance of this species cannot be attributed to a higher osmotic pressure.

NORTHERN ROCKY MOUNTAIN FOREST
AND RANGE EXPERIMENT STATION
MISSOULA, MONTANA

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