DROUGHT RESISTANCE OF ROOTS of white ash, sugar maple, and red oak

by Johnson Parker

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RICHARD D. LANE, DIRECTOR

The Author

JOHNSON PARKER did his undergraduate work at Harvard College, and later received Master of Forestry and Doctor of Forestry degrees from Yale University and Duke University respectively. He has also studied at the University of Munich. He joined the Northeastern Station as a plant physiologist at Hamden, Connecticut, in 1965. Previous employment included positions with the Bartlett Tree Research Laboratories (1963-65), Yale University's Valhalla Research Station (1957-63), the Southern Forest Experiment Station of the U. S. Forest Service (1956-57), the University of Idaho (1949-56), and the Oceanographic Institution (1941-44).

INTRODUCTION

IN the northeastern United States, sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus* americana L.), and red oak (*Quercus rubra* L.) are afflicted by dieback and decline diseases. The causes of these conditions have been discussed much in recent years, and the general consensus now is that one or more stress phenomena initiate them. Defoliation by insects is believed to be a primary factor in a decline of forest stands of sugar maple (called "maple blight" by *Giese et al. 1964*), and in the decline and mortality of red and scarlet oak (*Staley 1965*). Climatic factors too, especially drought, appear to play an important role in many of these diseases (*Westing 1966*).

It was suggested many years ago that drought alone might be the cause of certain diebacks and declines (*Balch 1927, Coover 1930*), particularly after the severe drought of the early 1930's (*Spaulding and Hansbrough 1935, Spaulding 1946, McIntyre and Schnur 1936; Parker 1965*). A more recent series of studies has given additional evidence that water deficiencies are important in the dieback and decline diseases (*Staley 1965, Hibben 1962, Ross 1964; Sinclair 1964*).

Although these recent studies have correlated periods of disease with periods of reduced precipitation, few researchers have attempted to measure either the resistance of tree tissues to desiccation or the ability of tree roots to retain moisture (*Stocker 1956 and Sullivan and Levitt 1959*).

Of the various organs of the tree, roots seemed most to deserve study. First, because there is evidence that in some of the dieback diseases the roots appear to be affected before the tops (*Greenidge 1953*). And second, because there have been suspicions for some time that roots are killed during drought periods because of the impairment of their absorptive capacity. Such impairment might result from plugging of the xylem with gums or bacterial clots, or from direct desiccation of rootlets.

The question then arises as to the relative drought resistance of roots of different tree species. Two aspects of resistance seem important: the ability of living root cells to withstand low moisture levels (desiccation resistance), and the tendency for whole root segments to retain water under extremely dry soil conditions.

A study was made to determine (1) the relative levels of desiccation resistance in roots of white ash, sugar maple, and red oak and (2) the relative rates of water loss through the root bark.

METHODS AND MATERIALS

Trees used in this study were growing in two similar forested areas in southern Connecticut. These areas bore overstories composed of various species of oak, maple, ash, and birch, and had understories of such species as wild cherry and dogwood.

Ten root segments, 8 to 10 cm. in length and 1 to 2 cm. in diameter, dug from the upper 0.3 m. of soil about 1 m. from the bole, were collected from three individual trees of each of the three species. Roots of this size were selected because in some studies they accounted for most of the water absorbed (*Kramer and Bullock 1966*). Segments were kept overnight in plastic bags at 4.0°C. Experiments were then performed to determine desiccation resistance of cells and transpirational water loss via bark.

Desiccation Resistance

Root segments were collected in December 1965, April 1966, and August 1966. From each group of ten segments collected, three were selected at random. From each of these three, 16 thin (about 25 μ) tangential sections were made of the inner bark with a single-edged razor blade. These sections were dipped in tap water according to the procedure of Sullivan and Levitt (1959), and were exposed to one of four relative humidities (RH's) for 24 hours.

The 16 sections from each segment were divided evenly among four humidity chambers (1-quart bottles), each of which possessed a different RH as described below. With three different segments supplying three bottles held at one particular RH, and each of these three segments being used to make sections for four different bottles, this may be summarized as 3 segments x 4 RH x 3 species x 3 replications — a total of 108 bottles.

In the December experiment, the four RH's were maintained at 89, 95, 97, and 99 percent by using 30-ml. quantities of sucrose solutions of 2.0, 1.5, 1.0, and 0.1 M. at about 22°C. In the April and August experiments, 85, 90, 95, and 100 percent RH's were obtained by using 2.2, 1.9, 1.1 M. sucrose solutions and distilled water, respectively, at 22°C. to 26°C. RH values were verified before beginning the experiments by using the appropriate relative humidity probe inserted through a rubber stopper fitted tightly to a hole in the screw-cap top (fig. 1). The probe connected to a strip recorder.[1]

Sections were transferred with an artist's paint brush to the bottoms of 50-ml. beakers inverted in the widemouth bottles that contained the sucrose solutions.

After sections were exposed to the various humidities for 24 hours, measurements of viability were made by soaking sections for 1 hour in an aqueous solution of 12 ppm. neutral red containing 0.1 N. of $CaCl_2$. (Vacuoles of living cells absorb and hold the dye; dead cells do not absorb the dye or do so

[1] The narrow-range "Hygrosensor" probes and the strip recorder, Model 15-4050E, were manufactured by Hydrodynamics, Inc., Silver Springs, Md. Mention of a particular product should not be taken as an endorsement by the Forest Service or Department of Agriculture.

Figure 1.—A typical humidity chamber with its inverted beaker, solution, and root sections on the beaker. A humidity probe for testing relative humidity is also shown in the chamber.

only weakly.) Sections were then transferred to a slide, mounted in a drop of water and examined for viability under the microscope at 100X. Counts were made of cells in the area delineated by the field of an ocular micrometer and the percentage of living phloem ray cells for each was calculated. Observations were limited to ray cells because they comprised a large component of the living root tissues, were homogeneous, large in size, and of a regular pattern that facilitated measuring.

Water Loss through Root Bark

The rate of water loss by transpiration from exhumed root segments was determined in two experiments. The first, performed in June, utilized roots from one locality; the second, carried out in August, utilized roots from a similar area 30 miles distant. Segments were selected as before (three roots from each of three trees for each of the three species) and washed free of loose soil. After the segments had drained for 15 minutes and their severed ends had been coated with melted paraffin to prevent water loss, they were kept under room conditions of temperature and RH (22°C., about 60 percent RH in June; 22°C. to 26°C., about 75 percent RH in August). Weighings were made at the intervals shown in the results. Both the fresh weight and oven-dry weight (105°C. for 48 hours) were used as bases for calculation of water loss.

RESULTS

Desiccation Resistance

Viability of cells subjected to the various RH's in different seasons increased from nearly zero at 89 to 90 percent RH to a maximum at 95 to 100 percent RH (fig. 2). It can be seen in these three graphs that there are, in some cases, apparent differences between certain species in their viability levels. Howver, considering all three experiments together and considering

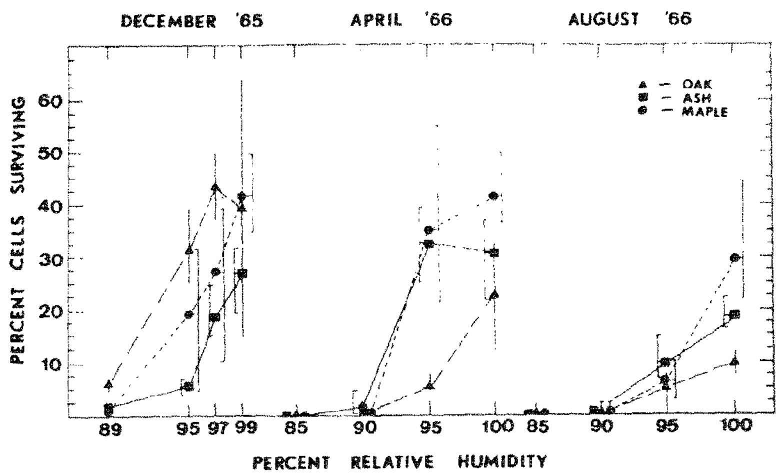


Figure 2.—Effects of 24 hours of dessication on thin sections of root bark kept at various relative humidities in three experiments. Viability as percentage of cells retaining neutral red per total cells counted is plotted for the three species over the various relative humidities. Each point is the average of three measurements of three roots from the same tree. Vertical lines indicate limits of data scatter.

the scatter in the data (the limits of which are shown on the graphs), I found no statistically significant differences in desiccation resistance among species.

Some indication of seasonal differences can be seen by comparing the three graphs in figure 2. In general, there appeared to be a decline in viability at the optimum RH (99 or 100 percent) from December to August.

Root Transpiration

Maple root segments dehydrated more rapidly in both experiments than did those of the other two species (fig. 3 and 4). Since dry weight is often considered a more consistent basis for comparison, results were based on dry weight. An analysis of variance of the data for the fifth day in each experiment showed that there were significant differences among species at the 5-percent level, but not at the 1-percent level. Water content of maple was significantly different from that of either ash or oak. These last two did not differ significantly from each other. Maple reached a state of equilibrium after about 7 days but the other

Figure 3.—Water content of whole-root segments as percentage of dry weight is plotted over time since start of experiment. Each point represents the average of nine roots. Data of North Madison, Conn., June 1966.

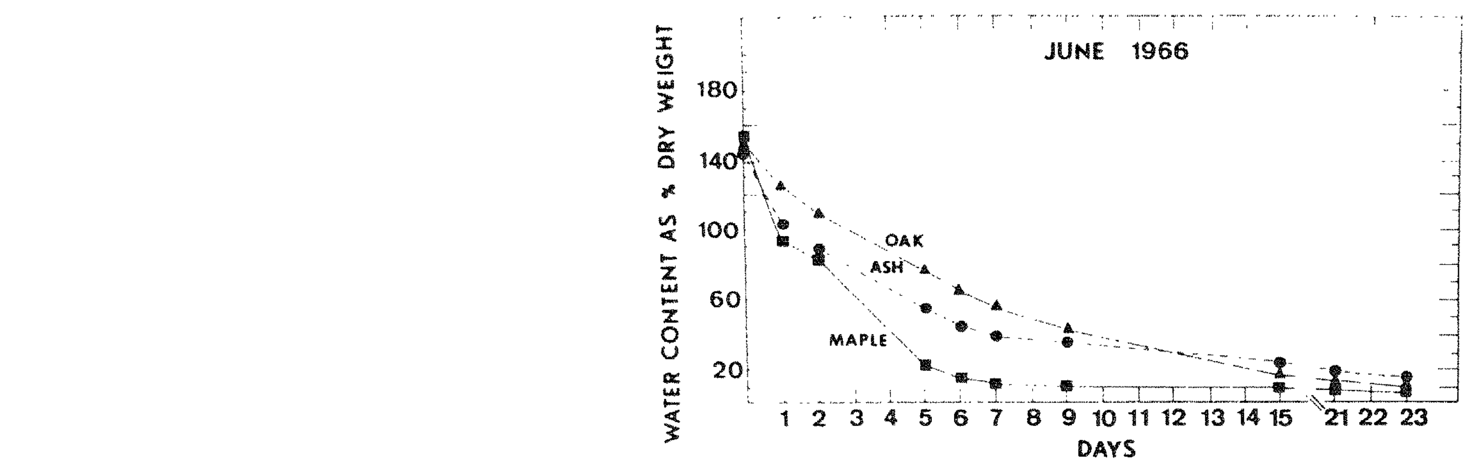
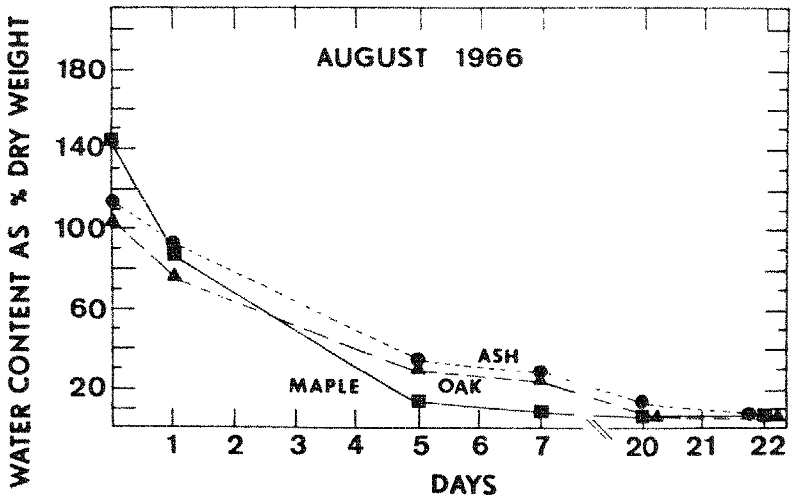


Figure 4.—Water content of whole root segments as percentage of dry weight is plotted over time since start of experiment. Each point represents the average of nine roots. Data of Haddam, Conn., August 1966.



two species continued to transpire appreciably after this. Eventually, water content of all three species fell to the same level (figs. 3 and 4).

DISCUSSION

The cells of the inner bark of the three species studied would not seem to possess any usually great resistance to the effects of a lowered moisture content. At least, their levels of survival compare closely to those of leaves of two species of oak (*Sullivan and Levitt 1959*). It would not be surprising then, that roots of the three species studied here would be injured during a protracted drought.

Under severe drought conditions, water loss by transpiration from the roots into the soil atmosphere could occur under certain soil conditions (*Slatyer 1956*). If root transpiration does occur under very dry soil conditions, the tendency of whole roots to retain water, as by means of heavily suberized outer layers, might be of importance to survival. Certainly maple roots appeared to lose water by bark transpiration more rapidly than did roots of ash or oak. This might help to explain why sugar maple is generally less likely to survive on dry soil than the oaks. On the other hand, although maple roots transpired water more rapidly than did those of ash, it would be difficult to say, based on field observations, that white ash is more drought resistant than sugar maple.

The differences observed in root transpiration might indicate, too, that similar differences exist among these species in their rates of water absorption. Preliminary experiments indicate that dry maple roots absorb water more rapidly than do those of the other two species.

There are, of course, other differences among these species that might influence their drought resistance. It was observed in digging the roots for these experiments that the surface roots of oak angled downward at about 20 degrees from the horizontal, while the "ropelike" (*terminology of Lyford and Wilson 1964*) surface roots of maple and ash remained near the surface throughout their lengths. While there is mention in the literature of the relatively great depth of oak roots as compared with some other common trees (*Weaver and Kramer 1932, Brinkman 1957*), root depth varies greatly with soil characteristics and general rules are difficult to make. Biswell (*1935*) described a red oak 6 years old with roots 7 feet deep, while sugar maple 10 years old had roots to 10 feet. This is one of the few positive comparisons given in the literature for red oak and sugar maple trees older than seedlings and is, in itself, poor proof of any advantage of oak over maple.

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