Stomatal resistance and growth of drought-stressed eastern cottonwood from a wet and dry site

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Summary

Stomatal resistance measurements were used to make a preliminary classification of the drought resistance of four Oklahoma clones of eastern cottonwood. The effect of drought-stress on clones from a dry site in northwestern Oklahoma were compared to clones from a wet site in southeastern Oklahoma. Within site differences, based on comparison of two clones, were not detected. The dry-site plants had lower stomatal resistance values than the wet-site plants, even under well-watered conditions.

Total leaf area expansion stopped at a stomatal resistance of 17.5 s cm $^{-1}$ for the dry-site plants after 23 days of severe drought-stress. Leaf area expansion of the wet-site plants stopped after 25 days at a stomatal resistance of 60 s cm^{-1}. Leaf area expansion of the wet-site plants was greater than that of the dry-site plants. Total height growth was greater for the dry-site than the wet-site plants. Height growth of the dry-site plants was not inhibited by moderate drought-stress. Height growth stopped for the dry-site plants at a stomatal resistance of 18.5 s cm^{-1} after 23 days of severe drought stress. The wet-site plants stopped height growth after 21 days at a stomatal resistance of 55 s cm^{-1}.

Differences in stomatal resistance between plants from the two Oklahoma sites were discernible with or without drought stress. This suggests that screening under common environmental conditions may distinguish drought resistant from drought susceptible clones. It follows that field testing to identify drought resistant clones is feasible. Decreased stomatal sensitivity (i.e. lower resistance) under drought stress was shown to convey greater adaption to drought in that a clone which can tolerate the least increase in stomatal resistance apparently will grow the fastest or continue to grow the longest and thus be the best to select.

Key words: Drought resistance, stomatal resistance, moisture stress, *Populus,* cottonwood.

Zusammenfassung

Zur vorläufigen Klassifizierung der Trockenresistenz von 4 *Populus deltoides*-Klonen aus Oklahoma wurden Messungen der Stomaresistenz vorgenommen. Verglichen wurde der Einfluß von Trockenheits-Stress auf Klone eines trockenen Standortes im nordwestlichen Oklahoma mit dem auf Klone eines feuchten Standortes im südöstlichen Oklahoma. Innerhalb eines Standortes wurden auf der Grundlage eines Vergleiches zweier Klone keine Unterschiede festgestellt. Jedoch hatten die Pflanzen von trockenen Lagen geringere Stomaresistenzwerte als Pflanzen von feuchten Lagen, sogar unter gut mit Wasser versorgten Verhältnissen.

Nach 23 Tagen schwerem Trockenheits-Stress war festzustellen, daß Pflanzen von trockenen Lagen die Vergrö-
ßerung der Blattfläche bei einem Stomaresistenzwert von 17,5 s cm^{-1} beendeten. Die Pflanzen aus feuchten Lagen beendeten ihre Blattflächenvergrößerung nach 25 Tagen bei einer Stomaresistenz von 60 s cm^{-1}. Die Blattflächenvergrößerung war bei Pflanzen feuchter Lagen größer als bei denen trockener Lagen. Das Gesamthöhenwachstum war bei Trockenlagenpflanzen größer als bei denen von feuchten Lagen. Das Höhenwachstum der Trockenlagenpflanzen wurde durch gemäßigten Trockenheits-Stress nicht gehemmt. Der Höhenwuchs wurde bei Trockenlagenpflanzen beendet bei einem Stomaresistenzwert von 18,5 s cm^{-1} nach 23 Tagen schwerem Trockenheits-Stress. Die Feuchtlagenpflanzen beendeten ihr Höhenwachstum nach 21 Tagen bei einer Stomaresistenz von 55 s cm^{-1}.

Unterschiede in der Stomaresistenz zwischen Pfanzen der 2 Oklahoma Standorte waren mit oder ohne Trockenheits-Stress deutlich erkennbar. Mit dieser Methode können unter üblichen Umweltbedingungen offenbar trockenresistente und trockenempfindliche Klone unterschieden werden. Daraus folgert, daß Feldprüfungen zur Identifizierung trockenresistenter Klone möglich sind. Pflanzen mit abnehmender Stomaempfindlichkeit (d.h. geringerer Resistenz) scheinen unter Trockenheits-Stress der Trockenheit besser angepaßt zu sein und schneller und größer zu wachsen, weshalb solche Klone selektiert werden sollten.

Introduction

Eastern cottonwood *(Populus deltoides* Bartr.) is an important hardwood pulp and timber species. It achieves maximum growth on rich bottomland soils of high agricultural value. In the Mississippi River Delta Region, which contains the best eastern cottonwood sites and nearly one-half of the current eastern cottonwood inventory in the southern United States, the forested acreage is shrinking at an alarming rate due to conversion to agriculture (Sternitzke, 1976). Land-use demands on forested acreage for non-timber products and for environmental protection are also growing. Coupled with the shrinking land base is an increasing demand for fiber for conventional uses (Sternitzke, 1976; U.S.D.A. Forest Service, 1974) and now also for energy(Drew and Bazzaz, 1978). McKnight (1976) reported that there will be a 100 percent increase in the use of "poplar" wood in the United States by the year 2000. This, he states, represents a tripling in the current acreage of eastern cottonwood planted.

To meet the demand for fiber, more eastern cottonwood will be grown on less-than-optimum sites, where drought resistance may be critical to plantation establishment in dry years. Farmer (1970) reported the effect of drought on growth, shoot/root ratios, and wood properties of eastern cottonwood. Transpiration rates of drought-stressed eastern cottonwood have been reported (Bonner, 1967; Farmer, 1969; Regehr et al., 1975) and considerable anatomical work on eastern cottonwood stomata has been done (Siwecki and Kozlowski, 1973; Isebrands and Larson, 1973; Kozlowski, 1976). But no published study examines the relationship of stomatal resistance and drought in eastern cottonwood. Farmer (1969) did estimate diffusion resistance (stomatal +

cuticular + boundary-layer resistances) of eastern cotton-wood using leaf energy-balance, water vapor, and temperature-gradient measurements. Stomatal resistance can be estimated by this method when boundary-layer resistance is low (KANEMASU et al., 1969). REGEHR et al. (1975) calculated approximate values of stomatal resistance for eastern cottonwood using similar methods, and took into account boundary layer resistance. Stomatal resistance of several *Populus* clones, including on of eastern cottonwood, was related by PALLARDY and KOZLOWSKI (1979) to environmental and plant factors by multiple regression analysis. Using KANEMASU et al. (1969) type porometers, pronounced stomatal sensitivity of some clones to vapor pressure deficit was suggested to be related to drought resistance in the clone's parentage.

Stomatal sensitivity to water stress is an important component of drought resistance (COWAN and MILTHORPE, 1967; HEATH, 1967; BAARS, 1968). Effective selection for a plant character can be achieved only if genetic variation exists within the population of interest. POSEY (1969) reported that genetic variation for drought resistance among geographic sources of eastern cottonwood in Oklahoma is of sufficient magnitude (based on first year survival of field-planted cuttings under natural drought conditions) that origin of plant material should be considered in a selection program for eastern cottonwood in Oklahoma. Selection can be practical only when the character of interest is easily measured and the environmental component of variation can be minimized. Stomatal resistance, as an indicator of drought resistance, can be simply measured with the KANEMASU et al. (1969) type diffusion porometer. With environmental variation minimized in a controlled environment chamber, this study was conducted to make a preliminary classification of the drought resistance of several Oklahoma clones of eastern cottonwood using stomatal resistance measurements.

Methods and Materials

Four clones of eastern cottonwood which originate from two natural stands in Oklahoma were used in this study. Two of the clones originate from two dominant trees of a stand along the Cimarron River in Beaver County, a dry site in northwest Oklahoma. The other two clones originate from two dominant trees of a stand along the Red River in Choctaw County, a wet site in southeast Oklahoma.

On July 7, 1978, 15-cm long tip cuttings with six to eight well-developed leaves were taken from the upper crown of the selected trees growing in a clonal test plantation. Cuttings were collected from ramets representing clones 2—6, 2—8, 16—3, and 16—5. These particular clones were selected for use at random, whereas the stands they represent were specifically chosen to allow comparison of sources from a wet site and a dry site.

Tip cuttings, rather than hardwood cuttings, were used for a number of reasons. Tip cuttings are actively growing when propagated, which eliminates the delay of an emergence period from dormancy to active growth of the hardwood cutting. The elimination of the hardwod cutting provided the opportunity for more normal root development and growth in the pots. Preliminary investigation showed tip cuttings to be more vigorous than hardwood cuttings, presumably due to the more controlled nature of the tip cuttings' propagation.

The tip cuttings were rooted under an intermittant mist system. On July 31, 1978, the now rooted cuttings were planted singly in 13,500 cc plastic bags filled with sand, bark, and peat in a 2:3:1 mix with approximately 190 g of time-release fertilizer incorporated.

The cuttings were placed in a greenhouse on September 19, 1978. On March 21, 1979, 15-cm long tip cuttings with

six to eight well-developed leaves were taken from the greenhouse plant material. Twenty-four cuttings of each of the four clones were taken. The cuttings were dipped in 0.01 percent indole-butyric acid and placed in 216 cc pots filled with peat and perlite in a 3:4 ratio plus approximately 2 mg of a time-release fertilizer mix and then put under an intermittent mist system. On April 22, 1979, the rooted cuttings were inserted, singly, in plastic pots (11 cm diameter, 14 cm deep) containing a potting mix of sand, bark, and peat in a 1:3:1 ratio plus approximately 15 g of time-release fertilizer. A few granules of Thimet, a systemic insecticide, were added to each pot. On May 15, 1979, 12 cuttings per clone were selected on the basis of uniformity within a clone and placed in a growth chamber. All cuttings were watered equally (360 ml/pot/day) for the first nine days preceding the start of the experiment. Just before the experiment began, the pots were enclosed in clear plastic bags, tied around the cutting stem, to prevent evaporation.

The experiment began on May 24, 1979 (day 1) and lasted 29 days. There were three treatments as follows:

control: 360 ml water added to pots daily
moderately-stressed: 240, 225, 210 ml water added to pots daily on days 1—9, 10—19, 20—29, respectively
severely-stressed: 120, 90, 60 ml water added to pots daily on days 1—9, 10—19, 20—29, respectively.

During the experiment, air temperature during the day was 30⁰C and at night was 25⁰C. The relative humidity, measured with a hygrothermograph, varied from 50 to 60 percent. From 0500 to 2100 hours, the light quantum flux density provided was 730 μ E m^{-1} s^{-1} at the top of the plants as measured by a quantum sensor (Model LI-190S, Lambda Instrument Company, Lincoln, Nebraska). From 2100 to 0500 hours, the chamber was dark.

Four measurements were taken every other day. First, the height of all plants was recorded. Second, leaf area of all leaves on each plant was measured using a clear plastic dot grid, with dots placed two cm apart. Third, adaxial stomatal resistance at the tip, and to the side of the midrib, of the fourth fully developed leaf from the plant top was measured with a calibrated stomatal diffusion porometer (KANEMASU et al., 1969) (Model LI-60 and Sensor LI-20S, Lambda Instrument Company, Lincoln, Nebraska). A calibration curve was developed for the sensor using perforated plates with calibrated resistance values. The calibration procedure was conducted in a controlled temperature room, with a constant air temperature of 25⁰C, according to the procedure described by KANEMASU et al. (1969). The calibration curve did not change during the experiment. Adaxial surface was measured because RAWSON et al. (1976) suggested that the leaf surface with the highest resistance (adaxial surface for eastern cotton-wood) should be measured in vapor-exchange studies, particularly if one is trying to determine differences due to different genotypes. Further, PALLARDY and KOZLOWSKI (1979) have since found that adaxial stomata of *Populus* clones are the more sensitive to changes in vapor pressure deficit, which supplements observations made by KANEMASU and TANNER (1969) concerning greater sensitivity of adaxial stomata to leaf water status. The fourth measurement recorded was pot weight, used to estimate transpiration rate.

The experimental design was a split-plot with four clones, three treatments, and four replications, for a total of 48 pots. The main-unit treatments were the water regimes (control, moderately-stressed, severely-stressed) while the sub-unit treatments were the clones. Data were subjected to an analysis of variance (α = .05) followed by Duncan's new multiple range test (STEEL and TORRIE, 1960). Analysis

of variance showed that clones 2-6 and 2-8 responded similarly to the three treatments, as did clones 16-3 and 16-5. Clonal data were, therefore, summed and analyzed as two populations to be known as the wet site and dry site, respectively. Although results suggest little or no local (within-site) variation, it is apparent that such a small sample (two clones) is highly unlikely to detect such differences. Discussion will be limited to comparisons of the two populations defined above.

Results and Discussion

Stomatal Resistance

Stomatal resistances of the wet-site control plants were higher than those of the dry-site control plants *(Figures 1 and 2)*. Wet-site control plants had resistances from 3 to 12 s cm^{-1} while the dry-site plant values ranged from 2 to 5 s cm^{-1}. Even under well-watered conditions, there was a difference in stomatal resistance between the two sites. This would suggest that differences in drought resistance as reflected by stomatal resistance may be detected with little or no stress as long as the plants are maintained under the same soil moisture regime.

There was little discrepancy in resistance between the two stress treatment groups for the dry-site plants. Resistance of the moderately-stressed dry-site plants were from 5 to 17 s cm^{-1} while resistances of the severely-stressed plants ranged from 7 to 34 s cm^{-1}. Although stomatal resistance did increase immediately following a reduction in water, the dry-site stress groups were found to equilibrate soon thereafter and respond similarly to the porometer. Though resistances increased more for the dry-site severely-stressed than for the moderately-stressed plants initially (after a reduction in water) both dry-site stress groups equilibrated to approximately similar resistance within a few days. This would suggest that stress within the realm tolerated by a tree can be withstood by an initial increase in stomatal resistance followed by a gradual equilibration to the new environment.

The moderately and severely-stressed wet-site plants had greater resistance values than the corresponding dry-site plants. There were statistically significant ($\alpha = .05$) differences between the moderately and severely-stressed wet-site plants. Resistances of the moderately-stressed wet-site plants were from 7 to 28 s cm^{-1} while resistances of the severely-stressed plants ranged from 18 to 60 s cm^{-1}. Resistances of the stressed wet-site plants were seen to increase with increasing water stress. Resistances of the stressed dry-site plants were not increased substantially
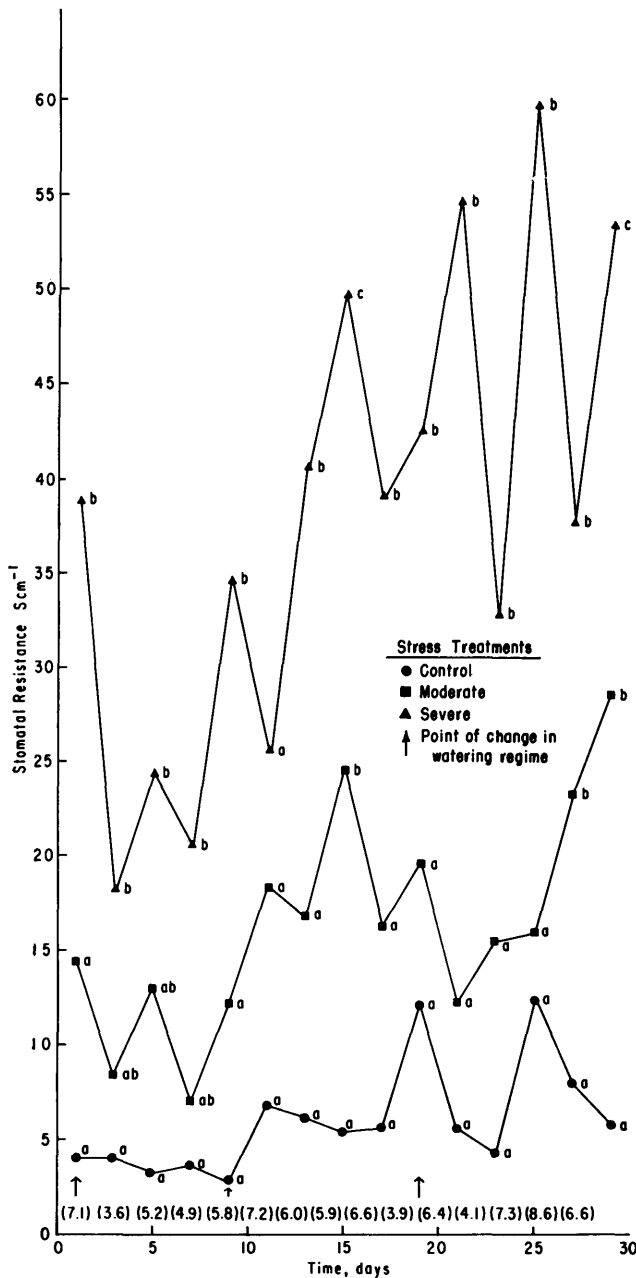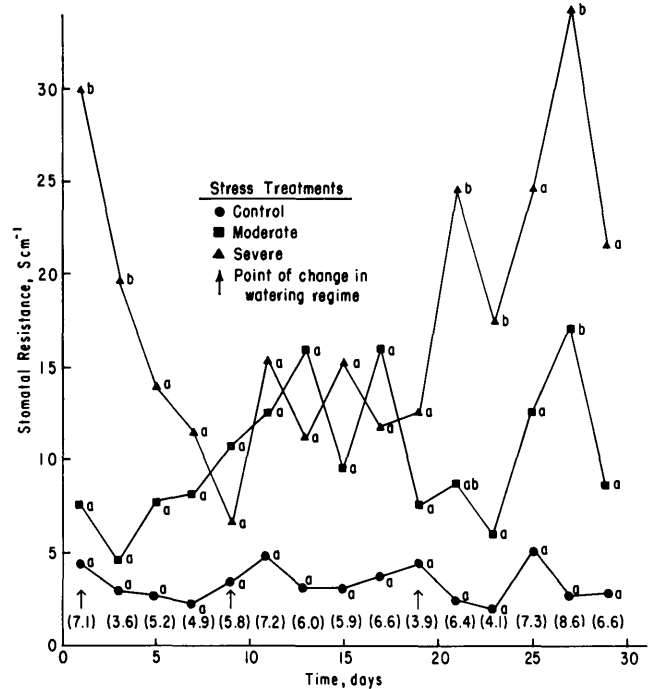

Figure 1. — Stomatal resistance of wet-site eastern cottonwood under three watering regimes. Numbers in parentheses are standard errors. Symbols for one measurement day, followed by the same letter, are not significantly different ($\alpha = .05$) according to DUNCAN's new multiple range test.

Figure 2. — Stomatal resistance of dry-site eastern cottonwood under three watering regimes. Numbers in parentheses are standard errors. Symbols for one measurement day, followed by the same letter, are not significantly different ($\alpha = .05$) according to DUNCAN's new multiple range test.

by increasing water stress which suggested a difference in drought tolerance between plants from the two sites.

Because water loss from the plant is controlled primarily through stomatal resistance (Cowan and Milthorpe, 1967; Heath, 1967; Barrs, 1968) measurement of stomatal resistance can indicate drought resistance. There was a difference in resistance between plants from the two sites even under well-watered conditions, which suggests that differences in drought resistance can be discerned with or without stress. Screening under common environmental conditions may distinguish drought resistant from drought susceptible clones. It follows that field testing to indentify drought resistant clones may be feasible using the diffusion porometer to measure stomatal resistance. Field testing would be easier and cheaper than laboratory testing, as drought resistance screening could be conducted in conjunction with clonal testing and other breeding objectives. This would eliminate the need for additional plant material and propagation since techniques used in the screening procedure are non-destructive. Screening in the field also facilitates management under actual commercial production methods, providing a more realistic test for usable drought resistance.

Transpiration Rate

Transpiration rate was found to be highly dependent on the amount of water available to the tree, as observed by many other workers (Farmer, 1969; Doughfrty, 1973; Regehr et al., 1975). Since transpiration rate directly reflects water loss from the plant, a lower rate represents an index of water stress illustrating the detrimental effect (i.e. less growth) of drought-stress on the plant. Control plants from both sites had the highest transpiration rate while severely-stressed plants had the lowest rate.

Leaf Area

Leaf area expansion of the moderately-stressed plants from the wet site was inhibited by water stress relative to growth of the control plants (Figure 3). Wet-site control plants increased their leaf area by 1200 cm^2 while the moderately-stressed group increased by 730 cm^2. The same pattern of response was observed for the dry-site plants as the controls increased their leaf area by 1000 cm^2 while the moderately-stressed increased by 600 cm^2 (Figure 4). It is apparent that even mild stress as inflicted on the moderately-stressed group will inhibit leaf area expansion (Zahner, 1968).

Leaf area expansion under the severely-stressed treatment stopped on day 23 for the dry-site plants and on day 25 for the wet-site plants. On day 23, the dry-site plants had a stomatal resistance of 17.5 s cm^{-1}, and on day 25, the wet-site plants had a stomatal resistance of 60 s cm^{-1}. Leaf area of the severely-stressed, dry-site plants barely increased, but the same treatment group from the wet site increased in leaf area, although slowly, until day 25. Apparently, as an adaptation to the drought-stress conditions, the dry-site plants did not increase in leaf area as much as the wet-site plants. Leaf abscission (though minimal) was greater for the dry-site, stressed plants. This would suggest that the leaves of the dry-site plants were able to maintain a more favorable water balance for growth than the leaves of the wet-site plants despite drought-stress conditions imposed.

Leaf area expansion appears to be a sensitive indicator of stress (Zahner, 1968) providing a warning of impending
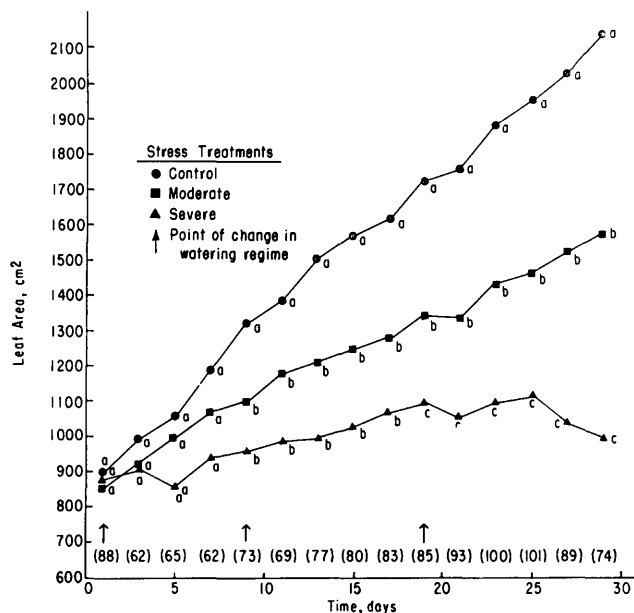

Figure 3. — Leaf area of wet-site eastern cottonwood under three watering regimes. Numbers in parentheses are standard errors. Symbols for one measurement day, followed by the same letter, are not significantly different ($a = .05$) according to Duncan's new multiple range test.
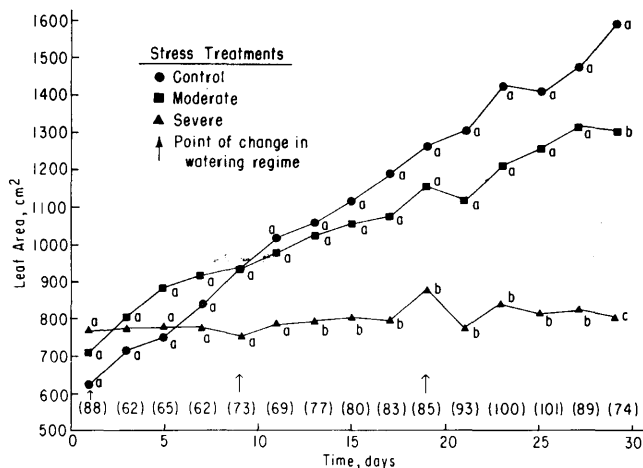

Figure 4. — Leaf area of dry-site eastern cottonwood under three watering regimes. Numbers in parentheses are standard errors. Symbols for one measurement day, followed by the same letter, are not significantly different ($a = .05$) according to Duncan's new multiple range test.

growth cessation. Thus, the stomatal resistance at which leaf area expansion stops seems to be important in terms of selecting drought resistant clones. Though more difficult to measure than stomatal resistance, especially on larger trees, leaf area measurements may be useful to indicate performance under drought-stress during preliminary screening.

Height

Total height growth for the control plants from the dry site was greater than that of the wet-site control plants (figures 5 and 6). Control plants from the dry site grew 36 cm while the wet-site control plants grew 33 cm.

There was no significant difference in height growth between the control and moderately-stressed plants from the

169

dry-site except for the final measurement day. There were statistically significant differences between the control and moderately-stressed, wet-site plants. The stressed plants from the dry site grew more than those from the wet site. The moderately-stressed, dry-site plants grew 27 cm while the severely-stressed plants grew 12 cm. The corresponding values for the wet-site plants were 18 and 8 cm, respectively. This suggests that clones which grow faster, even under moderate drought-stress, can be identified.

Height growth of severely-stressed plants from the wet site stopped on day 21 when stomatal resistance was 55 s cm^{-1}. Though resistance later decreased, plants never resumed height growth. Height growth of severely-stressed, dry-site plants stopped on day 23 when stomatal resistance was 18.5 s cm^{-1}. The data suggest that leaf and height growth respond differently at a given stage of drought, possibly because of differences in water stress among the contrasting tissues.

Height growth results suggest that the wet-site plants possess little or no ability to deal with drought. Even under moderate stress, height growth was inhibited for the wet-site plants.

Height growth of the dry-site plants was not significantly inhibited by moderate stress except for the final measurement day. Duration of growth was similar for all treatment groups, but the dry-site plants grew more than those from the wet site, perhaps partly because of their lower stomatal resistance. This would seem to indicate that decreased stomatal sensitivity (i. e. lower resistance) under water stress conveys greater adaption to drought. A clone which can tolerate drought stress with the least increase in stomatal resistance apparently will grow the fastest or continue to grow the longest under drought, and thus, be the best to select.

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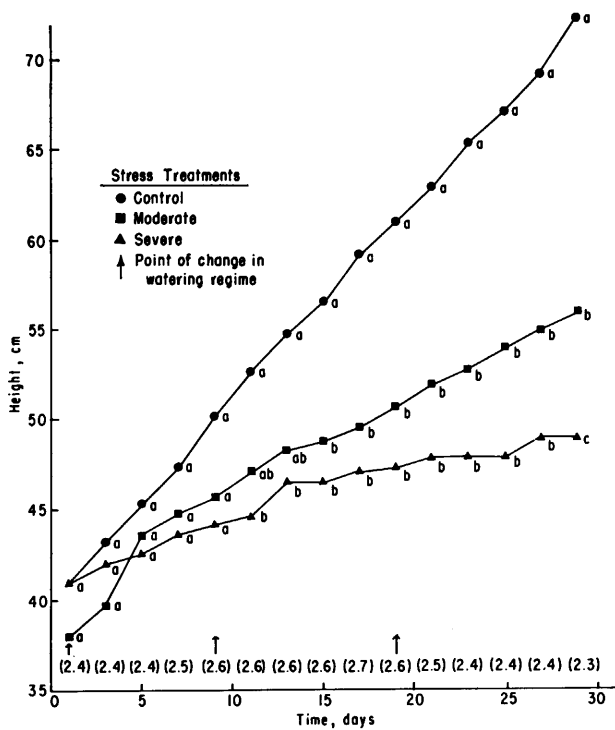
Figures 5. — Height of wet-site eastern cottonwood under three watering regimes. Numbers in parentheses are standard errors. Symbols for one measurement day, followed by the same letter, are not significantly different (α = .05) according to DUNCAN's new multiple range test.
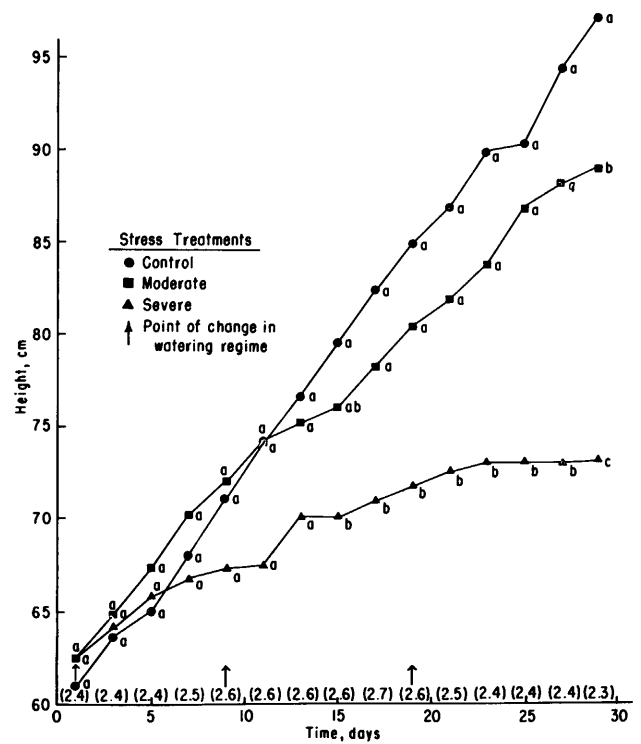

Figure 6. — Height of dry-site eastern cottonwood under three watering regimes. Numbers in parentheses are standard errors. Symbols for one measurement day, followed by the same letter, are not significantly different (α = .05) according to DUNCAN's new multiple range test.

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Variability of Quercus macrocarpa Michx. in an eastern Nebraska provenance study[1])

By St. G. Dicke and W. T. Bagley[2])

Summary

A provenance plantation of *Quercus macrocarpa* Michx. was established in eastern Nebraska during 1966. Morphological, phenological, and acorn characteristics were studied to determine the effect of provenance or variability.

Variation among provenances was discontinuous. Height growth maximized with trees originating 100 miles south of the plantation at 40 degrees north latitude. Correlation of juvenile-mature growth rates was high based on performance at 11 years. Between and within source variation was apparent in growth and acorn characteristics. Phenological information indicates that natural crossing among provenances over a wide geographic area would be possible. Fast growing trees were the last to drop their leaves in the fall.

Key words: Bur oak, *Quercus macrocarpa*, genetic variation, provenance test, phenology.

Zusammenfassung

Im Jahr 1966 wurde ein Provenienzversuch mit *Quercus macrocarpa* Michx. in Ostnebraska angelegt. Viele morphologische, phänologische und Eichelmerkmale wurden untersucht, um den Einfluß der Herkunft auf die Variabilität zu bestimmen.

Die Variation zwischen den Herkünften war diskontinuierlich. Das Höhenwachstum erreichte bei Bäumen aus Herkunftsgebieten 100 Meilen südlich des Prüfortes, bei 40 Grad nördlicher Breite, ein Maximum. Enge Jugend-Alters-Korrelationen über den Wachstumsgang konnten für das Verhalten im Alter von 11 Jahren nachgewiesen werden. Die Variation im Wachstum sowie in anderen Merkmalen war sowohl zwischen als auch innerhalb der Herkünfte offensichtlich. Natürliche Kreuzung zwischen Herkünften über ein weites geographisches Gebiet erscheint möglich. Schnellwüchsige Bäume warfen im Herbst ihre Blätter als letzte ab.

Introduction

Bur oak, *Quercus macrocarpa* Michx., is native in the north central United States and southern Canada (*Figure 1*). It is found in scattered natural stands throughout much of the Great Plains Region where it is adapted to dry sites and competes well with prairie vegetation. Bur oak has been harvested in Nebraska for firewood, lumber, posts, and barrel staves. It is also valuable in protection and ornamental plantings.

Past research has shown differences among provenances of bur oak in response to various day lengths. Vaartja (1961) found small differences in reaction to length of photoperiod between Manitoba and Nebraska sources. He concluded that bur oak was less responsive to photoperiod than other tree species. However, Read and Bagley (1967) found that bur oak seedlings of Nebraska origin grew significantly taller than under continuous light than under normal growing season daylengths. Long (1965) discovered that bur oak seedlings of northern sources produced shorter flushes of growth with less time between flushes than seedlings of southern sources. Long also found that the size of bur oak acorns decreases from east to west and south to north throughout the natural range of the species.

Santamour and Schreiner (1961) recorded differences in height and date of leaf coloration among bur oak seedlings of different origin growing in a nursery. After three growing seasons seedlings of South Dakota origin were 65 percent of the height of seedlings originating from Kansas. Leaves of trees of northern origin colored earlier in the fall than those of southern origin.

Acorns for this study were collected from natural stands of bur oak trees throughout their range with the most intensive sampling in the Great Plains Region (*Figure 1*). Seedlings and seed were planted on the University of Nebraska Field Laboratory near Mead in 1966. This report evaluates the growth of these trees during the first eleven years and interprets variation in morphological and phenological characteristics.

Methods

Acorns were collected from one to five trees in fifty native stands during the years 1963 through 1965 in cooperation with the Soil Conservation Service and Agricultural Experiment Stations. The plantation was established during