

DEVELOPMENT AND APPLICATION OF A TECHNIQUE TO
CLASSIFY THE DROUGHT RESISTANCE OF EASTERN
COTTONWOOD CLONES THROUGH MEASUREMENT OF
STOMATAL RESISTANCE

By

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PREFACE

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CHAPTER I

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 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 (44). Land-use demands 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 (44, 48) and now also for energy (10). For example, the use of wood for fuel has been rising at a rate of 15 percent per year since 1973 (38). McKnight (28) reported in 1976 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 of 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. The plant-water relations of a number of tree species, including eastern cottonwood, under drought-stress have been investigated (39, 29, 40, 5, 49, 16, 33, 53, 35, 47, 26, 27, 15, 32, 45, 2, 7). Quaking aspen (Populus tremuloides Michx.)

and European aspen (Populus tremula L.) have been studied under wet conditions (19, 42, 46, 13, 14). Farmer (12) reported the effect of drought on growth, shoot/root ratios, and wood properties of eastern cottonwood. Transpiration rates of drought-stressed eastern cottonwood have also been reported (3, 11, 37). Considerable anatomical work on eastern cottonwood stomata has been done (41, 20, 25). But no published study examines the relationship of stomatal resistance and drought in eastern cottonwood. Farmer (11) did estimate diffusion resistance (stomatal + cuticular + boundary-layer resistances) using leaf energy-balance, water vapor, and temperature-gradient measurements. Stomatal resistance can be estimated by this method when the boundary-layer resistance is low (24). Regehr et al. (37) calculated approximate values of stomatal resistance using similar methods, and took into account boundary-layer resistance. In an unpublished thesis, Dougherty (9) attempted to characterize stomatal resistance over four drying cycles for two Texas clones of eastern cottonwood using diffusion porometers of the type described by Van Bavel et al. (51). An increase in stomatal resistance was observed as the experiment progressed, which was attributed by Dougherty (9) to be more of a response to changes in atmospheric conditions (the experiment was conducted in a greenhouse) rather than a treatment effect (soil drought). Due to these changes, no valid statistical test could be made.

Stomatal sensitivity to water stress is proposed to be an important component of drought resistance (17, 1, 8). Effective selection for a plant character can be achieved only if genetic variation exists within the population of interest (4). Posey (34) reports that the genetic variation between geographic sources of eastern cottonwood in Oklahoma

is of sufficient magnitude for drought resistance (based on first year survival of field-planted cuttings under natural drought conditions) that origin of plant material must be considered in a selection program for eastern cottonwood in Oklahoma. Selection is practical only when the character of interest is easily measured and the environmental component of variation can be minimized (4). Stomatal resistance is simply measured with the Kanemasu-type diffusion porometer (24) and variability in the environment is minimized in controlled environment chambers. Because valid measurements of stomatal resistance of eastern cottonwood were not available, this study was designed to develop a technique to classify the drought resistance of eastern cottonwood through measurement of stomatal resistance. A simple and rapid measurement technique was developed through a pilot experiment. The technique was then applied to make a preliminary classification of the drought resistance of several Oklahoma clones of eastern cottonwood.

CHAPTER II

LITERATURE REVIEW

Water and Plant Water Relations

Water is essential to the life and growth of trees, often comprising as much as 90 to 95 percent of the fresh weight of succulent plant tissue (50). Water provides certain plant parts with their mechanical strength through cell turgor, since much vegetative tissue is composed of cells with non-lignified walls. Such plastic cells become mechanically stable under the influence of hydrostatic pressure developed by water. Water is the raw material in metabolism and synthesis reactions that occur in living trees, even though this amounts to a small fraction of the total amount of water that passes through the tree. By far the largest amount of water moves into the roots, through the stem, into the leaves, and out into the atmosphere in what can be termed a "transpiration pathway" (50).

Trees are capable of transpiring large amounts of water by exposing an extensive leaf area perforated with numerous stomata. Kozlowski (25) reports that forested areas in the southern United States may transpire up to 1200 liters of water per hectare per day. Trees normally exhibit daily internal water deficits due to their high rates of water loss through transpiration. If soil moisture is not adequately replenished, these temporary water deficits tend to persist longer each day as leaves become incapable of recovering turgidity at night (25). Such water

deficits negatively affect all important physiological processes including transpiration, photosynthesis, and growth.

Tolerance and avoidance of plant water deficit are known collectively as drought resistance (21, 25). Drought tolerance is protoplasmic tolerance to extreme desiccation without injury. Drought avoidance involves adaptations in the leaves, stem, and roots to reduce water loss or increase water uptake.

Measurement and Effect of Drought-Stress

An early report by Shirley (39) described an apparatus for testing drought resistance of trees. This machine consisted of a thermostatically-controlled, illuminated plant chamber with apparatus for drying air over calcium chloride and forcing it through the chamber. The severity of the drought was considered, with other factors constant, to be a function of the evaporative power of the air; the saturation deficit. Plants were tested at ambient temperatures of 35 to 40°C, a temperature which most plants were apparently able to withstand but which at low humidities gave a high saturation deficit.

Two to four week old seedlings, potted in cans filled with sand, were watered to a predetermined soil moisture content, sealed in paraffin and placed in the desiccation chamber. The machine was run continuously until all seedlings were dead. Time until death, and soil moisture content at death, were used as the criterion for drought resistance.

Shirley's first run (39) was described as a test of three seedling classes of white spruce (Picea glauca (Moench) Voss) seedlings. Two-year old (2-0), three-year old (3-0), and three-year old seedlings which had spent one year in the transplant bed (2-1) were used. The ambient

temperature averaged 38°C and the relative humidity was about ten percent. The soil moisture content at death was determined to be about 14 percent for all pots. The 2-0 and 3-0 seedlings lived 20 and 21 days respectively, while the 2-1 stock lived only 13 days. Shirley (39) concluded that the transplanted stock was less drought resistant than either of the other two classes of seedlings.

Meuli and Shirley (29) tested for drought resistance in green ash (Fraxinus pennsylvanica var. lanceolata (Borkh.) Sarg.) seedlings using Shirley's (39) machine. Seedlings grown from open-pollinated seed collected from 83 trees, located in five plains states (North Dakota, South Dakota, Nebraska, Kansas, and Oklahoma), were grown for one year in the greenhouse and then tested for drought resistance by Shirley's so-called "death test". The first seedling to die was assigned the number "one", the second "two", and so on. The figure obtained by averaging the numerical order of death for the trees of a given sub-region was called the mean score. These scores were used as a criterion for rating drought resistance.

Clinal variation in drought resistance of the green ash was described and regions of differing drought resistance were established by Meuli and Shirley (29). Seed from the northwestern portion of the study yielded the most drought resistant plants while plants from the southern and eastern seed sources were least resistant. No local differentiation into drought-resistant ecotypes was found. Because differences were also noted in size of seedling, color of foliage, and time of resumption of growth in the spring, the existence of climatic races within the species was suggested.

Shirley and Meuli (40) also used the drought resistance quantification technique of Shirley (39) on pine. The species used in the tests were red pine (Pinus resinosa Ait.), eastern white pine (Pinus strobus L.), and jack pine (Pinus banksiana Lamb.). The tests were run at an ambient temperature of 35 to 37°C and at a relative humidity of 20 percent. The seedlings were said to be dead when the needles were determined to be "brittle" (easily broken). The seedlings died in four to six days. With a seedling moisture content of around ten percent, oven-dry-weight basis, there was no question that the seedlings were dead. However, it was questionable as to how long such seedlings had been dead. For example, Brix (5) reported that leaf-moisture content of 110 percent, oven-dry-weight basis, indicated a critical plant water balance in loblolly pine (Pinus taeda L.), below which seedlings did not recover even after rewatering. In another study of loblolly pine, Ursic (49) found that when leaf-moisture content was reduced to 80 percent, oven-dry-weight basis, leaf turgor was never regained. In addition, "hardening off" of the plant during a longer period of drought might have changed the results of the very short, severe test done by Shirley (39). Ferrell and Woodward (16) found that proper assessment of the behavior of Douglas-fir (Pseudotsuga menziesii Franco.) after drought, such as occurred in nature, required more than a "few days".

Ferrell and Woodward (16) planted Douglas-fir seedlings and sunflower seeds in pots filled with soil. The seedlings were placed in a greenhouse and watered regularly until the sunflowers developed a pair of secondary leaves, at which time the drought period began. At the permanent wilting point of the sunflower, the tree seedlings were no longer watered and were placed in a controlled environment chamber until

death. Two types of tests were made to determine the ability of the seedling to resist death under severely dehydrating conditions. So that transpiration and root absorption differences would determine seedling survival, half the pots were sealed in paraffin to prevent water loss by evaporation from the soil. The soil surface of the remaining pots was covered with sand to slow evaporation from the soil. Using this technique, differences in survival were due to internal tolerance of the seedling to extreme desiccation (measured transpiration accounted for only ten percent of the water loss). Results suggested that different degrees of drought resistance have developed in populations of Douglas-fir representing the various environments of its range in Oregon. Dry-site (inland) seed sources were found to be more drought resistant than wet-site (coastal) seed sources, although local variability (north versus south slope seed source) was also present.

Pharis and Ferrell (33) used two measures of drought resistance of Douglas-fir; time until death and soil moisture content at the death point. The soil surface of all pots was covered with sand so that evaporation from the soil surface accounted for only ten percent of total water loss. Results confirm Ferrell and Woodward's (16) work. Inland sources of Douglas-fir were found to be more drought resistant than those from coastal sources in Oregon. Pharis and Ferrell (33) also showed that needle-moisture content might be a workable index for determination of coniferous seedling viability except near the "death point". Seedlings were classified into coastal and inland groups according to their needle-moisture content under well-watered conditions.

In terms of the so-called "death test" method, difficulty was encountered in assessing the viability of the plant following such

severe dehydration. Ferrell and Woodward (16) found it difficult to determine time of Douglas-fir seedling death with greater accuracy than plus or minus one day. Furthermore, Brix (5) noted that it is not the death of a certain plant organ (such as the leaves), but rather the ability of the plant as a whole to recover after dehydration which should be studied. Brix (5) concluded that an accurate method for determining this "threshold of survival" is the key for comparisons of plant hardiness following simulated drought conditions.

More recent investigations have advanced beyond the short, severe "death test" approach to a more quantitative methodology with emphasis on measurement of the plants' physiological parameters. Even terminology has been upgraded with changes from the unclear "droughty conditions" to the more specific "soil or plant moisture stress" described by standardized quantitative methods. Transpiration, water potential, and leaf turgidity measurements have replaced the vague "time until death" of previous work.

Under conditions of different levels of soil moisture stress, Zavitkovski and Ferrell (53) determined rates of photosynthesis, transpiration, and respiration in Douglas-fir seedlings from Oregon. The seedlings were grown from seed collected on a wet and a dry site. Photosynthetic rates were found to decline sharply after soil moisture stress of one atmosphere was reached, with no major differences between seedlings from the two sources. At both high and low soil moisture tension, respiration and transpiration rates were higher for seedlings from the wet-site source than for the dry-site seed source. Seedlings from the dry-site seed source had higher photosynthetic rates at higher relative turgidities of the leaves and lower rates at low relative

turgidities than seedlings from the mesic seed source. Over a range of soil moisture tension from field capacity to permanent wilting point, relative turgidity of seedlings from the dry site varied less than that of seedlings from the wet site source. Drought resistance of the dry site seedlings effectively prevented excessive water loss and prevented relative turgidity from falling below its level under well-watered conditions.

The effects of soil water stress on seedlings of Eucalyptus rostrata Schl., E. polyantemos Schau., and E. sideroxylon Cunn var. rosea Hort. were studied by Quraishi and Kramer (35). Transpiration rate, shoot growth, and leaf area growth were found to be most affected in E. rostrata and least affected in E. sideroxylon. Leaf water deficit at stomatal closure was greater and leaf water potential, at the wilting point of sunflower plants, was lower in E. rostrata than in E. sideroxylon. Excised twigs of E. rostrata also lost water faster than twigs of the other two species. Root growth did not differ significantly among the three species. It was suggested that E. rostrata suffered more injury from soil water stress than the other two species because its stomata closed more slowly when leaf water stress developed and because it had a higher transpiration rate.

Townsend and Roberts (47) compared red maple (Acer rumbrum L.) seedlings grown from open-pollinated seed collected from wet and dry sites. The seedlings were subjected to three levels of plant water stress. At both high and low water potential, transpiration rates were higher for seedlings from the wet-site than from the dry-site. Growth rates were also found to be greater for the wet-site seedlings at all levels of stress than for the dry-site seedlings. However, wet-site

source seedlings came to temporary and permanent wilt sooner than seedlings from the dry site which suggested that dry-site source seedlings would probably grow more under drought conditions.

Ladiges (27) found six-month old seedlings of Eucalyptus viminalis Labillardiere from two dry sites exhibited greater resistance to desiccation, and were less damaged by drought, than seedlings from two wet sites in Australia. The dry-site seedlings maintained higher rates of transpiration under moisture stress, not merely avoiding drought by quickly closing stomata. The wet-site seedlings wilted at a higher relative turgidity than did those from the dry sites. It was suggested that the greater protoplasmic tolerance of the dry site seedlings resulted in their greater tolerance of drought.

The advent of the diffusion porometer to provide direct, rapid measurement of stomatal resistance (24) has followed the recent "electronic" approach to plant water relations research. Diffusion porometers, thermocouple psychrometers, leaf area meters, and other assorted instrumentation have become the basis for recent investigation of the effect of drought-stress on trees (15, 32, 45, 2, 7). Recent investigation presently would seem an "absolute" quantitative approach.

Measurement of stomatal resistance has received particular attention as seen in the standard use of the diffusion porometer cited in recent literature (15, 32, 45, 2, 7). The reason for the emphasis on stomatal resistance becomes apparent from a description of the pathway of water through the so-called "soil-plant-atmosphere" continuum. The pathway of water is down a diffusion gradient from the soil moisture "reservoir" to the atmosphere "sink". It is apparent that decreasing the flow of

water through the soil-plant-atmosphere continuum results from increasing the resistance to flow at any point along the pathway.

The main effect of resistances from plant part to plant part is to restrict the replacement of water lost by transpiration. Stomatal resistance restricts water loss to the atmosphere. Consequently, resistances in the plant are to be considered potentially "harmful" while stomatal resistance is "protective" (17). A large increase in resistance within the plant would reduce transpiration, but the leaves could be desiccated and killed before a "water equilibrium" could be attained. It is apparent, then, that control of water transport through the plant is primarily through stomatal resistance because control elsewhere would result in the ultimate desiccation of the plant.

In a northern hardwood forest in central New Hampshire, Federer and Gee (15) artificially subjected several trees to soil moisture stress by trenching around them and covering the soil with plastic. After three weeks with rain excluded, soil water potential ranged from -0.4 to -0.8 bars (considered dry for this site). Daytime abaxial (lower surface) stomatal resistances of yellow birch (Betula alleghaniensis Britton), sugar maple (Acer saccharum Marsh.), and American beech (Fagus grandifolia Ehrh.) had doubled, which indicated significant stomatal closure caused by water stress. However, daytime xylem potential (measured with pressure bomb apparatus on excised twigs) on stressed trees were the same as, or higher than, those on unstressed trees. Stomatal closure effectively prevented excessive water loss and prevented xylem potential from falling below its normal level. This would suggest that moderate stress within the realm withstood by a tree can be tolerated through increasing stomatal resistance.

Pereira and Kozlowski (32) measured daytime changes in needle water potential and stomatal resistance of young jack pine and red pine during a single growing season in northern Wisconsin. During the growing season, water potentials in the early morning were lower each day as the season progressed. Needle water potential decreased more during the day in red pine than in jack pine. Stomata of jack pine were seen to close earlier in the day. Jack pine's superior performance was also reflected in lower transpiration rate and slower soil water depletion associated with lower leaf area and stomatal closure at a higher needle water potential than in red pine.

In a field study of Douglas-fir on Vancouver Island, British Columbia, Tan et al. (45) investigated the relationship between stomatal resistance and environmental variables. During the day, stomatal resistance was found to be related mainly to soil water potential and vapor diffusion deficit of the canopy air. Stomatal resistance of Douglas-fir was found to increase with decreases in soil water potential and increases in vapor diffusion deficit. During the study, there were two dry periods separated by a period when the soil was completely rewetted. This "stress history" had little effect on the relationships studied. The authors suggested measurement of soil water potential to describe the stomatal resistance characteristics of a Douglas-fir stand; however, direct measurement of stomatal resistance would seem much simpler to this author.

Clemens and Jones (7) investigated potted plants of Acacia and Eucalyptus species from Australia grown under different levels of shading, nutrition, and irrigation to assess the effect of these factors on plant water use. Water use was affected only by the irrigation treatment.

Control plants that had been watered daily used appreciably more water than plants repeatedly subjected to water stress. Conditioned plants (repeatedly subjected to water stress) exhibited control of transpiration associated with a more pronounced tendency for stomata to close prior to wilting. Conditioned plants also maintained a higher level of stomatal resistance than controls at lower leaf water potentials and thus controlled excessive water loss.

Bennett and Rook (2) investigated stomatal control of gas exchange as a possible factor in the survival ability of two clones of Monterey pine (Pinus radiata D Don) from New Zealand known to differ in their transpiration and survival rates. Stomatal resistance, apparent photosynthesis, and transpiration rates were measured in response to increased evaporative demand. The response of apparent photosynthesis to carbon dioxide concentration was also measured. Clone 457, which had a low survival rate in the field, showed a transpiration rate up to twice that of clone 456, which had a high survival rate. The stomatal resistance of clone 457 was about half that measured for clone 456 under all experimental conditions. Though the two clones showed a similar response to increased evaporative demand, the greater absolute value of stomatal resistance for clone 456 resulted in a lower overall transpiration rate in that clone. The measured rate of photosynthetic response to carbon dioxide concentration for clone 456 was half that of clone 457. It was suggested that a factor in determining the relative survival rates of the two clones was the greater ability of clone 456 to limit transpiration through increased stomatal resistance.

Effect of Drought-Stress on Eastern Cottonwood

The literature is limited in terms of drought-stress studies dealing specifically with eastern cottonwood. Broadfoot (6) discussed some of the soil and forest conditions associated with dieback of eastern cottonwood following a severe drought in the lower Mississippi River Delta Region during the 1950's. Cottonwood dieback was observed to be consistently associated with soil conditions. Stands on sandy sites showed the most rapid and severe dieback in dry weather, compared to other cottonwood sites. Johnson and Krinard (22) reported that cottonwood trees with more than two-thirds of their crown affected by such drought-caused dieback were found to be unlikely to survive. Trees with less than one-third crown dieback were found to recover. Trees in intermediate dieback classes were proposed to be lost for commercial harvest according to Johnson and Krinard (22). While such trees might recover, breakage and rot that ultimately followed drought-caused dieback was found to reduce the trees' potential merchantability.

Bonner (3) conducted a growth chamber study to determine the effect of increasing soil moisture tension on growth, transpiration, and leaf moisture stress in juvenile eastern cottonwood from Mississippi. The plants were grown in two soils of different texture, sandy loam and clay. Transpiration rates began to decrease at leaf water deficits of 2.5 percent in the sandy loam group and 4.5 percent in the clay group. Terminal growth ceased when leaf water deficits reached 4.0 percent for the sandy loam group and 5.0 percent for the clay group. It was concluded that, although eastern cottonwood used large amounts of soil moisture, its needs were apparently reduced at relatively low levels of moisture stress.

Farmer (11) found that the degree of transpirational cooling in juvenile eastern cottonwood from central Mississippi was negatively correlated with internal leaf water deficit. Leaf diffusion resistances (leaf + cuticular + boundary layer resistances) estimated from leaf energy balance, water vapor, and temperature gradient measurements, were less than 1.0 s cm^{-1} (seconds per centimeter) for freely transpiring plants and from 20.0 to 40.0 s cm^{-1} for plants under severe moisture stress.

Farmer (12) grew cuttings from 30 randomly selected eastern cottonwood clones from central Mississippi in pots for one season under favorable and drought-stress soil moisture regimes. Clonal variation in growth under stress was clouded as a result of experimental procedure. As rewatering followed observable wilting, drought-prone clones received more water than drought-resistant clones. Even so, clone-by-treatment interaction variance accounted for a substantial portion of the variation in growth. Genetic variation between treatments was statistically significant in leaf, stem, and root weight. Shoot/root ratios differed among clones under both treatments. Variation in drought resistance, under the conditions of the experiment, was concluded to be under moderate genetic control.

In an unpublished thesis, Dougherty (9) characterized stomatal resistance over four drying cycles for two Texas clones of eastern cottonwood using diffusion porometers of the type described by Van Bavel et al. (51). Soil water content, photosynthetically active radiation, wind speed, leaf temperature, leaf water potential, ambient air temperature, relative humidity, solar radiation, and carbon dioxide concentration were also measured.

Low levels of light quantum flux density were found to trigger stomatal opening. Rapid changes in stomatal resistance were observed from 0 to $50 \mu\text{E m}^{-2} \text{ s}^{-1}$ (micro-Einsteins per meter² x seconds) for the adaxial (upper) leaf surface and from 0 to $115 \mu\text{E m}^{-2} \text{ s}^{-1}$ for the abaxial (lower) surface. The experiment was conducted in a greenhouse without supplemental lighting.

No relationship was found between stomatal resistance and leaf water potential. However, a critical range of leaf water potential between -8 and -12 bars was found to trigger rapid stomatal closure.

Soil water content was found to condition the influence of the measured atmospheric variables on stomatal resistance. When soil moisture content was greater than 20 percent by volume, an increase in air temperature and vapor pressure deficit (calculated with relative humidity measurements) had little effect on stomatal resistance. However, when soil moisture content dropped below 20 percent, an increase in air temperature and vapor pressure deficit resulted in rapid increases in stomatal resistance. Soil moisture content was concluded to be the dominant factor characterizing stomatal resistance for both clones.

It should be noted that an increase in stomatal resistance was observed as the experiment progressed and that this was attributed by Dougherty (9) to be more of a response to changes in atmospheric conditions rather than a treatment effect. Due to these changes, no valid statistical test for treatment could be made.

Regehr et al. (37) found gas exchange in eastern cottonwood showed a high sensitivity to low leaf water potential. Photosynthesis was seen to fall from a maximum at -3 to -8 bars to near zero at -11 bars leaf

water potential. Trends in transpiration rate and leaf conductance (inverse of stomatal resistance) were similar to those exhibited by photosynthesis.

Stomatal resistance of several Populus clones, including one of eastern cottonwood, was related by Pallardy and Kozlowski (31) to environmental and plant factors by multiple regression analysis. Regression equations accounted for up to 80 percent of the variation in stomatal resistance data. Light intensity and vapor pressure deficit varied among clones in importance in influencing stomatal resistance. Pronounced stomatal sensitivity of certain clones to vapor pressure deficit was suggested to be related to drought resistance in the clones parentage. The importance of several environmental factors observed to determine stomatal resistance was found to suggest inclusion of several independent variables in equations describing stomatal resistance of eastern cottonwood.

CHAPTER III

PROCEDURE AND RESULTS

Pilot Experiment

Procedure

A pilot experiment was conducted to develop a simple and rapid technique to classify the drought resistance of Oklahoma clones of eastern cottonwood in a subsequent screening experiment. Two clones of eastern cottonwood (S7C1 and S7C13), obtained from Texas A & M University, were used. The clones, initially selected for their fast growth rate, were from the Colorado River in Bastrop County, Texas (Figure 1). The material obtained was propagated in a cutting bed at Oklahoma State University's Kiamichi Forestry Field Station, Idabel, Oklahoma. On 6 February 1978, 30 20-cm long cuttings of uniform diameter were collected for each clone. The cuttings were kept in cold storage until 16 April 1978 when they were transported to Stillwater, Oklahoma. They were soaked in water for four days and then planted singly, 14 cm deep, in plastic pots (11 cm diameter, 14 cm deep) containing a soil mixture of three parts loam to one part sand. The pots, perforated for drainage, were watered daily. Bud break began on 27 April and the pots were placed in a growth chamber (Sherer Model CEL-512-37) on 8 June. The plants were left to adapt to the chamber environment during the summer. All cuttings were watered equally (175 ml/pot/day) prior to the start of the

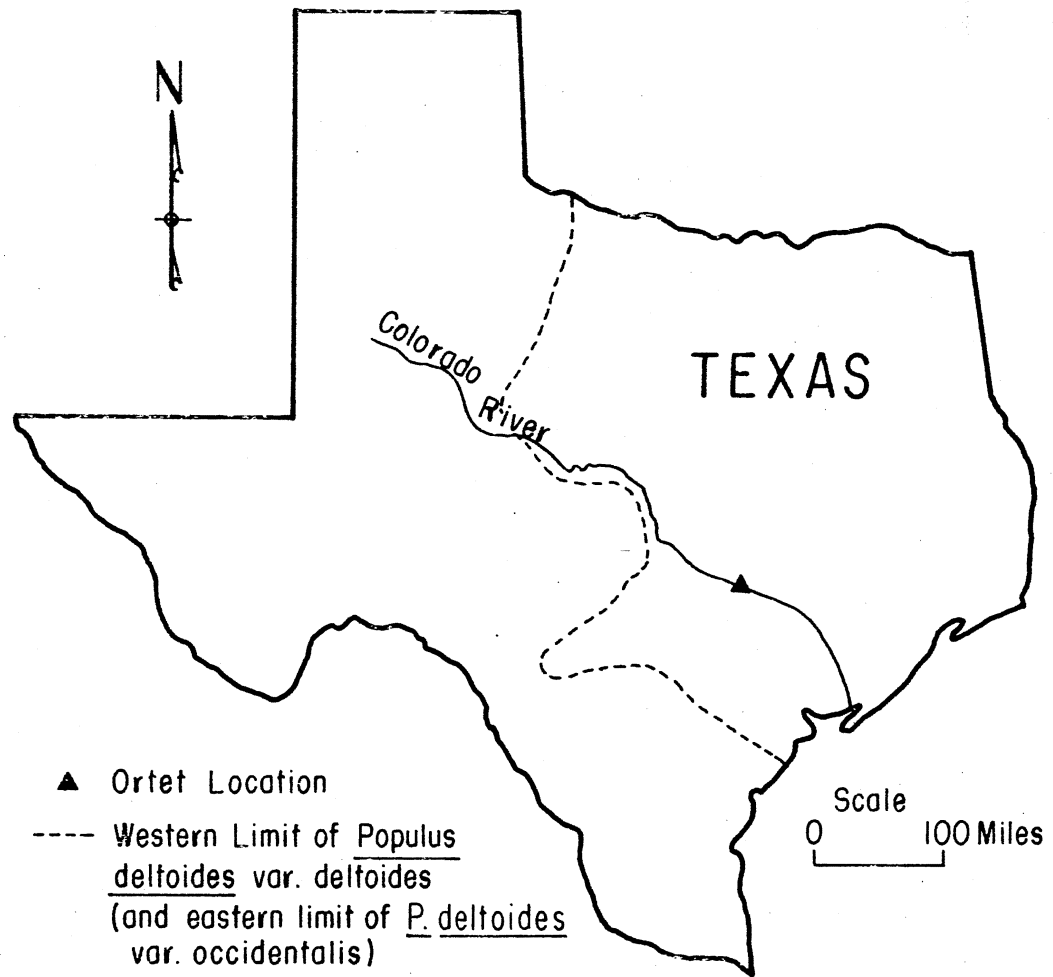


Figure 1. Geographic Origin of Clones Used for Pilot Experiment

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 6 September (day 1) and lasted four weeks. On day 1 the cuttings were 45 to 55 cm tall with 20 to 25 fully developed leaves. There were three treatments as follows:

Control: 175 ml water added to pots daily

Moderate-Stress: 175, 125, 75, 25 ml water added daily during weeks 1, 2, 3, 4 respectively

Severe-Stress: 175, 100, 25, 0 ml water added daily during weeks 1, 2, 3, 4, respectively

During the experiment, air temperature during the day was 30°C, and at night was 25°C. The relative humidity, measured with a hygrothermograph, varied from 50 to 70 percent. From 0500 to 2100 hours, the light quantum flux density, provided by cool-white fluorescent and incandenscent lights, was $630 \mu\text{E m}^{-2} \text{s}^{-1}$ at the top of the plants as measured with a quantum sensor (Model LI-190S, Lambda Instrument Company, Lincoln, Nebraska). From 2100 to 0500 hours, the chamber was dark.

On days 1, 8, 15, 22, and 28, two measurements were taken. First, the height of each plant was measured. Second, leaf area of all leaves on each plant was measured using a clear plastic dot-grid, with dots placed two cm apart. Dots were counted to obtain leaf area. A third measurement, taken every day, was adaxial stomatal resistance of the fourth fully developed leaf (from the top) of each plant. Each measurement was taken toward the tip and to the side of the midrib of the leaf with a calibrated stomatal diffusion porometer (24) (Model LI-65 and Sensor LI-20S, Lambda Instrument Company, Lincoln, Nebraska). A reading

was stopped if, after two minutes, the meter on the porometer did not register. These "no readings" were not included in the statistical analysis. Loss of water due to transpiration was determined by weighing the pots daily. The experiment ended on day 28 when the stomatal resistance of most of the moderately-stressed plants did not register on the meter.

The experimental design was a split-plot with two clones, three treatments, and nine replications, for a total of 54 pots. The main-unit treatments were the water regimes (control, moderate-stress, severe-stress) while the sub-unit treatments were the clones. A statistical test showed that the two clones responded similarly to the three treatments. Therefore, the two clones were considered as one population in the data analysis, which consisted of an analysis of variance ($\alpha = 0.05$), followed by Duncan's new multiple range test (43).

Results

Stomatal Resistance. The stomatal resistance of the control plants at 14 to 28 $s\ cm^{-1}$ (Figure 2) was higher than the resistances calculated for well-watered plants by Farmer (11) and Regehr et al. (37), who observed resistances less than 5 $s\ cm^{-1}$. There are at least three possible reasons for this discrepancy. First, Farmer (11) and Regehr et al. (37) calculated only a generalized resistance and did not differentiate resistance on the adaxial or abaxial surfaces. Their method might have determined abaxial resistances, which are usually lower than adaxial resistances in tree species (13). Federer (13) found that during an abnormally wet spring, quaking aspen had abaxial resistances of 5 to 7 $s\ cm^{-1}$ and adaxial resistance of 30 $s\ cm^{-1}$. The adaxial surface was

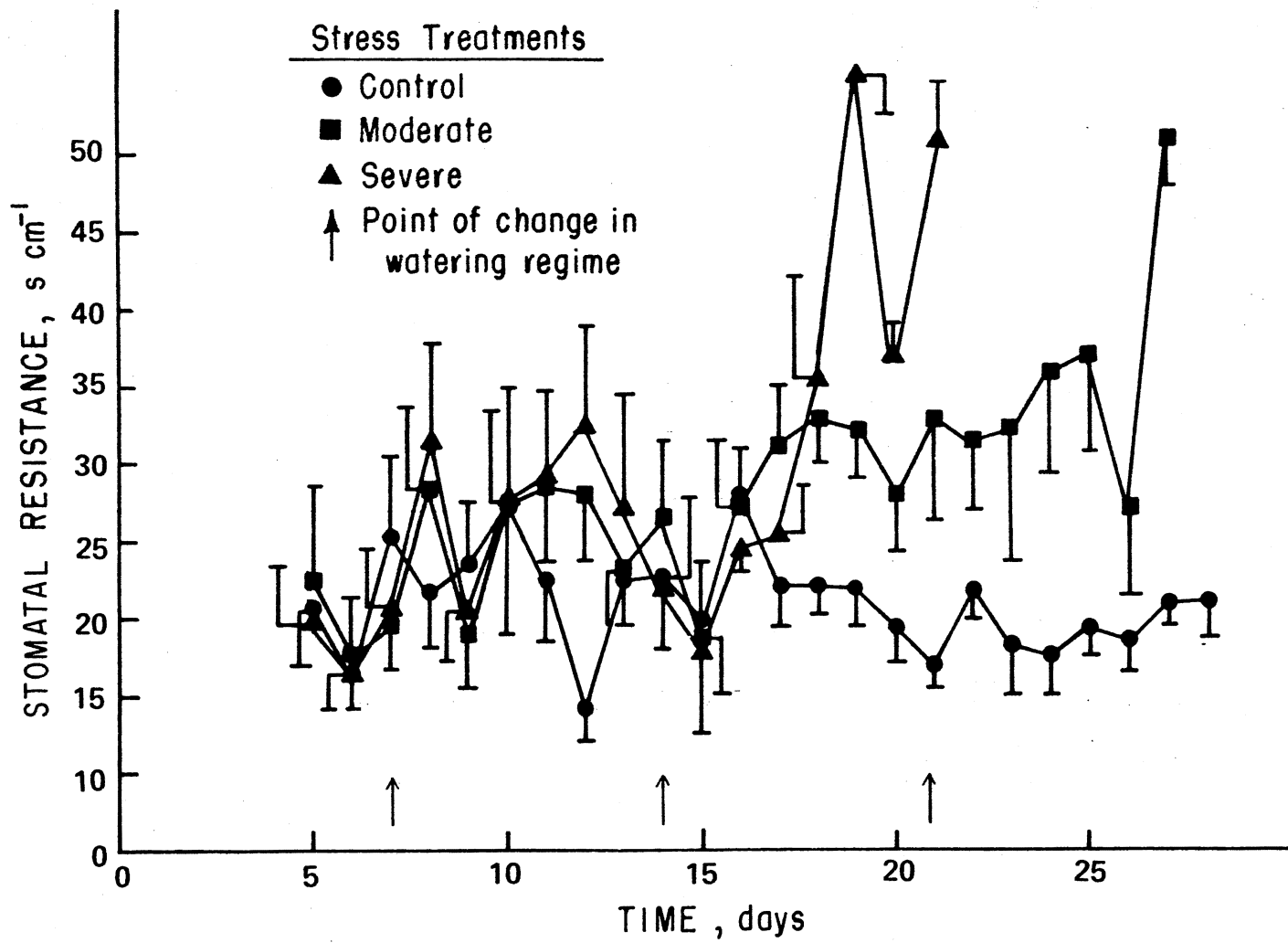


Figure 2. Stomatal Resistance of Texas Clones of Eastern Cottonwood Under Three Watering Regimes. Vertical Bars are Standard Errors.

measured because Rawson et al. (36) suggested that the leaf surface with the highest resistance should be measured in vapor-exchange studies, particularly if one is trying to determine differences due to different genotypes. Further, Pallardy and Kozlowski (31) found adaxial stomata of Populus clones to be more sensitive than abaxial stomata to changes in vapor pressure deficit, which supplements observations made by Kanemasu and Tanner (23) concerning greater sensitivity of adaxial stomata to leaf water status.

Second, the clones in the pilot experiment originated from a semi-arid region (Texas). These clones probably are adapted to moderate drought conditions and naturally have a higher resistance than eastern cottonwood plants from mesic areas (Mississippi in Farmer's (11) study and Minnesota in the study by Regehr et al. (37)). Third, the control plants may simply not have been watered adequately. Stomatal resistance was measured just prior to daily watering such that control plants may have been under some stress. Dougherty (9) found soil water content to affect stomatal resistance of eastern cottonwood. Apparently aberrant stomatal resistance values for the first four days conflicted with the initially high transpiration rates and thus will not be included in Figure 2 or further discussion. The sensor was replaced on day 5 with another being used for the remainder of the experiment.

On days 5 through 7, variation due to treatment was found to be non-significant (Table I). That is, variation among plants from different treatment groups was not so great as to produce significant differences in stomatal resistance. All plants received the same treatment during the first week. It was concluded that the uniformity in response, observed during the first week, provided an unconfounded base upon which

TABLE I

DUNCAN'S NEW MULTIPLE RANGE TEST FOR STOMATAL RESISTANCE
OF TEXAS CLONES OF EASTERN COTTONWOOD UNDER
THREE WATERING REGIMES

Day	Range Test ($\alpha = 0.05$)		
	Control	Moderate-Stress	Severe-Stress
5	20.8(a)*	22.6(a)	19.8(a)
6	16.6(a)	17.7(a)	16.0(a)
7	25.2(a)	19.4(a)	20.8(a)
8	21.9(a)	28.7(a)	31.6(a)
9	23.4(a)	19.0(a)	20.3(a)
10	28.2(a)	27.6(a)	28.0(a)
11	22.4(a)	28.5(a)	28.8(a)
12	14.1(a)	28.0(b)	32.5(b)
13	22.6(a)	23.8(a)	27.2(a)
14	22.8(a)	26.8(a)	21.9(a)
15	19.9(a)	18.9(a)	18.5(a)
16	28.2(a)	27.5(a)	24.5(a)
17	22.6(a)	31.3(a)	25.3(a)
18	22.5(a)	33.0(b)	35.4(b)
19	22.5(a)	32.3(b)	60.0(c)
20	19.4(a)	28.1(ab)	36.7(b)
21	17.5(a)	33.2(b)	49.3(b)
22	22.3(a)	31.6(a)	
23	18.4(a)	32.2(a)	
24	17.8(a)	35.9(a)	
25	19.4(a)	37.1(b)	
26	18.5(a)	27.1(b)	
27	21.1(a)	50.8(b)	
28	21.2		

* Numbers for one measurement day, followed by the same letter, are not significantly different.

to evaluate variation and compare treatment groups once the different watering regimes began.

Reduction in soil moisture began during the second week of the experiment, but differences between treatment groups were not visibly apparent that week. Also, variation due to treatment was not statistically significant ($\alpha = 0.05$) during the second week (except for day 12) despite a reduction in watering.

Considerable differences among treatment groups became apparent after an additional reduction in water during the third week. On days 18, 19, 20, and 21, there were significant differences in stomatal resistance between the control and stressed plants. However, only on day 19 was there a statistical difference between the two stress treatment groups. Despite the lack of quantitative difference in response between the moderate and severely-stressed plants, there were obvious qualitative differences. The severely-stressed plants were noticeably wilted and many of the lower leaves had yellowed and abscised. Some of these plants did not respond to the porometer, which suggests that their stomata were completely closed. The moderately-stressed plants were only slightly wilted and had not lost as many leaves as the severely-stressed plants.

Eleven of the 18 severely-stressed plants died due to the drought conditions during the final week of the experiment. The severely-stressed plants were not watered during that period. Though severely wilted during the fourth week, the moderately-stressed plants did survive but did not respond to the porometer on day 28 at which time the experiment was terminated. It is apparent that the stress treatments were too severe since it is unlikely that, in nature, a tree would succumb

after just three weeks of soil moisture stress. Such a severe test is unrealistic. Accordingly, the treatments were modified for the screening experiment.

Transpiration Rate. Transpiration rates are shown in Figure 3 and the comparison of treatment means by Duncan's new multiple range test is shown in Table II. Transpiration rate was related to stomatal resistance. Control plants had the highest transpiration rate and severely-stressed plants had the lowest transpiration rate. The transpiration rates were about an order of magnitude less than those reported by Farmer (11) and Regehr et al. (37). This, again, suggests that the clones from Texas were adapted to dry conditions and transpired less, even when well-watered, than clones from Mississippi and Minnesota. In addition, transpiration rate is highly dependent on the amount of water available to the tree (11, 9, 37, 7) so that transpiration rates of the pilot experiment plants may have been more comparable to others reported (3, 11, 37) if more water had been available.

Transpiration rates were found to respond directly to the amount of water applied. During the first week of the experiment, there was no difference in transpiration rate among the three treatment groups. However, a progressive reduction in watering during the experiment resulted in a correspondingly progressive reduction in transpiration rate. Duncan's new multiple range test separated all three treatment groups after the different watering regimes began (and for the remainder of the experiment). During the fourth week, the severely-stressed group was not watered and transpiration rate fell to near zero. Therefore, transpiration rates of the severely-stressed plants during the fourth week are not presented in Figure 3.

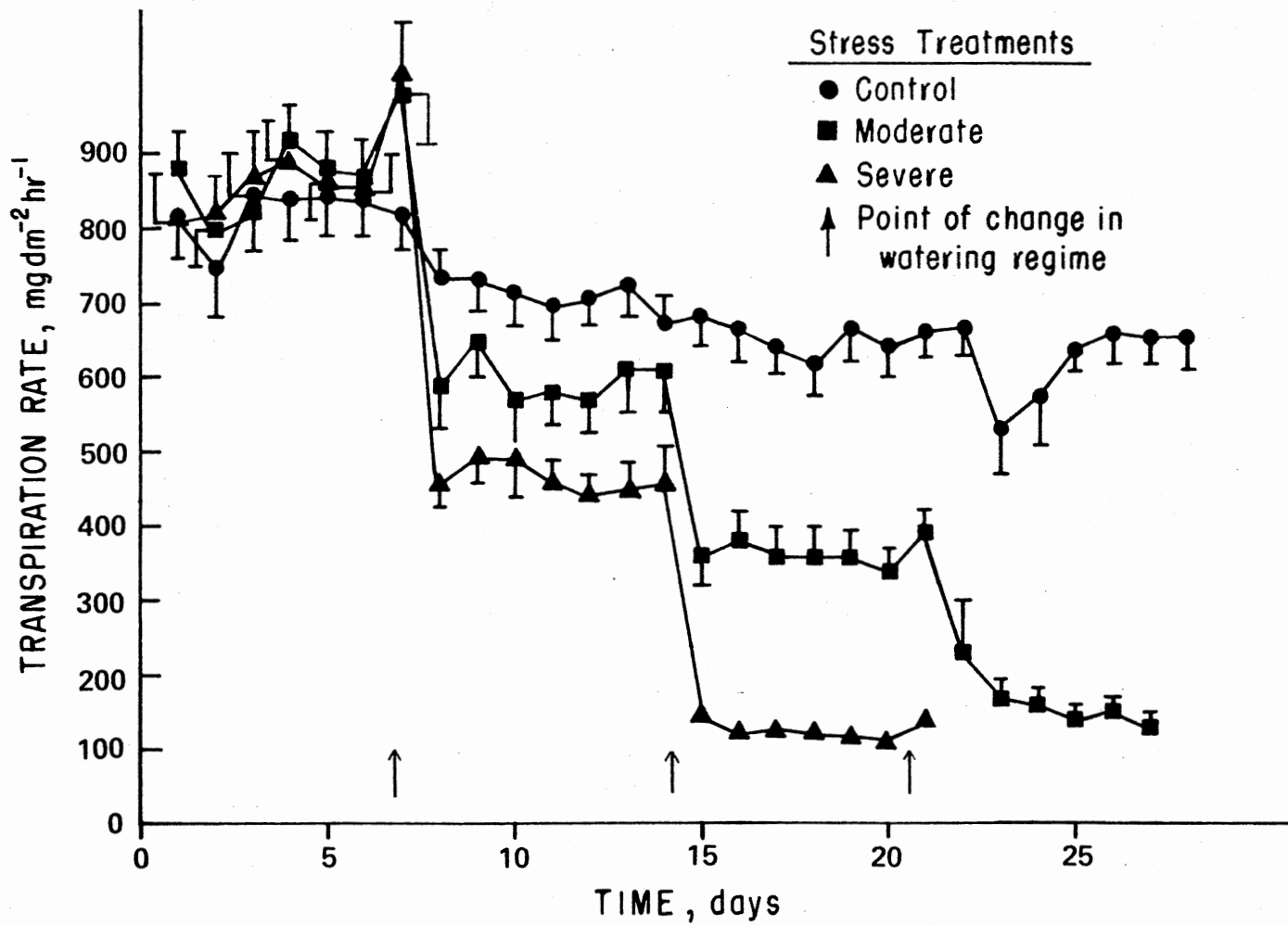


Figure 3. Transpiration Rate of Texas Clones of Eastern Cottonwood Under Three Watering Regimes. Vertical Bars are Standard Errors. Standard Error Was Negligible for Data Points Without Vertical Bars.

TABLE II
 DUNCAN'S NEW MULTIPLE RANGE TEST FOR TRANSPIRATION RATE OF
 TEXAS CLONES OF EASTERN COTTONWOOD UNDER THREE
 WATERING REGIMES

Day	Range Test ($\alpha = 0.05$)		
	Control	Moderate-Stress	Severe-Stress
1	812(a)*	883(a)	804(a)
2	750(a)	800(a)	808(a)
3	862(a)	821(a)	871(a)
4	846(a)	925(a)	892(a)
5	842(a)	875(a)	875(a)
6	842(a)	825(a)	871(a)
7	821(a)	979(ab)	1008(b)
8	738(a)	592(b)	458(c)
9	738(a)	546(b)	496(b)
10	717(a)	567(b)	488(c)
11	696(a)	579(b)	458(c)
12	708(a)	575(b)	442(c)
13	725(a)	608(b)	450(c)
14	675(a)	625(ab)	512(b)
15	683(a)	362(b)	146(c)
16	667(a)	375(b)	125(c)
17	638(a)	375(b)	129(c)
18	621(a)	375(b)	117(c)
19	667(a)	375(b)	117(c)
20	646(a)	342(b)	117(c)
21	662(a)	392(b)	138(c)
22	671(a)	229(b)	
23	533(a)	167(b)	
24	575(a)	154(b)	
25	638(a)	142(b)	
26	662(a)	150(b)	
27	658(a)	133(b)	
28	654		

* Numbers for one measurement day, followed by the same letter, are not significantly different.

Leaf Area. Leaves under the moderately and severely-stressed treatments stopped expanding on day 8 (Figure 4). Leaf area expansion was shown to be a sensitive indicator of stress, in agreement with Zahner (52). On day 8, the moderately-stressed plants had a stomatal resistance of 28.7 s cm^{-1} and the severely-stressed plants had a resistance of 31.6 s cm^{-1} . The drop in leaf area exhibited by the moderately and severely-stressed plants following day 15 reflects leaf abscission which was considerable for the stressed plants. Increment in leaf area of the control plants, though actively growing, was offset by leaf abscission as well. Apparently, control plants were actually under some stress or limited by pot size. It is suggested that stomatal resistances of greater than 30 s cm^{-1} in these clones indicate severe moisture stress, at which point the plants will soon succumb without sufficient soil moisture recharge.

Height. Height growth (Figure 5) was less sensitive to water deficit than leaf area growth. Moderately-stressed plants continued height growth, although slowly, until the end of the experiment. Height growth in the severely-stressed plants was inhibited after the third week. Total height growth for the control plants was greater than that of the two stressed groups. Height growth stopped at a stomatal resistance between 30 and 40 s cm^{-1} . The reduction in height growth of the severe treatment group in the final measurement was a reflection of a reduced sample due to the death of many plants during the final week of the experiment. At a given stage of drought, leaf and height growth were seen to respond differently, possibly because of differences in water stress among the contrasting tissues.

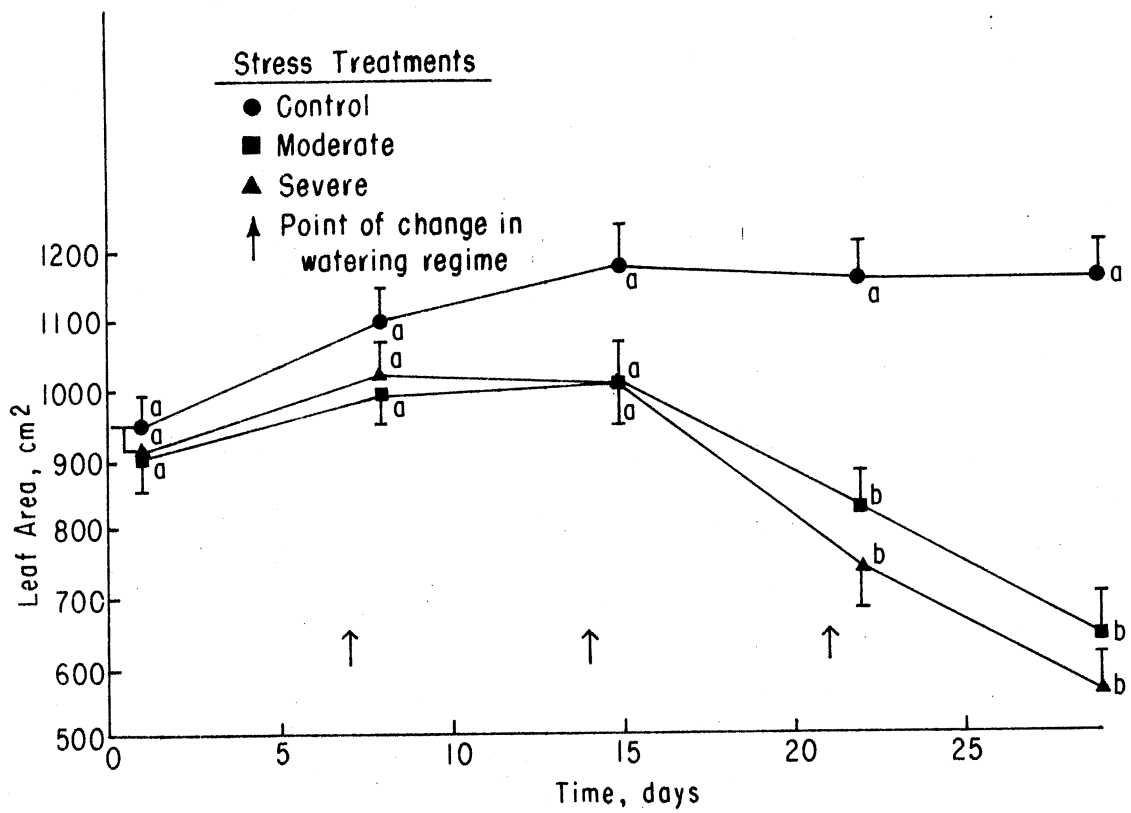


Figure 4. Leaf Area of Texas Clones of Eastern Cottonwood Under Three Watering Regimes. Vertical Bars are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

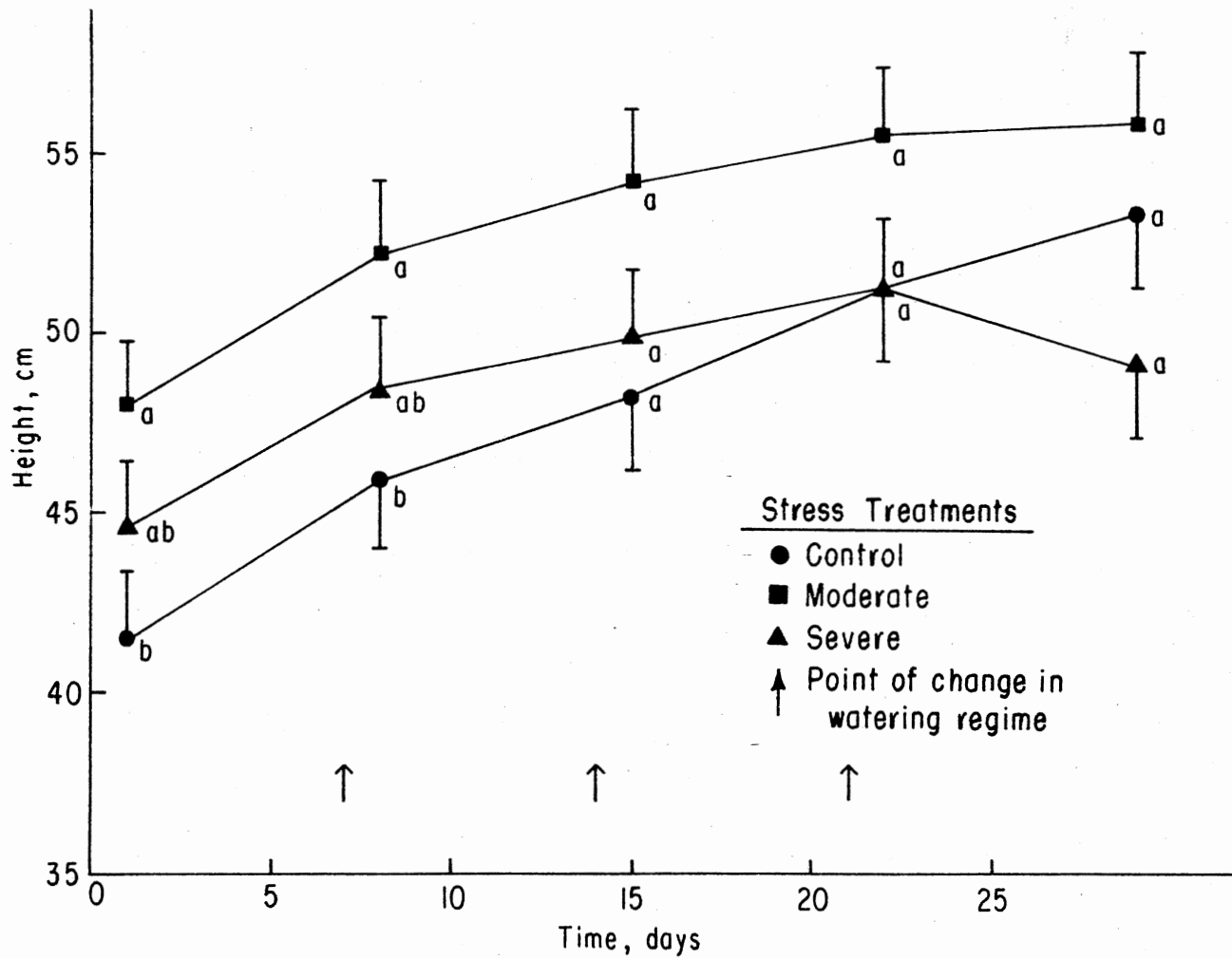


Figure 5. Height of Texas Clones of Eastern Cottonwood Under Three Watering Regimes. Vertical Bars are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

Screening Experiment

Procedure

Four clones of eastern cottonwood which originate from two natural stands in Oklahoma were used in the screening experiment. Two of the clones originate from two dominant trees of a stand along the Cimarron River in Beaver County, a dry site (Figure 6 and Table III). The Beaver County stand is Oklahoma State University's cottonwood sample stand 16 and the two trees selected from that stand for this study are clones 16-3 and 16-5. The other two clones originate from two dominant trees of a stand along the Red River in Choctaw County, a wet site (Figure 6 and Table III). The Choctaw County stand is Oklahoma State University's cottonwood sample stand 2 and the trees selected from that stand for this study are clones 2-6 and 2-8.

An eastern cottonwood clonal test plantation was established in 1969 at the Oklahoma State Forest Tree Nursery, Washington, Oklahoma (Figure 6). The plantation consists of ramets grown from cuttings collected from Oklahoma State University's 133 sample ortets representing 24 stands across Oklahoma. On 7 July 1978, 15-cm long tip cuttings with six to eight well-developed leaves were taken from the upper portion of trees growing in the 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 chosen to allow comparison of sources from a wet site and a dry site.

Tip cuttings, rather than hardwood cuttings, were used for the screening experiment for a number of reasons. Tip cuttings are actively

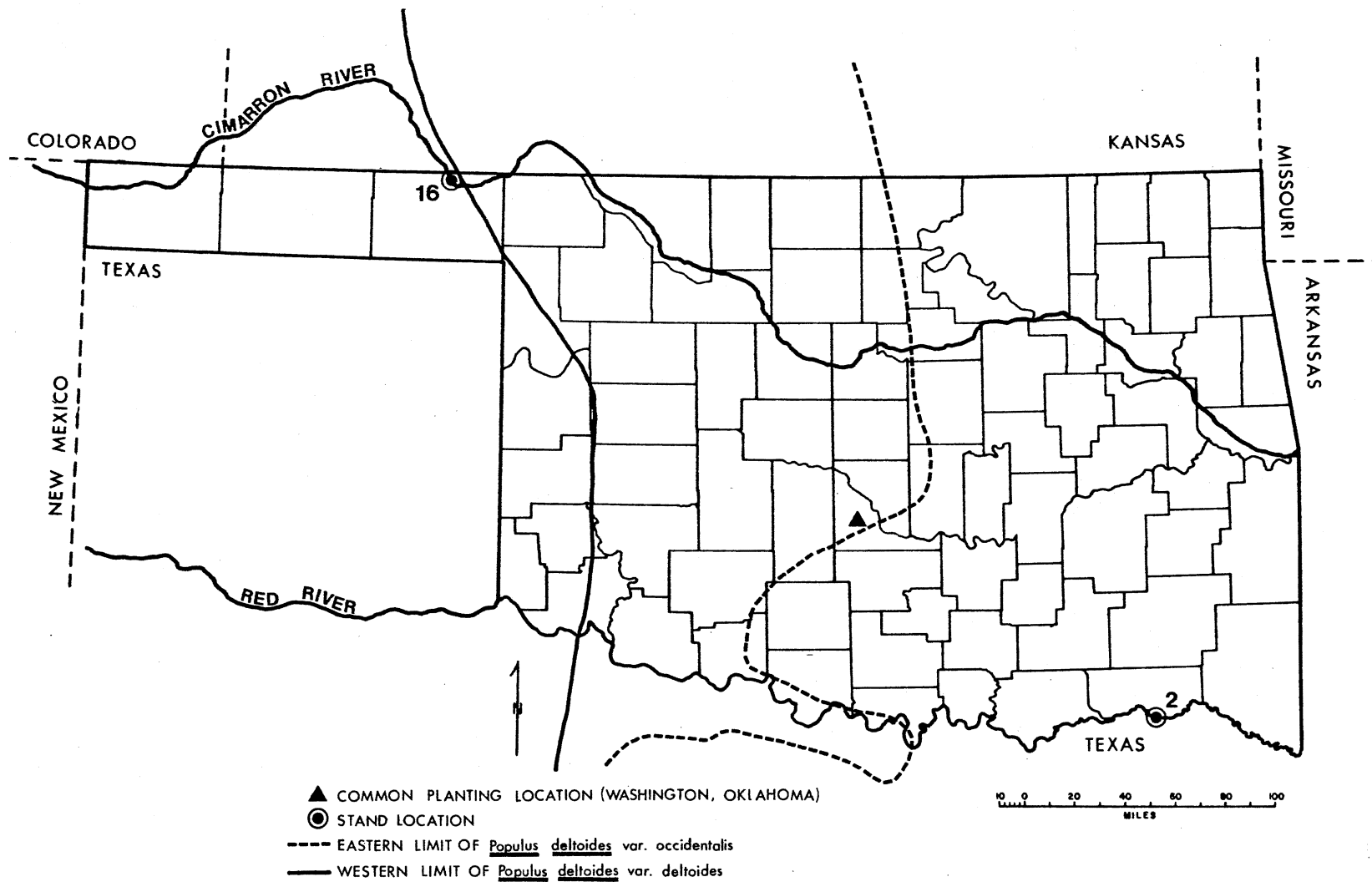


Figure 6. Geographic Origin of Clones Used for Screening Experiment

TABLE III
 AVERAGE MONTHLY AND ANNUAL PRECIPITATION AT GEOGRAPHIC
 ORIGINS OF CLONES USED FOR SCREENING EXPERIMENT

Month	Precipitation (cm)	
	Dry-Site*	Wet-Site**
JAN	1.07	7.21
FEB	2.08	8.31
MAR	2.46	10.21
APR	3.43	13.54
MAY	8.23	15.32
JUN	8.58	11.56
JUL	8.08	8.66
AUG	7.06	9.78
SEP	5.12	12.01
OCT	4.01	8.89
NOV	1.75	7.67
DEC	1.47	7.82
	<u>53.34</u>	<u>120.98</u>

Source: National Oceanic and Atmospheric Administration. 1978. Climatological Data Oklahoma. U. S. Dept. of Commerce, National Climatic Center, Asheville, North Carolina, Vol. 87.

* Weather Station at Beaver, Oklahoma (Lat. $36^{\circ}48'$, Long. $100^{\circ}32'$)

** Weather Station at Hugo, Oklahoma (Lat. $34^{\circ}00'$, Long. $95^{\circ}31'$)

growing when propagated, which eliminates the delay of an emergence period from dormancy to active growth of the hardwood cuttings. The elimination of the hardwood 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 packed over ice and transported to Stillwater, Oklahoma. They were 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. The cuttings were then placed under an intermittent mist system. On 31 July 1978, the now-rooted cuttings were planted singly in 13,500 cc plastic bags, perforated for drainage, and 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 19 September 1978. On 21 March 1979, 15-cm long tip cuttings with six to eight well-developed leaves were taken from the greenhouse plant material. Twenty-four cuttings of clone 2-6, 2-8, 16-3, and 16-5 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 22 April 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 15 May 1979, 12 cuttings per clone were

selected on the basis of uniformity within a clone and placed in the same growth chamber used for the pilot experiment. All cuttings were watered equally (360 ml/pot/day) prior to 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 24 May 1979 (day 1) and lasted 29 days. Results of the pilot experiment indicated that transpiration rates of the control plants were about an order of magnitude less than those of well-watered cottonwood as reported by other workers (11, 37). Transpiration rate is highly dependent on the amount of water available to the tree (11, 9, 37, 7) so that transpiration rates of the pilot experiment plants may have been more comparable if more water had been available. Additionally, the stress treatments of the pilot experiment were found to be too severe as indicated by the death of many plants during the final week of the experiment. Such a severe test is unrealistic. Accordingly, the treatments were modified for the screening experiment. 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

Severely-Stressed: 120, 90, 60 ml water added to pots daily
on days 1-9, 10-19, 20-29

During the experiment, air temperature during the day was 30°C and at night was 25°C. The relative humidity, measured with a hygrothermograph, varied from 50 to 60 percent. From 0500 to 2100 hours, the light quantum flux density was $730 \mu\text{E m}^{-2} \text{s}^{-1}$ at the top of the plants as measured with

a quantum sensor (Model LI-190S, Lambda Instrument Company, Lincoln, Nebraska). From 2100 to 0500 hours, the chamber was dark.

To facilitate a direct comparison between stomatal resistance, transpiration rate, and growth, four measurements were taken every other day. First, the height of all plants was determined. 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 top was measured with a calibrated stomatal diffusion porometer (24) (Model LI-60 and Sensor LI-20S, Lambda Instruments Company, Lincoln, Nebraska). Loss of water due to transpiration was determined by weighing the pots.

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 while the sub-unit treatments were the clones. Data analysis consisted of an analysis of variance ($\alpha = 0.05$), followed by Duncan's new multiple range test (43). A statistical test showed that clones 2-6 and 2-8 responded similarly to the three treatments and were, therefore, analyzed as a single population to be known as the wet site. A statistical test also showed that clones 16-3 and 16-5 responded similarly to the three treatments and they were analyzed as a single population to be referred to as the dry site. 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

Stomatal Resistance. The stomatal resistance of the control plants (Figures 7 and 8), at 2 to 8 s cm⁻¹, was less than the resistance of control plants in the pilot experiment, (Figure 2) whose values ranged from 14 to 28 s cm⁻¹. A number of differences in the two experiments may account for this discrepancy. First, different clones from a different area were used for the screening experiment. Second, the watering regimes were changed for the screening experiment which may have affected stomatal resistance as supported by the work of Dougherty (9). Third, a fertilized potting medium was used for the screening experiment while an unfertilized soil mix was used in the pilot experiment. Bonner (3) showed soil differences to have an effect on plant water relations of juvenile eastern cottonwood under drought-stress. Fourth, the tip cuttings used for the screening experiment were obtained during the growing season and appeared more vigorous and hardy than the hardwood cuttings used for the pilot experiment.

Stomatal resistance of the wet-site control plants was higher than those of the dry-site control plants (Figures 7 and 8). 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 stands. This would suggest that differences in drought resistance as reflected in stomatal resistance may be detected as long as the plants are maintained under the same soil moisture regimes.

There was little discrepancy in resistance between the two stress groups for the dry-site plants. Resistances of the moderately-stressed

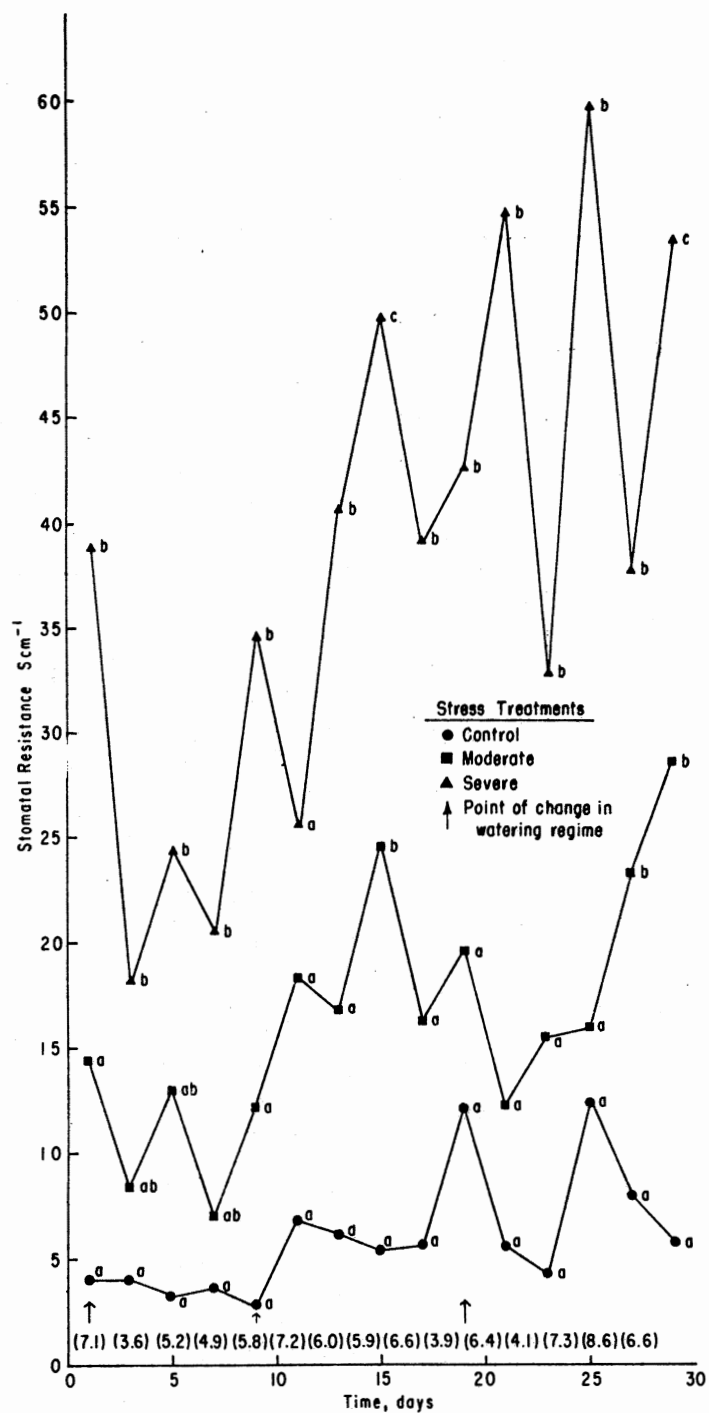


Figure 7. Stomatal Resistance of Wet-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parentheses are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

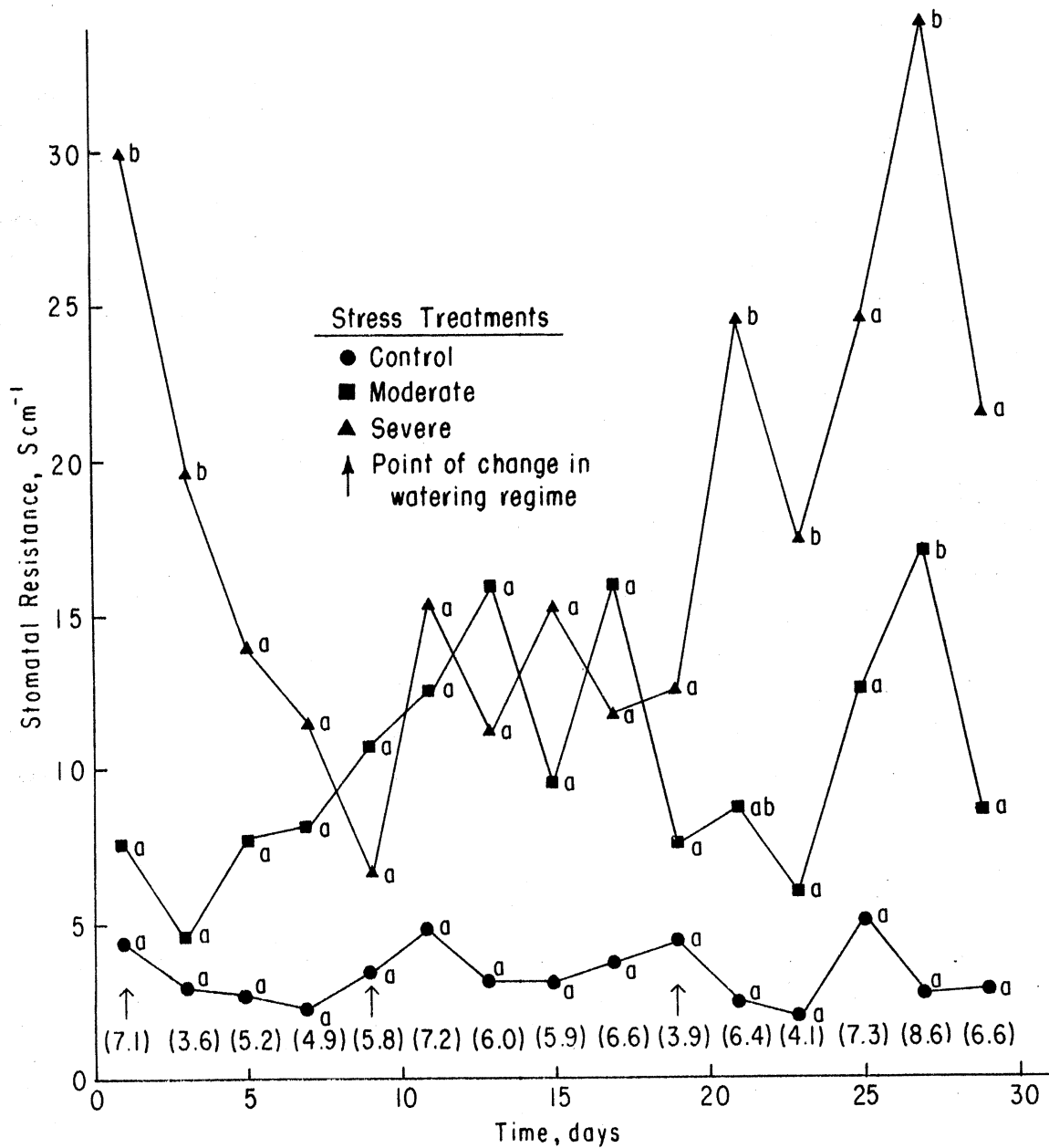


Figure 8. Stomatal Resistance of Dry-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parentheses are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

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. That is, although resistances increased more for the severely-stressed plants initially (after a reduction in water), both stressed groups decreased to similar resistances in a few days. This would suggest that stress within the realm withstood by a tree can be tolerated by increasing stomatal resistance until the tree can equilibrate with 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 ($\alpha = 0.05$) 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} . The corresponding values for the dry-site plants were 5 to 17 s cm^{-1} and 7 to 34 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 by increasing water stress.

Because water loss from the plant is controlled primarily through stomatal resistance, measurement of stomatal resistance can indicate drought resistance. There was a difference in resistance between the two stands even under well-watered conditions. These data suggest that differences in drought resistance can be discerned with or without 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 may be feasible using the diffusion porometer to measure stomatal resistance.

Transpiration Rate. Transpiration rates of the Oklahoma clones used for the screening experiment were higher than those of the Texas clones used in the pilot experiment (Figures 9 and 10). In addition to the previously outlined differences between the two experiments (see stomatal resistance section of screening experiment results), transpiration rate is highly dependent on the amount of water available to the tree (11, 9, 37, 7). Transpiration rates of the pilot experiment plants may have been more comparable to those of the screening experiment plants if more water had been available.

The decrease in transpiration rate of the control plants may have been due to stress caused by a change in the plant's environment from the greenhouse to the controlled environment chamber. As the plants were placed in the chamber only nine days prior to the start of the screening experiment, the plants may not have equilibrated with their new environment until day 15 for the wet-site plants and day 20 for the dry-site plants, when transpiration rates of the control plants were seen to stabilize. Transpiration rates of the pilot experiment plants did not decrease substantially over time, perhaps because those plants had more time to equilibrate with the environment of the chamber prior to the start of the experiment.

Transpiration rate was related to stomatal resistance. It can be seen as an index of water stress illustrating the detrimental effect

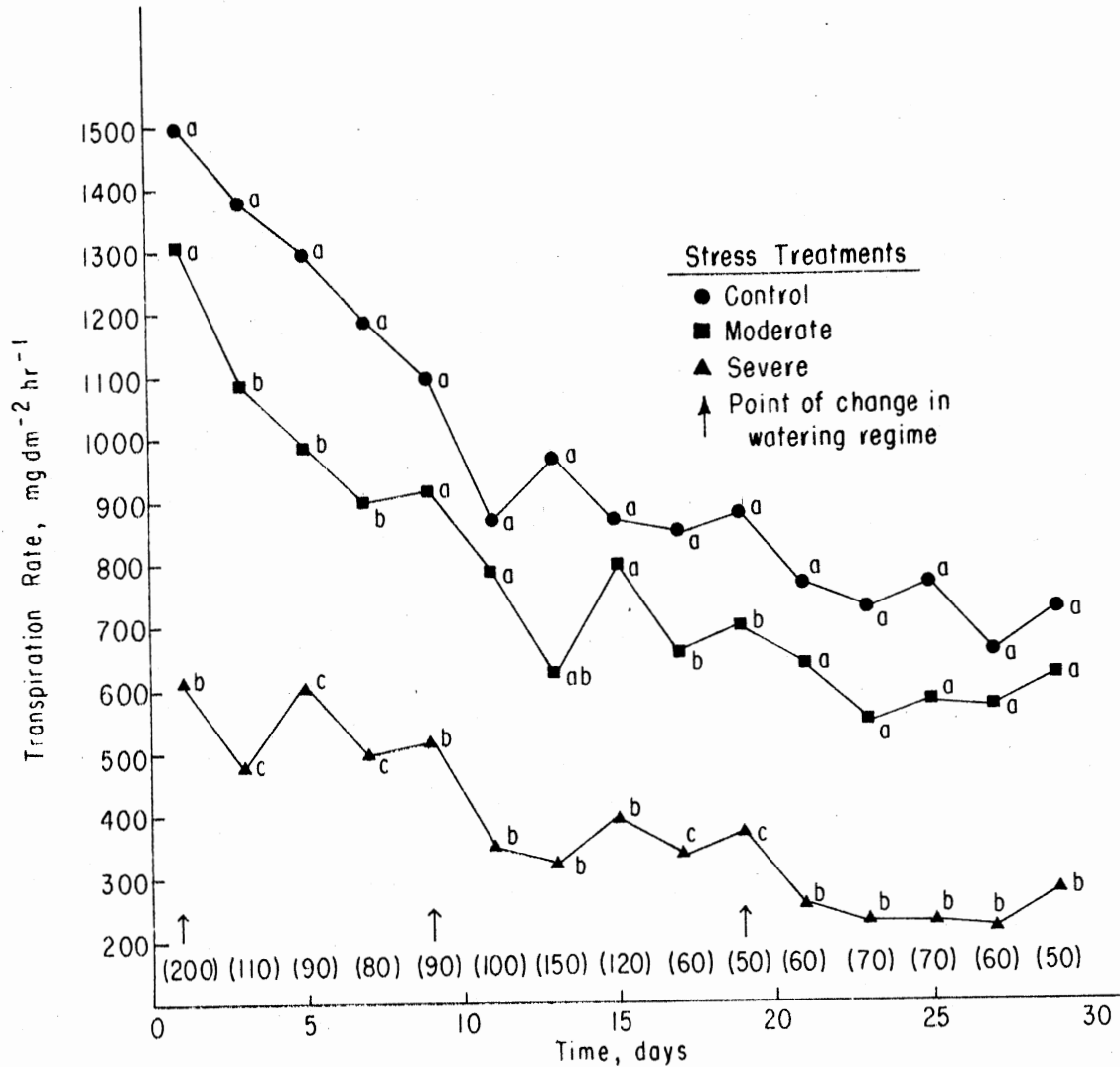


Figure 9. Transpiration Rate of Wet-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parentheses are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

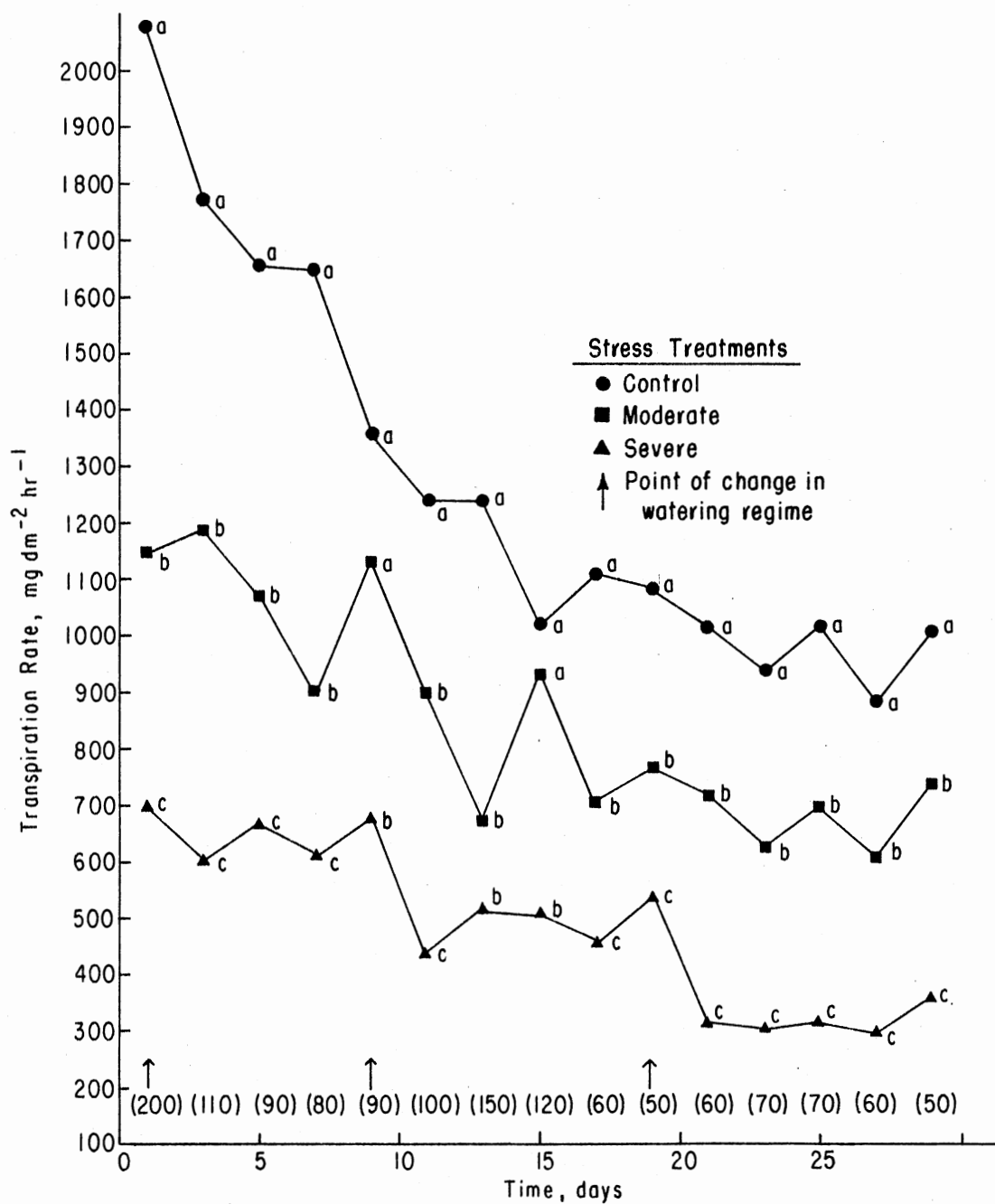


Figure 10. Transpiration Rate of Dry-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parentheses are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

(i.e. less growth) of drought-stress on the plant. Thus, control plants 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 (Figures 11 and 12). 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 exhibited by the dry-site plants as the controls increased in leaf area by 1000 cm^2 while the moderately-stressed by 600 cm^2 . It is apparent that even mild stress as inflicted on the moderately-stressed group will inhibit leaf area expansion (52).

Leaf area under the severely-stressed treatment stopped increasing 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.

Leaf area expansion appears to be a sensitive indicator of stress (52), providing a warning of impending growth cessation. 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. When leaf expansion stops, severe moisture stress is indicated, and the plants will soon stop growing without sufficient soil moisture recharge.

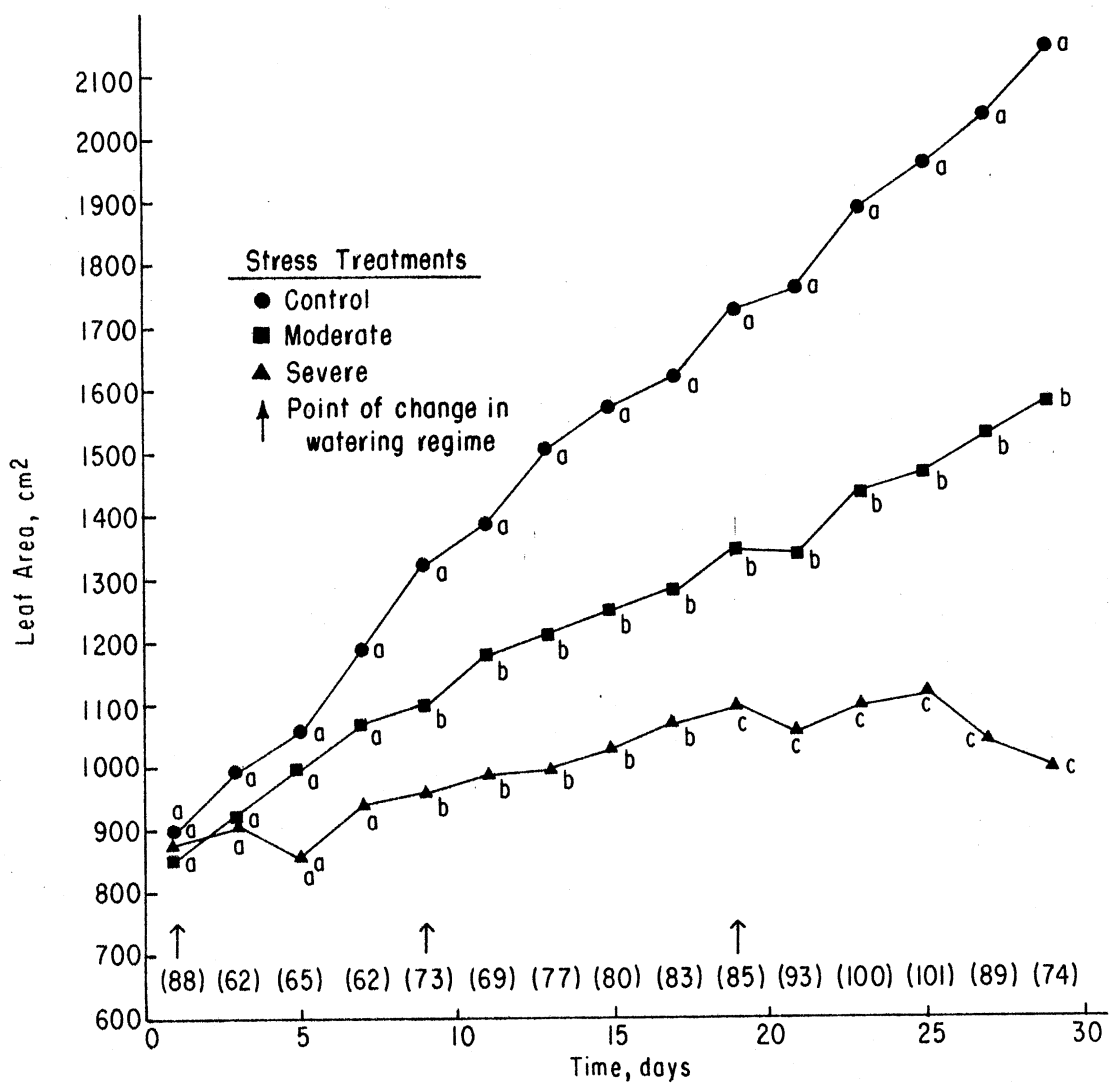


Figure 11. Leaf Area of Wet-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parentheses are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

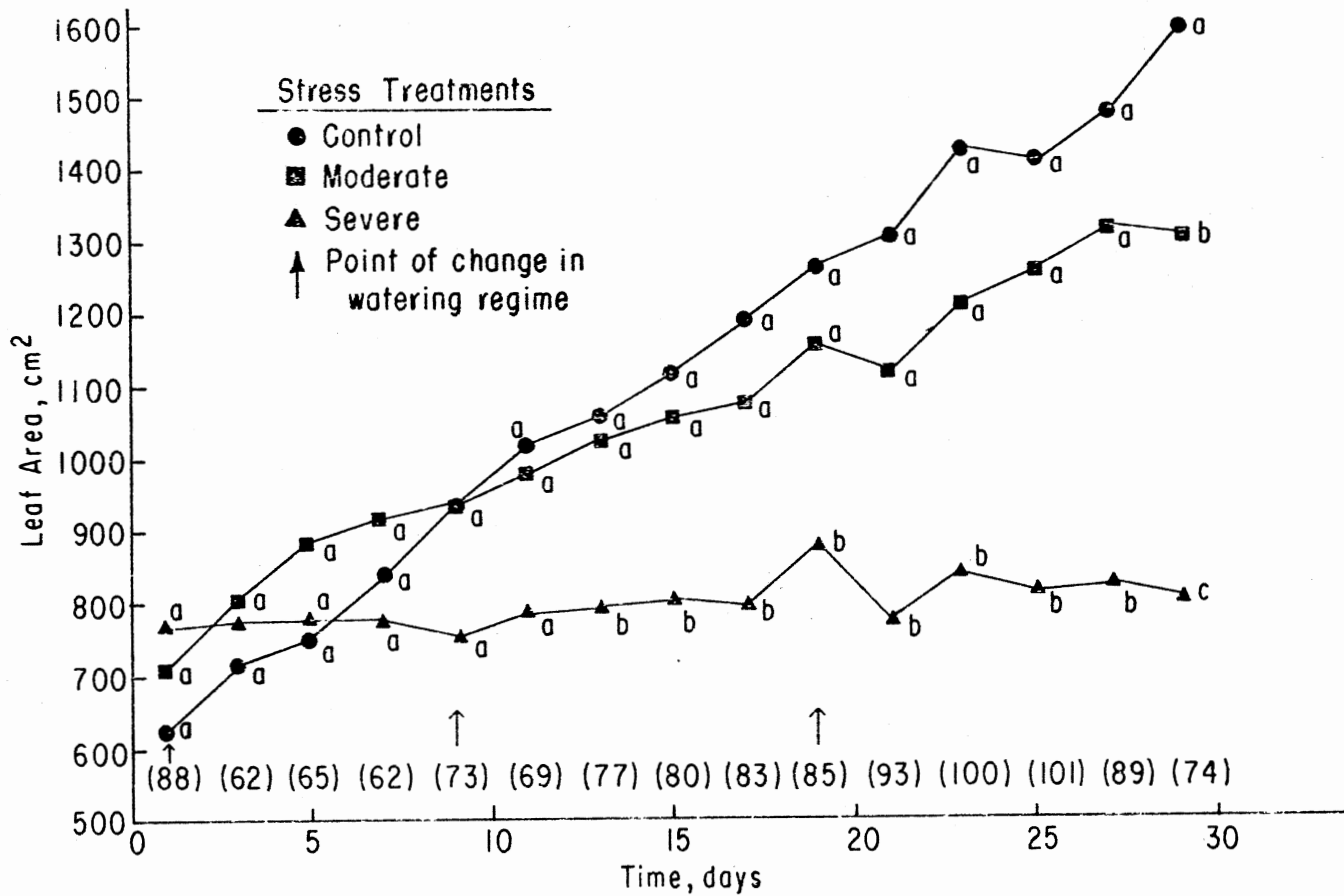


Figure 12. Leaf Area of Dry-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parentheses are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

Height. Total height growth for the control plants from the dry site was greater than that of the wet-site control plants (Figures 13 and 14). Control plants from the dry-site grew 36 cm while the wet-site plants grew 33 cm.

There was no significant difference in height growth between the control and moderately-stressed plants from the dry site. There were statistically significant differences between the controls and moderately-stressed, wet-site plants. The stressed plants from the dry site grew more than the wet-site plants. 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 will grow faster, even under moderate drought-stress, can be identified.

Severely-stressed plants from the wet site stopped growing on day 21 when stomatal resistance was 60 s cm^{-1} . Though resistance later decreased, the plants never resumed height growth. Height growth of the severely-stressed, dry-site plants stopped on day 23 when stomatal resistance was 18.5 s cm^{-1} .

Results suggest that the wet-site plants possess little ability to deal with drought. Even under moderate stress, height growth was inhibited for the wet-site plants. Severe moisture stress resulted in stomatal closure and, despite a later decrease in resistance, height growth never resumed. On the other hand, height growth of the dry-site plants was not inhibited by moderate stress. Duration of growth was similar under all experimental conditions, but the dry-site plants grew more than those from the wet site by virtue of their lower stomatal resistance. This indicates that decreased stomatal sensitivity under

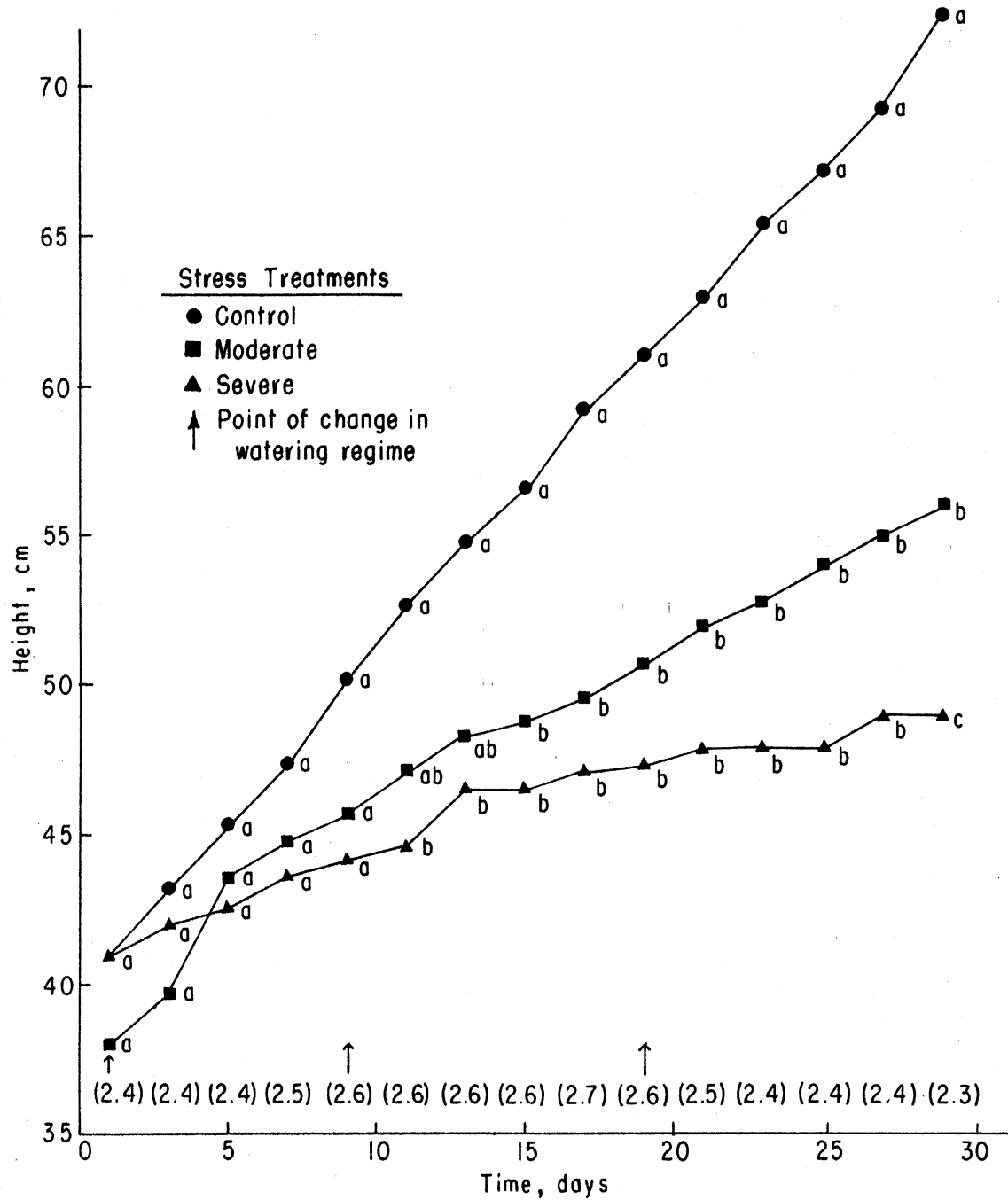


Figure 13. Height of Wet-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parenthesis are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

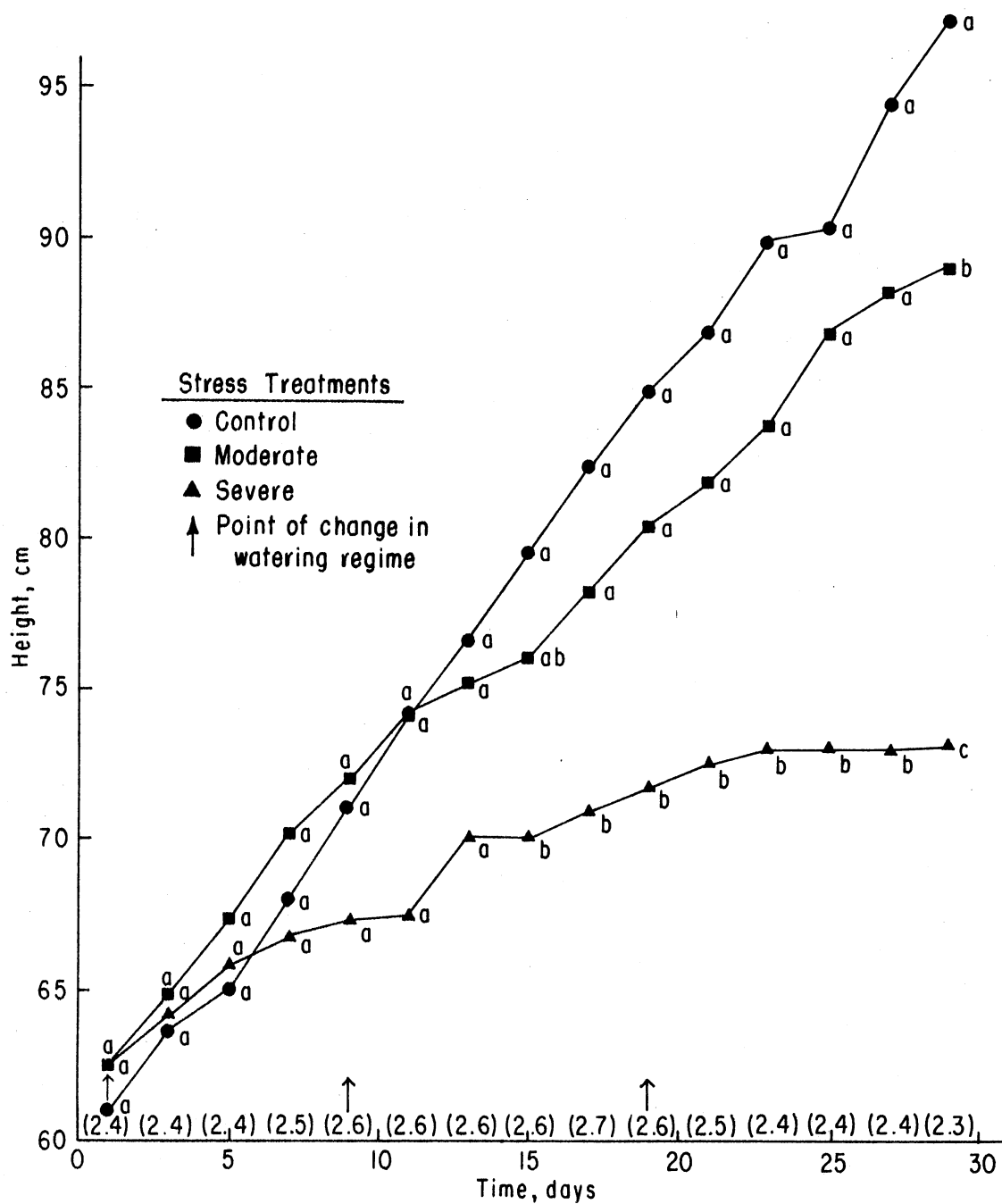


Figure 14. Height of Dry-Site Eastern Cottonwood Under Three Watering Regimes. Numbers in Parentheses are Standard Errors. Symbols for One Measurement Day, Followed by the Same Letter, are Not Significantly Different ($\alpha = 0.05$) According to Duncan's New Multiple Range Test.

water stress conveys greater adaption to drought (18). That is, a clone which can tolerate water stress with the least increase in stomatal resistance will grow the fastest and thus be the best to select.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Stomatal resistance, transpiration rate, leaf area, and height were measured on two Texas clones of eastern cottonwood grown in pots of soil maintained under three watering regimes, to determine the effect of drought on plant-water relations and growth. Transpiration rate was related to stomatal resistance. Leaf area expansion stopped at a stomatal resistance between 28 and 32 s cm⁻¹. Height growth stopped at a stomatal resistance between 30 and 40 s cm⁻¹. Stomatal resistance measurements were an easy way to determine the threshold beyond which severe moisture stress resulted in leaf and height growth cessation and eventual plant death.

Stomatal resistance measurements were then applied to make a preliminary classification of the drought resistance of four Oklahoma clones of eastern cottonwood. The effect of drought-stress on plant material from a dry site in northwestern Oklahoma was compared to plants from a wet site in southeastern Oklahoma. Within site differences, based on comparison of two clones, were not detected. The dry-site plants had a lower stomatal resistance than the wet-site plants, even under well-watered conditions. Transpiration rate was related to stomatal resistance. Leaves stopped expanding for the dry-site plants after 23 days of severe drought-stress at a stomatal resistance of 17.5 s cm⁻¹. Leaves of the wet-site plants stopped expanding 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} . The wet-site plants stopped growing at a stomatal resistance of 60 s cm^{-1} .

Because water loss from the plant is controlled primarily through stomatal resistance (17, 15, 32, 44, 2, 7), measurement of stomatal resistance can indicate drought resistance. Differences in stomatal resistance between the two stands were found to be discernible with or without stress. This suggests that screening under common environmental conditions may be used to distinguish drought-resistant from drought-susceptible clones. It follows that field testing to identify drought resistant clones may be feasible. 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, eliminating the need for additional plant material and propagation (i.e. 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 was found to be highly dependent on the amount of water available to the tree, as observed by many other workers (11, 9, 37, 7). Directly reflecting water loss from the plant, transpiration rate represents an index of water stress. Control plants had the highest transpiration rate while severely-stressed plants had the lowest rate.

Leaf expansion was found to be a sensitive indicator of stress, in agreement with Zahner (52). Though more difficult to measure than stomatal resistance, especially on larger trees, leaf area measurements may be useful to indicate performance under drought-stress. When leaf expansion stops, severe moisture stress is indicated, and the plant will soon stop growing without sufficient soil moisture recharge. The stomatal resistance at which leaf expansion stops is thus important in identifying drought resistance.

Height growth results suggest that the wet-site plants possess little or no ability to deal with drought. Even under moderate stress, height growth of these plants was inhibited. However, height growth of the dry-site plants was not inhibited by moderate stress. This would suggest that clones which will grow faster, even under moderate stress, can be identified. Duration of growth under all experimental conditions was similar for both the wet and the dry-site plants, but the dry-site plants grew faster by virtue of their lower stomatal resistance. This suggests that decreased stomatal sensitivity under water stress conveys greater adaption to drought (18). That is, a clone which can tolerate water stress with the least increase in stomatal resistance will grow the fastest and thus be best to select. Additionally, leaf and height growth were found to respond differently at a given stage of drought, possibly because of differences in water stress among the contrasting tissues.

Information derived from this study is descriptive only of the particular population studied under the specific conditions imposed. Only as these experiments are typical of the natural environment of eastern cottonwood, are these conclusions reliable. Caution is advised

in their interpretation and particularly in their extension to other populations.

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