

GROWTH AND DISTRIBUTION OF PLATANUS OCCIDENTALIS
IN OKLAHOMA AS INFLUENCED BY CLIMATE
AND WATER RELATIONS

BY

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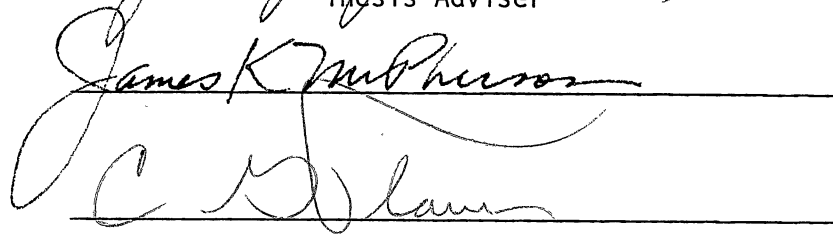
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Thesis Approved:


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CHAPTER I

INTRODUCTION

The distribution and growth of a forest tree species is dependent on that species' ability to respond to environmental stress. While these environmental factors may include amount and distribution of rainfall, severity of summer heat, extent and timing of freezing, or particular edaphic conditions, the impact of a single factor is difficult to isolate. Rather, plants respond to a complex of climatic, edaphic and biotic factors (Barbour et al. 1980). It is safe to say, however, that the most overriding factor in determining the distribution and growth of trees is water supply (Kozlowski 1979). Both actual precipitation, with subsequent soil moisture, and atmospheric moisture are influential.

On the North American continent the eastern deciduous forest is restricted to the wetter, more humid areas of the eastern half of the continent. Riparian species, of course, can extend far into the more arid mid-continental steppe as long as there is a source of moisture. Even species that occur on uplands in the east can penetrate into the prairie by taking advantage of the continuous moisture supply and protection from desiccating winds that are available in ravine bottoms (Daubenmire 1978). Within the prairie ecosystem, forests are generally restricted to floodplains, ravines and streambeds, the soils of which are frequently more productive than upland soils due to their alluvial

origin and better water holding capacity (Weaver 1968). In Oklahoma, mesic eastern deciduous forest communities generally merge with the tall grass prairie communities in the eastern third of the state and extend along streams for a considerable distance further west (Gray and Galloway 1959).

Numerous tree species reach their western geographic limits in Oklahoma, presumably because of the progressive moisture limitation from east to west. Platanus occidentalis L. is one example of a species whose range is limited to the eastern sector of Oklahoma (Little 1971).

Oklahoma is an ecotonal state between the cold temperate north and warm temperate south, and between the arid west and humid east. This unique position lends itself to distributional studies of many encroaching species. The average annual temperature for the state is 60.5 F, ranging from 64 F in the southeast to 57 F in the northwest (Gray and Galloway 1959). Precipitation shows even greater variation across the state with the annual average in the southeast at 54 inches and decreasing toward the panhandle, where it is 18 inches (Gray and Galloway 1959). This same trend is observed for humidity or Precipitation-Effectiveness (P-E) Index. The P-E Index is a measure established to distinguish humidity provinces on the basis of average precipitation related to average open pan evaporation (Thornthwaite 1941). In Oklahoma, it ranges from 64 (humid) in the east to 32 (dry sub-humid, almost semi-arid) in the panhandle. A low P-E Index exhibits high evaporation and is therefore less favorable for vegetation growth.

A pioneer, riparian species, P. occidentalis or sycamore, is

found along streams and rivers throughout eastern Oklahoma with it associates Populus deltoides, eastern cottonwood and Salix spp., willow (Little 1971). Cottonwood and willow extend into western Oklahoma but sycamore is limited to the eastern sector (Figure 1). Cottonwood and willow have the same general requirements and growth habit as sycamore but there appears to be some factor detrimental to only sycamore. The most obvious factors involved are climatic and are most likely lack of adequate rainfall and increased evaporative demand. Due to sycamore's riparian and phreatophytic nature, lack of rainfall should not prevent its distribution into western Oklahoma. Increased evaporative demand, however, could be a limiting factor and would most likely affect the internal water balance of the tree.

With this in mind, a study was initiated which would investigate the anatomical and physiological differences among sycamore individuals across a moisture gradient and to ascertain whether or not sycamore is prevented from extending further west due to lack of rainfall and increased evaporative demand. The latter should be evidenced by a lack of stomatal control and decreased water potentials near the edge of its range.

CHAPTER II

LITERATURE REVIEW

With the exception of Minnesota, sycamore is found in all states east of the Great Plains (Merz 1965). Its natural range extends from the Gulf of Mexico north to the Canadian border in the area of Lake Erie and from the Atlantic Coast west to the Great Plains (McAlpine and Applefield 1973). Sycamore occurs most frequently, however, in the coastal and southeast portion of its range where it thrives on an average annual temperature of 40 F-70 F and an average annual precipitation of 30-80 inches (Merz 1965). It is limited in the north by winter frost and low temperatures and in the west by a dry climate (Fogg and Kazkurewicz 1967).

The distribution of sycamore is highly influenced by flooding, ground water level, and drainage. Sycamore is distributed on the lowest terraces and slopes of drainage basins or watersheds which are flooded 29-40% of the year (Bedinger 1979). Although this species withstands high frequency of flooding, sapling and seedling mortality and stunting will result if the soil remains saturated for a prolonged period of time (McDermott 1954; Harris 1975; Kennedy and Krinard 1974).

This tree does best on medium textured silty or loamy, porous, deep soils of alluvial origin, with a 2-6 foot water table depth and good drainage. It is particularly favored by streambottom or floodplain soils with a pH of 5.5-7.5 and no profile development (Baker and

Broadfoot 1979). Good root development in sycamore is hindered by clay pans and soils containing high aluminum or iron (Daniels and Sarigumba 1980).

Sycamore is the predominant tree of two forest types: River Birch-Sycamore type in which Acer rubra and Salix nigra are the associates, and the Sycamore-Pecan-Elm type in which Acer negundo, Fraxinus spp., Populus deltoides and Salix interior are the associates (Merz 1965). The latter type is found in Oklahoma.

Generally classed as intermediate in tolerance, sycamore has in some cases been found to be very intolerant of shade (Preston 1978; Duba and Carpenter 1980). For instance, it may tolerate and succeed P. deltoides and Salix on a very moist site and yet be very intolerant and occur as a pioneer on a drier site (Merz 1965).

Reproduction is heavily influenced by moisture availability. The small seeds have hairs which act as parachutes and can be widely scattered by wind and water. They often are deposited on mud-flats or sandbars where conditions are usually favorable for germination, e.g. moist to wet soil and direct light. Under favorable conditions they develop a strong, spreading root system and grow rapidly, as much as three or four feet in height the first year (Merz 1965). Under less favorable conditions they have been known to act as a phreatophyte, developing a deep root system into the capillary fringe of the water table (Horton and Campbell 1974).

The inability of sycamore to tolerate both the decrease in precipitation and arid atmosphere of the prairie may be due to a number of factors, such as lack of stomatal control, intolerance to low tissue

water potential, sensitivity of seedlings to moisture stress, an inadequate root system or possible combination of these factors (Hall and McPherson 1980; Kozlowski 1979). In view of sycamore's riparian and phreatophytic nature, lack of precipitation and soil moisture availability would not be expected to cause physiological drought stress (Nilsen et al. 1981). The high evaporative demand and heavy heat load experienced on the prairie, however, could cause a serious imbalance in internal water status.

Water potential (Ψ) is the most widely used measure to describe the status of water in plant tissues or in any other part of the soil-plant-atmosphere continuum. It is defined as "the difference in chemical potential of water in a system and that of pure, free water at the same temperature" (Kozlowski 1979). The water or osmotic potential of cell sap is lower than that of pure water because of the presence of solutes. The absorption of water by cells causes an increase in pressure within them (turgor pressure) and the water potential of the cell is the result of these two opposing forces (Bannister 1976).

In cells the water potential has a negative value except that when fully turgid it is zero. The value becomes increasingly negative as water deficits in plant tissues increase, i.e. during drought and, may be responsible for reduced growth and metabolism. The water flowing through the soil-plant-atmosphere system moves upward as a result of the decreasing water potential gradient. Throughout the system, however, there is a resistance to flow called diffusive resistance (r), which is greater in the soil than in the plant and is maximal in the

transition from leaves to the atmosphere. Within the leaf, the total resistance involves mesophyll, stomatal and cuticular components. Stomatal resistance, however, is probably the only one the plant can control (Kozlowski 1979). The amount of water lost through stomata is proportional to the evaporative power of the air and by changing the degree of stomatal opening the plant can regulate its transpiration in accordance with the requirements for its water balance (Larcher 1973). The ability of a species to close stomata and increase internal resistance under moisture stress often affords the plant protection from excessive water loss. Under high evaporative demand, low water potential may develop in leaves as the soil dries. At a certain level of leaf water potential (the threshold potential) the guard cells of the stomata lose turgor and close (Ritchie and Hinckley 1975). The increased resistance to water loss usually prevents the development of severely low water potentials, which may result in metabolic damage to the plant (Tobiessen and Kana 1974). The ecological importance of this finding is debatable since stomatal closure has been known to occur without the presence of tissue water deficit. Differences seem to exist with changes in species, habitat and type of measurement.

The development of water deficits due to climatic effects rather than soil water availability is seen in citrus and pear when subjected to decreases in humidity (Camancho-B et al. 1974). Progressive decreases in water potential as transpiration increases indicates the presence of a substantial resistance to water flow. This response is viewed as a regulatory mechanism for water loss by which the species

combines strong regulation of water loss by stomata with low efficiency of its water transport system. The authors also feel that the low leaf water potential at large evaporative demands may be a consequence of the physical constraints exhibited by the structure of the woody species, i.e. high resistance between root and leaf.

The stomata of both Polypodium and Valerianella responded to the change between moist and dry air applied to the outer side of the epidermis (Lange et al. 1971). Shortly after the change from moist to dry air the stomata closed. The change from dry to moist air resulted in an opening of stomata. The advantage of this controlling mechanism would lie in the fact that with a decrease in humidity, water loss could be restricted by the increased stomatal diffusive resistance before the water potential of the other leaf tissues is affected.

Stomatal closure with increasing evaporation might increase the water use efficiency of a plant by restricting gas exchange and potential transpiration rates when evaporative demand is high. Populus clones exhibited significant increases in resistance when light intensity was low and evaporation was high (Pallardy and Kozlowski 1979). The clones had an accentuated stomatal closing response to the combination and an above the sum of responses to either factor alone. This behavior emphasizes the capacity of Populus to reduce water loss sharply when conditions for CO₂ fixation in relation to water loss are extremely unfavorable.

Transpiration directly from guard cells or "peristomatal" transpiration may allow these cells to act as sensors of vapor pressure

deficit. This mechanism causes stomata to close as vapor pressure deficit increases thus providing control of water loss that is independent of plant water potential (Lange et al. 1971; Federer and Gee 1976). The observance of higher xylem potentials in stressed Acer, Betula and Fraxinus during high atmospheric demand suggests stomata may close just enough to prevent the reduction of internal water potential below some critical value (Federer and Gee 1976).

The sensitivity of stomata to moisture stress has wide reaching ecological implications as an adaptive characteristic. Water potentials low enough to disturb metabolism are unlikely to develop if stomata close rapidly and completely, but CO₂ uptake through stomata is then eliminated and growth is reduced. On the other hand, less sensitive stomata may allow the development of water potentials low enough to reduce growth. Maximum growth is obtained then when the stomatal diffusive resistance is as low as possible without allowing damaging water potential to develop (Jarvis and Jarvis 1968).

The effect of drought and contrasting edaphic conditions on photosynthesis and transpiration in populations of Populus deltoides was examined by McGee et al. (1981). For those plants growing in a floodplain, photosynthesis and transpiration remained unchanged as water potentials declined to -10 bar but dropped sharply to zero at -15 to -16 bar. Strip mine plants nearly doubled photosynthesis and transpiration as water potential declined to -12 bar but growth declined with further decreases in water potential. Finally, in sand dune plants photosynthesis and transpiration rates were highest at potentials of -8 to -10 bar but did not become negligible until

-18 bar. The authors conclude that the enhanced photosynthesis of the strip mine and sand dune plants at more negative water potentials appears to be clearly adaptive and stomata seem to control the response to water availability since the trends are similar in each population.

The degree of diffusive resistance apparently differs among species and may depend upon the type of measurement. Direct measurement of resistance by diffusive porometry under field conditions has nearly always been less than 5 s/cm for unstressed broadleaved tree species (Federer and Gee 1976; Federer 1977). Indirect measurements, such as from leaf temperature and energy balance considerations, and from rates of evaporation into chambers show great variability with values ranging from 1 to more than 100 s/cm (Wuenschel and Kozlowski 1971; Federer 1977).

Threshold potentials have been found to differ among genera on the same site, especially under stress conditions. In Betula, Federer (1977) found stomatal closure to occur at potentials of about -15 bar and about -20 bar or lower in Quercus and Prunus, but Populus was intermediate at a potential of about -17 bar. Federer views site and size as secondary to genus in determining stressed potentials in these genera.

The habitat requirements of various species has been linked to water relations by several authors and different types of stomatal adaptations are apparent. Tobiessen and Kana (1974) studied Populus tremula, P. grandidentata and Fraxinus americana along a moisture gradient in New York. Their findings show that P. tremula had very

little control over its water loss. The very low leaf resistance suggests that the stomata were open even at low leaf water potentials. The absence of a mechanism to control water loss in this species could be a strong influence in limiting the species to relatively moist sites. On the other hand, both Fraxinus americana and Populus grandidentata exhibited stomatal "hypersensitivity" or stomatal closure at relatively higher water potential during drought stress. This mechanism could allow these species to survive, without severe damage, short dry periods at least for a short time but would probably reduce growth in the long run.

Hall and McPherson (1980) showed that seedlings of Quercus velutina were more sensitive to dry conditions than those of Q. marilandica. Q. velutina exhibited lower leaf water potentials at higher soil water potentials. The seedlings also showed a higher average transpiration rate with adequate water but with moderate stress there was a rapid decrease. The shutdown of transpiration could possibly be due to stomatal hypersensitivity and could act to restrict net gas exchange and subsequent growth.

The distribution of oaks in California has been correlated directly with xylem sap tension which is similar to resistance (Griffin 1973). The sharp summer rise in xylem sap tension in Quercus douglasii which occurs in dry woodland forests, strengthens the assumption that these trees do not reach the water table or at least draw from a limited ground water supply which is depleted by autumn. Drought deciduousness is the mechanism used by this species to cope with drought stress. When the late summer or autumn water

supply becomes critical, Q. douglasii can restrict transpiration by shedding much of its foliage.

The relationship of plant distribution and a plant's ability to conserve water is obvious. The mechanism which the plant employs, however, is less so and apparently differs with many factors. Xerophytic plants are capable of tolerating low internal water deficits without increasing resistance. Most mesic plants, however, cannot withstand low tissue water potentials and attempt to conserve water by closing stomata. Stomata may respond directly to increased evaporative demand as in Polypodium and close before the development of low leaf water potential. On the other hand, low leaf water potential may override all environmental factors and cause closure only at a particular threshold potential. The sensitivity of a species' stomata is often the main factor in determining how the plant balances CO₂ uptake with water loss and maintains growth.

Finally, aside from physiological changes, anatomical differences between stressed and unstressed trees have been noted. In comparison with plants grown under optimum conditions, those grown under an unfavorable water balance generally have reduced shoot size, increased root system, smaller and thicker leaves, smaller and more dense stomata and thicker cuticle (Daubenmire 1974).

CHAPTER III

MATERIALS AND METHODS

To study the effects of climatic gradients on the distribution of sycamore, five study sites were chosen to form a transect crossing the gradients from east to west within the range of the species. The transect began at the western limit of sycamore's range with a site near Perkins, Ok (site I) and ended near the eastern edge of the state at Elk Creek (site V). Sites II, III and IV were nearly evenly spaced between the border sites and were located from west to east near the towns of Shamrock (site II), Beggs (site III) and Zeb (site IV).

Although all sites were located in streambed bottomland forests with soils of alluvial origin, the specific soil series and climate differed between each site (Appendix).

On each site five trees were selected to serve as replicates. All trees selected for this experiment were, with one exception, between 10 and 28 years old, in full sun, within 50 feet of the water source, vigorous, apparently healthy and were no more than 100 feet from one another. All trees were easily accessible within the one hour time required to insure similarity of measurement.

Field Methods

On each tree a one time measurement of age, growth rate, height,

diameter, leaf area and stomatal density was made during the 1983 growing season. During the months of July, August, September and October of 1983, leaf water potential and diffusive resistance were measured three times on each tree once each month. Equipment failure prevented obtaining any June readings.

The height of each tree was determined using a Suunto Height Meter Type PM-5/360 PLP. The diameter at breast height of each tree was measured with a Lufkin Tree Tape. Growth rate was determined by use of increment cores. Tree borings at 4.5 feet produced cores of incremental growth from which the age and rate of growth of each tree could be determined. Since the youngest tree was determined to be 10 years old, the growth rate, in millimeters during the last 10 years was compared for each tree. Leaf area was measured using a LI-COR Model LI-3000 Portable Area Meter on three fully expanded sun leaves which were randomly chosen from each tree.

Stomatal density was determined for the same three sun leaves used to determine leaf area. Epidermal peels of the abaxial leaf surface were made using collodion. Leaves were first washed to remove both excess pubescence and debris. After drying, a few drops of collodion were deposited on the cleaned surface of the leaf with a glass rod, and allowed to dry. The collodion was gently peeled off the leaf, mounted on a microscope slide and examined with a compound microscope. The number of stomata per field view was counted and expanded by multiplication to the number per cm^2 .

Diffusive resistance rates were measured on three separate leaves on each tree once a month using a LI-COR Model LI-700 Transient

Porometer. The sensor was placed on the underside of a leaf in full sun while the necessary time for a given quantity of water vapor to be absorbed by the humidity sensing element was recorded (LI-COR Operators Manual 1981). This time was then converted to a diffusive resistance value using predetermined calibration curves.

Leaf water potential was measured at the same time and day as diffusive resistance using a PMS pressure bomb. Three separate determinations were made for each tree. A twig with at least two sun leaves was cut from each sample tree and placed immediately in the gas chamber.

Both diffusive resistance and leaf water potential were measured between 12:00 noon and 1:00 pm, the time of day considered most stressful for the plant, i.e. leaf water potential is generally at its lowest point and diffusive resistance at its highest (Larcher 1975).

Finally, on each sampling day, at each study site, temperature and relative humidity were measured and recorded using a sling psychrometer.

CHAPTER IV

RESULTS

Leaf Area

In 1983, the mean leaf areas, based on three measurements per tree, five trees per site, were 120.03 cm², 206.93 cm², 115.45 cm², 180.98 cm², and 146.81 cm² for sites I through V, respectively, with site II having the largest mean leaf area and site III having the smallest (Appendix). Using Student-Newman-Keul's (SNK) multiple comparison test (Steele and Torrie 1980), sites I, III, V and IV, and sites II, IV, and V were grouped as not significantly different ($\alpha=.05$). Site II, however, was significantly different from sites I and III. Site II also had the largest amount of within site variation while site V had the least (Figure 2).

Stomatal Density

The mean stomatal density, based on three measurements per tree, five trees per site, were 29,276, 24,344, 25,617, 31,397 and 28,958 stomata/cm² for sites I through V, respectively, with site IV having the largest value and site II having the lowest (Appendix). These values were not significantly different ($\alpha=.05$) using the SNK test. There does not appear to be any direct relationship between stomatal density and location (Figure 3) or between stomatal density and leaf area (Figure 4). It should be noted, however, that the site with the

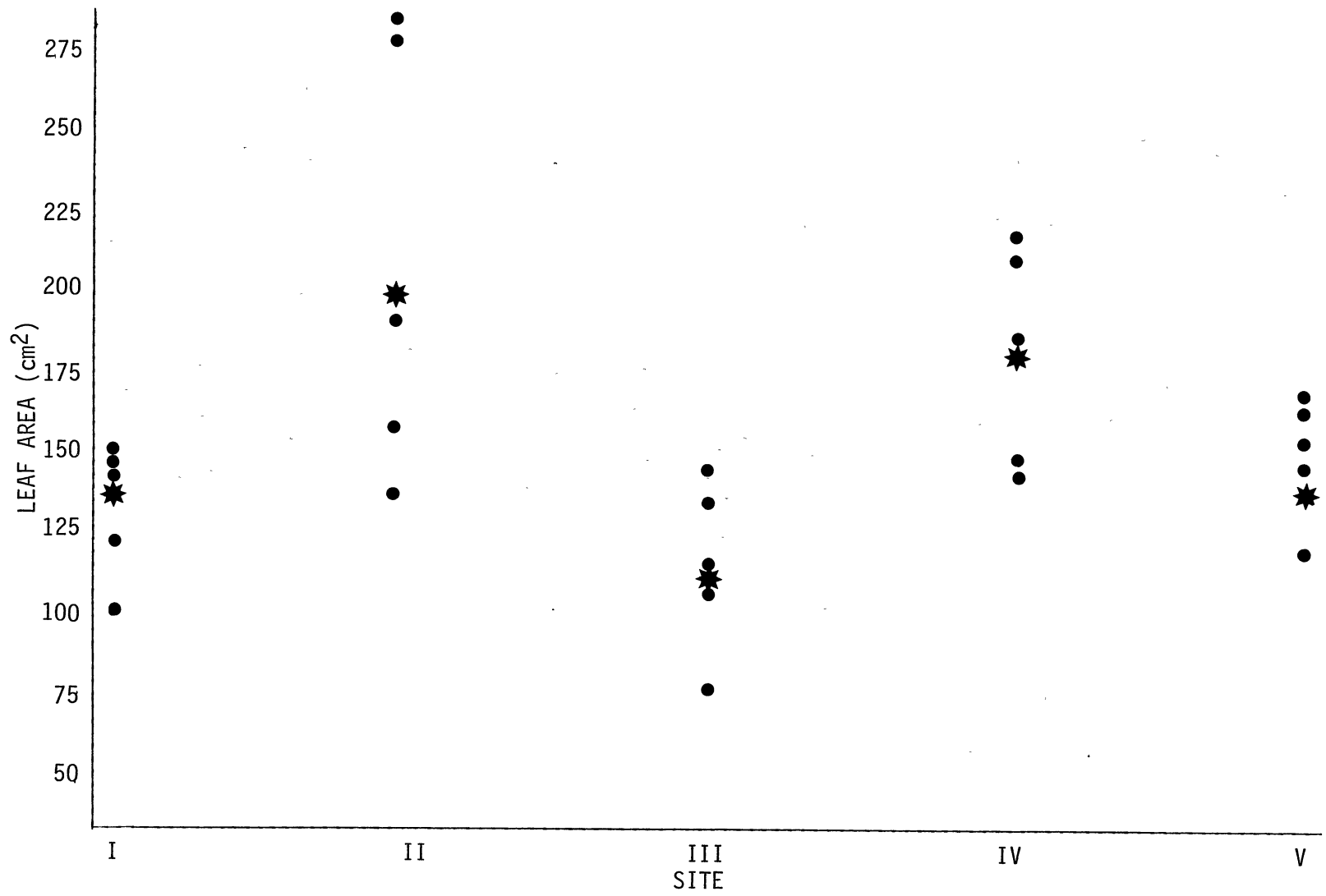


Figure 2. Range of mean leaf areas. Star represents location mean.

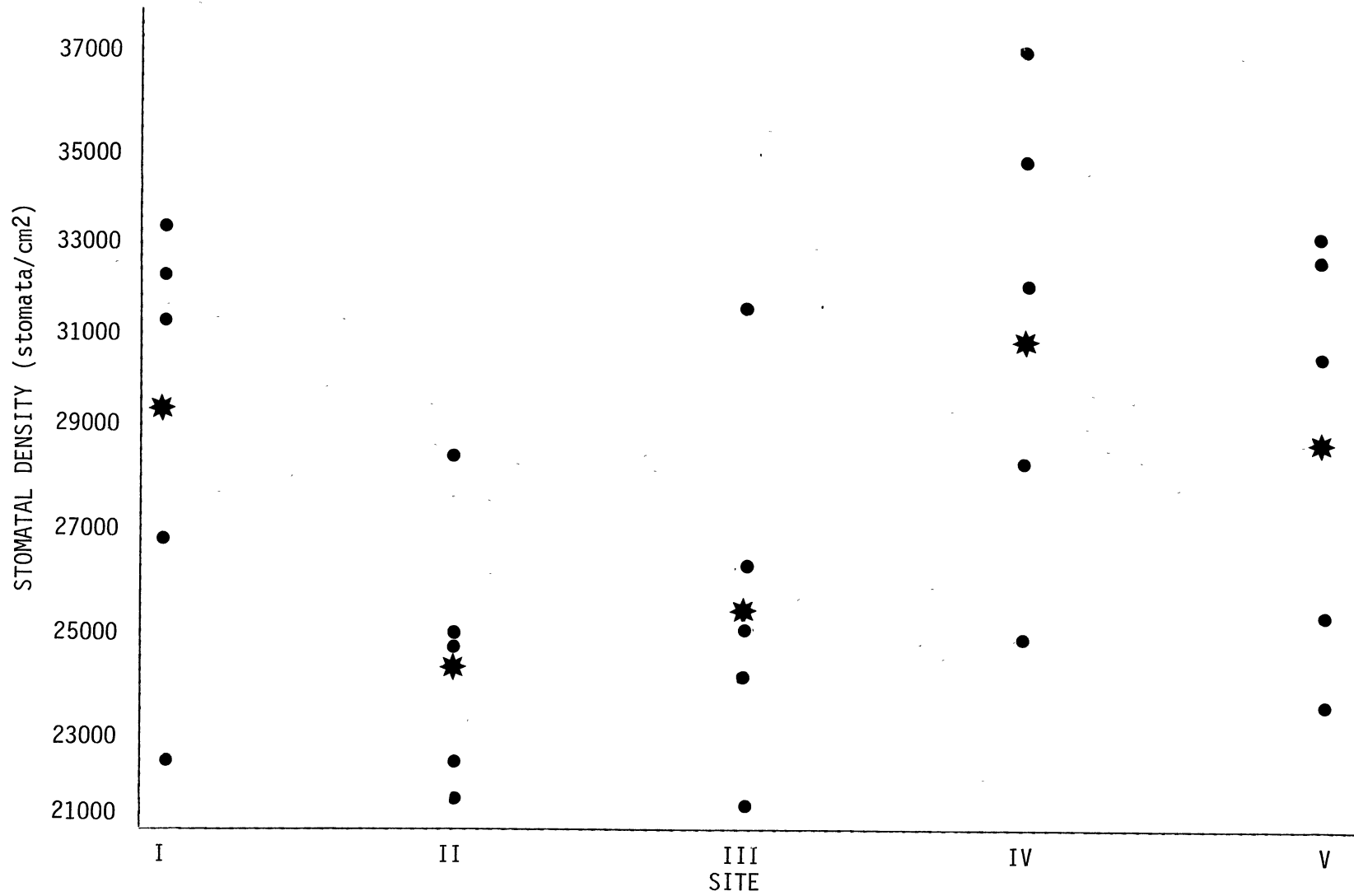


Figure 3. Range of mean stomatal densities. Star represents location mean.

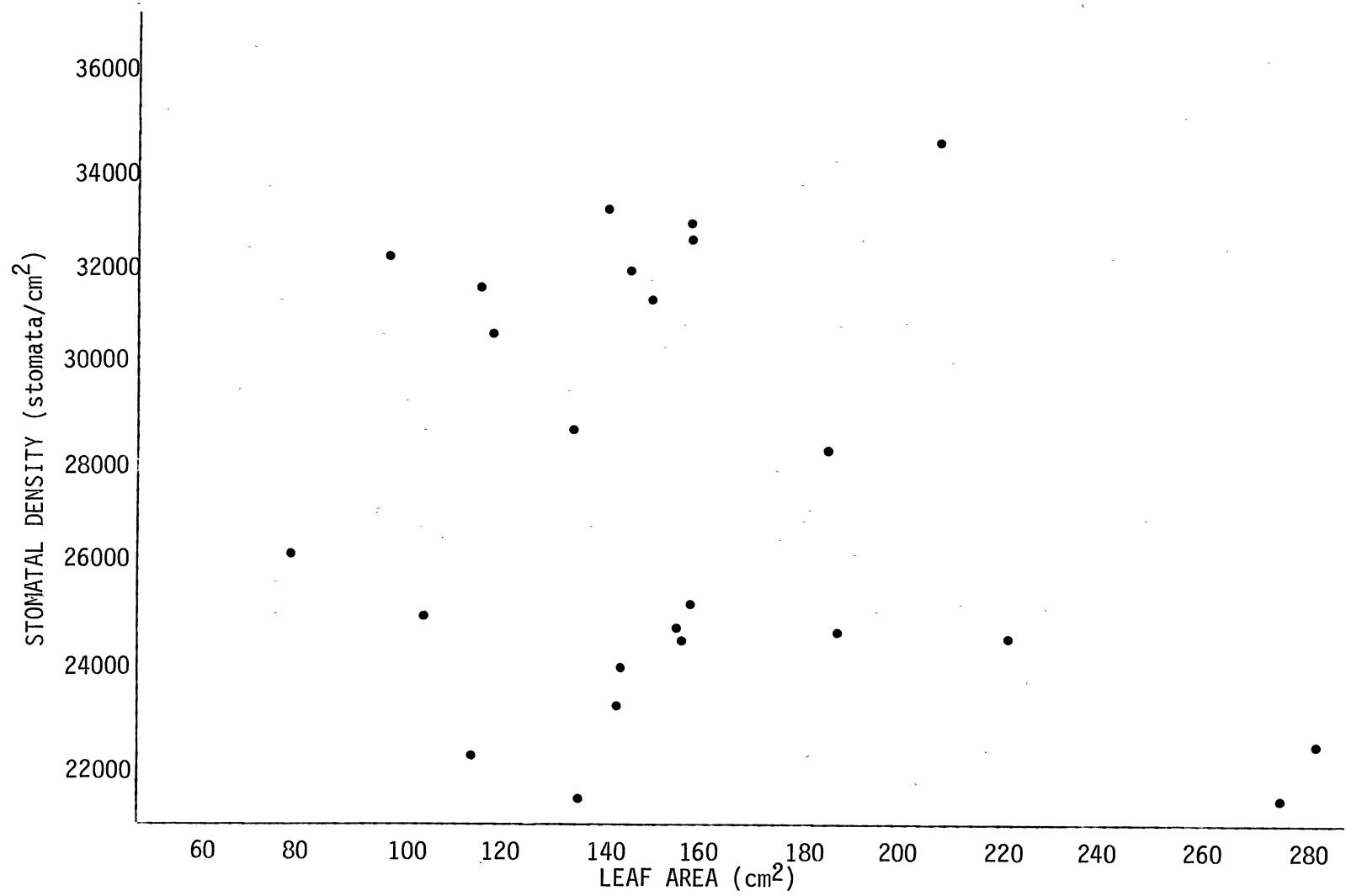


Figure 4. Stomatal density as a function of leaf area.

largest average leaf area (site II) also had the lowest stomatal density.

Growth Rate

Based on the last ten years of growth, the mean growth rate in mm/10 years were 532.40, 623.20, 903.60, 334.00 and 701.60 for sites I through V, respectively, with site III having the fastest growth rate and site IV having the slowest (Appendix). Using the SNK test only sites III and IV were significantly different ($\alpha=.05$) (Figure 5). At first it appeared that age might be correlated to the growth rate since site III had the youngest trees and site IV the oldest (Appendix, Figure 6). A covariance analysis, based on age as the covariant, was performed and showed that age was not correlated to the growth rate in this case. The difference in growth rate between sites III and IV would exist regardless of age.

Diffusive Resistance

During July of 1983, diffusive resistance values for sites I and III only were significantly different using the SNK test ($\alpha=.05$). August values showed no significant difference between sites. September values showed little difference among sites I through IV, while site V displayed a drastic increase in resistance (Figure 7). It was at this time that the leaves of all five trees at site V displayed wilting, yellowing and some necrosis. October readings were similar to September in that there were no real differences among sites I through IV. Conditions worsened at site V by early

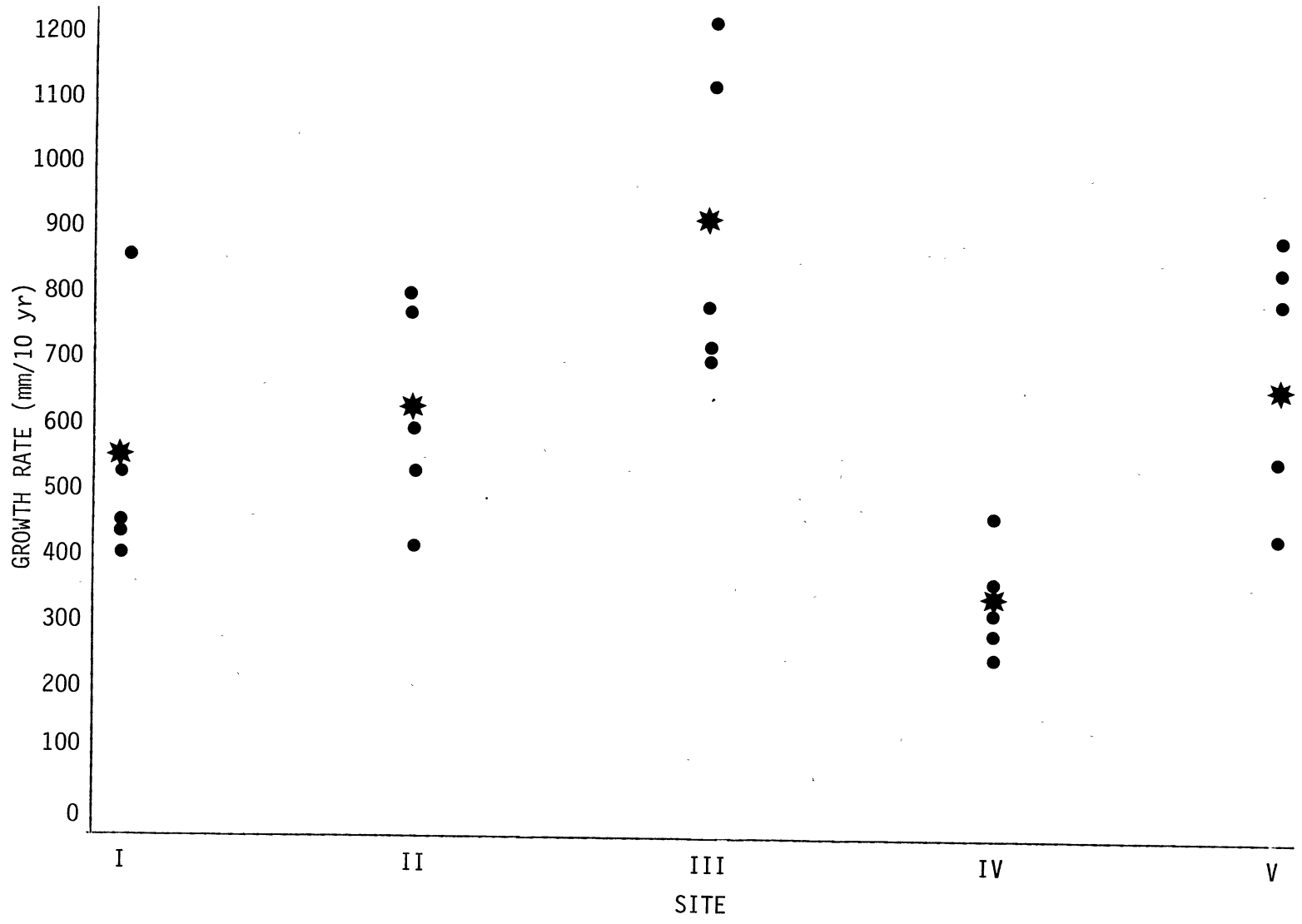


Figure 5. Range of growth rates. Star represents mean for each site.

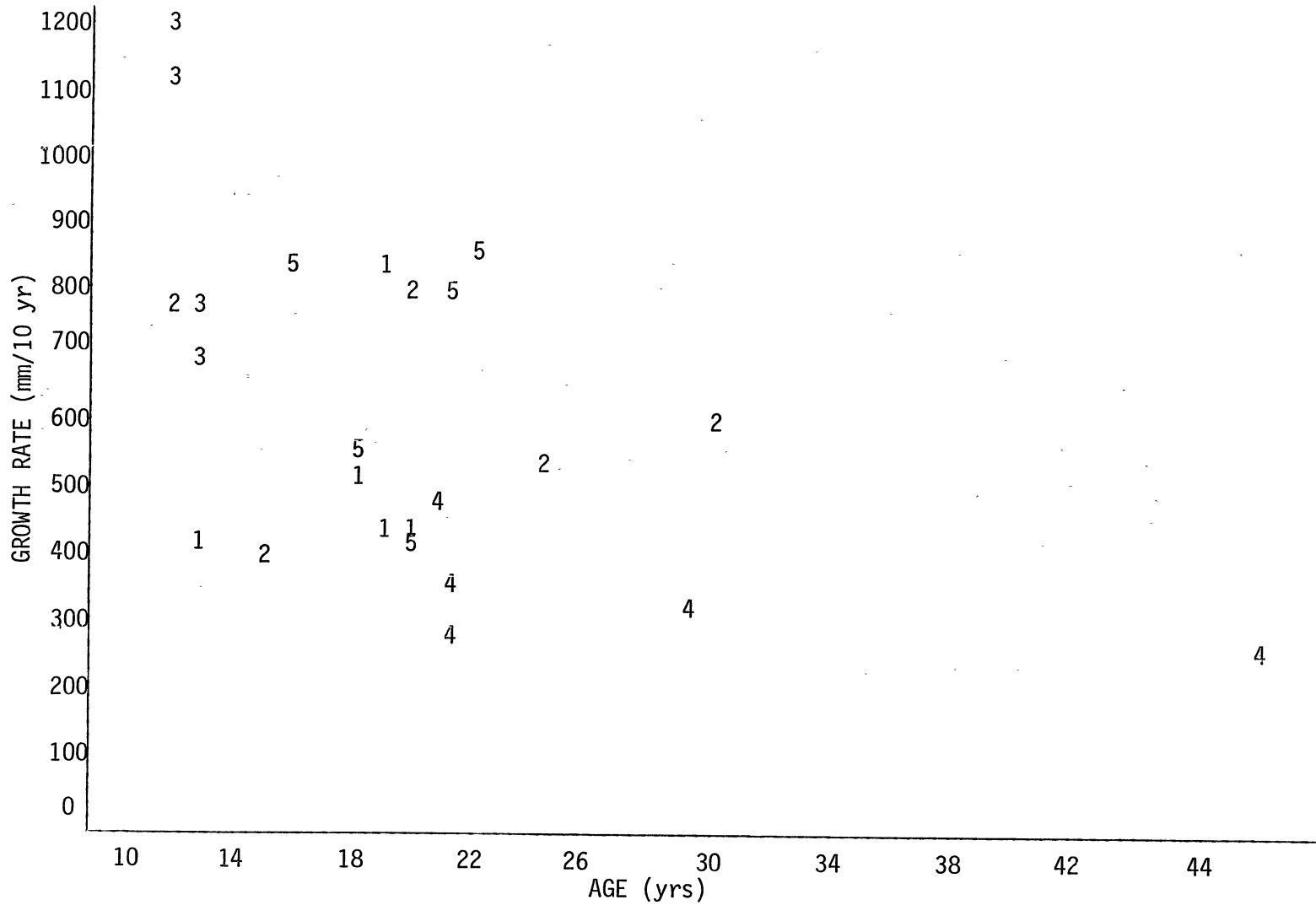


Figure 6. Growth rate as a function of age. Symbol represents site number.

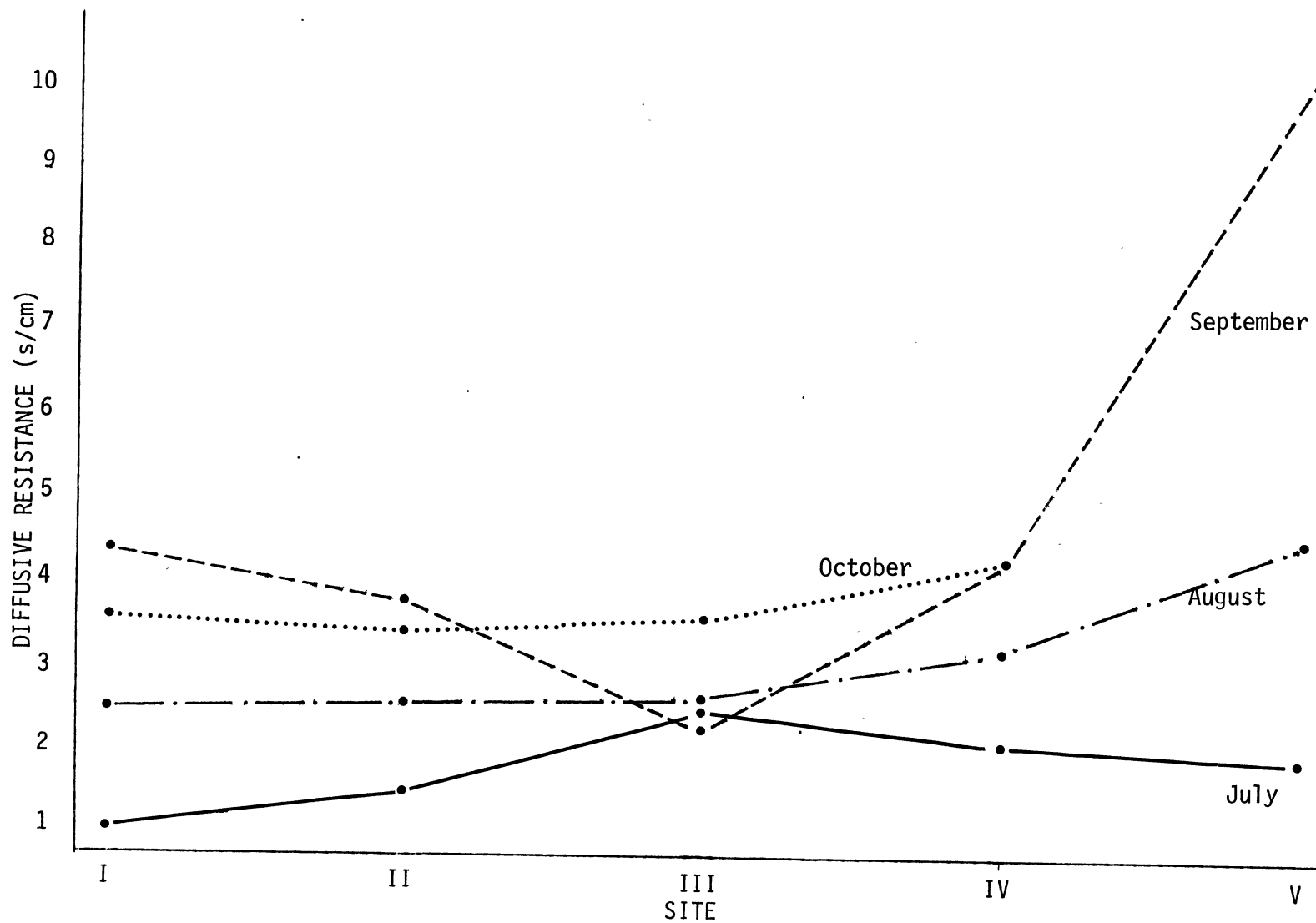


Figure 7. Mean diffusive resistance by site for each month.

October to the point where the leaves had dropped prematurely from the trees.

When each site is observed independently over time, the effects of the growing season become apparent. Regression analysis of these values showed a linear relationship for sites I through IV over the months of July through October (Figure 8). There was an average increase in resistance of 1.71 s/cm per month for these sites as the summer stress continued. Site V, however, displayed a positive quadratic relationship over this time period, i.e. the amount of increase in resistance increased from month to month.

Leaf Water Potential

The mean leaf water potential based on three measurements per tree five trees per site for July, 1983 show that site III was significantly different ($\alpha=.05$) from site V and that both sites III and V were significantly different from sites I, II and IV (SNK). The extremely high value at site III at this time could be associated with a rain event, overcast sky or measurement error (Figure 9). August values showed no significant difference between sites, yet values for site III were still higher than those for the remaining sites. September values showed only a significant difference between sites I and V, with site I having the lowest value (-16.3 b) and site V having the highest (-12.2 b). The high water potential value at site V was the result of high diffusive resistance there at that time and represents damaged leaves that were beyond recovery and ready to abscise. October values were generally higher than the previous months but showed no

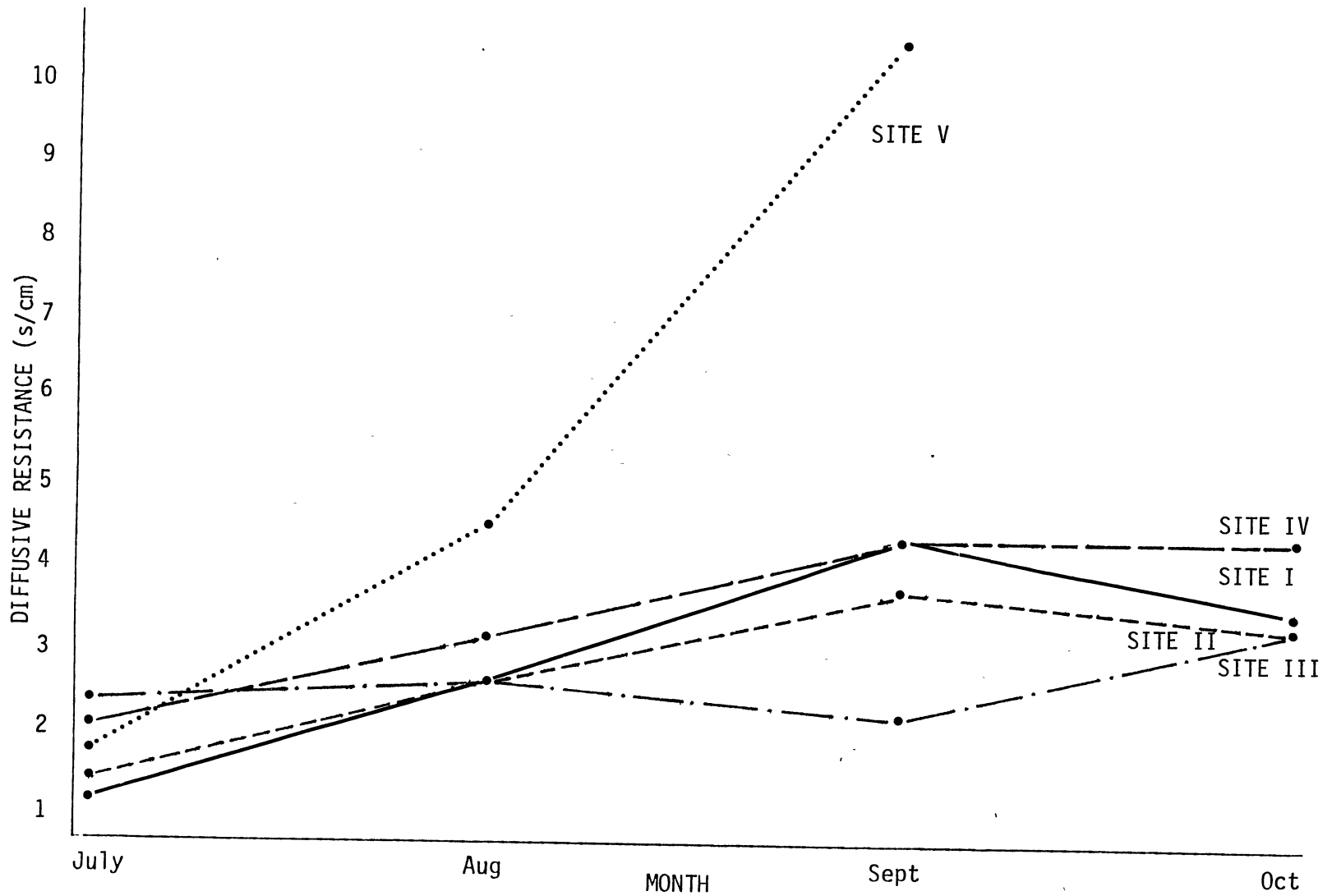


Figure 8. Mean diffusive resistance by month for each site.

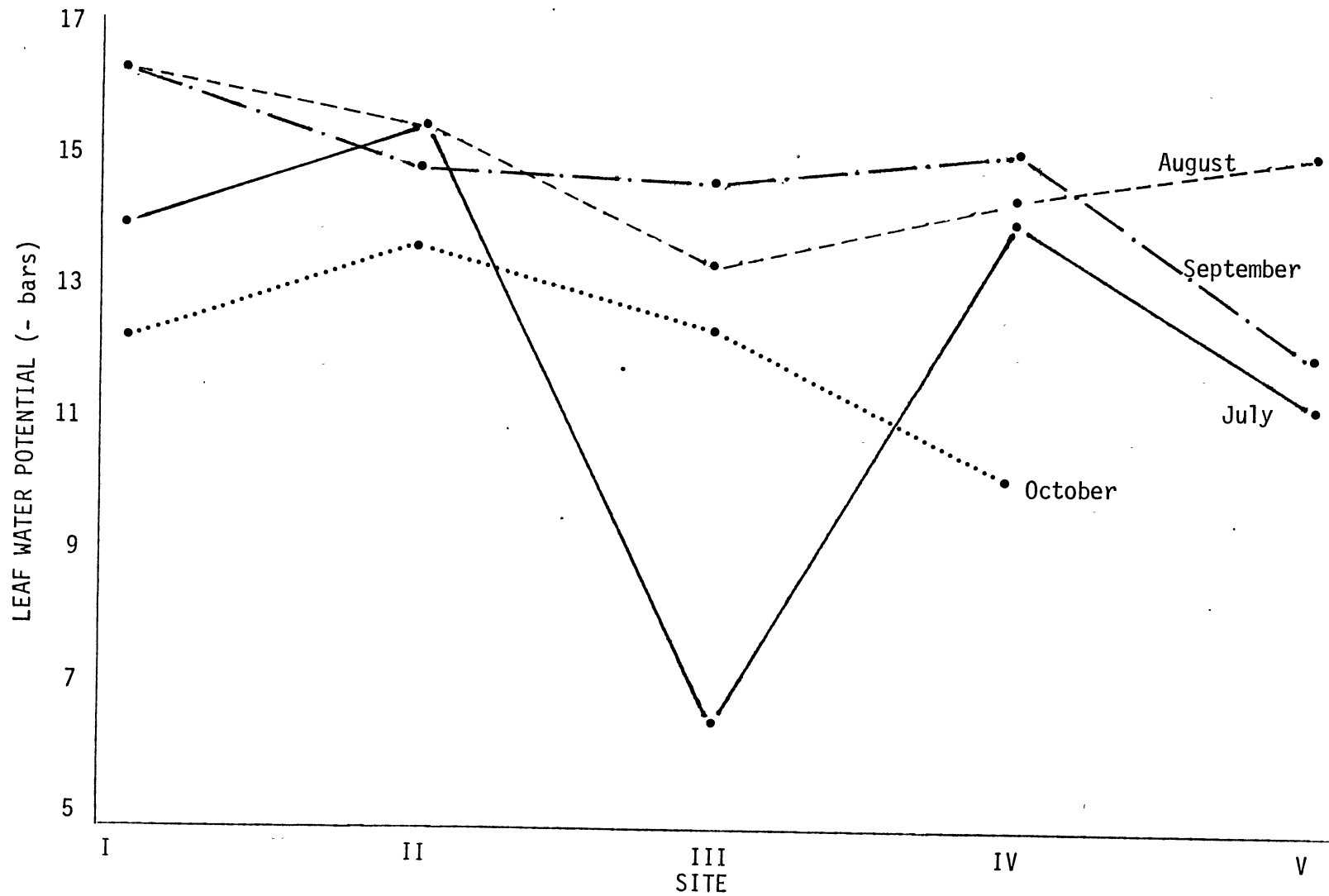


Figure 9. Mean leaf water potential by site for each month.

significant difference among sites I through IV. The trees at site V had dropped their leaves by this time making further measurements impossible.

When each site is observed independently over time a different pattern arises (Figure 10). Overall, a quadratic relationship was apparent over the months July through October for sites I through IV. There was a decrease in leaf water potential early in the season followed by a leveling off as they approach the peak of the summer stress. This was followed by an increase, most likely associated with rain events that occurred at that time. The increase at site V during September, again, can be associated with the increased diffusive resistance at that site.

The relationship between leaf water potential and diffusive resistance for the 1983 growing season was seen when the two were plotted graphically (Figure 11). A very low correlation coefficient (r) indicated that there was little, if any, linear relationship between the two measurements. One important feature was apparent, however, when these values were plotted. Over a range of leaf water potentials (-12.0 to -18.0 b), sites I through IV maintained a range of diffusive resistances between 1.0 and 6.0 s/cm. Over the same range of water potentials, however, site V displayed a larger range and higher values of resistance. The five highest resistance values were associated with the stressed conditions occurring during September, while the next two highest values were associated with August.

Finally, there appeared to be no relationship between relative

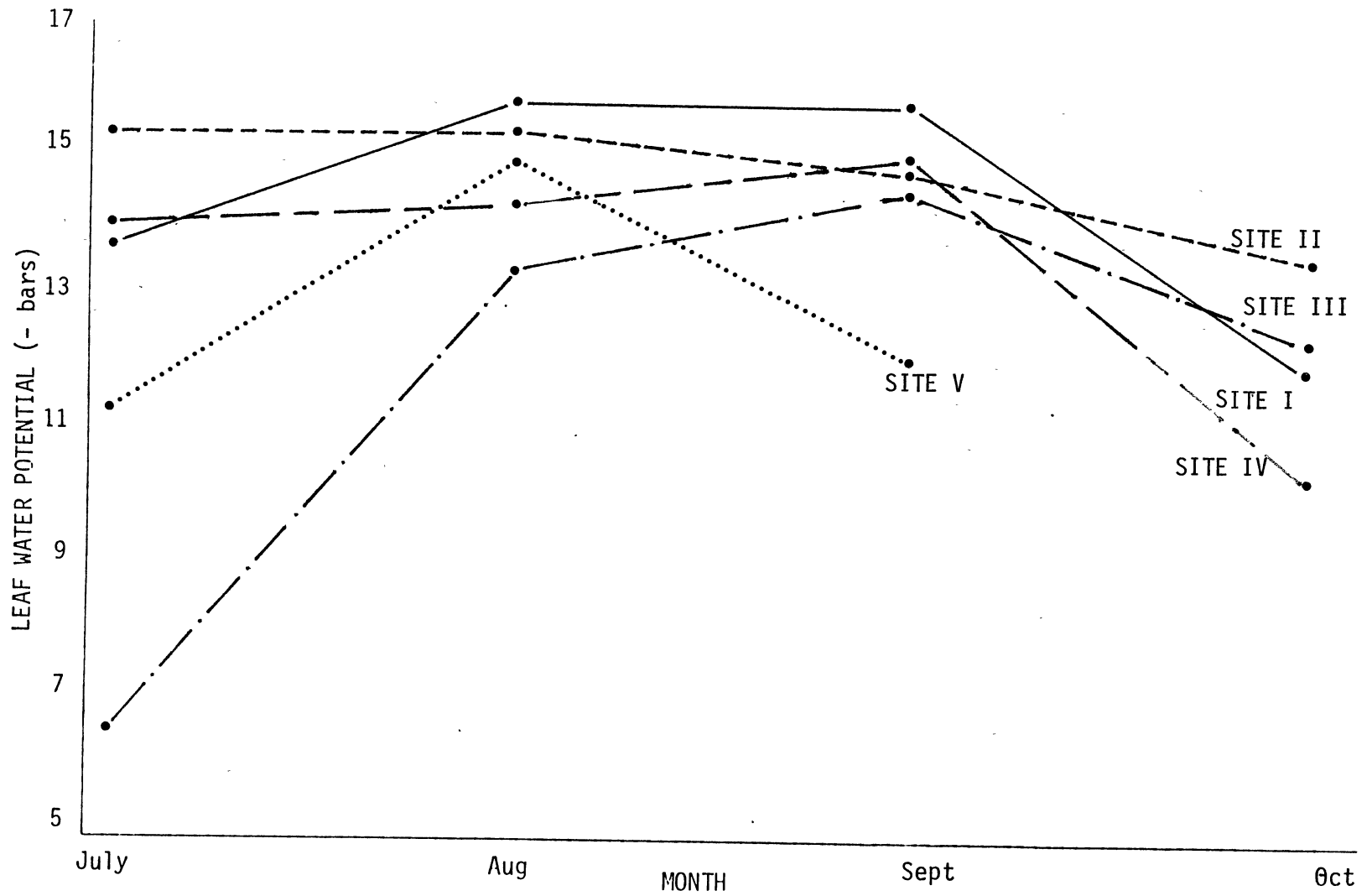


Figure 10. Mean leaf water potential by month for each site.

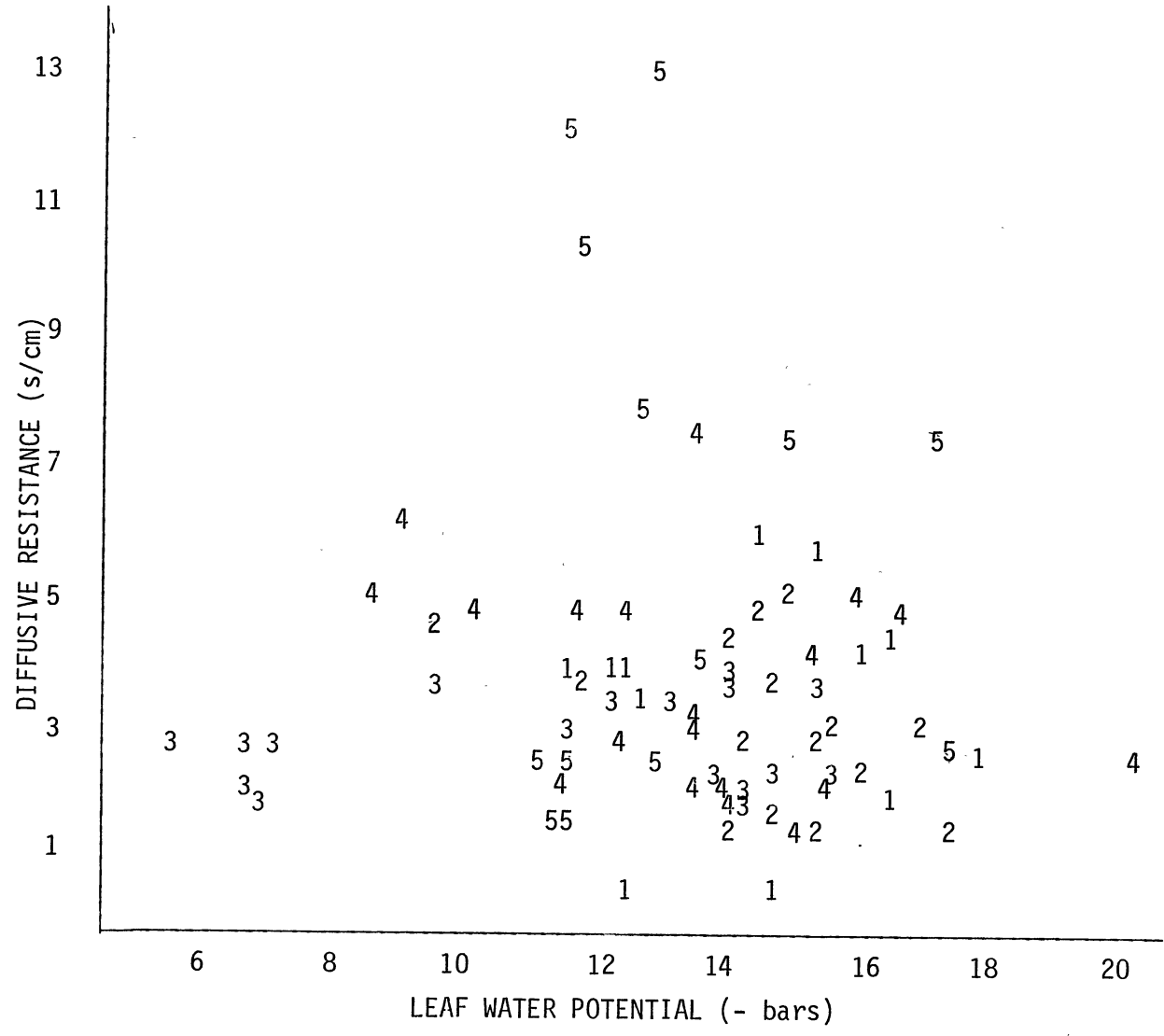


Figure 11. Diffusive resistance as a function of leaf water potential. Symbol represents site number.

humidity and its effect on diffusive resistance (Figure 12) or leaf water potential (Figure 13). This was seen when the two were plotted against the range of relative humidity values experienced over the growing season (Appendix).

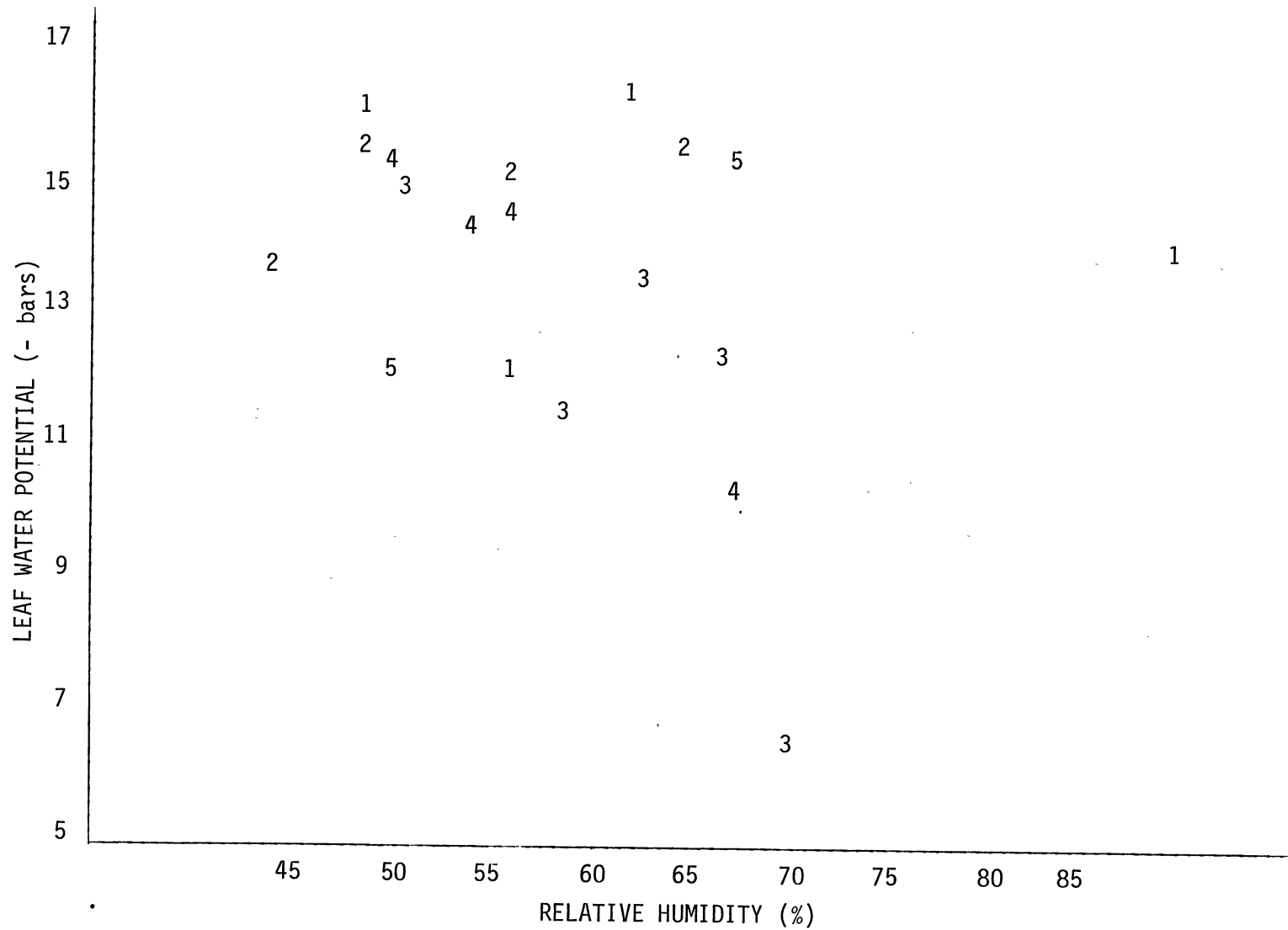


Figure 12. Leaf water potential as a function of humidity.
 Symbol represents site number.

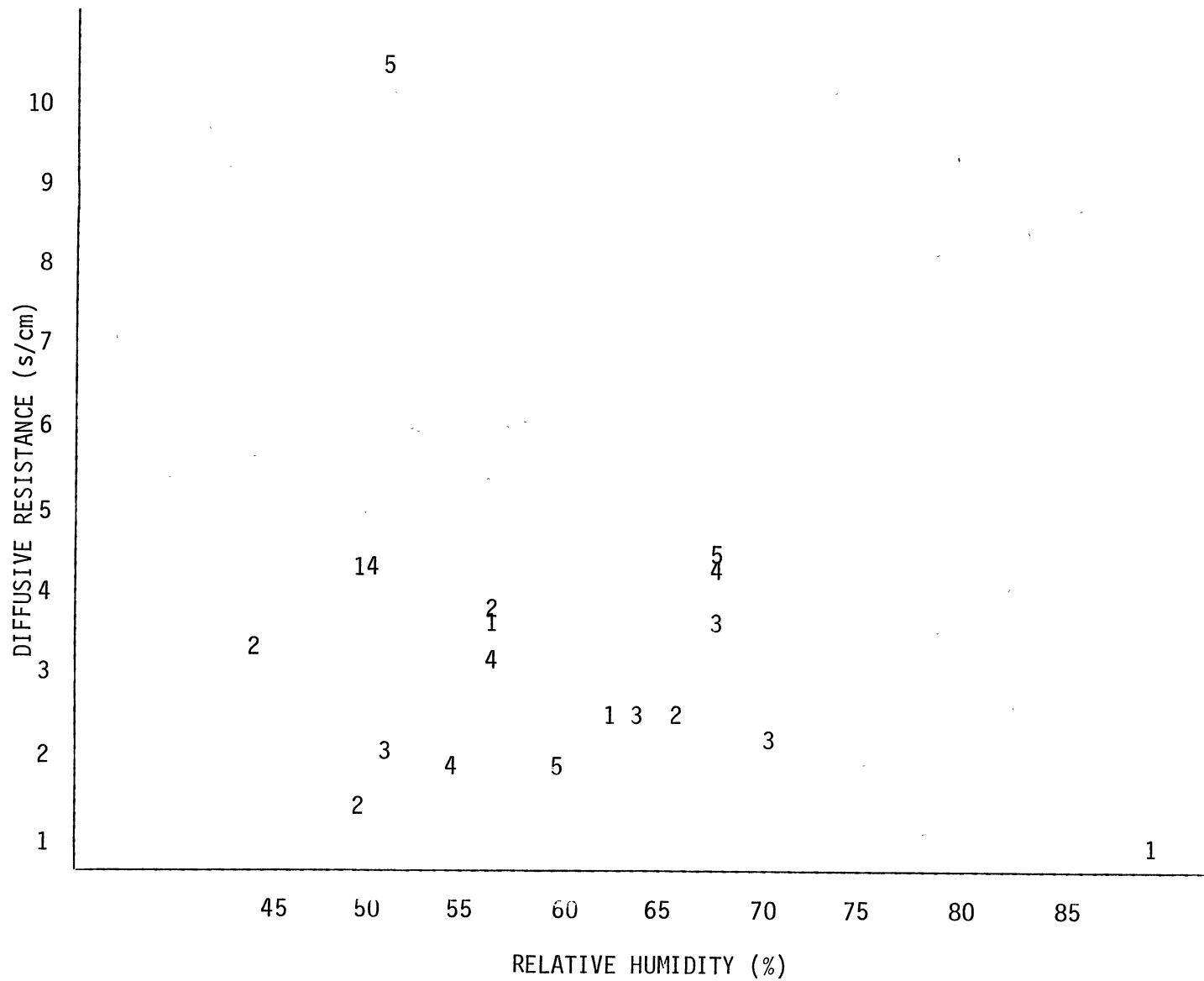


Figure 13. Diffusive resistance as a function of humidity.
 Symbol represents site number.

CHAPTER V

DISCUSSION

As the moisture conditions become less favorable from east to west across the state, the anatomical features of sycamore would be expected to adapt accordingly. Generally, leaf blades are expected to become smaller and thicker, and stomata smaller and more dense (Daubenmire 1974) in plants grown under unfavorable water balance. If this is true, it would be expected that those trees at the western edge of sycamore's distribution (sites I, II and III) would have the lower average leaf area and higher average stomatal density as compared with those trees in the eastern part of the study area (sites IV and V). This trend was not observed for the trees used in this study. Site II exhibited the largest average leaf area and the lowest stomatal density, while site III trees showed the smallest average leaf area and the second lowest stomatal density. The highest stomatal density was found at site IV, an eastern site.

The discrepancy between what was expected and what was found provides evidence for the possibility that lack of adaptation to the different climatic condition could restrict the species distribution. The ability to adapt to varying climates provides a species an increased and varied distribution (Pallardy and Kozlowski 1979). Inability to respond anatomically to an unfavorable moisture regime might very well reduce the individual's water-use-efficiency. Main-

taining a large leaf area, without adjusting stomatal number and/or size, contributes to large and expensive transpiring surface, which is expensive in terms of the amount of energy and water needed to support such biomass. Ability to transport water must be proportional to the need in order to survive summer moisture stress and/or high evaporative demand. When the need is greater than the amount transported (whether due to low soil moisture or high evaporative demand or both) gas exchange is decreased if not halted entirely. This could explain the situation which occurred at site V.

Aside from changes in anatomical features, the growth rate of trees in an unfavorable moisture regime would be expected to be less than those in a more mesic environment. This was indeed part of the hypothesis. However, the growth rate as well as anatomical features show no trend. A possible explanation for both of these discrepancies could lie in statistics. The sample size or number of trees measured may not have been large enough to show a significant trend across the gradients. Any small sample like this could be unintentionally biased, perhaps including trees that are not like the general population in their area.

The physiological responses were observed from two perspectives: geographically and chronologically. When sites are compared for one month at a time, or geographically, there appears to be no existing trend from east to west, no difference between stressed and unstressed sites, in either diffusive resistance or leaf water potential. There does not appear to be any physiological adaptation to the increased

evaporative demand or reduced moisture supply experienced in the western sites. Again, the ability of the species to adapt to the change in climate is questioned. Sycamore is generally adapted to moist soil and humid climates where it would not normally experience high evaporative demand. It would, therefore, not need such rigid stomatal control and resistance. Without the ability to control stomata and resistance under stress, the plant risks severe water loss and low internal water potentials. Both of which can contribute to prohibiting the species from extending into the less favorable sites in western Oklahoma.

Chronologically, sites I through IV showed a general increase in diffusive resistance as the season progressed through September. As expected, leaf water potential tended to reach a minimum during August and September, and increased by October. The continued increase in diffusive resistance for site III and IV during October is indicative of stressed conditions there, while the minor decrease in diffusive resistance for sites I and II was most likely the result of local rain events.

Of particular interest are sites III during July and site V during August, September and October. The significantly higher leaf water potential value for III in July has several possible explanations. It is suspected that either an early morning rain event or overcast sky occurred at the site and was replaced by clear skies preceding sampling. If this is in fact the situation, it emphasizes that local, transient events can lead to difficulties in understanding trends. Equipment failure and measurement error are, of

course, other possibilities.

The unusual physiological conditions experienced at site V during the months of August, September and October indicate severe stress at that site. Diffusive resistance values had already begun to rise higher than other sites by early August. This high resistance was associated with a significantly lower leaf water potential, indicating that the internal water balance had decreased enough to warrant stomatal closure. As transpiration diminished, the water potential began to rise again, slightly. Resistance did not respond to this increased water status, however, and increased drastically to the point at which gas exchange completely halted.

The general relationship between leaf water potential and diffusive resistance is such that when the former becomes sufficiently low, the latter increases and stomata close (Tobiessen and Kana 1974). Although this relationship was not encountered for all sites, stomatal closure did occur with a declining leaf water potential at site V as early as August. It appears that these trees could not tolerate the low leaf water potential experienced at that site. This stomatal hypersensitivity could be viewed as an adaptive mechanism for drought avoidance which the trees on the other sites do not possess. The trees at sites I through IV showed little change in resistance over a large range of water potentials. This lack of control or insensitivity could cause substantial water loss, especially during stress and contribute to limiting sycamore's range from extending further west.

The cause of the low internal water balance at site V may not necessarily be due to climate, however, but geography. Elk Creek

on which site V is located, is part of the Lake Tenkiller watershed. The regulation of water level in this lake may have reduced the water table of the creek, thus causing the drought effects. Also the creek-bed may have had a shallow impermeable bedrock which might have caused high drainage.

The effects of increasing evaporation on diffusive resistance and leaf water potential did not show the expected response. Generally, as evaporation increases, diffusive resistance increases and water potential maintains a specific range (Camanchó-B, et al 1974). The fact that no relationship between humidity and water relations for sycamore was found does not necessarily indicate that humidity has no effect on these parameters but that transpiration is regulated by some other factor.

Evidently, there is a significant discrepancy between the actual and expected results of this study. It can not be denied that the species' distribution does in fact end within miles of the most western site, site I, Perkins, Ok., regardless of the physiological and anatomical findings of twenty-five trees. The range of sycamore covers much of the eastern United States, of which eastern Oklahoma is only a small part. It seems quite possible that the study area did not incorporate a large enough area to show the expected trends and decreased growth rate. Had the study area included, for instance, the entire state of Arkansas along with the eastern sector of Oklahoma, the hypothesized trend may have been more obvious.

Another possibility is that there is indeed no gradual change in any growth parameter studied here. Evidence shows that sycamore

adults do not differ from eastern to central Oklahoma and that planted seedlings can survive in the extreme conditions experienced in the western part of the state, similar to Salix and Populus deltoides. Seedlings may have a higher transpiration rate than adults with adequate water supply while not having a large enough root system. This would reduce the survival rate of seedlings and subsequently the frequency of sycamore adults in western Oklahoma. This raises the prospect of a future study which could investigate the possibility of a decrease in frequency of sycamore as climate changes from east to west. The study could include not only adults but the frequency, density and physiological responses of seedlings and saplings.

CHAPTER VI

SUMMARY AND CONCLUSIONS

This purpose of this study was to ascertain whether or not Platanus occidentalis, sycamore, is prevented from extending into western Oklahoma due to lack of rainfall and increased evaporative demand. This was achieved by investigating anatomical and physiological differences among individuals across a moisture gradient.

It was hypothesized that the increased evaporative demand would cause an increased transpiration rate due to lack of stomatal control (or stomatal insensitivity) and growth would subsequently decrease. This would be evidenced by low diffusive resistance coupled with decreased water potentials. The associated anatomical responses would include leaf size and growth rate and smaller and more dense stomata. The results and conclusions of the study are as follows.

Leaf Area and Stomatal Density

Although significant differences were found between sites for leaf area, there did not appear to be the expected trend from east to west as conditions became less favorable for growth. The trees of the western sites displayed leaf areas similar to those in the eastern sites. Maintaining a large transpiring surface under high evaporative demand could increase water loss in these western site trees. In order to conserve water, stomatal density or size would

need to be reduced. Since neither response was evident it seems that there was no obvious anatomical adaptation to the change in climate (or weather). Although this appears to be a likely cause of the limited distribution, it should be noted that none of the adult trees at any of the western sites displayed signs of stress. It is possible, however, that the seedlings would show differences.

Growth Rate

A decreased growth rate was an assumed part of the hypothesis that has been proven incorrect. Like leaf area, the growth rate showed significant differences but not the expected east-west trend. This is added evidence that the trees at the western sites were possibly not stressed by increased evaporative demand, but, again, seedlings may be.

Diffusive Resistance and Leaf Water Potential

The physiological responses showed little differences among sites I through IV for any one month at a time. Over time, sites I through IV showed a gradual increase in diffusive resistance; while water potential decreased at first, reached a midsummer minimum, then increased by early fall. Site V showed the only significantly different response. In response to a decrease in water potential in August, resistance increased drastically and continued to increase until gas exchange halted and leaves abscised by mid-September.

If the events at site V are considered an adaptive mechanism against drought stress, then the hypothesis is at least partially correct. The

sites west of site V do not possess enough stomatal sensitivity to control water loss during summer stress. The trees of these western sites did not appear to respond to decreases in leaf water potential by increasing resistance. The hypothesis is still partially incorrect, however, since the growth rate and leaf area did not decrease or adapt to the changes in weather.

The question remains, however: is the stomatal hypersensitivity at site V a reoccurring, advantageous event? The possibility seems unlikely since gas exchange and photosynthesis are halted. The situation at site V is more likely not weather-related since it was so extreme and sudden. Also, site IV which was only twenty miles west showed no similarity.

In conclusion, sycamore does not display trends of decreased growth or increased stress along the moisture gradient from east to west across the study area. This is evidenced by no differences between east and west sites in leaf area, growth rate and stomatal density. Physiological responses are similar. There are no differences in leaf water potential or diffusive resistance among sites I through IV. The occurrence of drought stress at site V is quite likely the result of manipulation of the water table. The lack of change could possibly explain the limited distribution. Failure to adapt anatomically and physiologically may restrict this species to very moist and humid areas. Secondly, adult trees may, in fact, have no difficulty surviving summer stress whereas seedlings may. Seedling establishment and survival could be limited. Finally, it seems possible that the study area may not have incorporated a large enough area of sycamore's distribution to show the expected trends.

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APPENDIX

TABLE I

LOCATION, CLIMATE, AND SOIL SERIES (GRAY AND
GALLOWAY 1959) OF STUDY SITES.

<u>SITE</u>	<u>LOCATION</u>	<u>AVE. ANN. PRECIP.</u>	<u>P-E INDEX</u>	<u>SOIL SERIES</u>
I Perkins	SW $\frac{1}{4}$, Sec 3, T17N, R3E, on unnamed tribu- tary of the Cimarron Riv.	33 in.	53	Dougherty- Teller-Yahola light, sandy soil, low in fertility.
II Shamrock	SE $\frac{1}{4}$, Sec 26, T17N, R7E, on East Spring Creek.	36 in.	56	Verdigris silt loam- slightly acid, alluvial from dark prairie soil.
III Beggs	NE $\frac{1}{4}$, Sec 33, T15N, R12E, on Adams Creek.	37 in.	61	Broken Alluvial Land - alluvial soil ranging from fine sandy loam to clay loam.
IV Zeb	NW $\frac{1}{4}$, Sec 35, T16N, R21E, on Mill Creek.	42 in.	66	Elsah Soils - gravelly alluvial streambeds and loamy sediments from chert lime- stone and sand- stone.
V Elk Creek	SE $\frac{1}{4}$, Sec 31, T15N, R23E, on Elk Crk.	43 in.	68	Same as site IV.

TABLE II
 STOMATAL DENSITY (STOMATAL/CM²) AND LEAF AREA (CM²)
 VALUES BY TREE. PAIRED VALUES REPRESENT
 MEASUREMENTS MADE ON THE SAME LEAF.

SITE 1	-PERKINS	DENSITY	AREA	DENSITY	AREA	DENSITY	AREA
	TREE						
	1	27844.07	115.22	38186.16	199.44	34208.43	112.70
	2	41368.34	105.12	31821.80	85.75	23866.35	105.94
	3	36595.07	216.68	30230.71	118.84	27048.53	115.36
	4	24661.89	113.58	20684.17	85.73	21479.71	136.10
	5	27048.53	172.74	23866.35	111.58	30230.71	135.64
SITE 2	-SHAMROCK						
	TREE						
	1	27048.53	162.62	27048.53	173.18	19888.62	132.02
	2	23070.80	221.20	31821.80	178.54	19093.68	165.53
	3	31026.25	164.60	24661.89	91.20	30230.71	146.40
	4	20684.17	297.44	22275.26	269.12	23866.35	276.84
	5	20684.17	253.94	21479.71	258.60	22275.26	312.68
SITE 3	-BEGGS						
	TREE						
	1	25457.44	121.54	24661.89	102.14	24661.89	91.16
	2	27048.53	113.88	34208.43	109.74	53412.89	126.42
	3	23866.35	91.24	25457.44	182.56	22275.26	155.66
	4	27844.07	88.94	25457.44	60.67	25457.44	82.20
	5	17501.99	123.02	23866.35	135.98	23070.80	146.56
SITE 4	-ZEB						
	TREE						
	1	27844.07	181.25	30230.71	154.83	27048.00	219.06
	2	31026.25	195.99	38186.16	224.41	35003.98	205.64
	3	35799.52	200.09	25457.44	104.96	35003.98	132.71
	4	36595.07	130.50	36595.07	145.69	38186.16	155.07
	5	23866.35	154.96	25457.44	247.55	24661.89	262.57
SITE 5	-ELK CREEK						
	TREE						
	1	22275.26	168.92	28639.62	162.32	24661.89	141.62
	2	35003.98	194.33	25457.44	92.73	38186.16	184.63
	3	23866.35	161.41	23866.35	175.34	22275.26	95.77
	4	26252.98	108.55	35739.52	117.33	30230.71	130.38
	5	31821.80	127.83	34208.43	165.21	31821.80	178.32

TABLE III
GROWTH DATA BY TREE

SITE 1	-PERKINS	HEIGHT	DIAMETER	AGE	GROWTH
	TREE	(FT)	(IN)	(YR)	(MM/10 YR)
	1	51.5	8.60	17	445
	2	55.0	12.40	17	859
	3	55.0	8.10	18	443
	4	39.5	5.10	11	390
	5	46.5	6.40	16	525
SITE 2	-SHAMROCK				
	TREE				
	1	75.5	15.95	28	591
	2	40.0	5.90	13	412
	3	61.5	13.05	18	800
	4	67.0	13.40	22	535
	5	41.0	7.70	10	778
SITE 3	-BEGGS				
	TREE				
	1	35.0	8.55	10	1131
	2	34.5	9.90	10	1215
	3	28.0	6.05	11	688
	4	28.0	7.00	11	700
	5	35.0	9.70	11	784
SITE 4	-ZEB				
	TREE				
	1	73.0	11.05	27	318
	2	48.0	9.80	19	472
	3	57.5	8.90	19	273
	4	56.0	7.35	19	355
	5	80.0	18.50	46	252
SITE 5	-ELK CREEK				
	TREE				
	1	68.0	10.00	14	833
	2	52.5	12.30	20	881
	3	63.0	8.55	18	424
	4	41.5	13.15	16	560
	5	56.0	15.60	19	810

TABLE IV

LEAF WATER POTENTIAL (-BAR) VALUES BY TREE AND MONTH. (.) REPRESENTS MISSING DATA.

SITE 1 -PERKINS												
TREE	JULY 19 / 89%RH			AUGUST 13 / 62%RH			SEPTEMBER 13 / 49%RH			OCTOBER 16 / 56%RH		
1	12.0	14.5	11.5	17.0	14.5	15.5	15.5	16.0	15.5	13.5	11.5	12.0
2	14.5	16.0	14.0	15.5	17.0	17.0	18.5	18.5	19.0	13.0	13.0	12.0
3	12.0	14.5	12.0	15.5	13.5	17.5	14.5	13.5	15.5	16.0	11.0	11.5
4	15.5	15.0	15.0	18.5	17.5	18.5	16.5	17.0	16.0			
5	16.0	14.5	14.0	16.5	16.0	14.5	14.0	17.0	17.5	12.5	11.5	10.5
SITE 2 -SHAMROCK												
TREE	JULY 18 / 49%RH			AUGUST 14 / 65%RH			SEPTEMBER 20 / 56%RH			OCTOBER 14 / 44%RH		
1	15.0	13.0	11.5	16.0	16.0	16.5	15.0	14.5	13.0	9.5	9.5	10.0
2	15.5	15.0	15.5	12.5	15.5	16.0	16.0	15.0	16.5	16.5	14.5	14.0
3	16.0	16.5	14.0	17.5	17.0	17.0	15.5	14.0	15.5	15.0	15.5	17.0
4	17.0	18.5	17.0	16.0	16.0	13.0	15.0	13.5	14.5	17.5	13.0	16.5
5	16.0	15.0	15.0	17.5	14.0	13.5	15.5	17.5	14.0	12.5	11.5	12.0
SITE 3 -BEGGS												
TREE	JULY 16 / 70%RH			AUGUST 11 / 63%RH			SEPTEMBER 17 / 51%RH			OCTOBER 12 / 67%RH		
1	6.5	6.5	7.0	11.5	11.5	11.5	17.0	16.5	16.0	14.0	16.0	12.5
2	7.0	6.0	7.5	13.5	14.0	15.5	16.5	15.0	15.0	15.0	15.5	15.5
3	7.0	7.5	6.5	11.0	14.5	11.0	14.5	15.0	13.5	9.0	9.0	10.5
4	6.5	7.0	6.0	13.0	14.0	14.5	13.5	11.5	14.5	7.5	10.0	11.5
5	6.5	5.0	5.5	13.0	17.0	17.0	12.0	16.0	16.5	11.5	15.0	15.5
SITE 4 -ZEB												
TREE	JULY 8 / 54%RH			AUGUST 5 / 56%RH			SEPTEMBER 10 / 50%RH			OCTOBER 2 / 67%RH		
1	11.0	13.0	13.0	17.0	15.5	15.5	14.0	11.5	15.0	10.0	9.0	8.0
2	14.0	15.0	16.5	14.0	14.5	14.0	16.0	23.0	21.5	11.0	12.0	11.5
3	12.0	13.0	16.5	15.0	13.0	13.0	12.5	14.0	14.5	12.0	11.5	14.0
4	15.5	14.5	16.5	14.0	16.5	10.0	19.0	16.5	15.0	10.5	10.5	9.5
5	14.5	14.5	13.0	17.5	13.0	15.5	11.0	14.5	10.0	8.0	9.0	8.5
SITE 5 -ELK CREEK												
TREE	JULY 9 / 59%RH			AUGUST 6 / 67%RH			SEPTEMBER 11 / 50%RH			OCTOBER 3 / 68%RH		
1	11.0	11.5	11.5	13.5	14.5	13.0	12.0	12.0	11.5	.	.	.
2	11.5	12.0	11.0	13.0	13.5	12.5	12.5	13.0	13.0	.	.	.
3	12.0	11.5	11.0	14.0	15.5	15.5	13.0	9.5	12.5	.	.	.
4	11.0	11.5	11.0	16.5	20.0	15.0	12.0	11.5	12.0	.	.	.
5	12.0	11.5	11.5	18.0	16.5	17.5	13.0	13.5	12.5	.	.	.

TABLE V

DIFFUSIVE RESISTANCE (SEC/CM) VALUES BY TREE AND MONTH. (.) REPRESENTS MISSING DATA.

SITE 1 -PERKINS

TREE	JULY 19 / 89%RH			AUGUST 13 / 62%RH			SEPTEMBER 13 / 49%RH			OCTOBER 16 / 56%RH		
1	0.40	1.50	2.05	2.45	3.10	4.95	3.63	1.05	6.25	3.80	3.25	3.85
2	1.85	1.95	0.90	2.45	1.83	1.83	2.10	1.50	2.75	2.95	3.75	4.30
3	0.30	0.90	0.25	1.30	2.30	1.78	1.87	6.10	5.73	3.35	3.90	3.20
4	1.50	1.95	1.40	3.07	2.63	2.40	3.70	4.60	4.85			
5	0.40	0.30	0.40	2.90	3.37	3.35	3.20	4.87	4.13	3.85	3.20	3.90

SITE 2 -SHARROCK

TREE	JULY 18 / 49%RH			AUGUST 14 / 65%RH			SEPTEMBER 20 / 56%RH			OCTOBER 14 / 44%RH		
1	0.95	1.00	1.75	0.95	2.30	3.45	3.57	4.40	4.50	5.23	3.57	3.75
2	1.25	1.40	1.00	4.85	3.95	5.35	2.30	3.13	3.95	4.23	3.20	3.05
3	1.50	1.55	1.50	2.75	3.30	3.40	5.53	5.35	4.50	2.87	2.85	3.47
4	1.25	1.20	2.00	0.95	1.35	2.35	1.85	3.33	2.95	3.20	2.30	2.80
5	1.45	1.40	1.20	1.93	2.15	1.35	2.75	3.70	3.50	2.87	4.87	3.37

SITE 3 -BEGGS

TREE	JULY 16 / 70%RH			AUGUST 11 / 63%RH			SEPTEMBER 17 / 51%RH			OCTOBER 12 / 67%RH		
1	1.85	1.55	2.20	2.15	2.80	2.95	0.50	2.50	2.57	2.99	3.50	3.55
2	1.85	1.75	1.55	2.15	2.10	2.25	2.20	2.20	2.20	3.50	3.53	5.55
3	2.55	2.75	2.95	3.10	3.25	3.50	1.70	2.73	0.30	3.50	3.53	3.53
4	2.60	2.60	3.20	2.50	2.33	2.50	3.13	3.50	3.27	3.30	3.53	3.90
5	2.85	3.00	2.40	1.75	2.25	2.55	2.37	2.30	2.20	3.85	3.50	3.90

SITE 4 -ZEB

TREE	JULY 8 / 54%RH			AUGUST 5 / 56%RH			SEPTEMBER 10 / 50%RH			OCTOBER 2 / 67%RH		
1	2.50	2.75	2.60	5.20	4.85	4.87	6.83	6.83	8.50	7.40	5.30	5.20
2	1.75	0.85	1.70	1.50	1.95	2.75	2.73	2.57	1.50	1.90	2.13	2.37
3	2.85	1.60	2.70	2.60	2.90	3.80	2.30	2.60	3.10	2.37	6.00	5.35
4	1.85	2.00	2.35	1.27	2.35	1.93	4.00	4.05	5.20	4.30	4.43	4.90
5	1.70	1.60	2.00	3.80	3.57	4.35	3.20	4.85	5.95	5.00	4.75	5.17

SITE 5 -ELK CREEK

TREE	JULY 9 / 59%RH			AUGUST 6 / 67%RH			SEPTEMBER 11 / 50%RH			OCTOBER 3 / 68%RH		
1	0.85	1.50	1.40	3.30	4.35	0.90	0.50	13.45	11.40			
2	1.65	0.85	1.15	2.20	2.15	2.25	7.40	5.95	8.83			
3	2.75	2.30	1.85	6.50	7.25	7.85	3.95	10.70	15.10			
4	2.55	1.70	2.20	5.37	7.45	7.93	5.95	10.65	11.30			
5	1.70	1.35	2.20	3.40	1.35	1.87	12.90	13.80	11.90			

VITA

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Candidate for the Degree of
Master of Science

Thesis: GROWTH AND DISTRIBUTION OF PLATANUS OCCIDENTALIS IN OKLAHOMA
AS INFLUENCED BY CLIMATE AND WATER RELATIONS

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