

A COMPARATIVE STUDY OF THE WATER RELATIONS OF
QUERCUS MARILANDICA AND QUERCUS VELUTINA
WITH RESPECT TO THEIR GEOGRAPHIC
DISTRIBUTION

By

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PREFACE

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CHAPTER I

INTRODUCTION

Review of the Literature

The absorption of water from the soil was among the first physiological processes of interest to early workers (Kramer 1949). Since the time of Aristotle, researchers have worked to obtain answers to a multitude of questions regarding the importance of water to plant life. The majority of the basic concepts pertaining to plant and soil water relationships were developed fifty years ago (Kramer 1974). However, it has been only in recent years that development of accurate and practical methods for measuring the water status of plants has made possible field studies. It is now generally accepted that measurements of water potential in plant parts and soil are among the most useful parameters in explaining the distribution and ecological relationships of many plants.

Water potential is defined as the free energy per mole of water (Meyer et al. 1973). It is considered the best measure of the water status of plants not only because it can be measured on a wide range of plant tissues but also because a given level of water potential has the same physical significance in all kinds of systems and appears to have similar physiological significance (Kramer 1972). Water potential can be described by the following equation: $\Psi_w = \Psi_s + \Psi_p + \Psi_m$

The water potential (Ψ_w) consists of three components--the osmotic

potential (ψ_s) is due to the presence of solutes or ions; the pressure potential (ψ_p) or turgor pressure; and the matric potential (ψ_m) which is due to the adsorption of water molecules onto other molecules such as protein or soil colloids (Meyer et al. 1973). The turgor pressure of a cell is a positive value except in xylem vessels, the osmotic potential is a negative value, and in most plant tissues the matric potential is minor and can be disregarded. The resulting water potential will range between zero and the osmotic potential (Meyer et al. 1973).

Soil, too, has a water potential which is due primarily to its matric potential. At field capacity, the water potential of the soil is approximately -0.3 bar. As the amount of available water decreases in the soil, the water potential also decreases as does the availability of the remaining water to the plant (Kramer 1969). The water potential of soil at the wilting point for many plants is approximately -15.0 b and at this point and below, water movement from the soil into the roots is extremely slow (Downs 1975).

The water potential of the atmosphere is directly related to the relative humidity; at 100% relative humidity the water potential is 0.0 b, at 98% it is approximately -28.0 b, and at 50% it is -943.0 b (Slatyer 1967). It can be seen that even at a high relative humidity a gradient will exist from the soil, through the plant and to the atmosphere. Evaporation of water from the leaf cells lowers the cell water potential and causes movement of water into them from the xylem, thus reducing the potential in the xylem sap. The reduction of water potential is transmitted to the roots, causing mass inflow of water from the soil (Meyer et al. 1973). Differences in water potential

between the leaf and soil provide the driving force for water absorption across root and soil resistances.

The water potential of a plant is important not only because of its direct effects, but also because of the influence of its component parts. As Weibe (1972) stated, the only processes that are directly affected by water potential itself are those which depend upon diffusional movement of water across membranes. Turgor pressure, on the other hand, is very important in cell enlargement; with a reduction in turgor pressure growth can be greatly inhibited. In addition, turgor pressure plays an important role in phloem transport and water stress has been shown to result in a reduction in the translocation rate (Weibe 1972). Osmotic potential is an important factor in practically all biochemical processes within cells, influencing enzyme activity, rates of reaction and numerous other processes. Low water potentials may be damaging in many ways and it is of considerable advantage for a plant to avoid extremely low water potentials. Thus the level of water stress an individual plant is experiencing is reflected in the water potential it exhibits.

Plant water potential is known to be affected by numerous environmental factors such as availability of soil water, relative humidity, temperature, wind speed, and amount of available sunlight. Sucoff (1972) reported that with decreasing soil moisture, leaf water potential also decreased, but at a faster rate than soil water potential in order to maintain a sufficient gradient in water potential for water uptake. This has been noted by many other workers (Jarvis and Jarvis 1963, Haas and Dodd 1972, Ehleringer and Miller 1975, and Easter and Sosebee 1975).

Leaf water potential also varies greatly with variations in the evaporative demand of the atmosphere. Klepper (1968) showed diurnal fluctuations of water potential in pear and apricot trees as great as 10 b due to changes in the evaporative gradient throughout the day. The daily drop in water potential is a result of the increased transpiration brought about by a decrease in relative humidity and an increase in temperature and wind that often occur at midday. This results in a steepened gradient of water potential from the leaf to the atmosphere. Klepper concluded that the roots could not absorb water fast enough even though the water potential gradient steepened in relation to the roots. Similar daily cycles in water potential have been reported by Haas and Dodd (1972) in Prosopis glandulosa, by Griffin (1973) in three species of Quercus, and by Ehleringer and Miller (1975) in several herbaceous alpine species.

The amount of sunlight that is available also affects the water potential, not only by increasing the rate of transpiration, but also by affecting the osmotic potential. Leaves that are in full sunlight will have more negative osmotic potentials due to an accumulation of photosynthetic products. Klepper (1968) found that shaded leaves had water potentials that were as much as 8 b higher than those leaves in full sunlight. However, the magnitude of this difference is variable, for Sucoff (1972) found only a 2 b difference between shade and sun leaves in his studies of Pinus resinosa.

Studies comparing the rate of transpiration and water potential have been numerous, and the ability of a plant to control its transpiration when low water potentials develop has been considered to be advantageous to those species that experience frequent water stress

(Heth and Kramer 1975). Tobiessen and Kana (1974) found that Populus grandidentata which was adapted to drier conditions ceased transpiration at approximately -20 b whereas Populus tremuloides which was found only in wetter areas did not cease transpiration even at -60 b. In a study of Quercus velutina, Seidel (1972) found that at a soil water potential of -15 b, transpiration had decreased to 15% of the original rate at field capacity and leaf water potential was -22 b.

Although cessation of transpiration under moisture stress has its advantages, the effects of decreased CO₂ concentration and rate of photosynthesis also need to be considered. Boyer (1970) determined that as leaf water potential dropped, inhibition of photosynthesis did not occur unless stomatal closure and reduction in transpiration also occurred in his experiments with corn and soybeans. In a study of timberline meadow species Klikoff (1965) concluded that species from dry habitats had a higher percentage of initial photosynthesis at decreased water potential than did species from mesophytic or moist conditions. Dina and Klikoff (1973) studied streamside and scrub oak communities in Utah and determined that the distribution of Acer negundo was controlled in part by its photosynthetic response to water stress. Other species studied, especially Artemisia tridentata, were able to photosynthesize at water potentials as low as -37 b, but photosynthesis in Acer negundo ceased at -10 b. Cline and Campbell (1976) concluded that species which show a sharp decrease in transpiration in response to low levels of stress may be restricted to moist habitats because of reduced levels of gas exchange. Thus it is apparent that plants must maintain a balance between excessive transpiration and restricted photosynthesis.

Methods for studying plant water status have been extremely varied. The two most commonly used methods for measuring plant water potential are the thermocouple psychrometer (Boyer and Knipling 1965) and the Scholander pressure bomb (Scholander et al. 1965). While the thermocouple psychrometer is considered to be more accurate (Boyer and Knipling 1965), the advantages of the pressure bomb technique for field work are numerous. The amount of time required for equilibration to take place with the thermocouple limits the number of measurements that can be taken without accompanying changes in environmental conditions. In addition, with field measurement, variability using the thermocouple psychrometer may be greater than the discrepancy between it and the pressure bomb (Boyer 1967).

There is also disagreement as to what parameter is measured by the pressure bomb. Theoretically only the xylem pressure potential or xylem sap tension is measured, but since the contribution of xylem osmotic potential and matric potential to the xylem water potential tends to be minimal in most species, measurements are often treated as estimates of plant water potential. In this paper, water potential will be used synonymously with xylem pressure potential to refer to measurements obtained with the pressure bomb.

Purpose of the Study

Oklahoma exhibits great variation in climate, especially in terms of annual precipitation and range of temperatures. Summers are long and generally very warm, with average July temperatures ranging from 26⁰C to 28⁰C. In addition, temperatures above 38⁰C are not uncommon beginning in June and extending through September. Winters are

relatively short and mild; average January temperatures range from 7⁰C in the southeast portion of the state to 0⁰C in the extreme northwest (Gray and Galloway 1959).

In addition, considerable variation in rainfall occurs. Parts of the southeast region of Oklahoma receive in excess of 130 cm of precipitation per year. Only approximately 40 cm of annual precipitation occurs in the panhandle of northwest Oklahoma. This is a steep rainfall gradient accompanied by only a moderate change in elevation. Periods of extended drought throughout the state have also been recorded, and the average annual precipitation values fail to express the wide variability that may occur.

There are many species of trees that extend only as far westward as central Oklahoma, e.g., Quercus velutina, Q. shumardii, Carya texana, C. cordiformis, Diospyros virginiana, and Platanus occidentalis (Little 1971). It seems probable that this pattern of distribution is due in large measure to limitation of water availability. The inability of certain species to tolerate smaller amounts of moisture could be due to any number of factors, including lack of control over transpiration, an inadequate root system, seedlings sensitive to dry conditions, the inability to withstand low water potentials that facilitate absorption from relatively dry soils, or some combination of these factors.

The two species used in this investigation (Quercus marilandica and Q. velutina) are common in upland forest situations in the eastern third of Oklahoma. Q. velutina extends only to central Oklahoma; its western limit corresponds extremely well with the 90 cm annual rainfall isohyet. However the range of Q. marilandica extends much farther

westward into areas of only 65 cm annual precipitation. The purpose of this study was to ascertain whether or not Q. velutina is prevented from extending its range further west due to lack of adequate rainfall. This should be evidenced by decreasing water potentials near the edge of its range. In addition, laboratory experiments with seedlings of both species were used to assess their ability to tolerate extremely dry conditions such as those that periodically occur in western Oklahoma.

CHAPTER II

DESCRIPTION OF THE STUDY SITES

The three study areas were located in the cross timbers region of Oklahoma, a large wooded area which extends through east central Oklahoma from Kansas to Texas. It is characterized by stands of Q. stellata and Q. marilandica dominated forest on rocky ridges intermixed with tall grass prairies which usually occur on clayey lower slopes. The three sites chosen for study were located in such a manner as to extend from within the range of Q. velutina to west of its distribution (Figure 1). An effort was made to select forest stands of similar density since this can have an effect upon seasonal water potentials (Wambolt 1973). In addition only mature upland forests showing minimal disturbance were selected. Climatological data for each area is summarized in Table IX in the appendix.

The western site (Site 1) was located approximately 30 km west of Stillwater Oklahoma in Payne County (R1W, T19N, S28). It is included in the Central Redbed Plains geomorphic province which consists of gently rolling hills and broad, flat plains (Johnson et al. 1972). Soils in this area range from loams to clays, with clayey subsoils (Gray and Galloway 1959). This region of Oklahoma receives approximately 80 cm of annual precipitation (NOAA 1976). The study area consisted of a stand of Q. marilandica and Q. stellata surrounded by tall grass prairie that was lightly grazed. Symphoricarpos orbiculatus

was the predominant shrubby species and herbaceous vegetation was characterized by members of the Gramineae and Compositae. This site was approximately 65 km beyond the geographic limit of Q. velutina.

The central site (Site 2) was also located in Payne County, but is approximately 35 km east of Stillwater near the junction of state highways 51 and 18 (R5E, T19N, S21). This site was chosen to represent the western edge of the geographical range of Q. velutina. It is located in the Northern Limestone Cuesta Plains geomorphic province which consists of west-dipping cuestas and broad plains (Johnson et al. 1972). Soils in this region are dark-colored with clayey subsoils developed on either shales, sandstones, or limestone (Gray and Galloway 1959), and annual precipitation averages 90 cm (NOAA 1976). Vegetation in this area consisted mainly of Q. stellata, Q. marilandica, Q. velutina, and Carya texana. S. orbiculatus was again a prominent shrub species and many grasses and forbs were also present.

The eastern site (Site 3) was located near Keystone Dam in Tulsa County (R10E, T19N, S9). It is approximately 85 km east of Stillwater, well within the range of Q. velutina. This area consists of sandstone cuestas and broad plains typical of the Eastern Sandstone Cuesta Plains geomorphic province (Johnson et al. 1972). Soils are light-colored with reddish subsoils developed on various sandy materials (Gray and Galloway 1959). Annual rainfall averages 95 cm at nearby Tulsa (NOAA 1976). The vegetation here is similar to that of Site 2 with both Q. stellata and Q. marilandica being common. However, more Q. velutina and Carya texana were present with a greater diversity of forbs and fewer grasses.

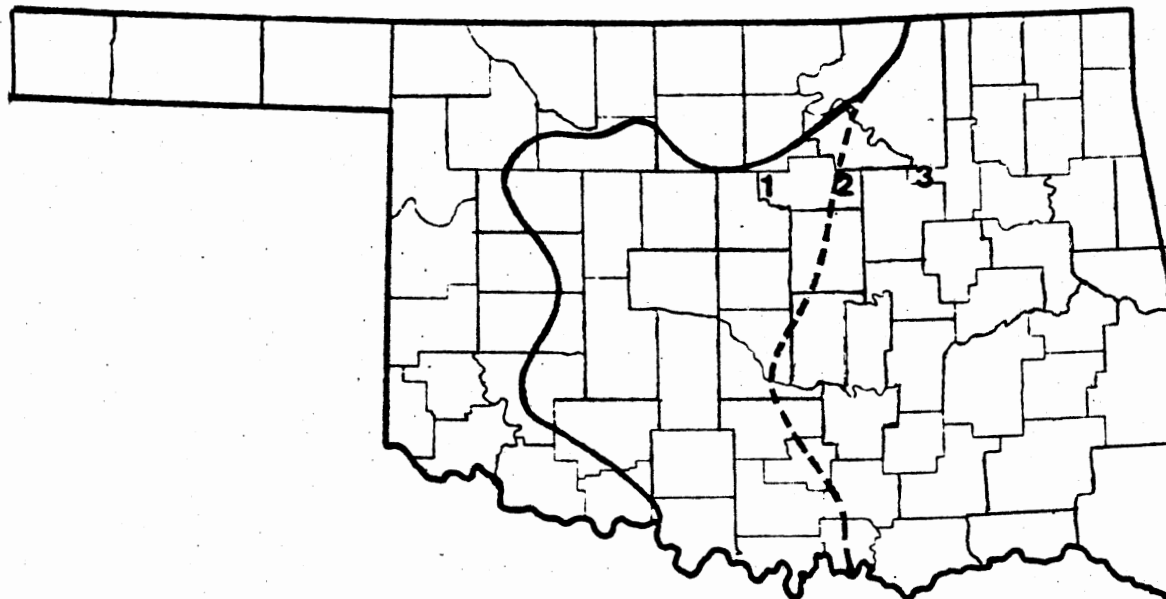


Figure 1. Distribution of *Q. velutina* (- - - -) and *Q. marilandica* (————) and Study Site Locations (1,2,3).

CHAPTER III

SEASONAL COURSE OF WATER POTENTIAL

Methods of Study

On 7 May 1977 measurements of water potential using a Scholander pressure bomb were made hourly from dawn until mid-afternoon. These were used to ascertain when periods of maximum and minimum water potential occurred. Five individuals of both Q. velutina and Q. marilandica were used, however there were no significant differences between the two at this early date. Thus each point in Figure 2 is the average of ten measurements.

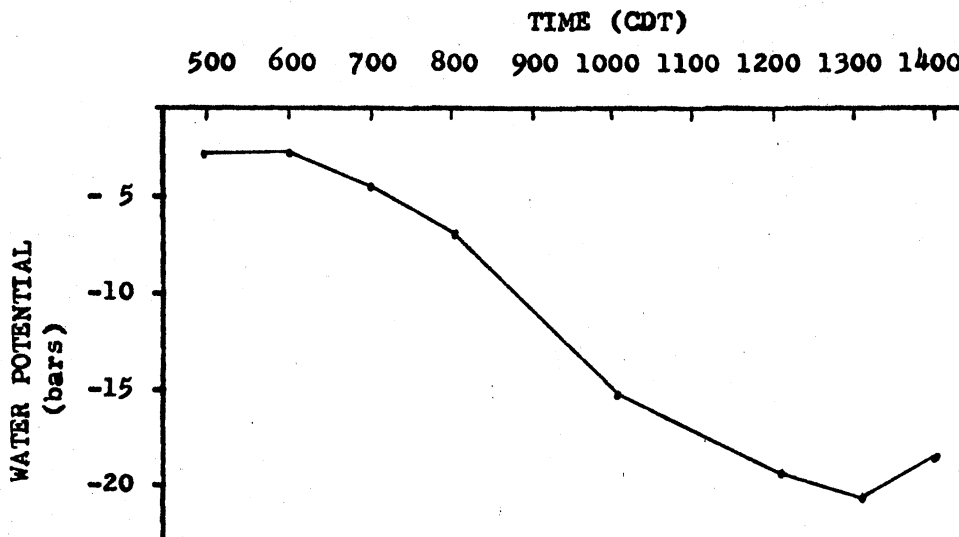


Figure 2. Diurnal Curve Showing Times of Minimum and Maximum Water Potential.

From these data it was apparent that maximum water potential occurred at 0530 hr and was at its minimum at 1300 hr. Therefore for the remainder of the season morning readings were taken between 0530 hr and 0600 hr, and afternoon readings from 1300 hr to 1330 hr.

During the months of May, June, September, and October measurements were obtained every two weeks, and in July and August this was done weekly. Measurements were taken on three consecutive days of sampling weeks with the sites sampled in a random order to avoid sampling bias due to climatic conditions. At Site 1 six trees of Q. marilandica were selected for study. Five individuals of both Q. velutina and Q. marilandica were chosen at Site 2 and at Site 3. Individuals studied were mature and approximately the same size.

Twigs of about 15 cm in length with at least two leaves were selected from each tree. These were cut off fully exposed branches on the south side at a height of 1.5 m. Twigs were immediately placed in the pressure bomb with no more than 60 sec elapsing between cutting and initiation of pressure. A uniform 1 cm of twig was left protruding from the pressure chamber top to eliminate a possible source of variation (Waring and Cleary 1967). Trees were sampled in random order, again to avoid bias due to environmental variation.

Once each month the water potential of seedlings and saplings of both species was also determined. The measurements were made only in the afternoon and involved three individuals of both Q. velutina and Q. marilandica at sites 2 and 3, and three of Q. marilandica at Site 1. Seedlings were considered to be less than 1.0 cm in diameter and less than 0.5 m in height. Saplings ranged from 1.0 to 5.0 cm in diameter and between 0.5 and 2.0 m in height. In most cases, the entire

seedling constituted a sample while saplings were sampled in a manner similar to that described for mature trees.

Results

The seasonal course of water potential for Q. marilandica at Site 1 is shown in Figure 3. Morning values in May (weeks 1-3) averaged -3.0 b and by October (week 24) they had decreased to -21.0 b. Afternoon readings ranged from -15.0 b to -33.0 b. The increases in water potentials at week 10 and week 16 correspond with rain events.

Seasonal water potential data from Site 2 for both Q. velutina and Q. marilandica are presented in Figure 4. Predawn water potentials ranged from approximately -3.0 b early in May (week 1) to less than -10.0 b at times in August and September (weeks 14-20). Afternoon water potentials early in the season averaged -13.0 b, while late in the season they were approximately -30.0 b.

Figure 5 illustrates the seasonal data from Site 3, the easternmost site studied. This site, anomalously, was the driest of all, especially through the month of August (weeks 14-17). This was the only time during the season at any site that statistically significant differences occurred between the two species (predawn water potential, weeks 14, 15, 16; $p < 0.05$). Morning values averaged approximately -2.0 b early in the season and by week 16 they had decreased to an average of -15.0 b. Afternoon averages varied from -22.0 b to -30.0 b.

Average monthly water potentials for seedlings are presented in Table I and those for saplings in Table II. At all sites and for both species there was a general trend for decreasing water potentials throughout the season, from -13.0 b to approximately -29.0 b.

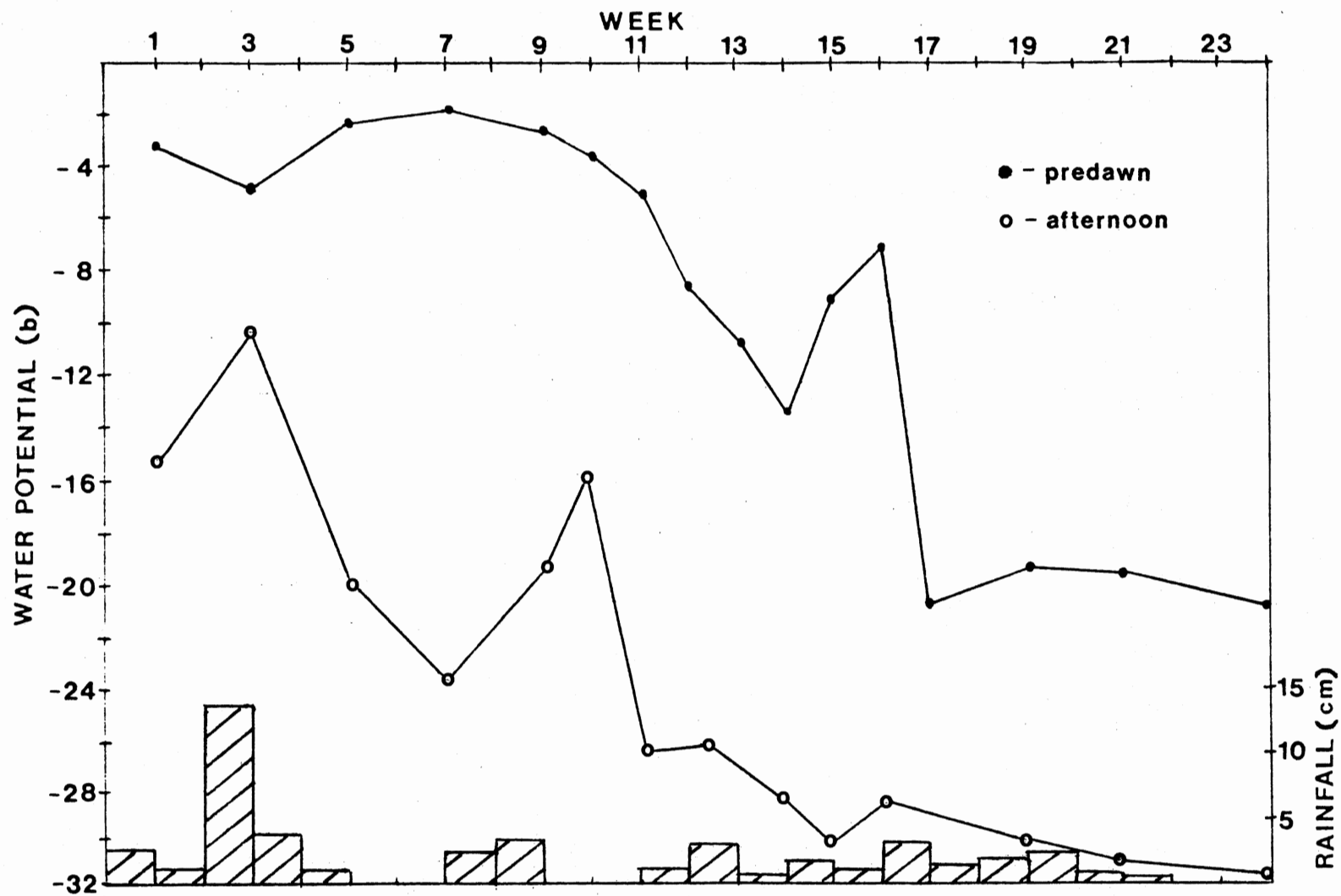


Figure 3. Seasonal Course of Predawn and Afternoon Water Potential of *Q. marilandica* in Relation to Weekly Precipitation at Site 1.

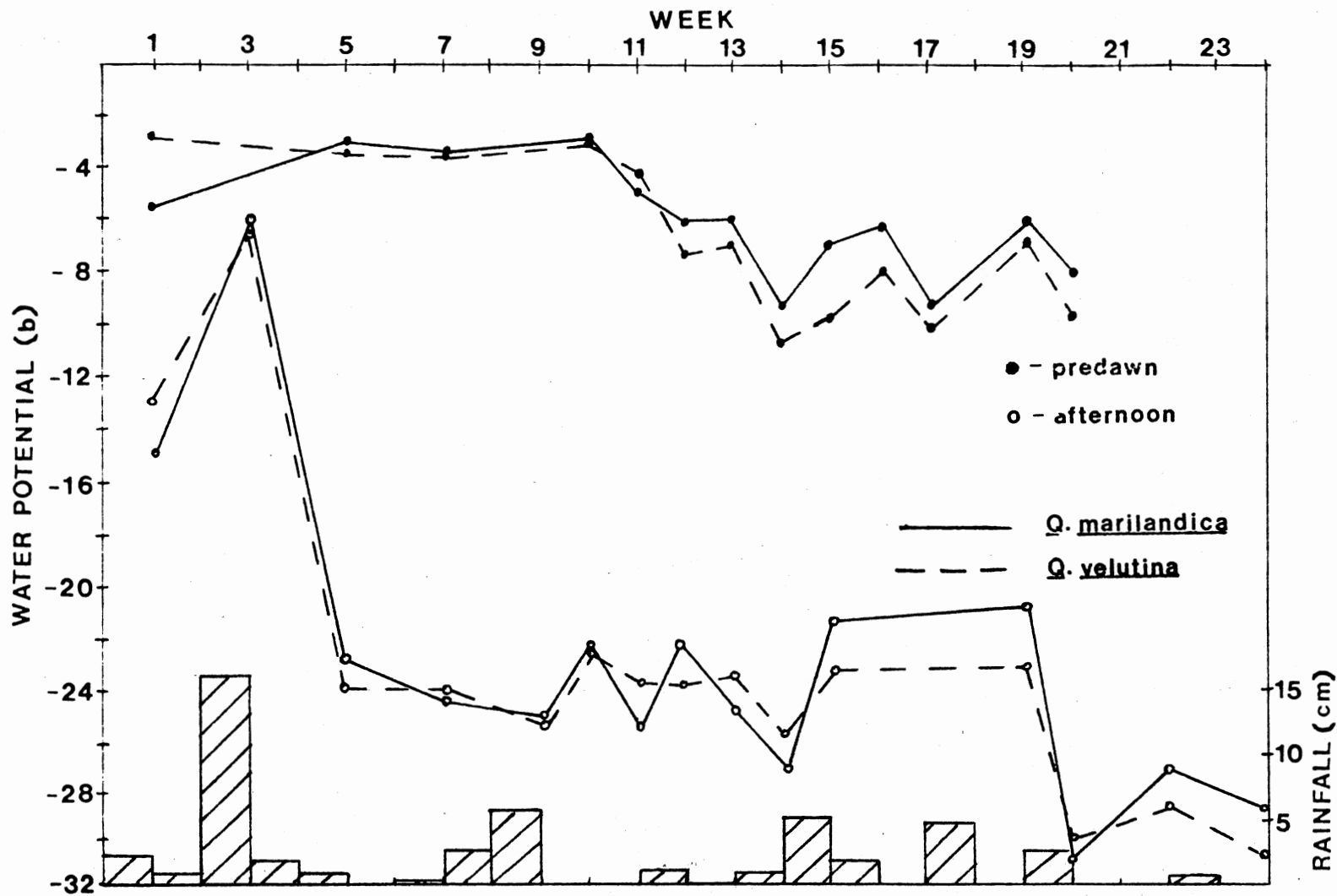


Figure 4. Seasonal Course of Predawn and Afternoon Water Potential of *Q. velutina* and *Q. marilandica* in Relation to Weekly Precipitation at Site 2.

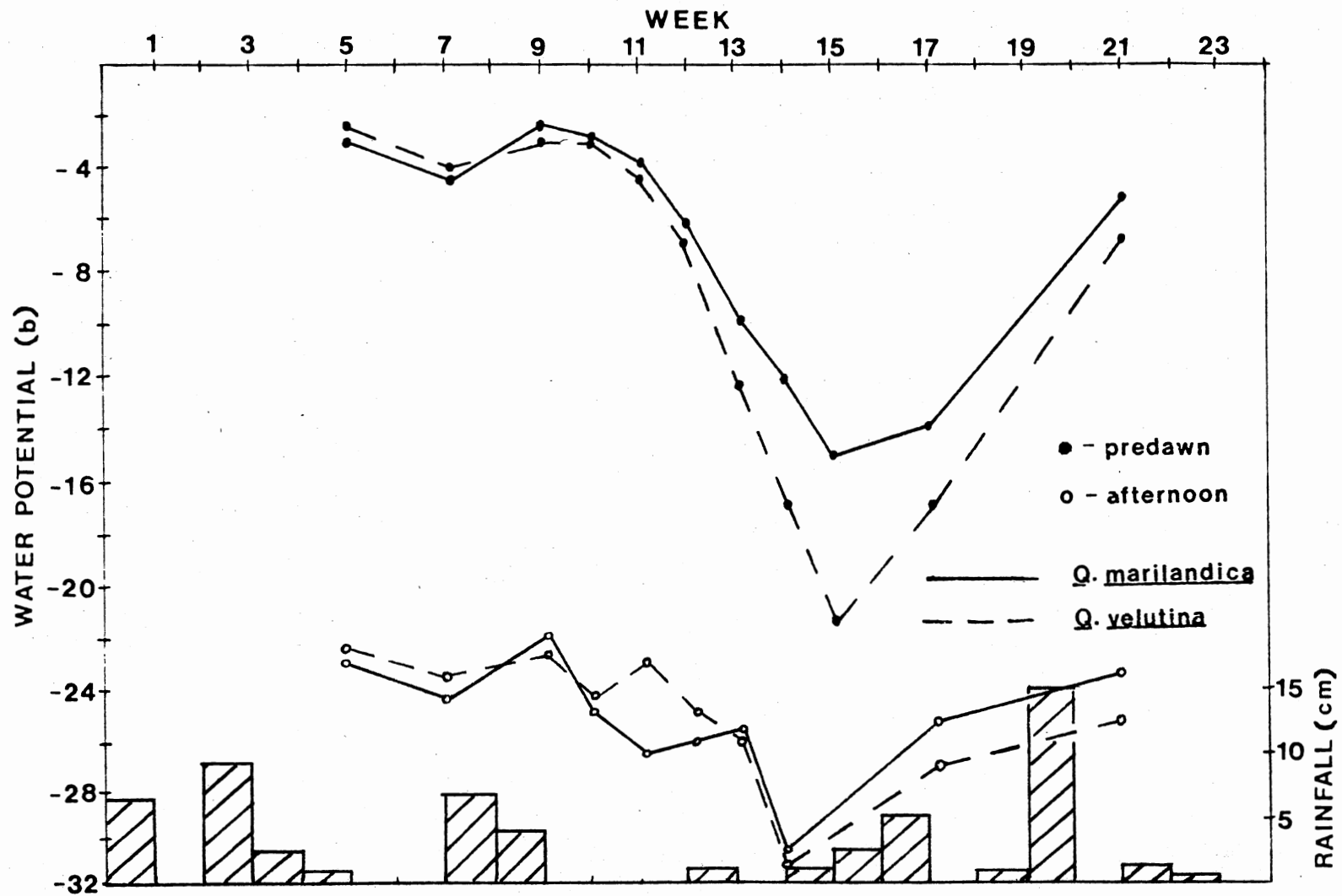


Figure 5. Seasonal Course of Predawn and Afternoon Water Potential of *Q. velutina* and *Q. marilandica* in Relation to Weekly Precipitation at Site 3.

TABLE I

AVERAGE MONTHLY SEEDLING WATER POTENTIALS (b)
AT ALL SITES

Month	Site	<u>Q. velutina</u>	<u>Q. marilandica</u>
June	1	-----	-16.2
	2	-14.2	-13.8
	3	-12.2	-10.8
July	1	-----	-18.2
	2	-20.8	-21.0
	3	-19.3	-18.3
August	1	-----	-28.2
	2	-25.7	-26.3
	3	-25.5	-24.5
September	1	-----	-27.7
	2	-31.2	-28.2
	3	-29.7	-28.8

TABLE II

AVERAGE MONTHLY SAPLING WATER POTENTIALS (b)
AT ALL SITES

Month	Site	<u>Q. velutina</u>	<u>Q. marilandica</u>
June	1	-----	-16.8
	2	-15.5	-13.8
	3	-13.0	-10.3
July	1	-----	-19.8
	2	-24.5	-24.3
	3	-23.8	-26.3
August	1	-----	-29.3
	2	-23.0	-25.2
	3	-25.7	-23.0
September	1	-----	-27.8
	2	-29.5	-28.3
	3	-28.8	-27.5

Discussion

A consistent pattern in the seasonal course of water potential was evident at all sites. Values early in the season when water was abundant were relatively high, but as the season progressed, water became more limiting and water potentials decreased dramatically. At Site 1 a rapid drop in both predawn and afternoon water potentials occurred in July. After this decrease, water potentials leveled off, but at much lower values than earlier in the season. The decrease in Q. velutina and Q. marilandica water potentials at Site 2 was not of the same magnitude as occurred at Site 1. Site 3, on the other hand, exhibited an extremely rapid decrease in predawn water potentials of both species during August. The lowest afternoon water potentials also occurred at this time. Much of the variation in the water potentials from week to week at all sites can be attributed to precipitation.

Predawn water potentials have been used as a measure of how well an individual can recover during the night with low evaporative demands and closed stomata. As seen in the predawn water potentials at all sites, the degree of recovery decreased significantly throughout the season. An increase in predawn water potentials of both species occurred during September at Site 3 in response to precipitation. This increase in soil moisture allowed more recovery during the night.

Early in the season until week 11 at Site 2 there was very little difference between the water potentials of the two species. However, beginning in week 12, Q. marilandica consistently had higher water potentials than did Q. velutina. This was true for both predawn and afternoon measurements. A similar trend also occurred at Site 3 with

respect to species differences in water potentials. Again, early in the season the difference was not great. By week 13, Q. velutina began to have consistently lower water potentials than Q. marilandica both in the morning and afternoon. The dramatic difference in predawn water potentials indicated that Q. velutina was not able to recover as well as Q. marilandica during the night.

In comparing the seedlings of the two species at sites 2 and 3, there is no consistent tendency for Q. velutina seedlings to exhibit lower water potentials as was expected. The same can be said for saplings. The reason for this lies in the observation that the seedlings and a majority of the saplings were not as exposed as were the mature trees. Seedlings and saplings were generally shaded by the larger trees surrounding them and were not subjected to as great a heating and drying by the sun and wind. There is a slight tendency for saplings to have lower water potentials than seedlings, perhaps due to them being somewhat less shaded and protected. This was not as hypothesized, since Griffin (1973) reported that seedlings developed much lower water potentials than did trees or saplings due to differences in rooting effectiveness. It is expected that in times of severe drought stress both seedlings and saplings would exhibit quite low water potentials due to their smaller and less extensive root systems.

CHAPTER IV

SEASONAL COURSE OF TRANSPIRATION

Methods of Study

Beginning in July and continuing into September, measurements of the transpiration rate of both species at each site were also obtained during the afternoon. Potometers were used to measure the amount of water transpired from an excised twig over a period of time. Twigs with at least two leaves were selected from each tree and were recut under water while the leaves were kept dry. With the stem remaining under water each was placed in a potometer and all air bubbles were removed from the system. Once the twig was secured in the potometer it was allowed to remain in the sun for 30 minutes. (Preliminary experiments showed less variation occurred when measurements were conducted in the sun as compared to the shade.) After this period the amount of water transpired was recorded and the leaves were removed and taken back to the laboratory to be dried in order to calculate the amount of water transpired per gram dry weight.

Later in the season a diffusion porometer as described by Kanemasu et al. (1969) became available for use. This device has the advantage of measuring attached, intact leaves and requires less time for measurements. This eliminates much of the possible environmental variation effects between measurements. The porometer was used at

Site 2 before excision and again after the 30 minute period in the potometer in an attempt to ascertain what effects excision might have on the transpiration rate.

Results

Figure 6 illustrates the transpiration rates obtained for the species present at each site. At Site 1 there was a consistent decrease in the transpiration rate of Q. marilandica as the season progressed. The most rapid drop occurred in the first three weeks of July (weeks 9-11). After this the transpiration rate remained consistently low at approximately 0.06 ml/g dry weight/hr. At Site 2 this same general pattern was followed. The transpiration rate of both species decreased by 50% from 5 July to 9 July. The seasonal trend for decreasing transpiration rates is not as consistent at Site 3 and the increase in transpiration during week 17 corresponds with a 2.5 cm rain that fell two days earlier.

Figure 7 illustrates both afternoon water potentials and transpiration rates for Q. marilandica at Site 1 for weeks 9 through 17. During periods of stress that are evidenced by low water potentials, the transpiration rate was also low. Table III summarizes transpiration rates in relation to water potential for both species at Site 2 and at Site 3. In many cases, when the water potentials of the two species were similar, so were their transpiration rates as at Site 2. At other times, only a slight difference in water potential of less than 1 b was accompanied by an approximate four-fold difference in the transpiration rate as seen during week 13 at Site 3.

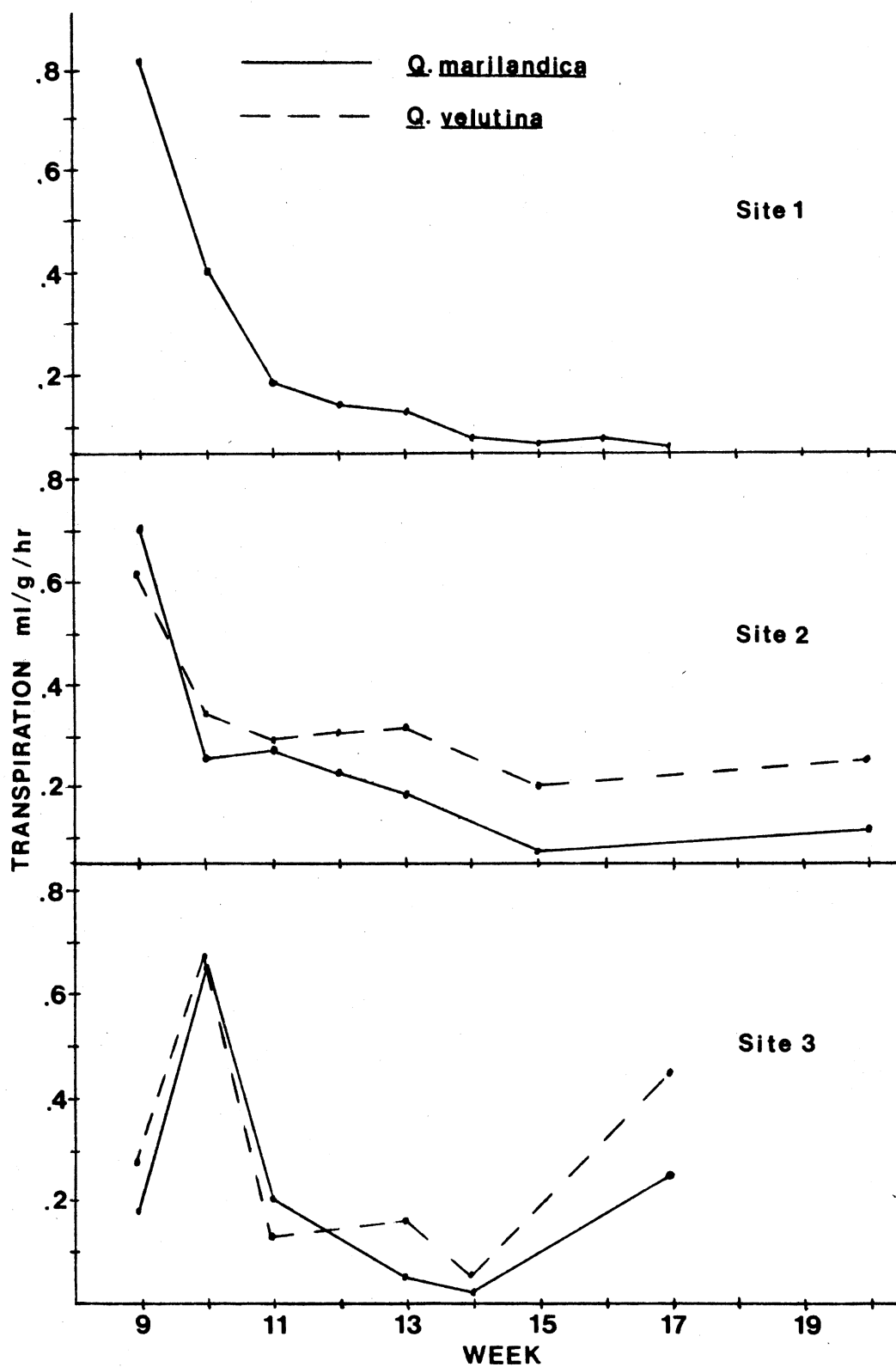


Figure 6. Seasonal Course of Transpiration Rate of *Q. velutina* and *Q. marilandica* at All Sites.

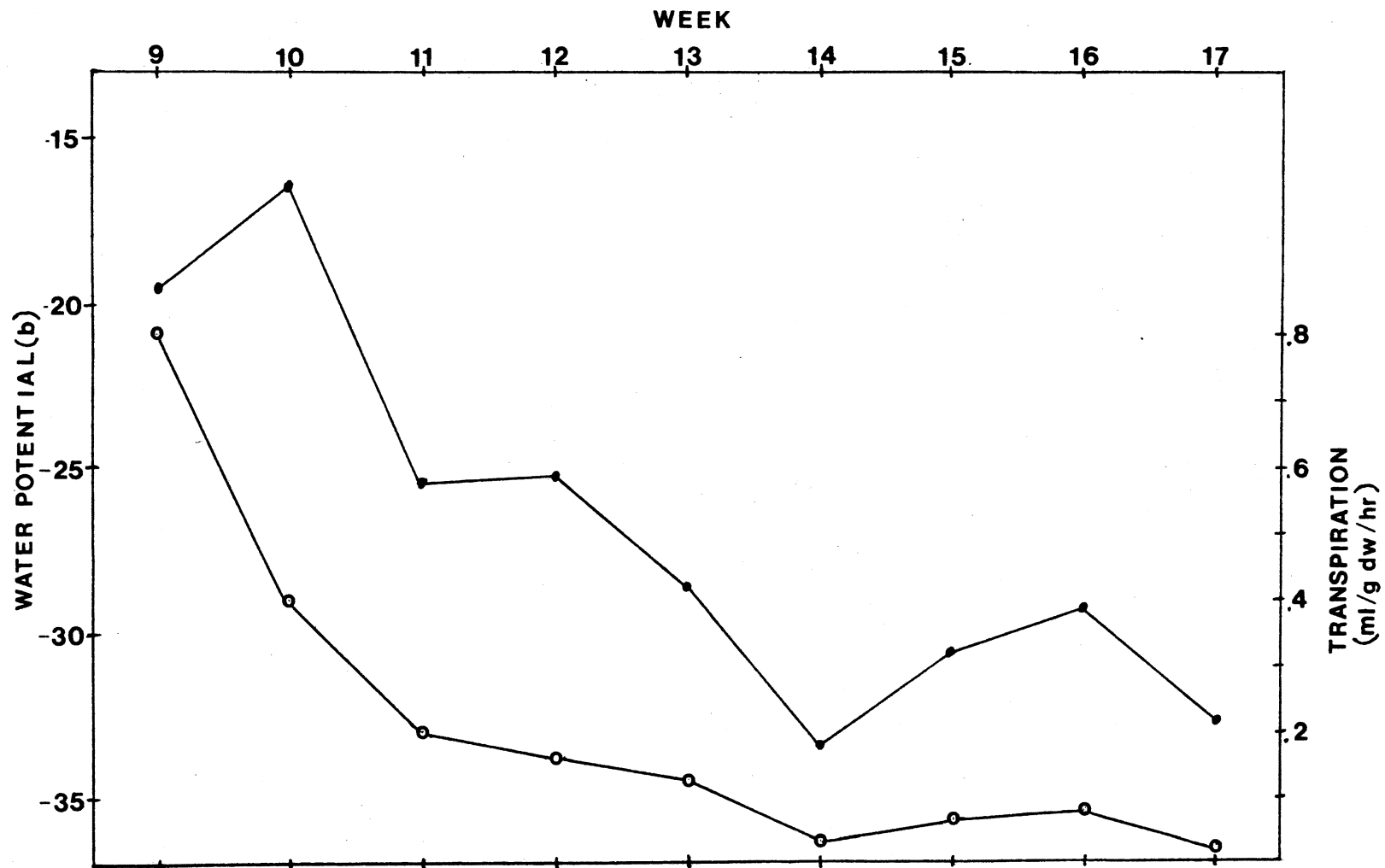


Figure 7. Water Potential (•) and Transpiration Rate (o) of Q. marilandica at Site 1 Over a Period of Nine Weeks

TABLE III

AVERAGE WATER POTENTIALS (ψ_w ; b) AND TRANSPIRATION
 RATES (TR; ml/g dw/hr) FOR BOTH SPECIES
 AT SITE 2 AND SITE 3

WEEK	SITE 2				SITE 3			
	<u>Q. velutina</u>		<u>Q. marilandica</u>		<u>Q. velutina</u>		<u>Q. marilandica</u>	
	TR	ψ_w	TR	ψ_w	TR	ψ_w	TR	ψ_w
9	0.62	-25.3	0.72	-25.0	0.27	-23.0	0.19	-22.0
10	0.33	-22.4	0.25	-22.3	0.67	-24.7	0.64	-24.9
11	0.28	-23.7	0.26	-25.6	0.12	-23.0	0.20	-26.5
12	0.30	-23.8	0.23	-22.3				
13	0.31	-23.4	0.18	-25.0	0.16	-26.1	0.04	-25.5
14					0.03	-31.7	0.01	-31.3
15	0.21	-23.0	0.04	-21.6				
17					0.45	-27.2	0.24	-25.4
20	0.24	-30.5	0.12	-31.7				

Discussion

At Site 2 both Q. velutina and Q. marilandica exhibited similar transpiration rates at the first of July, but as the season progressed the transpiration rate of Q. marilandica dropped much lower than that of Q. velutina. In all cases when low water potentials occurred, Q. marilandica showed more stomatal control and thus lower transpiration rates. Due to the restricted sample size and large amount of variation none of these differences are statistically significant, however the trend for Q. marilandica to transpire at a lower rate than Q. velutina becomes more apparent toward the end of the season. The difference between the transpiration rates of the two species was much smaller at Site 3. With the exception of one week, Q. velutina transpired at consistently greater rates than did Q. marilandica, but the difference was not as great as that shown at Site 2.

The diffusive resistance of both Q. velutina and Q. marilandica exhibited an increase after the 30 minutes in the potometer probably due to excision effects. However, the increase shown by Q. velutina (1280%) was more than twice that of Q. marilandica (600%). This must be taken into account when interpreting potometer data, for it appears that the transpiration rates of both species may be underestimated, especially that of Q. velutina. If this is the case, the difference in the transpiration rates of the two species later in the season would be even greater.

The correlation between water potential and transpiration rate of Q. marilandica at Site 1 indicates efficient stomatal control to conserve water and prevent extremely low water potentials from

developing. This relationship was not as consistent at Site 2 and Site 3. However the high transpiration rates of Q. velutina were generally associated with lower water potentials.

CHAPTER V

COMPARISON OF STUDY SITES

Predawn and Afternoon Water Potentials

Table IV summarizes the monthly average plant water potentials in relation to total monthly precipitation. Site 3 was the driest, especially in May and July when it received 17% and 34% less precipitation than sites 1 and 2. July figures show that the water potentials correspond well with the amount of precipitation received at each site. Site 1 received the most rain and also exhibited the highest average water potential. Site 3 on the other hand, received the least precipitation during July and had the lowest average afternoon water potentials. This was true for both Q. marilandica and Q. velutina. Again, in August and September the lowest average afternoon water potentials for each species corresponded to the site with the least amount of rainfall, and in October the site that received the most precipitation exhibited the highest water potential. The apparent discrepancy in June data can be explained by the distribution of the rainfall. Even though only 2.7 cm of precipitation occurred at Site 1, it was well distributed over a 5 day period prior to the measurements taken at the end of the month.

TABLE IV
 AVERAGE MONTHLY AFTERNOON WATER POTENTIALS (b) AND
 TOTAL PRECIPITATION (cm)

		MAY	JUNE	JULY	AUG	SEPT	OCT	TOTAL
Site 1	<u>Q. marilandica</u>	-13.0	-22.0	-23.0	-31.4	-33.6	-32.8	
	Rainfall	23.4	2.7	8.2	8.8	5.3	2.9	51.3
Site 2	<u>Q. marilandica</u>	-14.8	-23.7	-24.0	-24.6	-26.3	-27.4	
	<u>Q. velutina</u>	-12.7	-24.0	-23.7	-24.4	-26.8	-29.2	
	Rainfall	21.8	4.6	5.9	13.3	7.9	5.0	58.5
Site 3	<u>Q. marilandica</u>		-23.8	-25.0	-28.4	-23.4	-28.7	
	<u>Q. velutina</u>		-23.2	-24.3	-29.5	-24.7	-29.4	
	Rainfall	18.8	7.8	4.7	9.5	16.8	1.0	58.6

The same general relationship holds true in the average monthly predawn data as shown in Table V. This is especially evident during August and September. The site receiving the most precipitation had the highest average predawn water potentials and that with the least rainfall exhibited the lowest water potentials.

The trend in water potential with respect to site location is more apparent when early season averages are compared with late season averages. Table VI contains average water potentials from weeks 1 through 12 (early season), average water potentials from weeks 13 through 24 (late season), and the change in these averages for both

species at all three sites. The largest difference between early and late season averages was 12.6 b and occurred at Site 1 with afternoon water potentials of Q. marilandica. Both Q. velutina and Q. marilandica showed an increase in the difference between early and late season averages from Site 3 to Site 2. This trend continued with Q. marilandica from Site 2 to Site 1. This increase in the variation from early to late season water potentials was not as consistent with predawn measurements, but Site 1 still exhibited the greatest difference with respect to Q. marilandica.

TABLE V

AVERAGE MONTHLY PREDAWN WATER POTENTIALS (b) AND
TOTAL PRECIPITATION (cm)

		MAY	JUNE	JULY	AUG	SEPT	OCT	TOTAL
Site 1	<u>Q. marilandica</u>	- 4.1	- 2.2	- 6.3	-12.2	-19.9	-21.0	
	Rainfall	23.4	2.7	8.2	8.8	5.3	2.9	51.3
Site 2	<u>Q. marilandica</u>	- 5.7	- 3.3	- 5.1	- 8.2	- 7.0		
	<u>Q. velutina</u>	- 3.1	- 3.5	- 5.8	- 9.8	- 8.0		
	Rainfall	21.8	4.6	5.9	13.3	7.9	5.0	58.5
Site 3	<u>Q. marilandica</u>		- 3.8	- 5.2	-13.7	- 5.3		
	<u>Q. velutina</u>		- 3.2	- 6.0	-18.8	- 6.6		
	Rainfall	18.8	7.8	4.7	9.5	16.8	1.0	58.6

TABLE VI
 AVERAGE EARLY AND LATE SEASON
 WATER POTENTIALS (b)

TIME	SPECIES	PREDAWN			AFTERNOON		
		Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
Early in Season	<u>Q. marilandica</u>	- 3.2	- 3.9	- 3.3	-17.6	-21.9	-23.6
	<u>Q. velutina</u>		- 3.3	- 3.2		-21.7	-23.5
Late in Season	<u>Q. marilandica</u>	-12.6	- 7.1	- 9.5	-30.2	-24.9	-24.4
	<u>Q. velutina</u>		- 8.3	-12.4		-24.7	-24.8
Change in Average	<u>Q. marilandica</u>	9.4	4.8	6.2	12.6	3.0	0.8
	<u>Q. velutina</u>		5.0	9.2		3.0	1.3

Transpiration

Table VII summarizes the seasonal average transpiration rates of Q. marilandica and Q. velutina at all three sites. There are no significant differences between the sites, but the transpiration rate appears to be well correlated with the amount of precipitation received, as was water potential. Referring back to Figure 6, from week 10 through week 15, transpiration rates were lower at Site 3 than at Site 2 for both species. This time period coincides with the extremely dry period at Site 3 when low water potentials occurred (Figure 5).

TABLE VII
 AVERAGE SEASONAL TRANSPIRATION RATES (ml/g dw/hr)
 OF Q. VELUTINA AND Q. MARILANDICA
 AT ALL SITES

Site	<u>Q. marilandica</u>	<u>Q. velutina</u>
1	0.21	
2	0.26	0.36
3	0.22	0.28

Discussion

It was expected that both species would exhibit a decrease in water potential in relation to the geographic location of the study sites, with the westernmost sites having the lowest water potentials, however, this was not the case.

From one season of data it appears that water potential is directly related to the amount of precipitation an area receives. Thus over several seasons, the lowest average water potentials would be expected at Site 1, and the highest average values at Site 3, corresponding to the long term average annual precipitation. In addition, it appears that average transpiration rates over several seasons would be similarly affected, with the lowest average rates at Site 1 and highest rates at Site 3. Also, not only would Q. velutina tend to have lower water potentials than Q. marilandica, it would exhibit higher transpiration rates.

CHAPTER VI

LABORATORY EXPERIMENTS

Comparative Growth of Seedlings

In October 1977, acorns of Q. velutina and Q. marilandica were collected. These were stratified in moist sand at 4°C for two months. After this time they were planted in a mixture of sand and vermiculite until germination. Of the Q. marilandica acorns planted, 86% germinated while Q. velutina exhibited only 56% germination. Seventy Q. marilandica seedlings and 50 seedlings of Q. velutina were transplanted into plastic pots containing a sandy loam soil.

After two weeks, height, number of leaves and approximate total leaf area of each seedling were determined. This process was repeated four weeks later. The means of these measurements are presented in Table VIII. Both the difference in mean leaf area between species after 2 and 6 weeks and the difference in the average number of leaves were statistically significant ($p < 0.001$). In addition, the difference in mean height after 6 weeks was also significant ($p < 0.01$).

Even though Q. marilandica had a greater average estimated leaf area after both 2 and 6 weeks of growth, Q. velutina exhibited an increase of approximately 230% over a period of 4 weeks. In the same amount of time, Q. marilandica showed an increase of about 100%. Thus it appears that although Q. marilandica averaged over twice the

number of leaves than Q. velutina, those of Q. velutina were increasing in area at a much greater rate.

TABLE VIII

MEAN GROWTH PARAMETERS OF Q. VELUTINA AND Q. MARILANDICA SEEDLINGS AFTER TWO AND SIX WEEKS GROWTH

Parameter Measured	Weeks of Growth	<u>Q. marilandica</u>	<u>Q. velutina</u>
Leaf area	2	23.3 cm ²	14.8 cm ²
	6	65.1 cm ²	48.7 cm ²
Height	2	5.2 cm	4.9 cm
	6	6.7 cm	5.6 cm
# of leaves	2	5.3	2.9
	6	7.6	3.6

Transpiration of Seedlings

Ten seedlings (five of each species) were randomly selected in order to monitor transpiration rates in relation to decreasing soil moisture. All of the pots were securely covered with plastic wrap to prevent evaporation from the soil surface. Each seedling was weighed every 1 or 2 days to determine the amount of water lost. Four of these seedlings served as controls; the water they transpired was replaced every two days. Leaf areas were determined by tracing outlines on

graph paper in order to calculate the amount of water transpired per unit leaf area per day. In addition to transpiration, soil water potential was measured periodically with a thermocouple psychrometer.

Figure 8 illustrates the course of daily transpiration rates over 30 days for the Q. marilandica seedlings. Transpiration rates of the Q. velutina seedlings are presented in Figure 9. Through the tenth day after watering, transpiration rates for both species remained consistently high. The decrease in transpiration rate at this time was due to a decrease in temperature brought about by the initiation of air conditioning in the laboratory. Transpiration rates then remained fairly constant until the 13th day. After this, the transpiration rate of the experimental Q. marilandica seedlings began to decrease rapidly, while the Q. velutina seedlings did not show this decrease until 6 days later. Even though the experimental Q. marilandica and Q. velutina seedlings had similar transpiration rates by day 21 through day 30, the rate of Q. marilandica represented a decrease from an average of 132% of the controls to only 24%. Q. velutina, on the other hand, only dropped from an average of 76% of the controls to 23%, a decrease of less than half the magnitude of the decrease exhibited by Q. marilandica.

The point at which the transpiration rate of the droughted Q. marilandica seedlings began to decrease corresponded to a soil water potential of -9.8 b. The Q. velutina seedlings had an average soil water potential of only -3.0 b even though all seedlings started at approximately the same soil water potential (-3.0 b to -0.9 b). The gradual decrease in transpiration of droughted Q. velutina seedlings after day 19 was accompanied by an average soil water potential

of -7.5 b. By the end of the 30 day period without watering, the soil water potentials ranged from -28.5 b to -61.2 b; average soil water potential of the droughted Q. marilandica seedlings was -40.7 b while that of the Q. velutina seedlings was -33.2 b.

In a comparison of only the control seedlings of both species over the 30 day period, Q. velutina exhibited a higher average transpiration rate (significant at $p < 0.05$) of $84 \mu\text{l}/\text{cm}^2/\text{day}$ as compared to $67 \mu\text{l}/\text{cm}^2/\text{day}$ for Q. marilandica seedlings (Table X in appendix).

Seedling Water Potential and Diffusive Resistance

In addition to the 10 seedlings used in the previously described experiment, five additional seedlings of each species were selected for a comparative study of seedling water potential and diffusive resistance. Since the weighing method for transpiration rate determination only yields average daily measurements, a diffusion porometer was utilized approximately every 2 days to obtain a measure of instantaneous transpiration rate. Seedling water potential was measured psychrometrically each 2 or 3 days during the 30 day period. After this time, the final seedling water potential was obtained using a pressure bomb.

Figure 10 is a plot of seedling water potential in relation to diffusive resistance for both Q. marilandica and Q. velutina. At a water potential of approximately -30.0 b to -33.0 b, the diffusive resistance of both Q. marilandica and Q. velutina began to increase. The diffusive resistance values for Q. velutina showed much more variation, but it is evident that the response was approximately three times greater than that of the Q. marilandica seedlings.

At the end of the 30 day experiment, the average droughted Q. velutina seedling water potential was -51.2 b while that of the Q. marilandica seedlings averaged only -44.3 b. As stated before, the final average soil water potential of Q. velutina was -33.2 b and -40.7 b for the Q. marilandica seedlings.

Discussion

In comparing the early growth of seedlings of Q. marilandica and Q. velutina it is apparent that in a competitive situation during this time Q. marilandica seedlings would have an advantage due to both increased height and greater total leaf area. However, it is probable that after some period of time the differences in leaf area, number of leaves and height would diminish.

It appears that seedlings of Q. velutina are very sensitive to low water potentials, showing virtually complete stomatal closure. This response could be of a detrimental nature if gas exchange ceased. Cline and Campbell (1976) felt that some species may be limited to moist areas if at moderate stress levels they exhibited a sharp increase in diffusive resistance which hindered gas exchange.

In addition, during times of adequate soil moisture, Q. velutina seedlings exhibited higher transpiration rates and by the end of the experiment they had lower water potentials than Q. marilandica seedlings even though their soil water potentials averaged higher. Thus Q. marilandica seedlings were able to maintain higher water potentials even in drier soil.

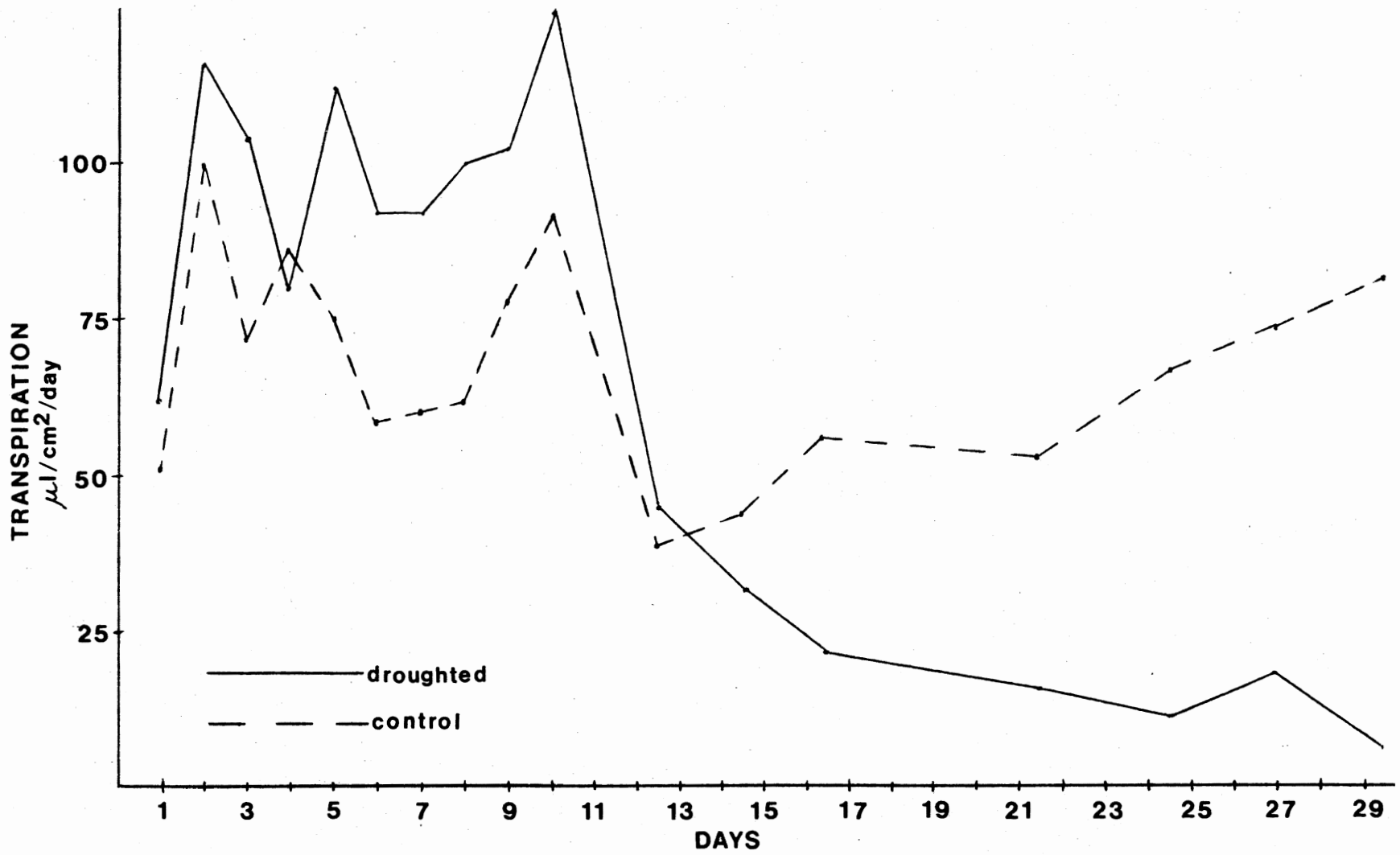


Figure 8. Mean Transpiration Rate of *Q. marilandica* Seedlings Exposed to Increasingly Dry Soil in the Laboratory.

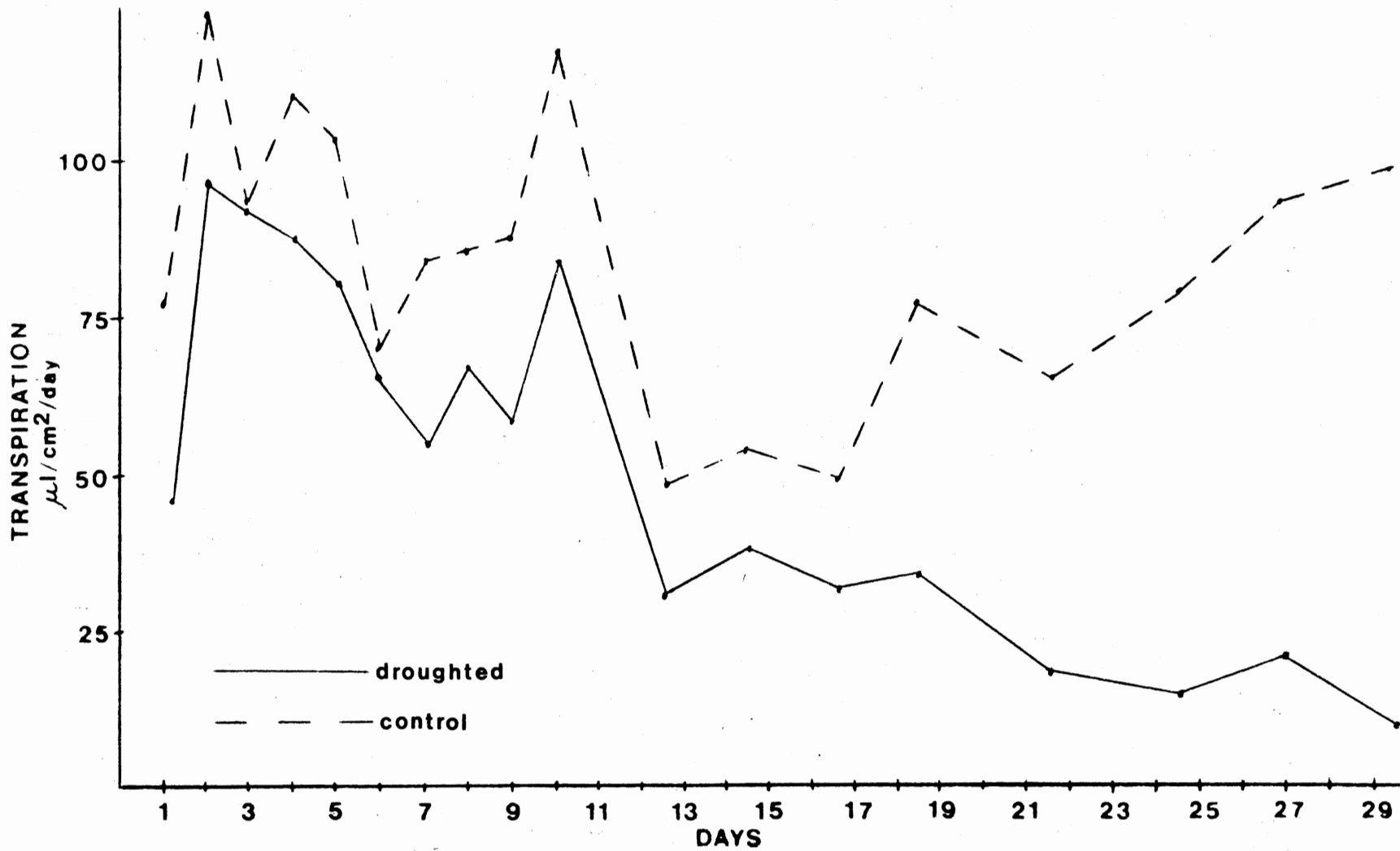


Figure 9. Mean Transpiration Rate of *Q. velutina* Seedlings Exposed to Increasingly Dry Soil in the Laboratory.

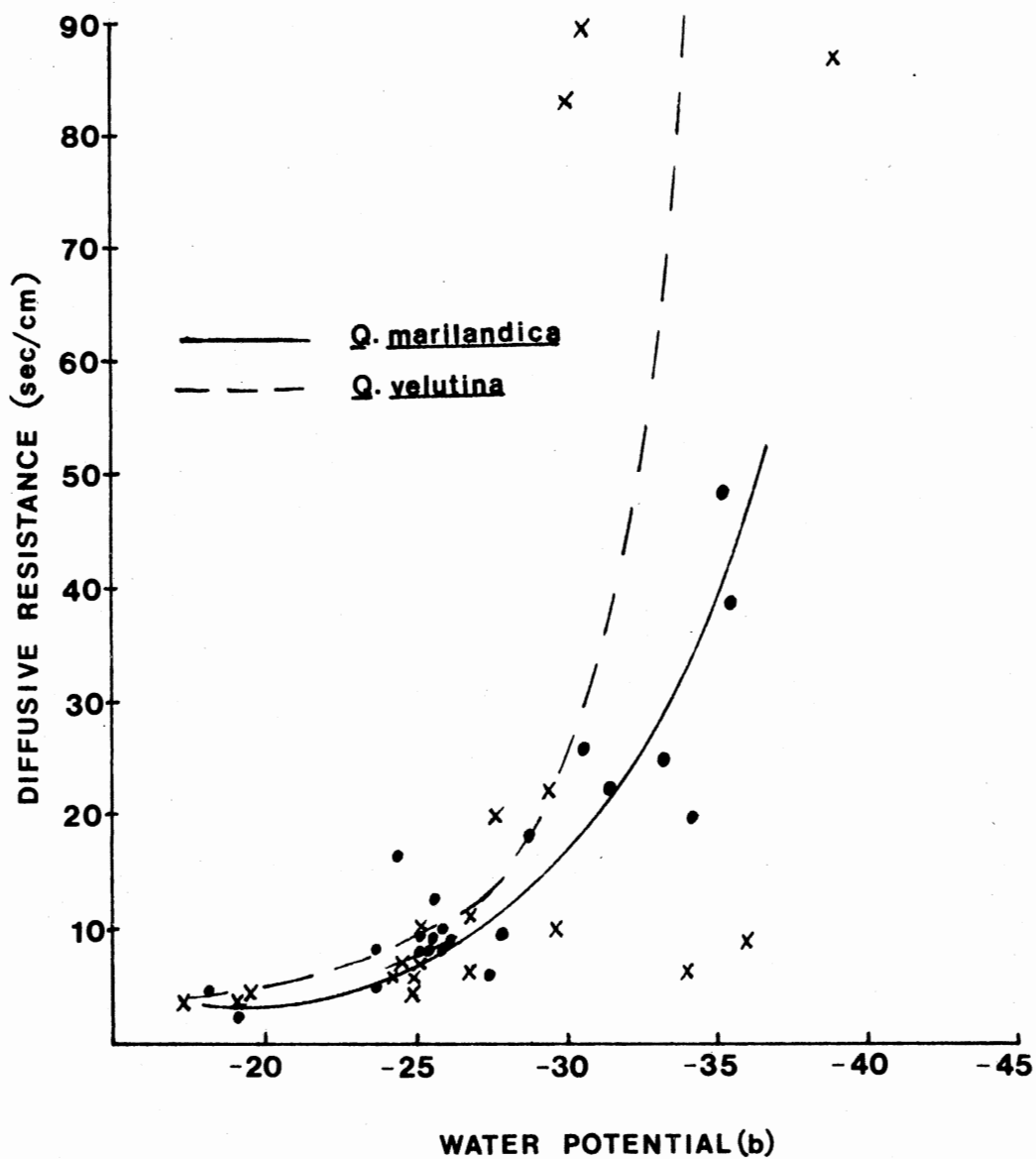


Figure 10. Diffusive Resistance in Relation to Water Potential of *Q. velutina* (x) and *Q. marilandica* (•) Seedlings.

CHAPTER VII

CONCLUSIONS

There was a distinct seasonal trend for decreasing water potential and transpiration as the soil moisture supply diminished. This was true for both Q. velutina and Q. marilandica at all study sites. In most cases, the decrease in predawn water potentials was greater than the corresponding decrease in afternoon water potentials. This indicates that the decrease in soil moisture had an important effect upon the degree of recovery. Afternoon water potentials are primarily dependent upon prevailing atmospheric conditions, however they are also influenced by the level of predawn water potentials.

Q. marilandica and Q. velutina had similar water potentials early in the season at both Site 2 and Site 3 when soil moisture was plentiful. As the season progressed, the predawn and afternoon water potentials of Q. velutina became consistently lower than those of Q. marilandica. This decrease was more exaggerated at Site 3 which experienced a longer period without rainfall, especially with respect to the predawn water potentials. In addition, there was good correlation between total monthly precipitation and average monthly water potential. This also suggests that over a longer period of time the average water potentials would correspond with average precipitation. Thus the lowest water potentials would be found at Site 1 and the highest average water potentials at Site 3. Long periods of dryness

which periodically occur in central and western Oklahoma would act to accentuate the difference in the water potentials of the two species. As was evident at Site 3, as conditions became drier, the difference in water potential between the species increased. It is probable that under these conditions Q. velutina water potentials could become critically low and act to restrict its range.

The higher transpiration rates of Q. velutina as compared to Q. marilandica may be one reason why Q. velutina showed lower water potentials. However, many other factors such as the rate of water uptake also play a role in determining the water potential. As stated earlier, the transpiration rates as measured by the potometer method may be underestimated; the transpiration rate of Q. velutina more than that of Q. marilandica. Thus it is possible for this difference in transpiration rate to be a major factor in the difference in water potentials of the two species.

Of the seedlings grown in the laboratory, Q. marilandica exhibited many seemingly superior drought resistance characteristics. Q. velutina seedlings exhibited a higher average transpiration rate with adequate water, but with moderate stress there was a rapid decrease. This was a response similar to that shown by Q. velutina in the potometers. Although Q. marilandica seedlings also exhibited a decrease in transpiration rate, it was much smaller than that of Q. velutina. This rapid, possibly complete, shutdown of transpiration exhibited by Q. velutina could possibly act to restrict gas exchange, and in turn the rate of photosynthesis. In addition, after the same period of time without watering, Q. marilandica seedlings were able

to maintain a higher water potential at somewhat lower soil water potentials.

In conclusion, it is evident that Q. marilandica is much better adapted for existing in dry habitats than is Q. velutina. The fact that Q. velutina is limited to the eastern third of Oklahoma may be due in part to the decrease in precipitation. However, it is more likely that periodic droughts would be the major factor in preventing any extension of distribution. From laboratory experiments, the seedlings of Q. velutina appear to be especially sensitive to dry conditions as evidenced by lower water potentials and excessive response to moderate stress. This could put them at a competitive disadvantage with other species which can maintain lower water potentials without a complete shutdown of gas exchange.

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APPENDIX

TABLE IX
 AVERAGE MONTHLY TEMPERATURES ($^{\circ}\text{C}$) AND PRECIPITATION (cm)
 NEAR THE STUDY AREAS

MONTH	SITE 1 (Stillwater)		SITE 2 (Cushing)		SITE 3 (Tulsa)	
	Mean Temp	Rainfall	Mean Temp	Rainfall	Mean Temp	Rainfall
January	3.2	2.4	2.3	2.7	2.6	3.6
February	6.1	3.0	4.9	3.4	5.1	4.4
March	9.7	4.5	8.9	5.4	9.1	6.4
April	16.4	7.4	16.1	8.4	16.0	10.6
May	20.6	12.4	20.6	13.8	20.4	13.0
June	25.3	10.5	25.2	12.4	25.2	11.9
July	27.8	9.2	27.9	10.6	27.8	8.9
August	27.6	8.4	27.6	6.9	27.4	7.5
September	23.2	10.2	23.1	10.6	22.9	10.3
October	17.4	7.3	17.2	7.6	17.2	8.2
November	10.0	3.8	9.6	4.1	9.7	4.7
December	4.9	3.0	4.3	3.4	4.3	4.2
Total		82.1		89.3		93.7

TABLE X
 AVERAGE TRANSPIRATION RATES ($\mu\text{l}/\text{cm}^2/\text{day}$) FOR CONTROL
 AND DROUGHTED SEEDLINGS

DAY	CONTROL		DROUGHTED	
	<u>Q. velutina</u>	<u>Q. marilandica</u>	<u>Q. velutina</u>	<u>Q. marilandica</u>
1	77	51	46	51
2	123	100	96	100
3	93	72	92	72
4	110	86	87	86
5	103	75	80	75
6	69	64	65	64
7	84	65	55	65
8	85	66	67	66
9	87	78	59	78
10	117	92	84	92
12	48	39	31	45
13				
14	54	39	38	38
15				
16	49	44	32	32
17				
18	77	61	34	22

TABLE X (Continued)

Day	CONTROL		DROUGHTED	
	<u>Q. velutina</u>	<u>Q. marilandica</u>	<u>Q. velutina</u>	<u>Q. marilandica</u>
19				
21	65	53	18	16
22				
24	79	67	15	12
25				
27	93	74	21	19
29	98	82	10	6
30				

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