COMPARATIVE WATER RELATIONS OF FOUR SPECIES OF

UPLAND DECIDUOUS TREES ALONG A

MOISTURE GRADIENT

By

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PREFACE

I would like to thank Mr. Dan Sisson and Mr. Ray Hodgkins for their enthusiastic assistance in the field. I also wish to thank Dr. Jerry Crockett, Dr. James Ownby, and Dr. Glenn Todd for their valuable suggestions. To Dr. James McPherson, major adviser and friend, I give my deepest appreciation and special thanks for his careful guidance, prudent suggestions, and invaluable assistance throughout this project.

In addition, I would like to express my thanks to my parents, Mr. and Mrs. Carl Alleman, whose support was greatly appreciated.

Finally, for her patience, encouragement, support, understanding, and assistance during the last three years, I wish to express heartfelt thanks and special appreciation to Melodie, my wife.

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INTRODUCTION

It has long been accepted that plant distributions are often
related to moisture availability and the water relations of a given
species, especially in warm, dry regions. Several workers have
examined the relationship of water relations to habitat requirements
(Griffin 1973, Poole and Miller 1975) and geographic distribution
(Cline and Campbell 1976, Hall and McPherson 1980). In general,
these studies showed that water relations parameters such as water
potential, diffusive resistance, and moisture availability can be
correlated to explain or clarify the habitat requirements and geographic
range of a species. Other studies have shown that different species
growing on the same site will exhibit different water potential and
stomatal sensitivity behavior (Hinckley and Ritchie 1973, Havrenke and
Beneke 1978). Thus, a water relations study of several species along
a moisture gradient in a small area should help to explain the
geographic distribution and habitat requirements of the species
involved.

Oklahoma exhibits a strong precipitation gradient from southeast
(> 130 cm/yr) to northwest (< 40 cm/yr). The temperatures across
the state vary considerably with temperatures above $38^{o}C$ not uncommon
in the summer and mean July temperatures ranging from $28^{o}C$ in the
southeast to $26^{o}C$ in the northwest. Oklahoma winters are typically
mild and short with mean January temperatures not ranging below $0^{o}C$

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(Gray and Galloway 1959).

Black hickory (<u>Carya</u> <u>texana</u> Buckl.), post oak (<u>Quercus</u> <u>stellata</u> Wang.), blackjack (Q. <u>marilandica</u> Muenchh.), and chinquapin oak (Q. <u>Muehlenbergii</u> Engelm.) share much the same range throughout much of the Eastern and Central United States and are commonly associated in the upland forests of Oklahoma. The western geographic boundary of each of these species crosses Oklahoma (Little 1971). The range of black hickory extends westward only to Central Oklahoma while the ranges of chinquapin oak, blackjack, and post oak extend progressively farther west (Fig. 1).

Even though these species often occur together, post oak and blackjack appear to be more drought hardy than others (Seidel 1972, Hall and McPherson 1980). Black hickory tends to occur on dry sandy upland sites while blackjack occurs more often on finer textured sandy clay soils and post oak on more coarse-grained sandy soils. Chinquapin oak is typically found on moister, deeper soils (Sargent 1926).

Because the western geographic limits of these species essentially parallel isohyets on a state precipitation map, it is probable that this pattern of geographic distribution is established in large part by limited moisture availability. Comparison of these distributions to a state soils map shows no correlation to major soil differences and it is unlikely that early fires would have determined these present day range limits since the range limits are all different.

The major goal of our study is to make a comparative study of the water relations of <u>Carya</u> <u>texana</u>, <u>Quercus</u> <u>stellata</u>, Q. <u>marilandica</u>, and
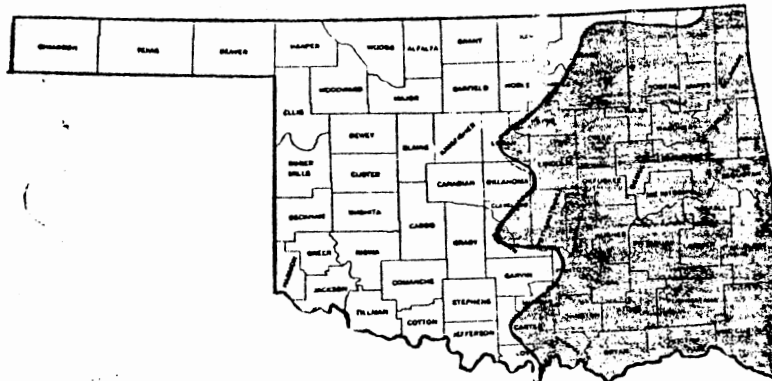
Carya texana
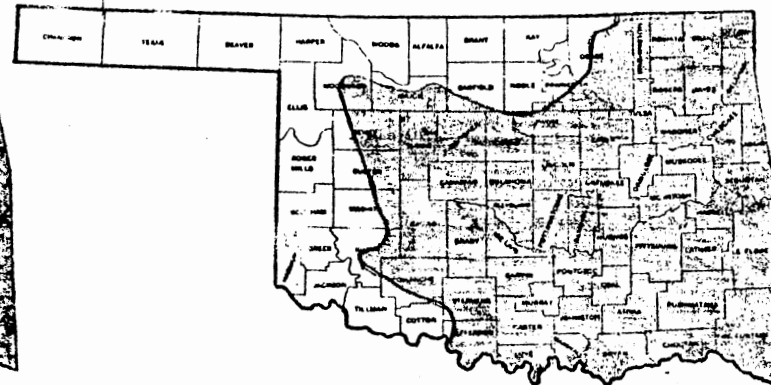
Quercus marilandica
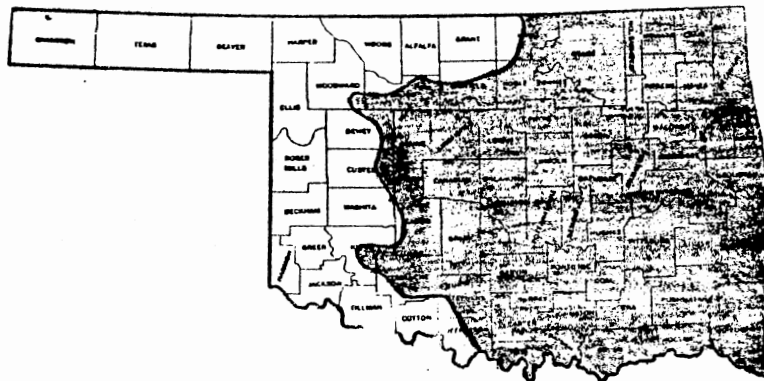
Quercus muehlenbergii

Quercus stellata

Figure 1. Geographic limits of the study species with shaded area representing the geographic range of each species in Oklahoma (Little, 1971).

$\underline{Q}$. $\underline{Muehlenbergii}$ along a moisture gradient at a single locality in an effort to elucidate their habitat requirements and geographic range.

METHODS AND MATERIALS

The study area is located in the cross-timbers region of north-central Oklahoma in Payne County about 35 km south of Stillwater (R3E-T17N-S3). The regional vegetation is predominantly post oak-blackjack forest intermixed with tallgrass prairies. The study area is in the Central Redbed Plains geomorphic province with generally undulating, dissected old stream terrace topography (Johnson et al. 1972). Soils are in the Dougherty-Teller-Yahola series typified by light sandy soils which are generally low in fertility (Gray and Galloway 1959). Average annual precipitation for the area is about 90 cm.

The study area consists of a gentle slope about 250 m long with about 9 m relief and ranges from a rather dry upland at site I to a moist, stream-terrace bottomland with an intermittent stream at site IV. Four study sites were selected along this gradient about 75 m apart with about 3 m relief between sites. All four species post oak, blackjack, chinquapin oak, and black hickory occurred within 20 m of each other at each site.

During the growing seasons of 1980 and 1981, measurements of water relations parameters were taken for the four species at each of the four sites. Measurements began in May after full leaf expansion and continued until very low and erratic water potentials indicated abscission layer formation in the fall.

In 1980 we measured leaf water potential (Ψ_L), relative humidity

(RH), soil moisture, and temperature weekly throughout most of the growing season. Water potential measurements were taken at 0500 h and 1300 h to correspond to maximum and minimum water potentials (Klepper 1968, Haas and Dodd 1972, Griffin 1973, Ehrlinger and Miller 1975). Measurements at all sites were taken on the same day within one hour (0430–0530 h and 1230–1330 h) and in random order to avoid bias due to environmental changes. Twice during the season, Ψ_L at all sites were taken hourly for 24 h to determine actual times of minima and maxima and to compare the daily course of Ψ_L between sites and between species.

In 1981, diffusive resistance using a diffusive resistance porometer (Kanemasu et al. 1969) was measured in addition to the other parameters. During this second season, bi-weekly measurements of all parameters were taken hourly from 0400 through 1500 h.

Leaf water potential was measured using a pressure chamber (Scholander et al. 1965) pressurized with dry nitrogen gas. Twig samples were about 10 cm long with at least two leaves and were taken from fully exposed branches. Twigs were placed in the chamber within one minute of cutting and the chamber pressure increased at about 0.5 bars per second (Waring and Cleary 1967, Griffin 1973, Ritchie and Hinckley 1975, Hall and McPherson 1980).

Some researchers doubt the accuracy of the pressure chamber in measuring Ψ_L (Boyer 1967, Kaufman 1968, Ritchie and Hinckley 1971). Earlier work in our lab showed that pressure chamber readings were accurate to $\pm$ 1 bar when compared to thermocouple psychrometer readings. However, we are concerned with relative Ψ_L of these species and no attempt was made to compare these values to values obtained with a thermocouple psychrometer. To establish the consistency or relative

accuracy of our pressure chamber technique, readings of 10 twigs during a twenty minute period were taken for each study species. The variation within samples was less than $\pm$ 1 bar.

Percent soil moisture at each site was determined gravimetrically from a depth of 1 m and conversions to soil water potential (Ψ_S) were made using a calibration curve based on pressure membrane extraction values. Relative humidity was taken at each site using a sling psychrometer and temperature was measured at a single location for each sampling hour.

RESULTS

In 1980, Ψ_S was significantly different between each site
(p < .05) with mean Ψ_S being -11.1 b, -9.2 b, -7.1 b, and -4.9 b at
sites I-IV, respectively (Appendix). During 1981, mean Ψ_S values
were -8.5 b, -6.8 b, -4.9 b, and -3.8 b at sites I-IV, respectively.
Only site I and II were not significantly different.

Relative humidity corresponded with the soil moisture gradient
with mean values of 43%, 48%, 53%, and 58% at sites I-IV, respectively
in 1980. In 1981, mean RH was 56%, 58%, 62%, and 66% at sites I-IV,
respectively (Appendix). All sites were significantly different
during each season (p $\leq$ .0473). Mean predawn Ψ_L values in 1980 also
increased significantly between sites with site IV being the highest.

At site I there was very little difference between species early
in the season but after 18 July chinquapin oak and black hickory showed
a decline in predawn Ψ_L while post oak and blackjack had an increase
(Fig. 2). At site II, black hickory had the highest mean Ψ_L and
chinquapin oak, again with the lowest mean was lower than at site I.
The same general pattern occurred here with post oak and blackjack
recovering to higher values late in the season. At site III the same
general trend occurred at higher Ψ_L values.

Site IV, the most mesic, showed greatly increased predawn
for all species except blackjack which had a lower mean than at site I.
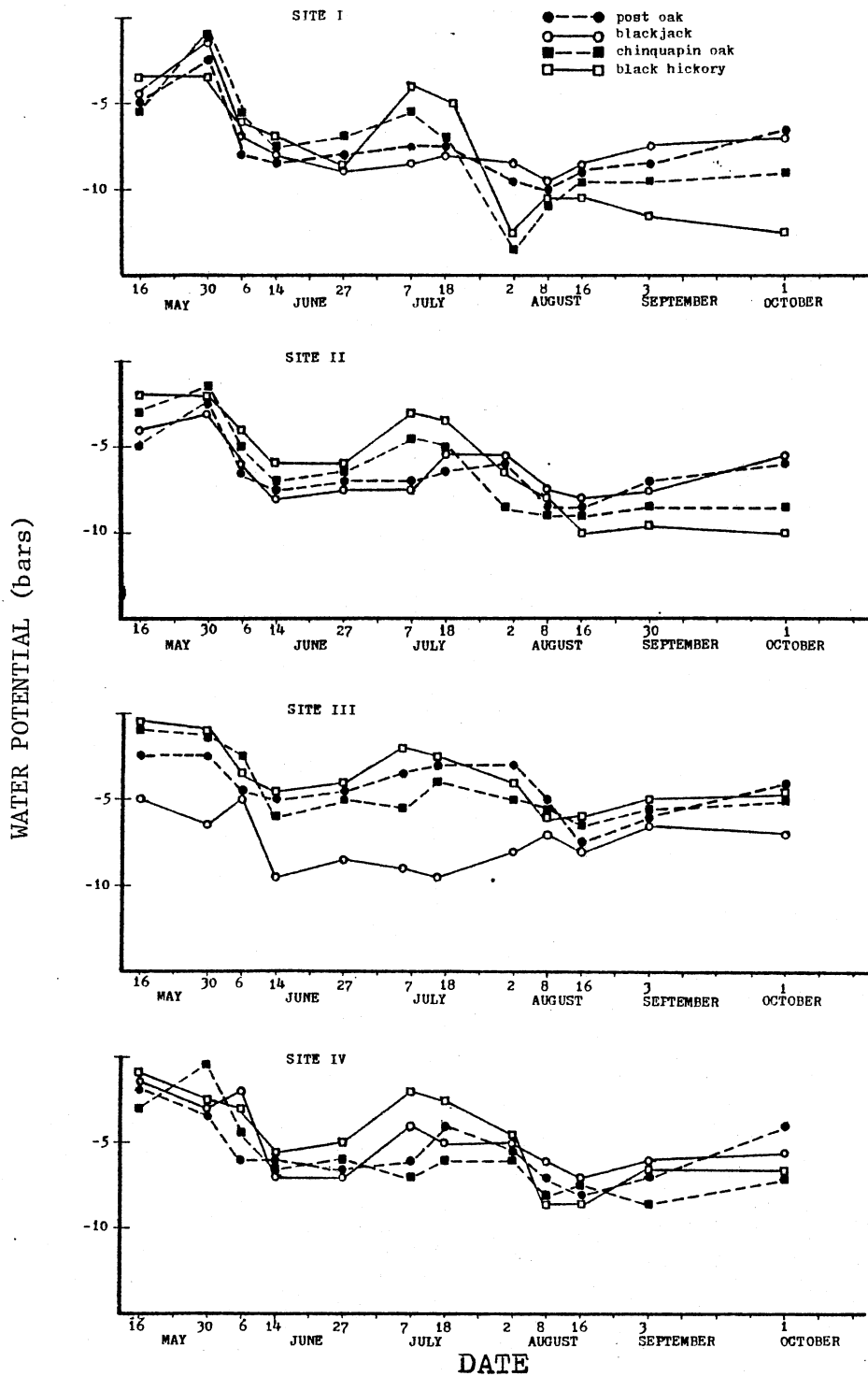Black hickory and chinquapin oak had a higher mean than the other

Figure 2.   Seasonal course of predawn (0500h) leaf
water potentials, 1980.

species even though their Ψ_L values declined late in the season.

Similar patterns occurred in 1981 (Fig. 3). At sites I, II, and III, black hickory and chinquapin oak showed a decrease in predawn Ψ_L late in the season while post oak and blackjack showed an increase. At site IV, black hickory had a higher mean than the other species and blackjack was noticeably lower than the others and actually had a lower mean than at site I.

In 1980, the general trend at all sites was a substantial decline in afternoon Ψ_L values through the early part of the season (Fig. 4) and then fluctuation about relatively low values through the rest of the season. At site I, post oak had the lowest seasonal mean of -28.4 b and black hickory had the highest mean at -23.8 b. Blackjack at site I reached -38 b on 25 July, the lowest value recorded in 1980.

At sites II and III post oak again had the lowest mean afternoon Ψ_L values with -26.4 b at site II and -24.1 b at site III. Black hickory showed the highest mean values with -23.0 b at site II and -21.2 b at site III. At site IV however, blackjack had the lowest mean with -23.4 b and post oak the highest with -17.4 b.

Late in the season, post oak and blackjack showed an increase in Ψ_L at all sites and black hickory and chinquapin oak showed a decrease for the same period except for chinquapin oak at site IV which exhibits a slight increase. There was no corresponding precipitation to explain these changes.

In 1981 similar trends occurred with post oak again having the lowest mean Ψ_L at site I, II, and III with values of -25.8, -24.1, and -22.3 b, respectively (Fig. 5). At site IV blackjack again had the lowest mean with -20.6 b while black hickory had the highest with
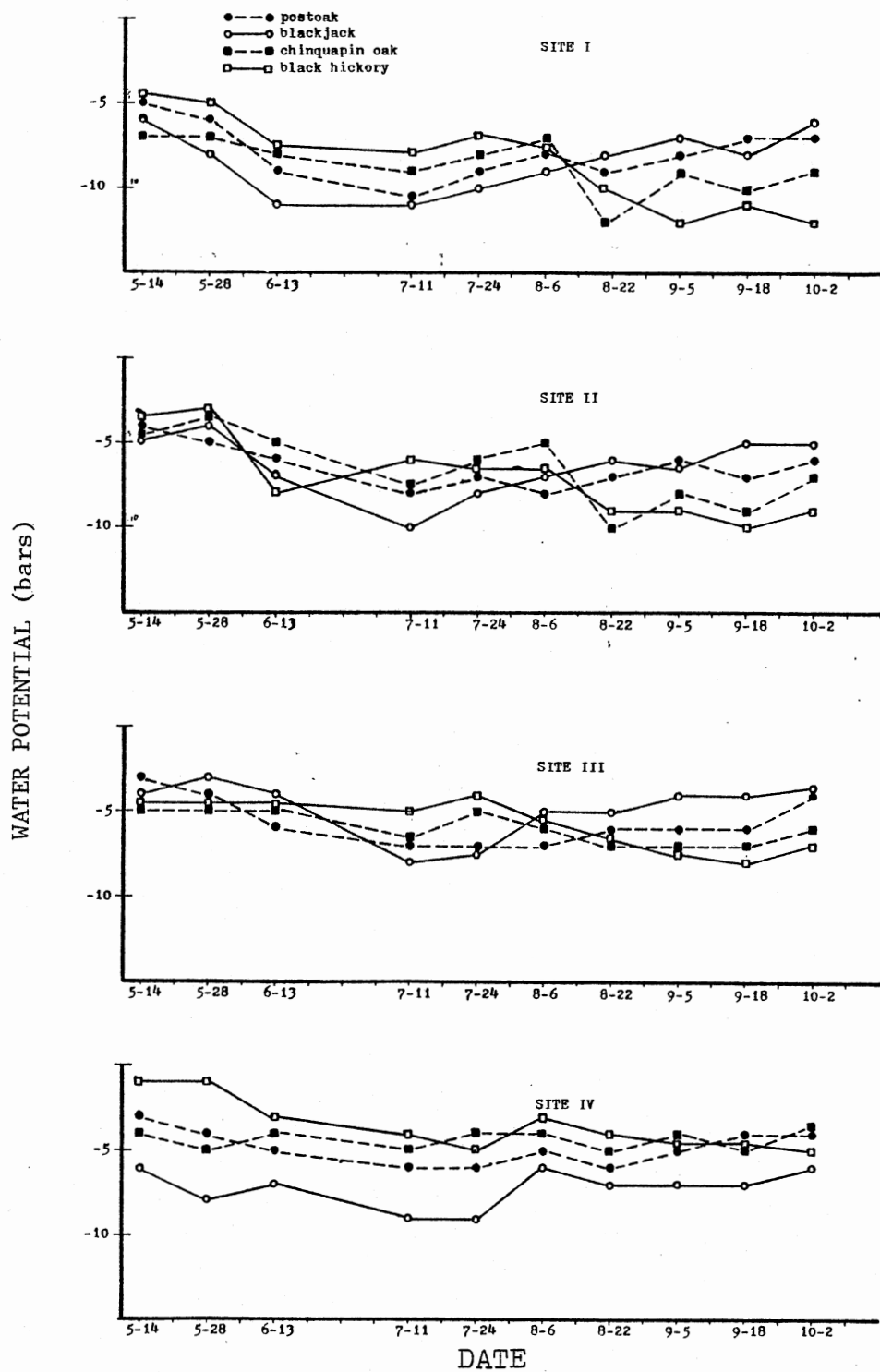
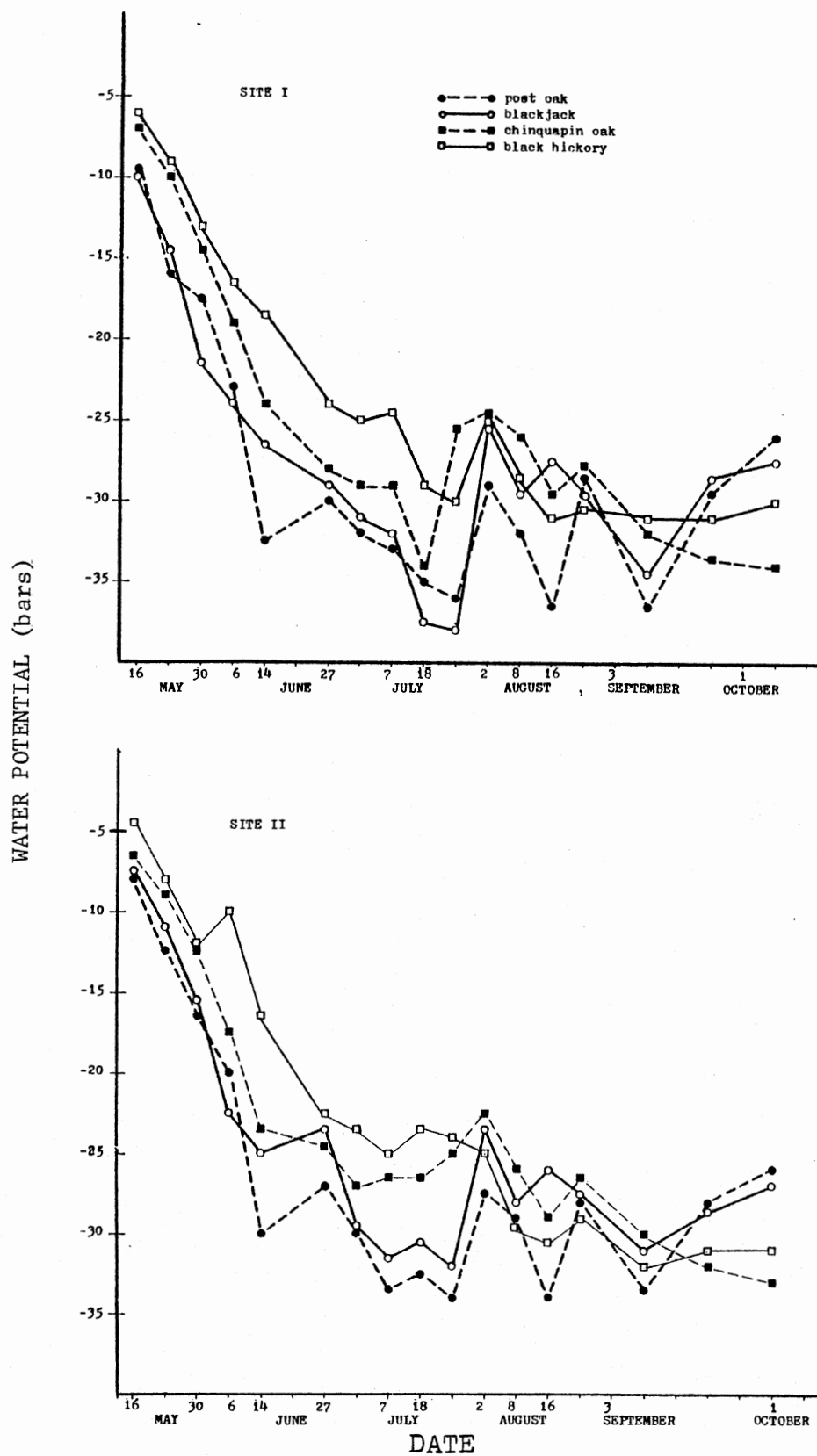Figure 3. Seasonal course of predawn (0500h) leaf water
potentials, 1981.

Figure 4. Seasonal course of afternoon (1300h) water
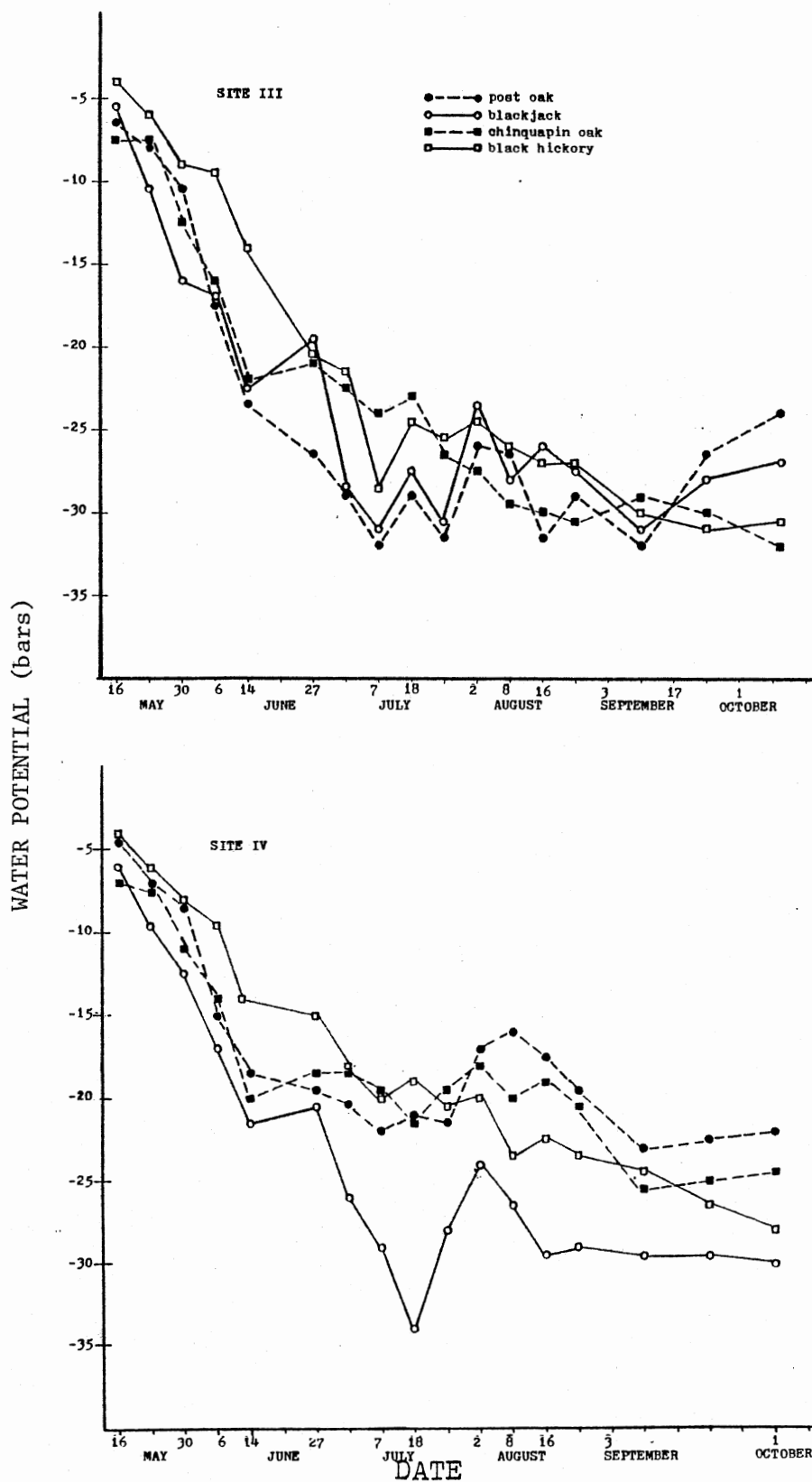potentials, 1980.
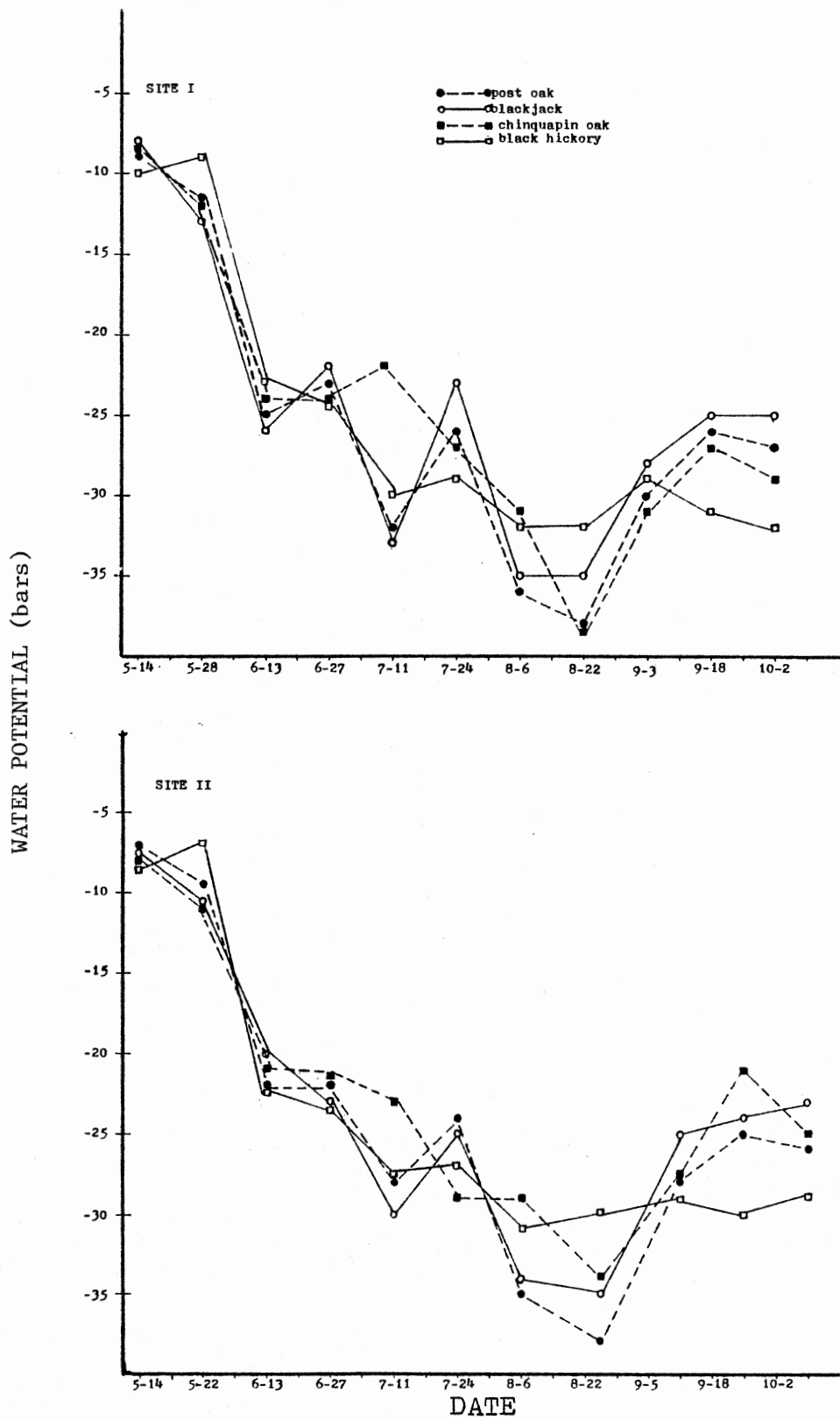
Figure 4. (Continued).

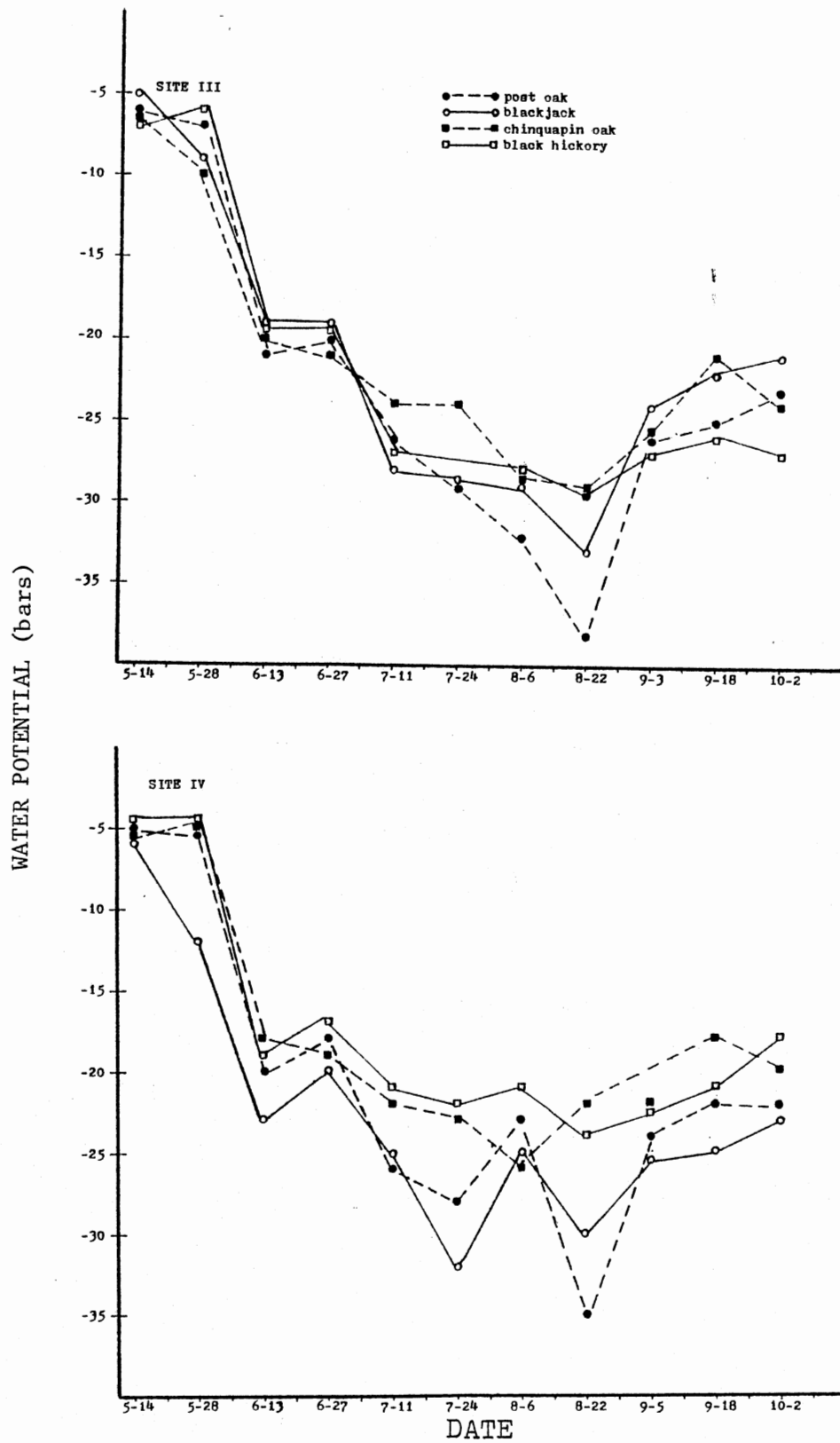Figure 5.   Seasonal course of afternoon (1300h) water potentials, 1981.

Figure 5. (Continued).

-19.5 b. Black hickory again had high to moderate values throughout most of the season and at the end of the season was the highest at all sites except IV.

Diurnal measurements at site I on 14 June 1980 showed Ψ_L for all species decreasing until 1100 h. After 1100 h, black hickory and chinquapin oak decreased only slightly to their minimum at 1300 h and maintained slightly higher values throughout the afternoon. The decrease for post oak and blackjack remained fairly uniform until 1300 h when their minima were reached and they increased only slightly until 1600 h (Fig. 6). This same general pattern was observed at higher values at the other sites.

On 12 July 1980 diurnal Ψ_L at site I showed that black hickory and chinquapin oak decreased slightly faster than that of post oak and blackjack until 1100 h when black hickory and chinquapin oak values began to decrease more slowly and troughed at 1300 h, then decreased very slightly through the heat of the afternoon. Blackjack and post oak continued to decrease rapidly until 1300 h when the values begin to oscillate from near their minima to higher values (Fig. 6).

The lowest Ψ_L values of 1981 were recorded at site I on 22 August (Fig. 4). Diurnal measurements of Ψ_L for this day (Fig. 7) showed that black hickory reached its lowest level at 1100 h and remained at about that level through 1600 h. Chinquapin oak decreased until 1100 h, decreased rapidly until 1300 h, then increased about 10 b by 1400 h with little change through 1600 h. The pattern for post oak and blackjack was similar to chinquapin oak through 1300 h. At 1400 h, post oak and blackjack had increased sharply by 1500 h and decreased to near their minima at 1600 h.
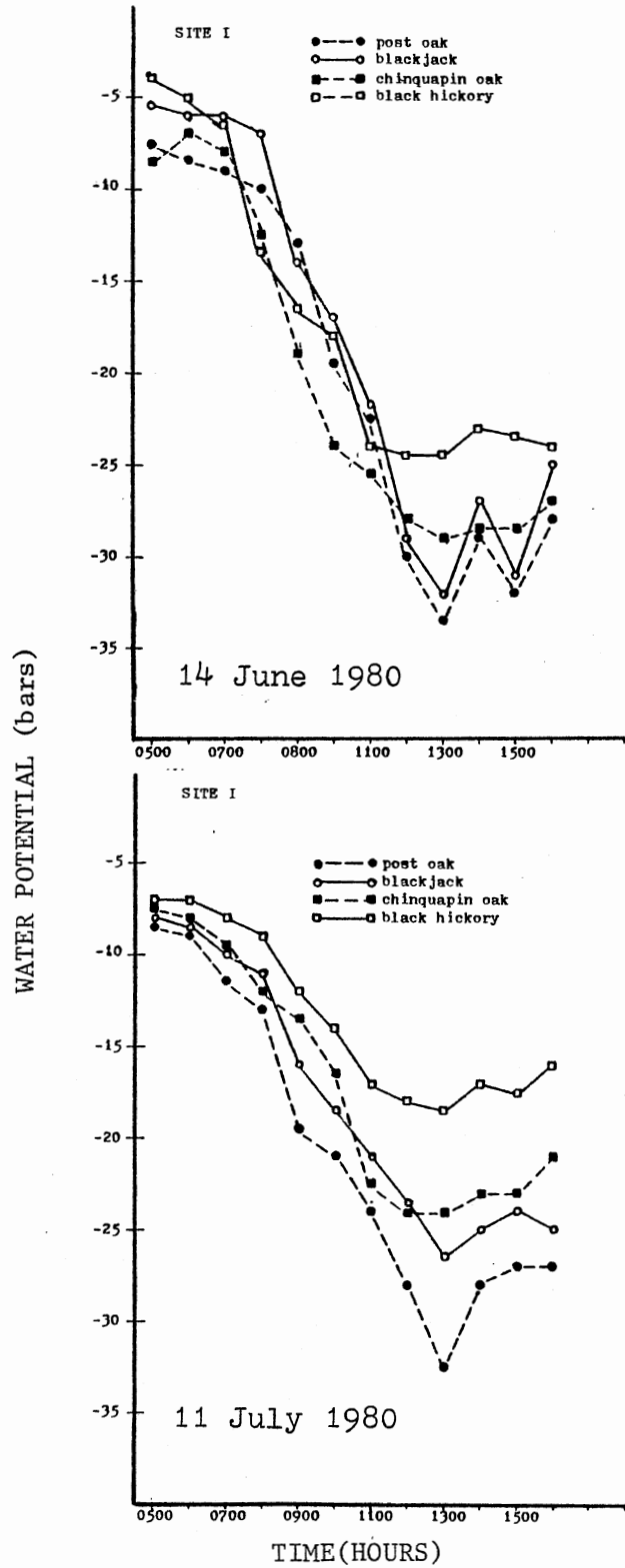
Figure 6.   Diurnal pattern of leaf
            water potentials at site I,
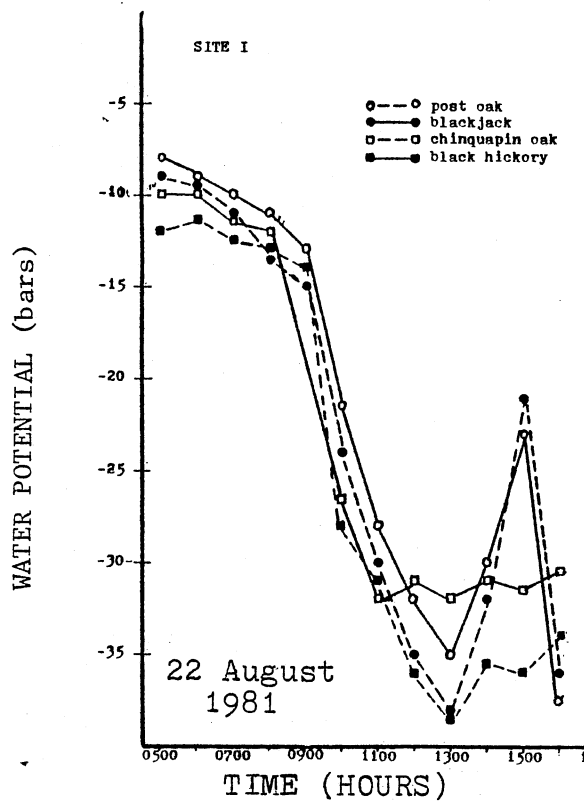   1980.

Figure 7. Diurnal pattern of leaf
           water potentials at
           site I, 22 August 1981.

Through 27 June 1981, diffusive resistance was similar for all species and sites. By 24 July however, diffusive ressistance for black hickory was much greater than for the others at sites I, II, and III and remained substantially higher than post oak and blackjack for the rest of the season (Fig. 8). At site IV, black hickory and chinquapin oak had consistently lower diffusive resistance than blackjack and post oak until late in the season when black hickory had the highest resistance of all species.

A comparison of diffusive resistance and Ψ_L for each species (disregarding site and date) in 1981 showed that when Ψ_L for black hickory and chinquapin oak exceeded -25 bars, diffusive resistance increased dramatically (Fig. 9). Even at higher Ψ_L values black hickory had substantially higher diffusive resistances than the other species.

Diurnal diffusive resistance for site I on 22 August 1981 (Fig. 10) showed that black hickory had lower diffusive resistance than other species early in the day. At 1100 h diffusive resistance for black hickory was higher than the others, reaching a peak at 1300 h and remaining very high throughout the day. Diffusive resistance for chinquapin oak reached a peak at 1300 h and remained high through 1600 h. Blackjack and post oak reached their maximum diffusive resistance at 1300 h then dropped substantially at 1500 h before rising again at 1600 h.

When Ψ_S was plotted against diffusive resistance for 1981, black hickory showed the most rapid increase in diffusive resistance with decreasing Ψ_L. Diffusive resistance for black hickory showed the highest correlation to Ψ_S with a correlation coefficient of 0.8965.
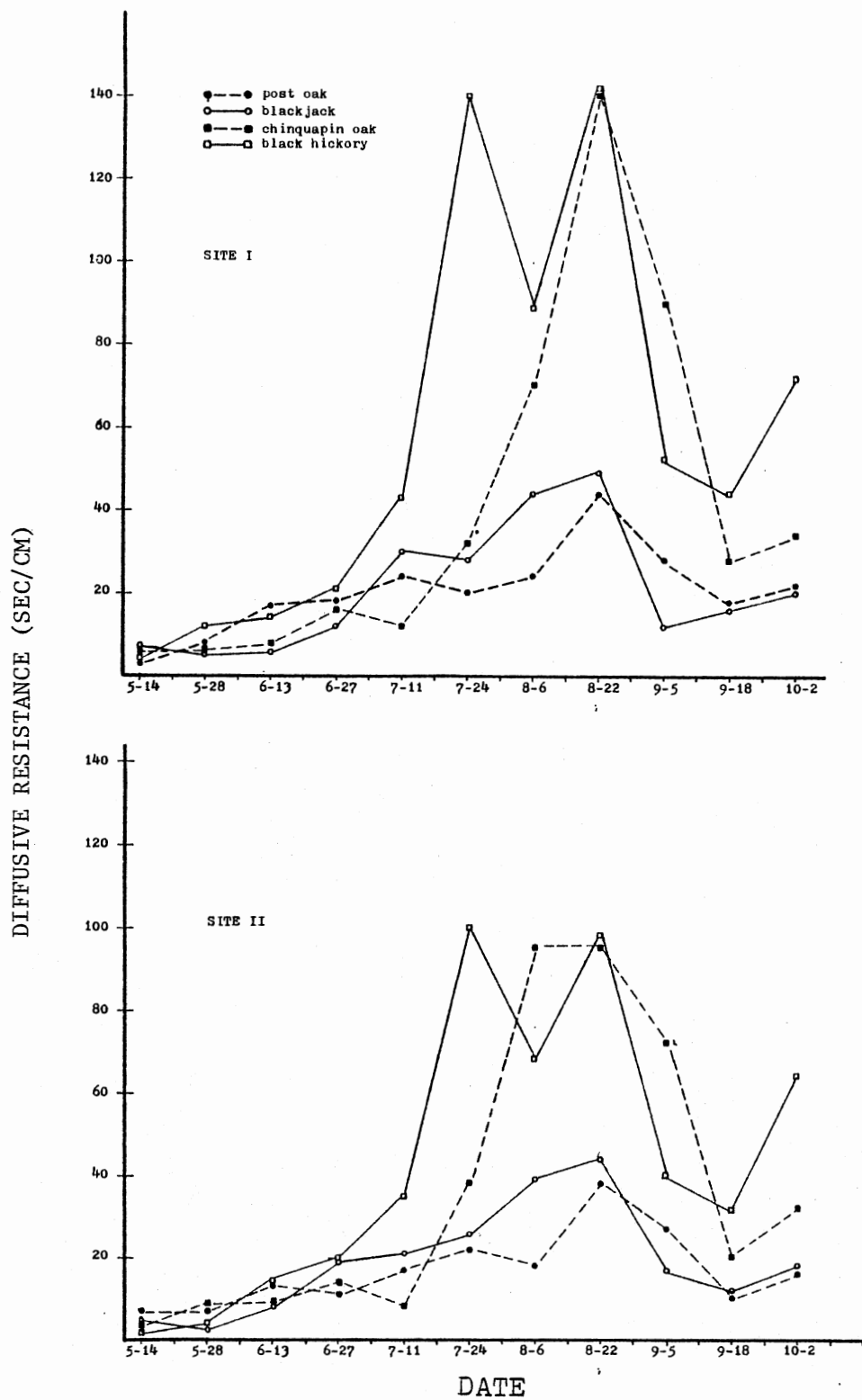
Figure 8.   Seasonal course of diffusive resistance, 1981.
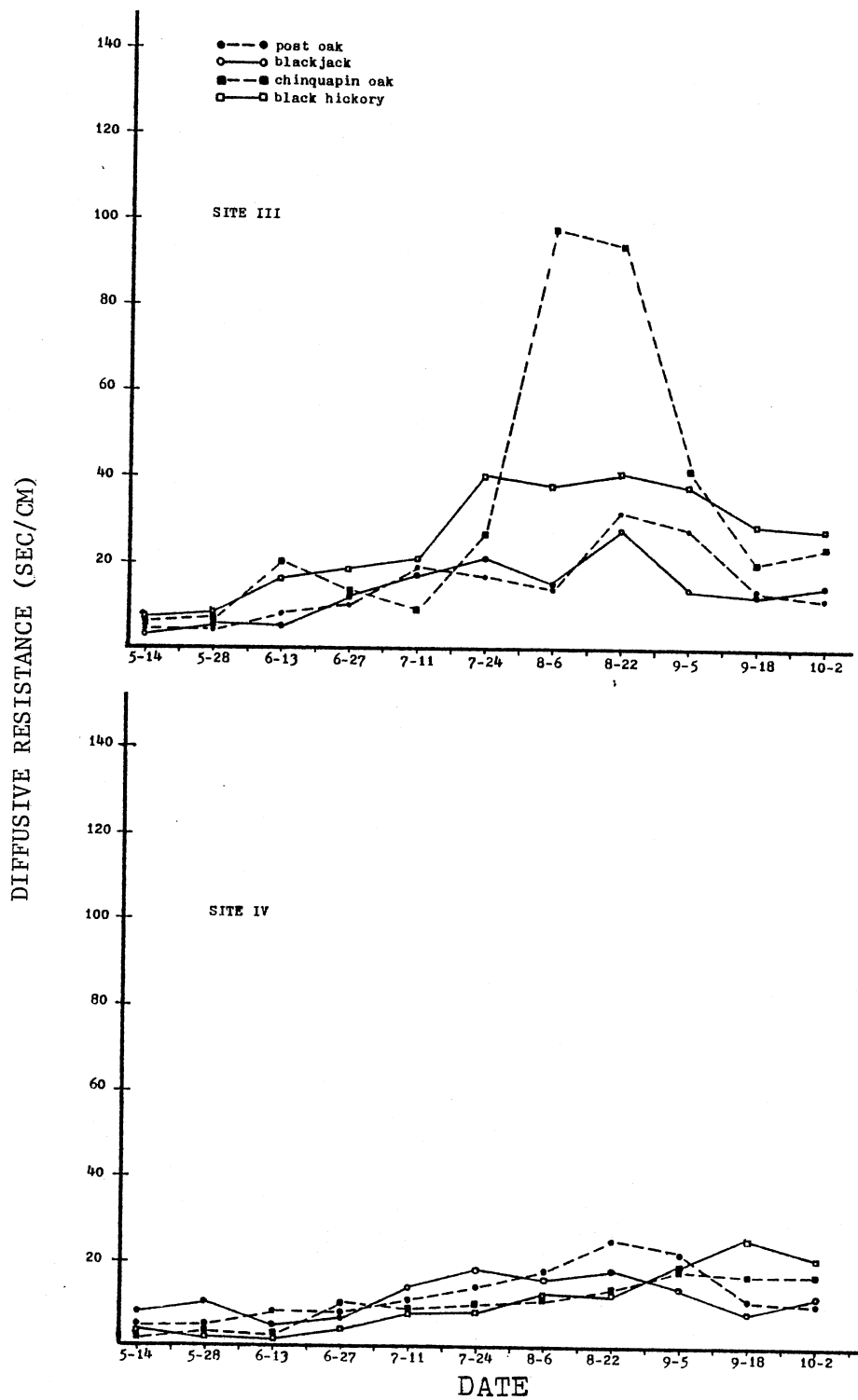
Figure 8. (Continued).
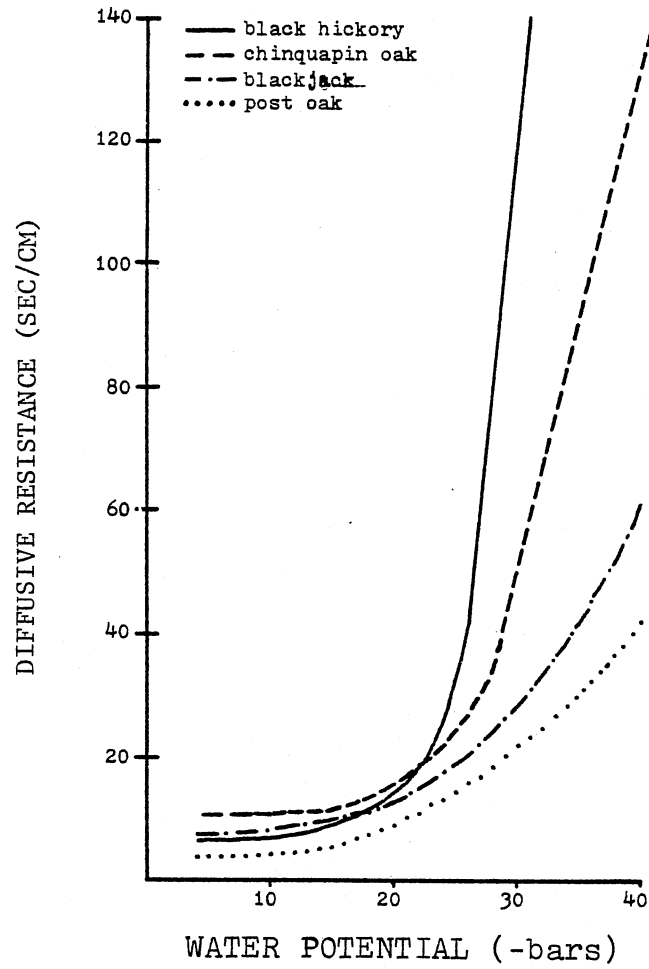
Figure 9. Diffusive resistance vs. water potential
for all sites showing estimated best
Pit lines, 1981.
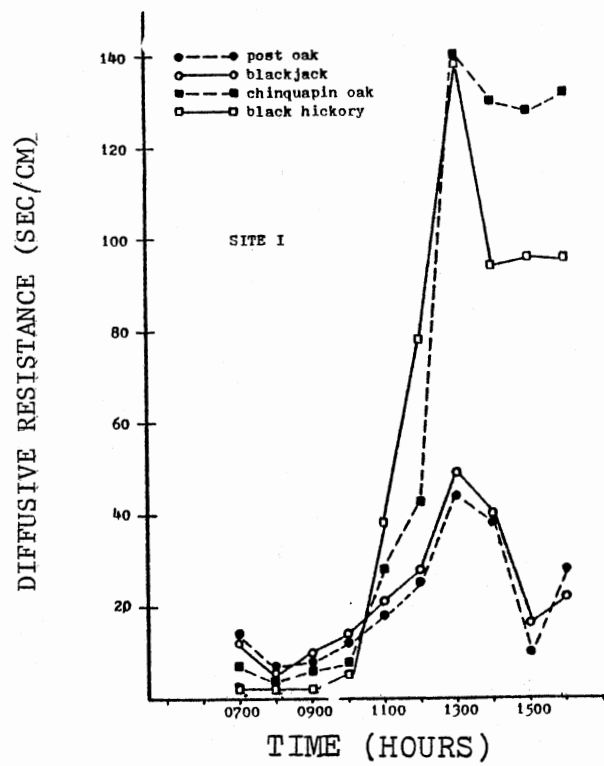
Figure 10.   Diurnal diffusive resistance
at site I, 22 August 1981.

Chinquapin oak showed slightly less increase in diffusive resistance with a decrease in Ψ_S and had a slightly lower correlation coefficient of 0.8729. Blackjack showed substantially lower diffusive resistance with decreasing Ψ_S and had a correlation coefficient of 0.8775. The diffusive resistance of post oak showed the least increase in response to Ψ_S and also had the lowest correlation coefficient of 0.8227.
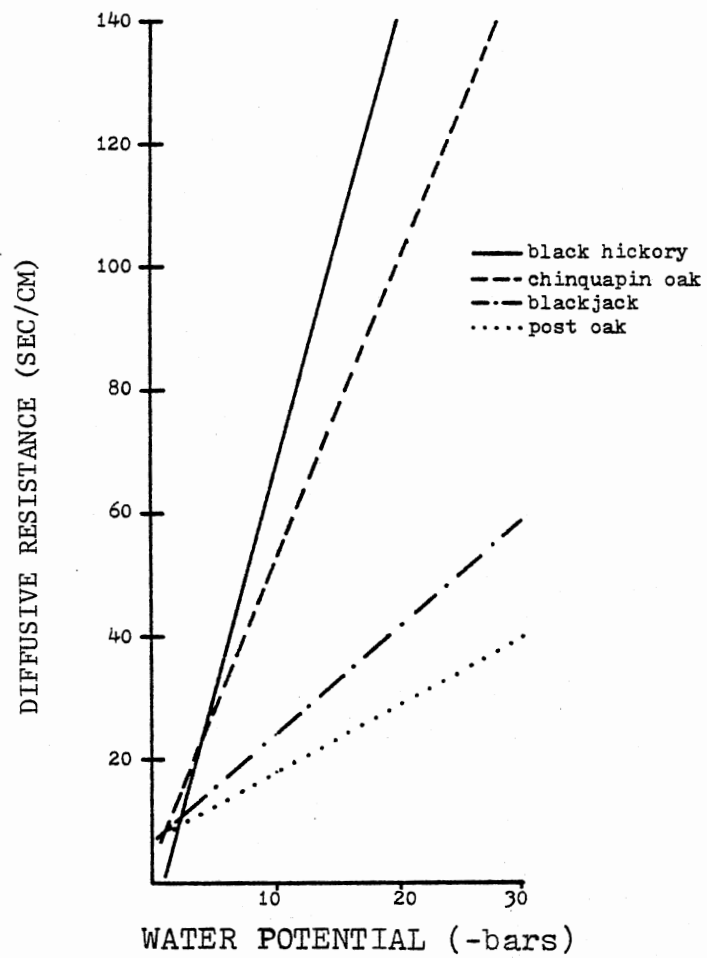
Figure 11. Diffusive resistance vs. soil water
potential by species, showing
calculated regression lines.

DISCUSSION

Soil water potential and RH were compared between sites to establish that the moisture regime was significantly different at each site. Thus, differences observed in Ψ_L and diffusive resistance were due to the differential response of each species to real changes in the moisture regime.

Predawn Ψ_L values are generally accepted to be directly related Ψ_S (Cunningham and Bark 1973, Slatyer 1967) and, as expected, predawn Ψ_L measurements generally showed that all study species recovered to higher values at the moister sites. Under mesic conditions such as those encountered early in the season and at the more mesic sites, all species showed similar predawn Ψ_L values. However, under less favorable moisture conditions, black hickory and chinquapin oak showed lower predawn Ψ_L than post oak or blackjack. This indicates that during periods of low moisture availability, the species whose geographic limits extend farther west are better able to recover from daytime water stress than those species restricted to more mesic ranges.

As expected, the seasonal course of afternoon Ψ_L values showed values decreasing early in the season and remaining at relatively low values through the remainder of the season (Hickman 1971, Hall and McPherson 1980). It was also expected that under a given set of conditions, those species whose ranges extend farther west would have higher Ψ_L values, indicating a lower level of water stress (Kramer 1972, Tobiessen and Kana 1974, Hall and McPherson 1980).

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The species-specific patterns observed in the seasonal course of afternoon Ψ_L values was unexpected since black hickory and chinquapin oak have the most restricted western limits and showed higher values than the other species at sites I, II, and III in each season.

During each season, the seasonal Ψ_L for black hickory tended to reach a floor in July and decline only slightly through the end of the season. At sites I and II, the other species showed much more variation and much lower Ψ_L values than black hickory.

In 1980, the Ψ_L values for 2 August at sites I and II showed an interesting phenomenon (Fig. 3). All species showed a sharp increase in Ψ_L when Ψ_S and RH were at the lowest values of the season, presumably indicating the most stressful conditions. It seems probable, since most of the species were near the lowest Ψ_L recorded for that species, that some minimum Ψ_L value had been reached for each species and some mechanism, probably stomatal closure, was responsible for the relatively high Ψ_L values.

Through both seasons, each species seemed to have a minimum level below which it rarely dropped regardless of environmental conditions. Black hickory seemed to reach a floor around −30 b and never went below −32 b. Chinquapin oak was more variable with values generally not lower than −32 b, but going as low as −38 b. Blackjack commonly had Ψ_L values of −24 b with a minimum of −38 b, while post oak frequently reached −36 b and reached a minimum of −38 b on several occasions.

Diurnal patterns showed results similar to seasonal patterns (Fig. 6). During June and July of both seasons, each species reached and tended to maintain a minimum Ψ_L. Black hickory had the highest

minimum with chinquapin oak, blackjack, and post oak showing
progressively lower values at site I. In August, diurnal patterns
showed black hickory decreasing to a Ψ_L of -32 b at 1100 h and
remaining at about this level throughout the afternoon. Under the
same conditions, the other presumably more drought hardy species
showed values as low as -38.5 b.

The seasonal diffusive resistance patterns were essentially
the opposite of Ψ_L patterns. When Ψ_L values for black hickory
seemed to reach a floor diffusive resistance increased rapidly at sites
I and II and remained high throughout the season. At site III under
more mesic conditions, black hickory showed much lower diffusive
resistance, and at site IV had lower diffusive resistance than the
other species through most of the season. Chinquapin oak developed
much lower Ψ_L values than black hickory during the season, but also
had very high diffusive resistances. At site III, chinquapin oak
showed diffusive resistances similar to that at site II, indicating
that it did not respond as well as the other species to the more mesic
conditions. Post oak and blackjack showed low diffusive resistance
even at very low Ψ_L values.

Diurnal diffusive resistance patterns showed further correlation
with Ψ_L values. In August, black hickory had a sharp increase
in diffusive resistance beginning at about 1100 h, corresponding to
a Ψ_L of -32 b. Diffusive resistance and Ψ_L both remained relatively
high through the rest of the day. Diffusive resistance for
chinquapin oak also increased rapidly for the same period but at
lower corresponding Ψ_L values. Diffusive resistance for post oak and
blackjack did not increase nearly so rapidly and even at low Ψ_L values

was substantially lower than for black hickory and chinquapin.

As Ψ_L for black hickory exceeded -25 b, diffusive resistance increased sharply (Fig. 9). Post oak did not show such extreme diffusive resistance even at low Ψ_L values. Chinquapin oak showed a pattern similar to black hickory although the rise in diffusive resistance was not so sharp. Blackjack showed a pattern similar to post oak with blackjack showing higher diffusive resistance at lower Ψ_L values.

Our data indicate than on a seasonal basis, post oak and blackjack are able to withstand very low Ψ_L values with open stomata thus allowing a high rate of net gas exchange for photosynthesis during most of the season while black hickory and chinquapin oak may be sacrificing gas exchange for water conservation. On a diurnal basis post oak is able to maintain open stomata for longer periods of each day than black hickory or chinquapin oak.

Under more mesic conditions, these differences are reduced and with abundant moisture may be reversed. The very low Ψ_L values for blackjack at site IV indicate that it may not be able to take up or transport water as rapidly as the other species when moisture is abundant.

In an attempt to ascertain whether any particular moisture parameter corresponded to the differential water relations of each species, temperature, RH, and Ψ_S were compared to both Ψ_L and diffusive resistance and subjected to regression analysis. Since the study area was small, precipitation was considered to be uniform for all sites and therefore not considered. Comparison of Ψ_S to diffusive yielded the only species-specific differences (Fig. 11).

From this one season of data, it appears that Ψ_S is a major factor in determining the ranges of these species.

Evidently, when moisture is abundant, black hickory and chinquapin are able to take up water fast enough to maintain a high Ψ_L . As Ψ_S decreases, they are not able to obtain available moisture as well as post oak and blackjack. Therefore, it appears that the differential response of these species to moisture availability, especially Ψ_S , is in large measure responsible for their different habitat requirements and geographic distributions.

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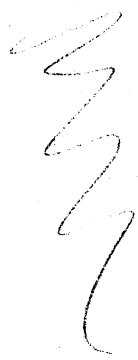
APPENDIX

Table 1. Soil water potentials (bars) for each year.

1980

Site	16 May	23 May	30 May	6 June	14 June	27 June	12 July	18 July	2 Aug	8 Aug	16 Aug	22 Aug	3 Sept	1 Oct
1	-2.0	-3.7	-2.5	-2.5	-7.5	-5.0	-8.5	-12.5	-21.0	-20.0	-22.3	-18.0	-12.1	-12.5
2	-1.5	-2.5	-1.7	-2.5	-6.2	-3.7	-7.2	-10.5	-20.0	-20.0	-20.6	-17.4	-11.6	-10.5
3	-1.5	-2.0	-1.2	-2.0	-3.8	-3.1	-6.0	-10.2	-12.5	-16.5	-17.2	-14.9	-10.2	- 8.5
4	-0.5	-1.7	- .08	- .10	-2.5	-2.0	-4.5	-7.0	- 8.5	- 9.0	-10.1	- 7.1	- 6.3	- 6.0

1981

Site	14 May		28 May		13 June	27 June	11 July	24 July		6 Aug	22 Aug	18 Sept	5 Sept	2 Oct
1	-2.2		-2.5		-3.5	-2.0	-7.8	-12.4		-17.3	-16.1	-9.2	-11.2	- 8.7
2	-1.7		-1.9		-2.8	-1.5	-6.0	-10.5		-14.2	-13.9	-7.3	- 8.2	- 7.0
3	-1.5		-1.4		-1.9	-1.3	-5.3	- 9.8		-10.1	-11.8	-5.4	- 6.3	- 5.2
4	-1.0		-1.0		-1.5	-0.5	-4.0	- 6.7		- 7.3	- 6.5	-4.1	- 5.0	- 4.0

Table 2. Percent relative humidity for each year.

1980

Site	16 May	23 May	30 May	6 June	14 June	27 June	3 July	12 July	18 July	25 July	2 Aug	8 Aug	16 Aug	22 Aug	3 Sept	17 Sept	1 Oct
1	72	69	57	59	43	50	49	49	48	33	23	27	25	35	42	37	38
2	73	70	63	65	45	53	52	51	50	35	31	30	28	38	45	38	41
3	78	74	67	66	47	57	58	57	56	49	45	36	35	41	51	42	43
4	86	86	84	69	48	61	61	60	59	54	48	42	40	46	57	48	48

1981

Site	14 May		28 May		13 June	27 June		11 July		24 July		6 Aug		22 Aug	5 Sept	18 Sept	2 Oct
1	72		84		74	77		50		42		57		38	39	42	40
2	73		87		78	78		52		43		59		41	41	44	41
3	75		90		81	80		57		48		63		47	46	48	46
4	79		94		86	84		61		51		69		52	53	51	49

VITA 1

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