

# WATER RELATIONS, SOIL FERTILITY, AND PLANT NUTRIENT COMPOSITION OF A PYGMY OAK ECOSYSTEM<sup>1</sup>

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**Abstract.** The water and nutrient relations of Buzzard's Roost, an unusual pygmy oak ecosystem in southwest Missouri, USA, were studied in 1976 and 1977 in an attempt both to characterize the ecophysiology of the individuals and find the causative agents for the existence of the pygmy forest. The stunted trees were mostly blackjack oak (*Quercus marilandica*) with some northern red oak (*Q. rubra*) and a few black oak (*Q. velutina*). In addition to being stunted, the trees were gnarled and twisted and had miniature leaves and acorns.

Results of soil analysis showed the pygmy forest soil to be very acidic ( $pH_w = 4.6$ ), with very low levels of Ca and Mg (0.25 and 0.12 meq/100 g, respectively) and very high levels of Al (600 ppm). Adjacent non-pygmy forest soils did not display these characteristics. Foliar analysis of blackjack, northern red, and black oak showed Ca and Mg to be much lower in pygmy foliage than in non-pygmy foliage, at three times during the growing season. Diurnal and seasonal patterns of xylem pressure potential, leaf conductance, and soil moisture content illustrated the development of very severe tree water deficits at Buzzard's Roost. Predawn and midday xylem pressure potentials declined to as low as  $-3610$  and  $-4200$  kPa, respectively, accompanied by complete daytime stomatal closure. However, water stresses in nearby non-pygmy oaks were greater than at two of three pygmy oak sites, implying that water stress was not the major factor or causative agent in the stunting process.

The evidence suggests that the very low nutrient levels in the soil, especially of Ca and Mg, plus the very high levels of Al, may be deficient (and/or toxic) for normal tree growth and development, and possibly responsible for the existence of the pygmy oak forest. Also, the xeric site characteristics add another severe stress to this ecosystem.

**Key words:** Buzzard's Roost; Missouri; plant nutrient composition; pygmy oaks; *Quercus marilandica*; *Quercus rubra*; soil fertility; water relations.

## INTRODUCTION

Areas of naturally dwarfed trees are rare and are usually associated with atypical flora, soils, geology, or climate. Stunted tree growth occurs at treeline (both in mountains and towards the Poles) and on some coastal dunes (Tranquillini 1976). The existence of stunted vegetation in other locations is less frequent, but the uncommon features of such systems have attracted the interests of many scientists (Jenny et al. 1969, Proctor and Woodell 1975, Westman 1975).

Buzzard's Roost, a sandstone bluff overlooking the Sac River Valley in St. Clair County, Missouri, is inhabited by an unusual pygmy oak community (Fig. 1). The trees are characterized by extremely stunted growth, gnarled and twisted limbs and trunks, miniature leaves and acorns, rosetting of leaves, and die-back of twigs, branches, and trunks. By examining environmental and plant factors, both spatially and temporally, we hoped to determine which factors influenced the development of the dwarfed condition. Specific objectives were:

1) to describe the seasonal and spatial patterns of

soil-plant moisture and nutrient relations for both the pygmy and non-pygmy forest,

2) to examine diurnal trends in plant water deficit, leaf conductance, and certain environmental variables, and

3) to describe differences between seedling growth of acorns from pygmy and non-pygmy oaks.

## MATERIALS AND METHODS

### Study site

Buzzard's Roost is  $\approx 10.4$  km west-northwest of Collins and 12.9 km south-southwest of Osceola in St. Clair County, Missouri (lat.  $37^{\circ}58'N.$ , long.  $93^{\circ}42'W.$ ). The climate is of the warm, humid, continental type (Critchfield 1966). Mean January, July, and annual temperatures are 0.6, 25.8, and  $13.3^{\circ}C$ , respectively. Average annual precipitation is 101.4 cm (United States Department of Commerce 1976). The bluff faces west-southwest and is  $\approx 50$  m above the Sac River. A slope,  $\approx 90$  m long rises  $\approx 12$  m from the bluff edge to the summit of a ridge (Fig. 2).

### Vegetation

Trees scattered along the very edge of the bluff are the most stunted (height 1.4 m). The pygmy forest begins 5 m from the edge of the bluff and continues for 52 m upslope (Fig. 2). At the transition between the pygmy and non-pygmy forests, tree heights double

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FIG. 1. View of the bluff at Buzzard's Roost, above the Sac River Valley, St. Clair County, Missouri.

from 5 to 10 m, trunks are straighter, and trees appear generally healthier.

The pygmy oak forest is almost entirely blackjack oak (*Quercus marilandica* Muenchh.), with a few northern red oak (*Q. rubra* Lam.) present. At the boundary with the non-pygmy forest, northern red oak is more common, and black oak (*Q. velutina* Lam.) can also be found. The non-pygmy forest is typical of the oak-hickory upland forest of southwest central Missouri (Braun 1972). The principal trees are white oak (*Q. alba* L.) black oak, northern red oak, post oak (*Q. stellata* Wangenh.), blackjack oak, and hickories (*Carya* spp.).

Many of the non-woody species found in the pygmy oak ecosystem are rare in that area of the state (Settergren 1974, Redfern, *personal communication*). Among those are several succulent species, including rock pink (*Talinum calyanum* Engelm.), widow's cross (*Sedum pulchellum* Michx.), and prickly pear cactus (*Opuntia compressa* (Salisb.) Macbr.). In addition, the ground is covered with lichens (e.g., *Cladonia furcata* Huds. Schrad., *C. subtenuis* Abb. Evans, *C. chlorophaea* Flk., Spreng) and bryophytes

(e.g., *Polytrichum juniperinum* Hedw., *Leucobryum albidum* Hedw. Angstr. ex Fr., *Dicranum sabuletorum* Ren. and Card).

Five sites along a transect were chosen for sampling and collecting data. Increment cores were collected from 19 trees at Sites 1 through 4. Average age of trees at the pygmy sites varied between 68 and 76 yr, in contrast to 108 yr at non-pygmy Site 4. Average stem diameter growth per year was less for blackjack oak than for white, black, or northern red oak.

Average leaf area index (LAI) of the pygmy forest trees ( $3.3 \text{ cm}^2/\text{cm}^2$ ) was less than half that of the non-pygmy forest trees ( $7.0 \text{ cm}^2/\text{cm}^2$ ). Lichens and bryophytes on the pygmy forest floor probably added another  $1 \text{ cm}^2/\text{cm}^2$  to the LAI of that part of the ecosystem.

### Soils

Soils at Buzzard's Roost are very similar in texture and color to the subsoil of a Bolivar soil, common in the uplands of southwest Missouri (Table 1). Bolivar soils have developed in weathered sandstone residuum (Scrivner et al. 1975), and probably the soils at Buzzard's Roost have as well. The bluff is composed of Pennsylvanian sandstone, of the Desmoinesian series, Cherokee group, and Krebs subgroup. This sandstone has a high quartz content and is cemented with iron oxide. Soils derived from this material are usually of low fertility.

The soils at Sites 1 through 3 are similar in profile development, texture, and color (Table 1). Surface horizons have eroded away, exposing the B1 horizon. Leaf litter does not accumulate to any great extent beneath the pygmy forest, and probably blows onto the ridge summit. This could help explain the lack of any O1 or O2 horizons. The pygmy forest soils are sandy loams or sandy clay loams, and both clay content and percentage stone content increase with depth.

The soil at Site 4 (non-pygmy forest) shows little signs of erosion; it has both O and an A horizons. Texture of all horizons is loam and over 50% of the soil is coarse fragments. This soil is stonier than the

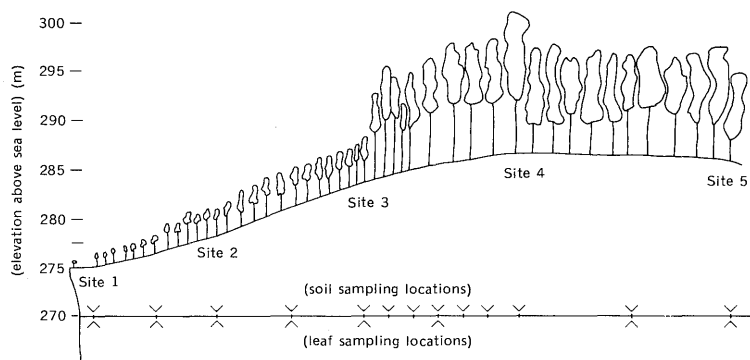


FIG. 2. Cross-sectional diagram of Buzzard's Roost, looking north.

TABLE 1. Average tree height, leaf area index (LAI), and soil profile descriptions for four sites at Buzzard's Roost and for a Bolivar soil in Henry County, Missouri.

Location	Horizon	Depth (cm)	Color (dry)	Sand (%)	Silt (%)	Clay (%)	Stone content (%)	Average tree height (m)	LAI (cm <sup>2</sup> /cm <sup>2</sup> )
Buzzard's Roost Site 1 (Slope 10–13%)	B1	0–10	10YR 4/3	62	25	13	0–5	1.4	3.9
	B2	10–20	10YR 5/5	63	21	16	10–15		
	B3t	20–30	7.5YR 5/6	60	20	20	20–25		
Buzzard's Roost Site 2 (Slope 14–16%)	B1	0–15	10YR 5/6	56	24	20	0–5	3.3	4.3
	B2	15–40	10YR 5/6	57	21	22	5–10		
	B3t	40–60	7.5YR 5/6	50	22	28	20–25		
Buzzard's Roost Site 3 (Slope 14–16%)	B1	0–15	10YR 5/4	55	31	14	0–5	4.9	4.6
	B2	15–40	10YR 6/5	57	26	17	10–15		
	B3t	40–60	7.5YR 5/6	54	16	30	20–30		
Buzzard's Roost Site 4 (Slope 0–2%)	O	3–0	10YR 3/1	...	...	...	...	15.0	7.0
	A1	0–10	10YR 3/2	61	29	10	50–65		
	A2	10–25	10YR 5/4	60	28	12	50–65		
	A-B	25–50	7.5YR 5/4	60	26	14	50–65		
Henry County Bolivar soil (Slope 8%)	A1	0–15	10YR 4/2	58	33	9			
	A2	15–30	7.5YR 6/4	60	33	8			
	B1	30–38	7.5YR 5/6	56	30	14			
	B2	38–65	5YR 4/7	52	23	23			
	B31	65–102	5YR 4/4	58	15	27			
	B32	102–120	5YR 5/6	70	11	19			

pygmy forest soils, but is texturally similar. In addition, fine root growth seemed good in the non-pygmy forest soils and poor in the pygmy forest soils.

#### *Experimental design and measurement techniques*

*Water relations.*—Diurnal patterns of leaf conductance ( $k_l$ ), xylem pressure potential (XP), leaf temperature ( $T_l$ ), vapor pressure deficit (VPD), photosynthetically active radiation (PAR), air temperature ( $T_a$ ), potential evapotranspiration (PET), and soil moisture content (SMC) were measured on 22 d at about weekly intervals from 15 May to 2 October 1976. Data were collected hourly from predawn to sunset on Sites 1–3, and at midday and predawn at Site 4. Leaf conductance, PAR incident upon the leaf surface (LPAR), and XP were measured for a "sun" and a "shade" leaf from two trees at Sites 1–3 and from four trees at Site 4. Sun leaves were defined as leaves currently in the sun. All but the XP readings were taken on the site from intact leaves. Then the leaves were cut from the twigs at the base of the petiole, and determinations of XP were made. Air temperature, VPD, PET, and incoming PAR incident upon the site (IPAR) were measured once for each site at each hourly reading.

Xylem pressure potential was determined on leaf petioles using the pressure chamber technique described by Ritchie and Hinckley (1975) and Millar and Hansen (1975). Leaf temperature was measured with a fine wire thermocouple contact thermometer (Gale et al. 1970). Leaf diffusive conductance was measured on the abaxial surface with a Lambda diffusive resistance meter and a horizontal sensor (Kanemasu et al.

1969). The meter and humidity sensor were stabilized before each reading and sensor response between 12° and 40°C was calibrated three times during the study period (Morrow and Slatyer 1971).

Ambient wet and dry bulb temperatures were measured with an aspirated Assman psychrometer, and used in determining  $T_a$  and VPD. Photosynthetically active radiation in the 400–700 nm range was measured with a Lambda quantum sensor (Biggs et al. 1971) in two ways. Measurements of LPAR were made by holding the sensor surface parallel to the leaf surface, while IPAR was measured in the open by holding the sensor parallel to the ground.

Soil samples for measuring soil moisture content (SMC) were collected at 0–10, 10–20, and 20–30 cm approximately 0.3 m from the study trees at each site, once each sampling day before 0900. The auger hit bedrock at Site 1 at ≈28 cm and stone content was high enough at Sites 2, 3, and 4 to prevent sampling below 30 cm with a hand auger. Soil samples were oven dried at 105°C for 48 h and SMC was expressed as percent of dry mass. Soil texture was determined by the hydrometer method (Bouyoucos 1951).

*Soil fertility.*—Soil pH, percent organic matter, P, K, Mg, Ca, H, S, B, Zn, Mn, Fe, Cu, Mo, Al, cation exchange capacity, and percent base saturation were measured at 13 points along a transect (Fig. 2). Soil cores from 0–15 cm depth were used in testing fertility because >50% of the roots in both pygmy and non-pygmy trees were found in the top 15 cm. These soil tests were made by A and L Agricultural Laboratories, Incorporated, Memphis, Tennessee. Calcium, Mg, K, Na, and S were extracted using 1 M ammonium ace-

tate at a pH of 7.0. Soil pH was determined using both distilled water ( $\text{pH}_w$ ) and a 1 N calcium chloride solution ( $\text{pH}_s$ ). A 1 N potassium chloride solution was used to extract aluminum. Zinc, Mn, Fe, and Cu were extracted with 0.1 N hydrochloric acid. A 1 N dichromate solution was used to extract organic matter. Phosphorus was extracted with a Strong Bray solution. Molybdenum was extracted with calcium oxalate and B analysis was done by the curcumin method. Exact procedures are available from the authors.

In addition, soil tests of samples from three depths at Sites 1–4 were made by the University of Missouri Soil Test Laboratory, Columbia, Missouri. Techniques used were similar to those of the A and L Agricultural Lab.

*Foliar nutrient composition.*—Foliar analysis was performed for both pygmy and non-pygmy trees at three times (30 April, 30 June, and 3 September) during the 1977 growing season. These dates were chosen in order to examine best the effects of stage of leaf development and season upon nutrient concentration. Bud burst occurred prior to 30 April and by that date leaves were rapidly expanding, but average leaf area was still <10% of mature leaf area. The date 30 June was chosen for sampling because leaves were mature and expansion had ceased, but the foliage had not experienced the prolonged water deficits of midsummer. Leaf sampling and foliage analysis were last done on 3 September, prior to senescence but after the hot and dry period of summer.

Foliage was sampled from five oak species at nine locations along a transect (Fig. 2), and the concentrations of N, P, K, Mg, Ca, Na, Fe, Al, Mn, B, Cu, Zn, and Mo were determined. Sampling tested for variation in foliar nutrients between and within pygmy and non-pygmy trees and sites. Additionally, lichens and bryophytes from the pygmy forest floor and foliage from pygmy and non-pygmy blackjack oak seedlings grown in a greenhouse in Columbia were analyzed for their nutrient concentration. Plant nutrient analyses were made by A and L Agricultural Laboratories. All elements were determined by atomic absorption, except B, P, S, and N, which were determined colorimetrically. Exact procedures used are available from the authors.

*Seedling growth study.*—In an indirect effort to test for genetic differences, 60 seedlings from both pygmy and non-pygmy blackjack oak acorns were grown under identical conditions in a greenhouse in Columbia, Missouri. The pygmy oak acorns were collected at Buzzard's Roost and the non-pygmy oak acorns were collected both at Buzzard's Roost and the University Forest, in Butler County, Missouri. Following 3 mo of stratification at 3°C, seedlings were grown from February to September 1977 in a 3:2:1 mixture (by volume) of peat, loam, and sand. Stem height and maximum length (L) and width (W) of every leaf were

measured for each seedling at 4-d intervals for the first 44 d of growth and at 8-d intervals thereafter. Correlation of L and W with leaf area measured with a Lambda portable area meter was significant and

$$\text{leaf area} = 1.117 + 0.509(L \times W); \quad r^2 = .94.$$

Stem diameter at 2.5 cm above the root collar was measured with Mitutoyo calipers (accurate to .0025 mm) in September before removing the seedlings from the pots. Each seedling was separated into leaves, stems, and roots, and oven dried at 70°C for 48 h to obtain root and leaf dry mass and total biomass.

## RESULTS AND DISCUSSION

### *Growth of pygmy and non-pygmy oak seedlings*

To explain the existence of and abrupt boundary between the pygmy and non-pygmy oak forests, we considered the possible effects of both site and genetic factors. We assumed that there must be site differences, because even if a pygmy oak genotype now exists, it would have evolved in response to some extraordinary environmental conditions. The abrupt boundary between the pygmy and non-pygmy forests and the small size and lack of physical isolation of the pygmy population led us to believe that the pygmy oaks were not genetically different from the surrounding oaks. If the pygmy oaks were a separate genotype, one would expect to find at least some intermingling of the genotypes; i.e., at least a few of the more tolerant pygmy trees would be able to compete on poorer microsites within the non-pygmy forest. However, this is not the case.

Growth differences of experimentally grown blackjack oak seedlings were apparently due to acorn mass rather than genetic potential (Table 2). Acorn size had significant linear correlation with leaf area ( $r^2 = .96$ ) and with total seedling biomass ( $r^2 = .92$ ). Acorns collected at Site 5 (non-pygmy) were almost as small as those from Site 1, and Site 5 seedlings were also small.

Non-pygmy blackjack oak acorns from the University Forest weighed much more than acorns from Buzzard's Roost. Seedlings from these acorns were much larger than either the pygmy or non-pygmy seedlings from Buzzard's Roost acorns (Table 2). In addition, leaves from University Forest seedlings had less mass per unit area (0.85 mg/dm<sup>2</sup>) than those from either the pygmy (1.12, 1.08, 1.11 mg/dm<sup>2</sup>, respectively) or non-pygmy sites (1.07 mg/dm<sup>2</sup>).

### *Variations in tree water status*

Because genetic differences were apparently not responsible for the existence of the pygmy oak forest, perhaps drought was the determining factor. The vegetative patterns at Buzzard's Roost led to the following hypotheses:

TABLE 2. Means and standard deviations of average leaf area, total leaf area per seedling, number of leaves per seedling, stem height, and initial acorn mass for five groups of blackjack oak seedlings.

Acorn source location	Parent tree condition	Per seedling					N
		Average leaf area (cm <sup>2</sup> )	Total leaf area (cm <sup>2</sup> )	Number of leaves	Stem height (cm)	Acorn mass (g)	
Buzzard's Roost (Site 1)	Pygmy	5.4 ± 0.3	50.7 ± 3.9	9.5 ± 0.5	4.5 ± 0.3	0.5 ± 0.1	11
Buzzard's Roost (Site 2)	Pygmy	9.2 ± 1.0	104.6 ± 17.5	10.7 ± 0.9	8.0 ± 0.9	0.8 ± 0.1	21
Buzzard's Roost (Site 3)	Pygmy	9.2 ± 1.4	97.5 ± 16.7	10.3 ± 0.6	6.1 ± 0.8	0.9 ± 0.1	11
Buzzard's Roost (Site 5)	Normal	9.3 ± 1.0	76.7 ± 11.8	8.1 ± 0.6	7.0 ± 0.6	0.5 ± 0.1	18
University Forest	Normal	14.5 ± 1.6	188.2 ± 32.0	12.6 ± 0.6	12.7 ± 1.6	1.7 ± 0.2	25

1) Because soil depth decreases from the summit to the edge of the bluff, a soil moisture gradient will exist due to decreasing soil volume.

2) Due to the open exposure of the bluff, atmospheric evaporative demand (measured as VPD,  $T_a$ , and PET) would be greatest near the bluff and decrease toward the summit.

3) Assuming these gradients are real, greater evapotranspirational losses coupled with decreasing available soil moisture supply would increase plant water deficits (more negative predawn and midday xylem pressure potential and decreasing leaf conductance) towards the bluff.

4) Summer droughts are common in Missouri, but their duration and severity vary greatly from year to year. During summers with prolonged droughts the severe moisture conditions could lead to dieback of leaves, twigs, and branches.

#### Seasonal trends in tree water status

Seasonal trends of tree and environmental factors are shown in Fig. 3. Patterns and values of  $T_a$ , VPD, IPAR, and SMC were similar at Sites 1, 2, and 3. Average midday  $T_a$  fluctuated considerably but generally increased to a maximum of  $\approx 35^\circ\text{C}$  on 24 July, and then slowly decreased. Average midday VPD also fluctuated greatly. In late spring and early summer VPD ranged from 1 to 2 kPa. Two long drought periods, interrupted by a rainy period, followed. During the droughts midday VPD was extremely high, averaging  $\approx 3.5$  kPa. Average IPAR fluctuated with cloud cover and haziness, but in general was  $\approx 1900 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  on clear days. On rainy, overcast days IPAR was  $\approx 550 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Early in the study SMC averaged  $\approx 23\%$ . It decreased until 31 July, increased slightly until 16 August, and decreased rapidly after that. Between 21 August and 11 September SMC remained very low (5–8%). With the onset of fall rains SMC increased to  $\approx 10\%$  on 25 September and 14% on 2 October.

Although XP, BXP (base or predawn XP), and  $k_i$  differed for the pygmy sites, seasonal patterns were similar. Base XP was high,  $\approx -100$  kPa, at the beginning of the study, and remained fairly constant until

declining soil moisture caused a decrease. This decline occurred at different times and varied in magnitude at each site. Base XP decreased sooner at Site 1 than at Sites 2 and 3. Minimum BXP, observed in early September, was  $-3610$ ,  $-1560$ , and  $-900$  kPa at Sites 1, 2, and 3, respectively. At Site 3, BXP in blackjack and northern red oak were nearly identical throughout the study. Moderate rains relieved the drought in mid-September and BXP recovered to  $-450$ ,  $-450$ , and  $-220$  kPa at Sites 1, 2, and 3 respectively.

Midday water deficit, measured as a decrease in XP, is primarily a function of available soil moisture and atmospheric evaporative demand (Hinckley et al. 1978). Therefore, on a seasonal basis, as SMC decreases and VPD increases, midday XP should decrease (Fig. 3). Since stomatal closure occurs with increasing water deficits, the rate of decrease of XP in relation to increasing VPD declines. In general, at the pygmy sites, midday XP was high from 15 May to 19 June, averaging between  $-1000$  and  $-2000$  kPa, and then steadily decreased with time to  $-4200$  kPa at Site 1 and  $-3500$  kPa at Sites 2 and 3.

Midday leaf conductance is a good indicator of plant water status, because it is dependent upon moisture supplies and demands, and is generally unaffected by light levels. As SMC and BXP decreased after 19 June at the pygmy sites,  $k_i$  in both blackjack and northern red oak responded with more or less parallel decreases. The magnitude and timing of changes in  $k_i$  varied with site and species, but were usually in response to microenvironmental changes, particularly soil moisture supply. At Site 1, average midday  $k_i$  decreased to  $<0.2$  cm/s by 24 July, along with a decrease in BXP to  $-1030$  kPa (Fig. 3). Leaf conductance and BXP increased slightly around 8–16 August and then dropped dramatically between 21 August and 11 September when BXP fell to  $-3610$  kPa. Decreases in  $k_i$  at Site 2 were slower than at Site 1. Average midday  $k_i$  peaked around 4 July near 0.63 cm/s and gradually decreased to a minimum of  $<0.1$  cm/s on 11 September. Seasonal changes of  $k_i$  in blackjack and northern red oak at Site 3 were similar, but average  $k_i$  was always higher in blackjack than in northern red oak. In both species midday  $k_i$  remained fairly high until

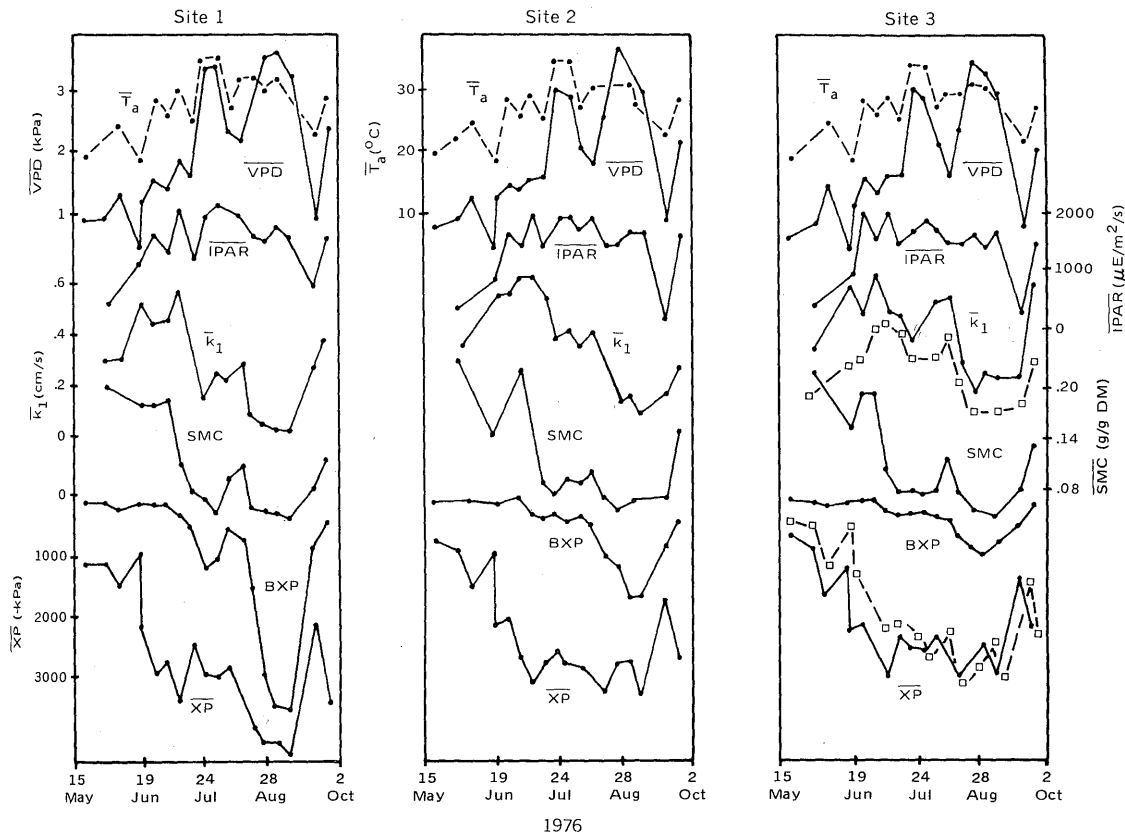


FIG. 3. Seasonal patterns of average midday (1000–1400) air temperature ( $\bar{T}_a$ ), vapor pressure deficit ( $\overline{VPD}$ ), incoming photosynthetically active radiation (IPAR), leaf conductance ( $k_l$ ), and xylem pressure potential (XP), plus predawn XP (BXP) and soil moisture content (SMC) for blackjack oak (solid circle) and northern red oak (open square).

decreasing BXP and high VPD caused lower rates from 21 August to 11 September.

*Diurnal trends in tree water status and leaf conductance*

Diurnal patterns of  $k_l$  and XP during the season reflect the influence of changing soil moisture and atmospheric factors upon tree water status. Predrought conditions were typified by 4 July, which was warm, clear, and moderately dry (Fig. 4). Patterns of XP and  $k_l$  were typical for well-watered or mesic conditions. Xylem pressure potential was maximum at predawn, declined to a minimum at midday, and increased in late afternoon. Leaf conductance showed bimodal peaks at 1000 and 1600. Although trends were similar, magnitudes and times of the changes differed by site and species. Similar diurnal patterns are well documented in the literature (Sucoff 1972, Hinckley et al. 1978).

Representing mid-drought conditions, 30 July was very hot and dry (Fig. 5). Soil moisture content averaged <10% throughout the pygmy forest soil. Trends in  $k_l$  and XP were similar for Sites 1–3, but timing and magnitude of changes were not. Differences in BXP apparently caused  $k_l$  to decrease earliest

and most severely at Site 1, followed in order by Sites 2 and 3. As was always found in this study, BXP in northern red and blackjack oak at Site 3 were almost identical, yet  $k_l$  in blackjack oak was always higher than it was for northern red oak. Even under similar atmospheric and edaphic conditions, stomatal closure in blackjack oak occurred later in the day than it did in northern red oak. These consistent patterns suggest an intrinsic difference in stomatal functioning between the two species.

Peak drought conditions were typified by 11 September, which was moderately hot and very dry (Fig. 6). Differences in BXP at Sites 1–3 were reflected in the diurnal trends of  $k_l$  and XP. At Sites 1 and 2,  $k_l$  was near zero all day. At Site 3,  $k_l$  in blackjack oak had three low peaks of  $\approx 0.3$  cm/s. In contrast,  $k_l$  in northern red oak was near zero all day. Even with low  $k_l$  levels in the morning, XP in blackjack oak decreased at Sites 1–3 to between  $-4000$  and  $-4500$  kPa, and in northern red oak at Site 3 to  $-3000$  kPa.

Observations of diurnal trends showed that during summer drought periods water deficits became large and stomatal closure occurred, sometimes throughout the entire day. So far, changes in  $k_l$  have been discussed in relation to midday

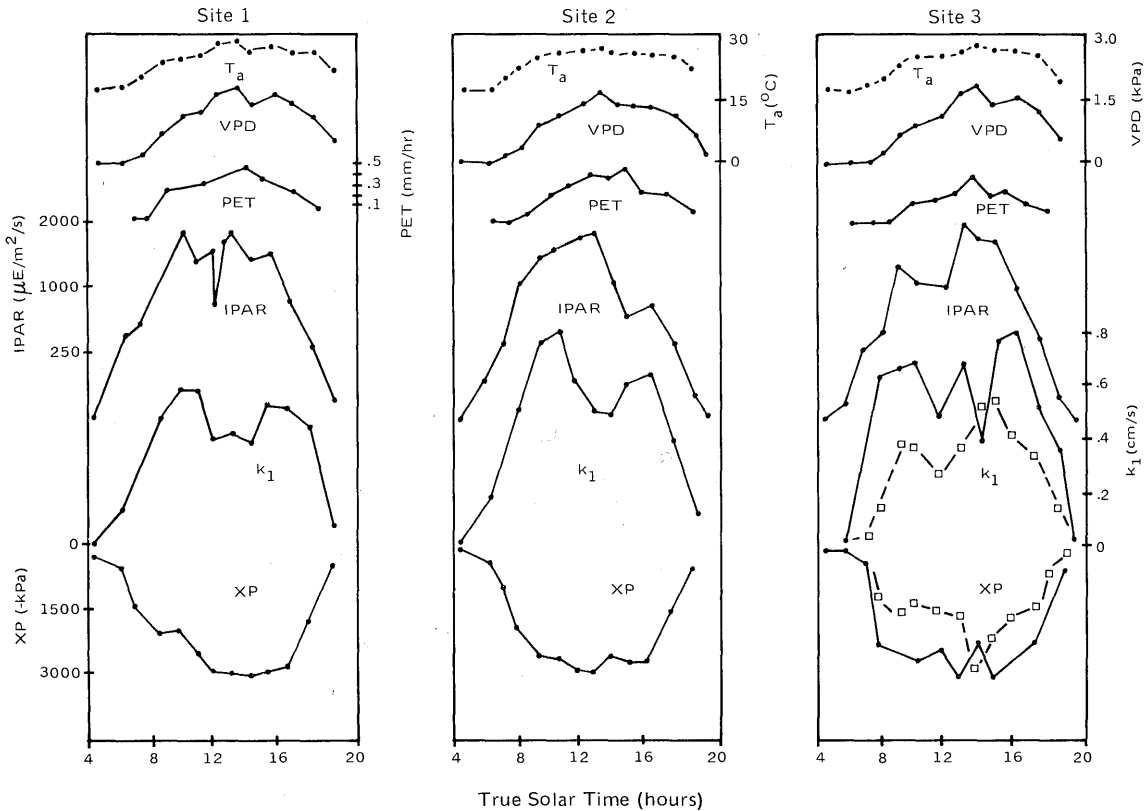


FIG. 4. Diurnal patterns of air temperature ( $T_a$ ), vapor pressure deficit (VPD), potential evapotranspiration (PET), photosynthetically active radiation incident upon the site (IPAR), leaf conductance ( $k_l$ ), and xylem pressure potential (XP) for blackjack oak (solid circle) and northern red oak (open square) on 4 July (predrought).

out knowing what triggers stomatal closure under light-saturated conditions. The system may be analogous to a feedback mechanism, with stomata beginning to close as XP approaches a critical value, cutting down on water loss and preventing XP from declining beyond the critical point. If BXP regulates the degree of stomatal opening, along with limiting XP or VPD, then the plant is responding to its prior, as well as current, internal water status. How this can be done is not known.

#### Functional relationships between plant and environmental factors

*Predawn tree water status with respect to soil moisture.*—Although SMC was measured only in the top 30 cm, significant correlation existed between BXP and SMC at all sites. As site soil depth increased, the coefficient of determination ( $r^2$ ) decreased (Site 1,  $r^2 = .95$ ; Site 3,  $r^2 = .69$ ). Had SMC in the entire soil profile been measured, as at Site 1, perhaps as much as 95% of the variation in BXP at all sites could have been explained by SMC. Similar patterns have been noted by Sucoff (1972) and Hinckley and Bruckerhoff (1975).

*Stomatal response to environmental and plant factors.*—Since changes in  $k_l$  are not closely related to any single plant or environmental factor, analysis was done in two ways. Multiple regression analysis was used to explain the variation in  $k_l$  due to combinations of other factors ( $r^2 = .67$  and  $.73$  for Site 1 sun and shade leaves, respectively), while boundary line analysis was used to interpret the response of  $k_l$  to single variables (Webb 1972, Jarvis 1976, Hinckley et al. 1978).

*Changes in  $k_l$  with respect to LPAR.*—Initially in both blackjack and northern red oak,  $k_l$  increased rapidly with small increases in LPAR. With continued increases in LPAR,  $k_l$  leveled off. Federer and Gee (1975) observed that  $k_l$  was independent of light levels above  $250 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  in yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), and American beech (*Fagus grandifolia* Ehrh.), while Chambers (1976) found light saturation levels for white, black, and northern red oak, and sugar maple saplings in the field to range from 50 to  $90 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . In this study, light saturation for northern red oak was  $92 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  as compared with  $65 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  reported by Chambers (1976). Light saturation in blackjack oak was  $116 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ .

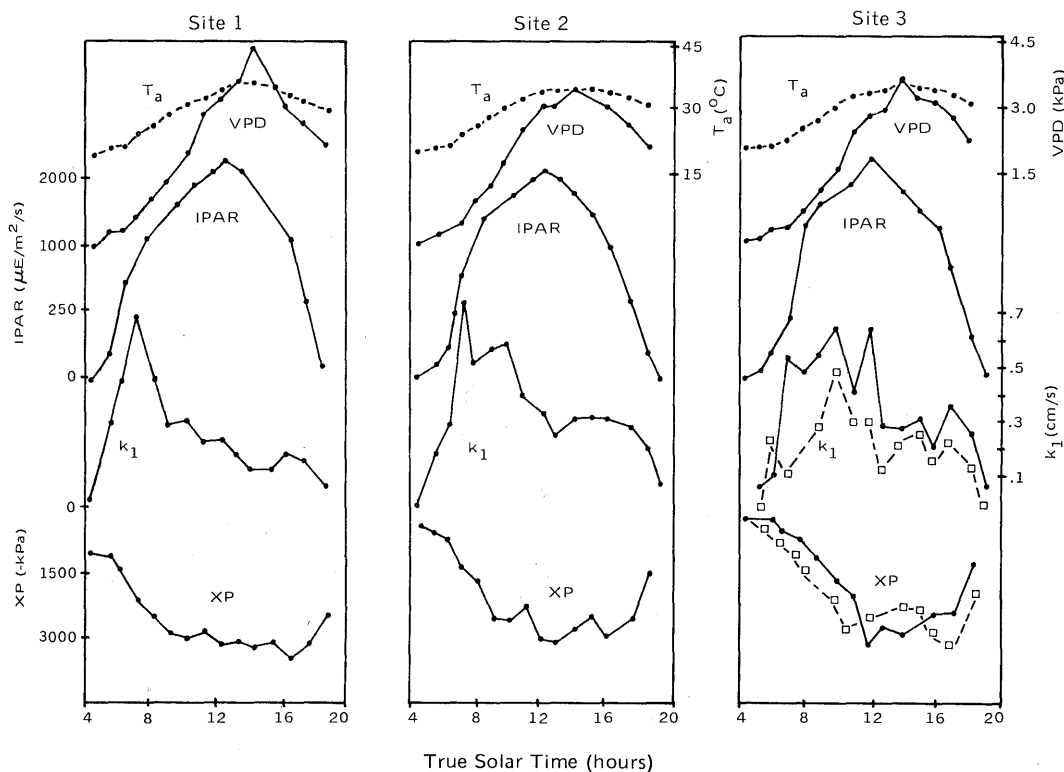


FIG. 5. Diurnal patterns of air temperature ( $T_a$ ), vapor pressure deficit (VPD), photosynthetically active radiation incident upon the site (IPAR), leaf conductance ( $k_l$ ), and xylem pressure potential (XP) for blackjack oak (solid circle) and northern red oak (open square) on 30 July (mid-drought).

*Changes in  $k_l$  with respect to VPD.*—Reductions in  $k_l$  are associated with increases in VPD (Davies and Kozlowski 1974, Federer and Gee 1976). The VPD threshold, above which  $k_l$  decreased, was 2.0 and 1.5 kPa for blackjack and northern red oak, respectively. Based upon regression analysis, VPD was the second most important independent variable (after BXP) in explaining variation in  $k_l$ .

*Changes in  $k_l$  with respect to  $T_a$ .*—Effects of  $T_a$  on  $k_l$  are difficult to separate from other variables, particularly VPD. In general, stomates will open slightly as  $T_a$  increases up to  $\approx 30^\circ\text{--}35^\circ\text{C}$  (Schulze et al. 1975, Hinckley et al. 1978). Maximum  $k_l$  in blackjack and northern red oak occurred at  $24^\circ$  and  $27^\circ\text{C}$ , respectively.

*Changes in  $k_l$  with respect to XP.*—Xerophytic species maintain higher levels of  $k_l$  under increasing levels of water deficit than do mesophytic species (Hinckley et al. 1978). Blackjack oak, probably the most xerophytic of the eastern oaks, had a lower threshold ( $-3700$  kPa), below which  $k_l$  decreases, than northern red oak ( $-2500$  kPa). Phelps et al. (1976) found thresholds of between  $-1700$  and  $-2450$  kPa for northern red, white, and black oak, and sugar maple. Maintenance of higher  $k_l$  at decreasing XP could be advantageous to species occupying xeric sites by al-

lowing both evaporative cooling of leaves and higher gas exchange rates to continue. Leaves would obviously have to tolerate more severe water deficits, however.

*Changes in  $k_l$  with respect to BXP.*—Boundary line analysis showed that as BXP decreased, daily maximum  $k_l$  decreased almost linearly in blackjack and northern red oak, but much more rapidly in the latter. For daily maximum  $k_l$  to decrease to  $<50\%$  of its seasonal maximum value, BXP in northern red and blackjack oak must decrease to  $<-600$  and  $-2100$  kPa, respectively. Also, regression analysis indicated that BXP alone explained 48, 38, and 32% of the variation in  $k_l$  of blackjack oak sun leaves at Sites 1, 2, and 3, respectively.

#### *Spatial trends in tree water status*

A transect (Fig. 2) was used to examine spatial, or site, variation in seasonal trends of BXP, SMC, and  $k_l$  from just prior to the onset of drought until recovery (Fig. 7). During drought periods the largest differences between sites occurred. In the original hypotheses, SMC,  $k_l$ , and BXP had been expected to follow a gradient of increasing deficit from the ridge to the bluff. These hypotheses appear correct for Sites 1–3, but not for Site 4. Instead of being greatest at Site 4,  $k_l$  and



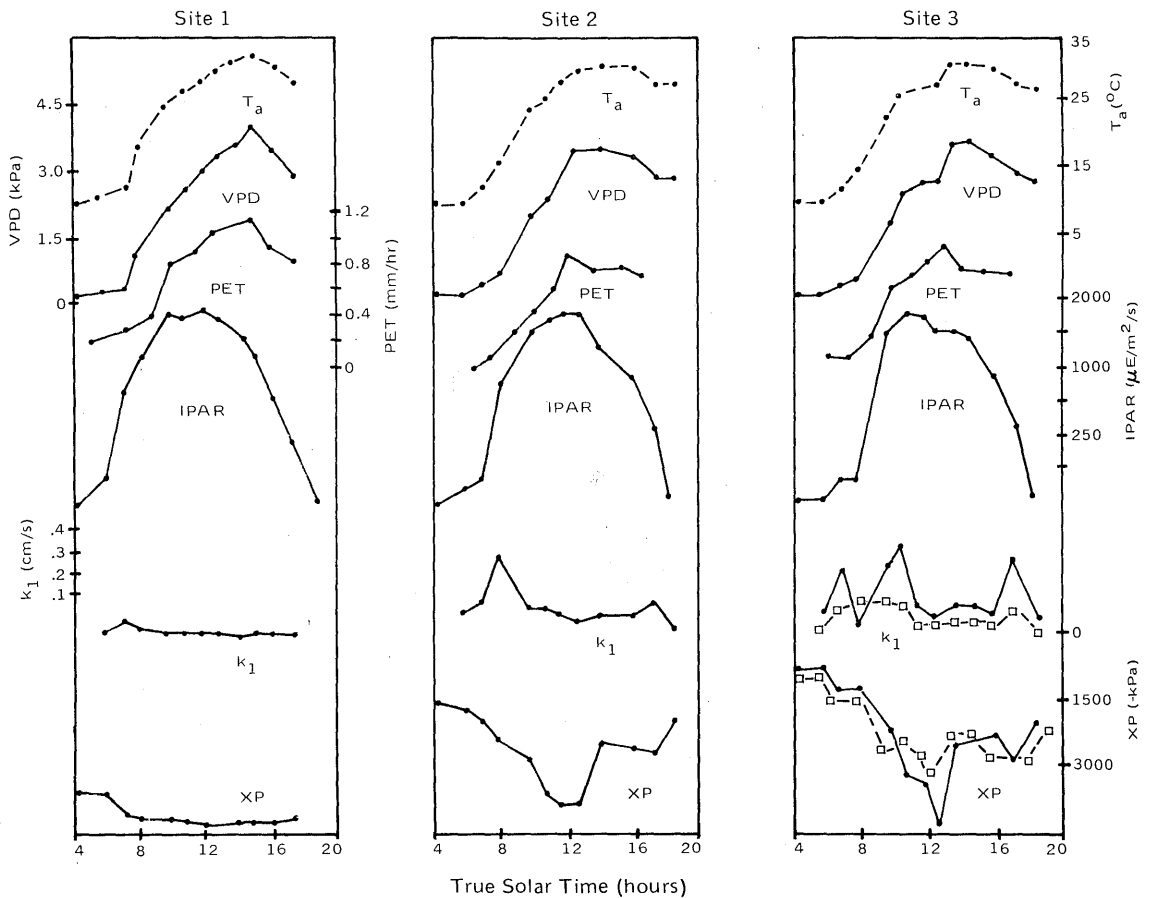


FIG. 6. Diurnal patterns of air temperature ( $T_a$ ), vapor pressure deficit (VPD), potential evapotranspiration (PET), photosynthetically active radiation incident upon the site (IPAR), leaf conductance ( $k_1$ ), and xylem pressure potential (XP) for blackjack oak (solid circle) and northern red oak (open square) on 11 September (peak drought).

SMC were lower than at the pygmy sites, and BXP was lower than at two of the three pygmy sites. Why did this occur? Site 4 was on the ridge and had a very rocky, well-drained soil with low water holding capacity. The rooting zone was only 35–50% of the soil volume because of stoniness (Table 1). In addition, leaf area at Site 4 was almost double that of the pygmy sites and transpiration during periods of adequate moisture supply would have been much greater, depleting the available moisture much more quickly than at the pygmy sites. These factors would in turn cause BXP and  $k_1$  to decrease to lower levels than at the pygmy sites.

The hypothesis that the dwarfing of the trees at Sites 1–3 was due to dieback caused by water deficit induced stress appears incorrect in light of the greater water stress in the non-pygmy forest than at two of the three pygmy sites. However, water deficits could still be involved in the causative process along with other factors such as soil acidity and nutrient deficiency.

### Soil fertility

The availability of adequate amounts of mineral nutrients in the proper ratios is of major importance to plant growth and survival. Calcium, Mg, P, B, Zn, Mn, S, Al, and pH varied considerably between the pygmy and non-pygmy forest soils, while K, Fe, Cu, and Mo did not (Table 3). Aluminum and S were higher, while pH, Ca, Mg, P, B, Zn, and Mn were lower in the pygmy forest soil than in the non-pygmy forest soil. Greatest changes in concentration of all elements occurred between Sites 3 and 4.

Soil  $pH_w$ , Ca, and Mg were fairly constant throughout the pygmy forest soil at  $\approx 4.6$ , .25 meq/100 g, and .12 meq/100 g, respectively (Table 3). They increased dramatically from the pygmy to the non-pygmy forest soils to maximums of 6.1, 4.0 meq/100 g, and 1.2 meq/100 g, respectively. In addition, pH, Ca, and Mg varied little with depth. Levels decreased slightly to depths of 60 cm in both pygmy and non-pygmy forest soils.

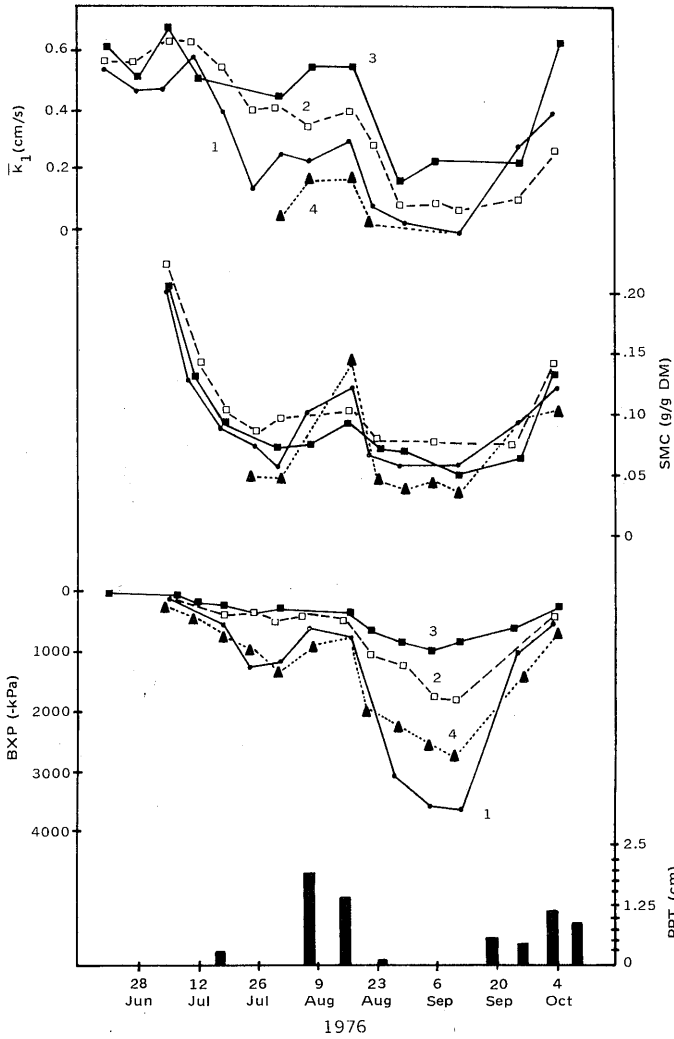


FIG. 7. Spatial patterns of midday leaf conductance ( $k_1$ ), soil moisture content (SMC), predawn xylem pressure potential (BXP), and precipitation (PPT) for blackjack oak at Sites 1 (solid circle), 2 (open square), 3 (solid square), and 4 (solid triangle).

Extractable P was lower in the pygmy forest soil than in the non-pygmy soil (Table 3). The high Al content of the pygmy forest soil probably reduced the availability of P (Baule and Fricker 1970). Because of minimal levels of Ca and Mg and high levels of Al, P was probably not limiting pygmy tree growth.

Zinc, B, and Mn content in the non-pygmy forest soil was much higher than in the pygmy forest soil (Table 3). Zinc, which ranges from 10 to 300 ppm total content in soils, is generally more available in acid rather than alkaline soils (Treshow 1970). However, in Buzzard's Roost soils Zn increased from 2.1 to 10.2 ppm as the pH increased from 4.6 to 6.1. Boron content of soils ranges from 5 to 200 ppm (Treshow 1970, Buckman and Brady 1974). The availability of B depends upon soil pH, organic matter, and moisture conditions. Although B content in the pygmy forest soils

was very low it was only slightly higher in the non-pygmy soil (Table 3). Manganese availability is believed to increase with decreasing soil pH (Tisdale and Nelson 1975), but Hewitt and Smith (1975) point out that as soil pH drops below 5.0, Mn availability decreases. At Buzzard's Roost, Mn was very low in the acidic pygmy forest soil and high in the less acidic non-pygmy forest soil.

Exchangeable  $Al^{3+}$ , along with the loss of Ca, Mg, and K, is responsible for the development of acid soils, and Al toxicity may limit plant growth in such soils (Adams and Pearson 1967, Tisdale and Nelson 1975). Extractable Al was extremely high in the pygmy forest soil and decreased to low levels in the non-pygmy forest soil (Table 3). Adams and Lund (1966) found that levels of Al required for toxicity varied in acid soils, because of differences in clay mineralogy. However,

TABLE 3. Soil test results from 13 points along a transect at Buzzard's Roost (see Fig. 2). A. Soil pH, organic matter (O.M.), Ca, Mg, K, P, cation exchange capacity (CEC), and percent base saturation (B.S.).

Distance from edge of bluff (m)	Site	pH <sub>w</sub>	pH <sub>s</sub>	O.M. (%)	P <sub>2</sub> (ppm)	Ca	Mg	K	CEC	B.S.(%)
						meq/100 g				
5	1	4.6	3.7	2.2	7	.25	.12	.08	9.65	4.7
17		4.5	3.8	2.4	12	.25	.12	.14	10.51	4.9
30	2	4.6	3.7	2.2	4	.25	.16	.18	9.60	6.3
45		4.8	3.8	1.7	4	.25	.12	.16	10.30	4.9
60	3	4.6	3.8	2.5	5	.25	.12	.16	8.63	6.1
65		4.7	3.9	2.7	3	.25	.12	.17	6.55	8.4
70		4.9	4.1	2.5	7	.25	.12	.21	6.49	9.1
75		4.9	4.1	1.6	12	.25	.12	.13	5.50	9.1
80		4.9	4.0	2.9	11	.50	.21	.13	6.94	12.1
85		5.4	4.4	3.9	14	2.50	.37	.20	9.08	33.9
90	4	5.6	4.5	2.9	22	2.50	.58	.15	9.34	34.7
115		5.6	4.6	2.8	22	2.75	.66	.15	8.67	41.2
140	5	6.1	5.2	3.2	20	4.00	1.20	.20	9.43	57.6

## B. Soil micronutrients.

Distance from edge of bluff (m)	Site	S	B	Zn	Mn	Fe	Cu	Mo	Al
		(ppm)							
5	1	73	0.3	2.3	1	42	1.1	2.3	585
17		79	0.3	2.1	1	44	0.9	2.1	616
30	2	60	0.2	2.4	2	43	0.9	1.8	437
42		64	0.3	2.6	1	41	0.8	2.8	598
60	3	56	0.3	3.0	1	59	1.0	1.8	299
65		72	0.2	4.0	1	65	1.8	1.8	261
70		37	0.2	3.5	1	51	1.4	1.9	178
75		50	0.4	2.1	1	43	0.6	1.5	149
80		11	0.4	2.8	5	88	0.8	1.2	24
85		16	0.5	6.4	44	109	1.4	1.2	16
90	4	16	0.6	5.2	48	60	0.8	1.5	16
115		13	0.6	5.9	47	37	0.8	1.0	7
140	5	14	0.7	10.2	84	18	0.8	0.8	3

levels of Al in the pygmy forest soil were so high that Al was probably at least somewhat toxic regardless of mineralogy.

Base saturation is an important factor in evaluating cation availability (Tisdale and Nelson 1975). Total base saturation considered optimum for plant growth is 90–100%, with partial base saturations of 65–80% Ca, 10–15% Mg, and 2–7% K (Ankerman and Large 1977). Optimum ratios are 5 to 7:1 for Ca:Mg and 2 to 4:1 for Mg:K.

Base saturation of the non-pygmy forest soils (35–58%) was much greater than that of the pygmy forest soils (5–6%; Table 3). Base saturation of Bolivar soils, which resemble Buzzard's Roost soils, ranges from 46–54% at seven depths between 0 and 135 cm (Scrivener *personal communication*). Fertility of Bolivar soils is low to very low and forests very similar to the non-pygmy forest at Buzzard's Roost are common on Bolivar soils (Grogger and Persinger 1976).

Between 80 and 85 m from the bluff (between Sites 3 and 4), base saturation increased dramatically from 12 to 34% (Table 3). This abrupt change coincides with

the transition from pygmy trees to straighter, taller trees.

The effects of acid soils are both direct and indirect (Hewitt and Smith 1975). First, there is direct injury due to high H ion concentrations. Indirect effects are:

1) impaired absorption of Ca, Mg, K, and P (Maas 1969, Lund 1970),

2) increased availability of Mn, Al, and at times Fe, Cu, and Ni, leading to toxicities,

3) reduced availability of P (Foy 1974b),

4) low concentrations of Ca, Mg, K, P, and sometimes Cu and other micronutrients as a result of prolonged leaching, and

5) unfavorable biotic conditions such as low mycorrhizal activity.

At pH levels where the H ion concentration is considered harmful, Al and Mn may be soluble in toxic quantities. These elements are considered more harmful to plants than H ions. Therefore, in acid soils, the harmful effects of high H ion concentrations are largely indirect (Foy 1974a).

Many of the above effects were present in the pyg-

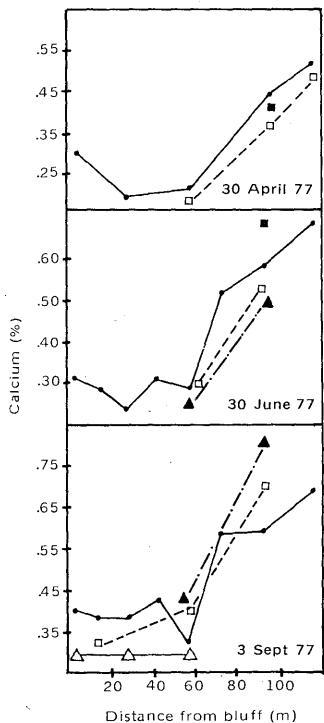


FIG. 8. Spatial patterns of foliar calcium concentration in blackjack oak (solid circle), northern red oak (open square), black oak (solid triangle), white oak (solid square), and necrotic blackjack oak (open triangle), at three times during the growing season.

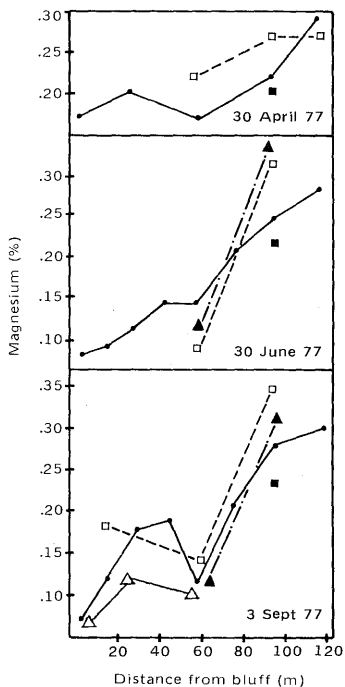


FIG. 9. Spatial patterns of foliar magnesium concentration in blackjack oak (solid circle), northern red oak (open square), black oak (solid triangle), white oak (solid square), and necrotic blackjack oak (open triangle), at three times during the growing season.

pygmy forest soil. For example, soil pH and levels of Ca and Mg were extremely low, probably due to a combination of inherently low concentrations in the sandstone, prolonged leaching, and lack of soil enrichment by organic matter. In addition, exchangeable Al was extremely high.

*Foliar nutrient composition*

Foliar analysis is widely used in assessing the nutrient status of forest trees, but the techniques and interpretations involved are not simple. Meaningful analysis must take into account variations within individual trees, such as those due to crown position, leaf age, and seasonal change. Cain (1959) found considerable variation of elements in apple leaves because of age and position on shoots. Concentrations in leaves from the center one-third of all shoots were least variable. The midshoot leaf is widely used in sampling for this reason, and was used in this study.

*Spatial trends in foliar nutrient concentration*

On 30 April, 30 June, and 3 September concentrations of Ca, Mn, and Mg differed appreciably between pygmy and non-pygmy foliage, while concentrations of other elements did not (Figs. 8, 9, and 10) (Reich

1977). Calcium, Mg, and Mn were all lower in the pygmy foliage than in the non-pygmy foliage in blackjack, black, and northern red oak. The major changes in concentrations occurred at the pygmy-non-pygmy boundary. Calcium concentration in blackjack oak leaves was fairly constant between Sites 1-3 and then increased dramatically between Sites 3 and 4. Magnesium concentration in blackjack oak leaves increased steadily upslope from Site 1 to 24 m beyond Site 4. White oak foliage, sampled only at Site 4, and post oak, sampled only at Site 5, followed the trend of increasing nutrient concentration with distance from the bluff. In addition, chlorotic leaves from pygmy blackjack oaks had lower Ca, N, Mn, Mg, and B, and higher Al, than healthy leaves from the same trees.

Foliar nutrient composition of pygmy and non-pygmy seedlings grown under identical greenhouse conditions was the same for all elements, except Al. Pygmy seedling foliage had more than double the Al of the non-pygmy seedling foliage. This could have been due to greater Al uptake by the pygmy seedlings, but was more likely the result of greater concentrations of Al in the pygmy acorns than in non-pygmy acorns.

Within a nutrient-poor environment such as the pygmy forest ecosystem, could there be a nutrient "sink," either in the soil or plants, which accumulates and

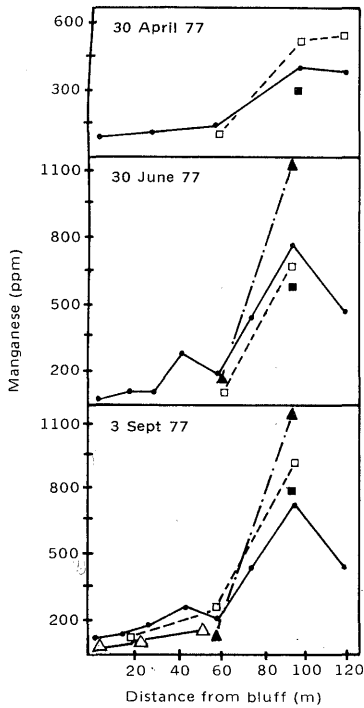


FIG. 10. Spatial patterns of foliar manganese concentration in blackjack oak (solid circle), northern red oak (open square), black oak (solid triangle), white oak (solid square), and necrotic blackjack oak (open triangle), at three times during the growing season.

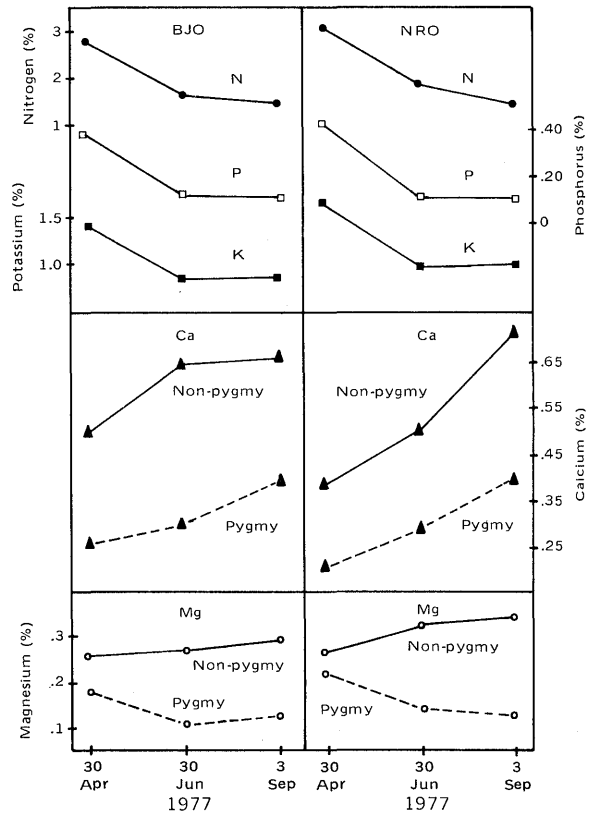


FIG. 11. Seasonal patterns of foliar concentrations of N (solid circle), P (open square), K (solid square), Ca (solid triangle), and Mg (open circle) for blackjack oak (BJO) and northern red oak (NRO).

withdraws nutrients from the system? To test whether lichens (*Cladonia furcata* Huds. Schrad and *C. subtenuis* Abb. Evans) beneath the pygmy forest could be nutrient accumulators, plant analysis was done. Nutrient concentrations in *Cladonia* at Sites 1 and 3 varied widely from those in tree foliage, yet surprisingly, there were much lower concentrations of every element, except Al and Fe, in *Cladonia* than in either pygmy or non-pygmy tree foliage. Levels of Fe and Al were about two to five times greater in *Cladonia* than in the tree foliage. Concentrations of all elements in *Cladonia* were slightly higher at Site 3 than at Site 1.

#### Seasonal trends in foliar nutrient concentration

Concentrations of N, P, and K in blackjack and northern red oak foliage at all sites decreased as the leaves matured, while Ca concentration increased (Fig. 11). Similar patterns have been observed in other deciduous tree species by Duvigneaud and Danaeyerde Smet (1970) and Likens et al. (1970). In contrast, seasonal changes in Mg concentration show no clear trend. Hoyle (1965) found Mg increased in some trees and decreased in others. In this study Mg concentration in non-pygmy northern red and blackjack oak foliage increased slightly, while decreasing in the pygmy

trees. No apparent differences were observed for other elements.

*Interpreting nutrient levels.*—As shown above, nutrient concentration varies considerably with site and season, and amounts, per se, of any element cannot always be declared adequate or deficient. For example, Titus and Boynton (1953) found apple (*Malus pumila* Mill.) leaf K (percent dry mass) to vary by as much as 400% at a given level of soil K. In this study, the concentrations of Ca and Mg in the pygmy foliage were much lower than oak foliage concentrations considered normal (Leaf 1973). In contrast, Mn concentration in the pygmy foliage, although much lower than in the non-pygmy foliage, was probably about normal.

#### Correlation of foliar and soil nutrient levels

There was no correlation between plant and soil P, but there was for Ca and Mg. Phosphorus concentrations in pygmy and non-pygmy foliage were always very similar, even while changing seasonally, but corresponding levels in the soil were 6 and 21 ppm, respectively (Table 3). In blackjack oak foliage, concen-

trations of Ca and Mg in spring, early summer, and late summer were significantly correlated with soil Ca and Mg. Coefficients of determination ( $r^2$ ) ranged from .75 to .94. The fact that foliar and soil Ca and Mg were significantly correlated is another indication that these elements were probably deficient. On the other hand, lack of correlation between foliar and soil P seemed to indicate an adequate supply of P.

#### THE EFFECTS OF NUTRIENT AND WATER RELATIONS UPON VEGETATIVE GROWTH AND FORM

The availability of water and nutrients to plants is of paramount importance in terms of growth, development, and survival. It seemed obvious from the beginning of this study that the pygmy oak morphology must be a result of the severe environment of the bluff site. However, it was difficult to determine what caused this particular vegetative condition. Modifications of growth and form by the pygmy oaks resemble those made by stunted trees in such diverse sites as dune sand, serpentine soils, coastal terraces in California, and pine barrens of New Jersey. The modifications were:

- 1) reduction in the size of leaves and reproductive organs,
- 2) shrubbiness of form and plagiotropism,
- 3) stunting of height and diameter growth,
- 4) greater glaucousness,
- 5) periodic dieback, and
- 6) rosetting of leaves and buds.

Many of these modifications are characteristic of xeromorphism. Proctor and Woodell (1975) found that leaves of stunted plants growing on soils derived from serpentine have thick palisade tissue, a lower epidermis with two layers of cells, and are often smaller and thinner and have fewer stomata than leaves of the same species growing on nonserpentine soils. Also, the predominance of xeric plant and soil characteristics led early investigators to assume that drought was largely responsible for the evolution of serpentine-soil vegetative form. Similarly, our preliminary thoughts and hypotheses about the pygmy oak ecosystem at Buzzard's Roost had been that drought was largely responsible for the existence of the pygmy oak forest. However, the 1976 results showed that soil moisture deficits and/or plant water stress per se, did not cause stunted growth.

Plant species in other "pygmy" communities differ from those found in adjacent "normal" communities, just as at Buzzard's Roost. Proctor and Woodell (1975) stated that in many parts of the world serpentine areas have large numbers of endemic species. For example, Whittaker (1954) found 30 endemic species on serpentine soils in the Siskiyou Mountains (Oregon, U.S.A.) as compared to only two in dioritic soils. Jenny et al. (1969), Westman (1975), and Westman and Whittaker (1975) reported that, in the pygmy forest region of

northern California, species distribution follows a podzolization gradient, and that the principal tree species were endemic conifers. In the pygmy pine forests of New Jersey, at least 55 plant species are present which are not known to grow elsewhere in New Jersey (Robichaud and Buell 1973).

In the pygmy pine forests of New Jersey, pygmy blackjack oak is the second most dominant species, following stunted pitch pine. These forests are common where fires occur as often as every 10 yr or less and it is generally believed that a long history of frequent and severe fires is responsible (Robichaud and Buell 1973). Both pitch pine and blackjack oak are capable of sprouting from the root crown and producing seeds in just a few years after a fire. The reoccurrence of fire kills the young sprouts, and the process repeats itself.

Although fires are fairly common in southwest Missouri, the ages of the pygmy trees at Buzzard's Roost show that a long period of time has elapsed since an exceptionally hot fire occurred. Therefore, the possibility is negligible that fire is the agent responsible for the existence of the pygmy forest at Buzzard's Roost.

Since neither genetic differences, fires, nor water deficits seem responsible for the dwarfed condition of the oaks, what is? We believe the soil differences between the pygmy forest and the non-pygmy forest, including low pH, low levels of Ca and Mg, and high levels of Al, are responsible for the existence of the pygmy oaks at Buzzard's Roost. Foliar analysis showed Ca and Mg to be very low and probably deficient, and levels of Ca and Mg in leaves and soil had significant correlations. Proctor and Woodell (1975) stated that the elemental composition of serpentine soils varied greatly, but usually included certain adverse characteristics which caused severe stunting of vegetation. Among those characteristics were low pH, low levels of N, P, K, and Ca, a high level of Mg, and unfavorable physical factors. Jenny et al. (1969) believed that intensely podzolized soils were largely responsible for the stunted growth of *Cupressus pygmaea*, *Pinus muricata*, and *P. contorta* ssp. *bolanderi* on terrace flats, in contrast to nearby giant coastal redwoods (*Sequoia sempervirens* Lamb. Endl.). The pH of the pygmy-podzol soils ranged from 2.8 to 3.9, while Ca, Mg, and K were <1 meq/100 g. Jenny et al. (1969) stated that soil impoverishment, once initiated by a particular feature of a site, could result in a reinforced feedback between nutrient loss, acidification, and changing ion solubilities. These would result in increasingly stunted vegetation, with shrinking nutrient pools held in the living mass and increasing acidity and loss of nutrients to lower soil horizons or groundwater. A similar feedback system seems to be working at Buzzard's Roost, although the process of podzolization is missing. Decreasing soil moisture also affects nutrient availability. Brown (1953) found that as the wilting point was approached, cation movement

slowed down. Hosner et al. (1965) found that nutrient content per seedling decreased as moisture stress increased. At Buzzard's Roost, soil moisture increased considerably from Site 1 to Site 3. At Site 4 on the ridge, a combination of

- 1) higher total transpiration due to more leaf area,
- 2) decreased soil volume due to high stone content, and

- 3) greater loss of soil moisture in subsurface flow due to landscape position is responsible for greater tree water deficits than those at pygmy Sites 2 and 3 and similar to those at Site 1. Soil fertility, on the other hand, decreased tremendously between Site 4 and Site 3, and differs only slightly between the three pygmy forest sites.

One would expect that the combination of the greatest water deficits and lowest soil fertility would influence tree growth at Site 1, as it does. Tree height, leaf area, leaf size, acorn mass, and stem diameter were lowest at Site 1, near the bluff, and increased slightly towards Site 3. Between Sites 3 and 4 tree height, leaf area, and leaf size increased dramatically. Tree water stress decreased considerably between Site 1 and Site 3, while fertility increased only minimally and was apparently still poor enough to cause stunting and dwarfed growth. At Site 4, tree water deficits were greater than at Sites 2 and 3, but fertility was so greatly improved that tree growth was about normal.

In late summer of both 1976 and 1977, leaf chlorosis and necrosis began first on pygmy trees near the bluff, and then progressed from Site 1 to Sites 2 and 3. Leaf tips appeared scorched, turned yellow and then brown, and necrosis moved in from the edges of the leaf blades. If water deficits alone were responsible then necrosis should have occurred earlier at Site 4 than at Site 2. If soil infertility were the sole cause, Sites 1, 2, and 3 should have experienced similar degrees of necrosis, because soil fertility at all three sites was similar. However, the pattern of necrosis, which was widespread at Site 1 (>50% of all leaves), moderate at Site 2 (<50%), and low at Site 3 (<10%), implies that the reduced uptake of an already minimal supply of nutrients, plus possibly increasing Al concentration as the soil dried, may have caused the leaf necrosis.

#### SUMMARY AND CONCLUSIONS

There are clearly diverse mechanisms by which pygmy oaks adapt/respond to the extreme conditions of the Buzzard's Roost site. The trees were growing in a very acid soil with low levels of Ca and Mg and high levels of Al. These factors are interdependent and function as a "feedback" system. Also, the pygmy trees occupy an exposed site with high irradiance, a moderate slope, a shallow, sandy soil with low water holding capacity and a limited volume available for rooting; in short, a very dry site with high potential evapotranspiration conducive to the development of

extreme plant water deficits during droughts. These xeric site characteristics compound the problem of ion uptake by reducing an already minimal supply.

The demanding environment at Buzzard's Roost has resulted in the altered morphology of the pygmy oaks. These trees exhibit severe stunting of growth, reduction in the size of leaves and acorns, and rosetting of leaves and buds. Also, they have a twisted, gnarled appearance due to the periodic dieback of limbs, branches, and upper parts of the trunk. The adversity of the site conditions increases towards the bluff along with decreases in tree height, leaf and acorn size, and increases in rosetting (Fig. 1). The growth of seedlings from pygmy vs. non-pygmy acorns did not seem to differ due to acorn source, but due to acorn size.

Blackjack oak appears to be more drought tolerant than white, black, or northern red oak. Stomatal closure did not occur in blackjack oak until a XP of -3700 kPa was reached, in contrast to a threshold range of -1850 to -2500 kPa for white, black, and northern red oak (Phelps et al. 1976). Tolerance to acidic soil, low levels of Ca and Mg, and high levels of Al may also be greater in blackjack than in other oaks. Post oak, considered as drought tolerant as blackjack oak, did not occur on the pygmy bluff site and was found only at Site 5, the most nutrient-rich site. Northern red, black, and white oak, all less drought tolerant than post oak, were found on less favorable sites than post oak. By evaluating species distribution among the various soil types at Buzzard's Roost, the ranking of the oaks in order of "infertility" tolerance was: Blackjack > Northern Red > Black > White > Post. These rankings are very different from those for drought tolerance. Since this classification is based on only this one ecosystem, more research in this area is obviously needed.

The ability of the pygmy oaks to survive at all must be viewed as an indication of the tenacity with which vegetative life seeks to preserve its existence. This ecosystem seems to have come to a steady state condition in which the plants are able to sustain themselves, but conditions are too poor for good growth to occur.

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