

Oak mortality in sand savannas following drought in east-central Minnesota¹

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ABSTRACT

FABER-LANGENDOEN, D. AND J. R. TESTER. (Department of Ecology, Evolution and Behavior, University of Minnesota, Minneapolis, MN 55455). Oak mortality in sand savannas following drought at Cedar Creek, Minnesota. Bull. Torrey Bot. Club 120: 248-256. 1993.—Savanna plots that were established and sampled in 1984 at Cedar Creek Natural History Area in east-central Minnesota were resampled in 1989, towards the end of a major drought period. Tree diameter was measured and mortality was assessed for all stems ≥ 10 cm dbh in eleven 50 × 75 m plots. *Quercus ellipsoidalis* E. J. Hill (northern pin oak) and *Q. macrocarpa* Michx. (bur oak) dominate the savannas, accounting for >95% of all stems ≥ 10 cm dbh. In 1984, diameter distributions and species composition were significantly different on different soil types. Zimmerman soils had a larger proportion of stems in the 10–25 cm dbh size classes (62%) than did the Sartell soils (36–60%), and a significantly larger proportion overall of *Q. ellipsoidalis* stems (93%) than did the Sartells (51–84%). Plots burned during the previous 20 years had fewer stems in the 10–25 cm dbh size class (45%) compared to unburned plots (58%). These differences were not changed by mortality over the 1984–1989 period, nor did diameter distributions within a plot change significantly over this period. Average five-year mortality rates per plot from 1984–1989 for *Q. ellipsoidalis* (21.4%, range 0.0–60.0%) were significantly higher than for *Q. macrocarpa* (6.1%, range 0.0–33.3%). Five-year mortality rates of *Q. ellipsoidalis* declined from 60% to 15% with higher total stem basal area and density. Drought or large moisture changes may have been primary factors responsible for oak mortality. Other factors, such as percent organic matter, depth to water table, and fire frequency were not correlated with mortality rates. The inverse relation between mortality and stand density suggests that the possible effects of drought varied with stand structure. Closed savannas or woodlands had lower mortality rates than open savannas. These findings emphasize the role of climate in maintaining sand savannas in the prairie-forest border region.

Key words: *Quercus*, savanna, mortality, drought, Palmer Index, climate.

Variations in recruitment, growth and mortality of trees along the prairie-forest border of the upper Midwest of the U.S. are of interest in understanding the origin and maintenance of oak savannas or barrens. At the regional level such

variation is in part dependent on interactions between climate, topography and fire regimes (Grimm 1984; Sharpe et al. 1987; Clark 1990). European settlement led to reductions in fire frequency, causing oak savannas to rapidly change to oak woodland (Cottam 1949; Grimm 1984). Conversely, heavily logged and burned sites further east of the border favored oak establishment (Nowacki et al. 1990). These newly formed woodlands appear to be relatively stable, at least in the short term, even in the presence of re-introduced fire regimes, particularly for trees >20–25 cm dbh (White 1983). However, their long term stability seems doubtful, as older oak woodland stands elsewhere are dominated by red and sugar maple in the understory, a pattern thought to be related as much to climatic change as disturbance (Kline and Cottam 1979; Crow 1988; Abrams 1992).

These observations raise important questions about how savannas can be restored, as well as how they might have originated. For example, Grimm (1984) and others (Transeau 1935; An-

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erson 1990) have suggested that an interaction between climate and fire was responsible for the origin of savannas, whereby periodic droughts increased the flammability of the vegetation.

Studies on oak savanna dynamics have been underway at Cedar Creek National History Area since fire management was introduced in 1964. The occurrence of a drought period in 1988 following a relatively wet period permitted some assessment of the role of moisture changes in oak savanna. The objectives of this study were to 1) measure oak mortality and recruitment during the five year period that included the drought; and 2) determine the influence of fire frequency, soil type, stand structure, and other site factors on oak mortality rates.

Study Area. The oak savanna (or oak barrens) area of Cedar Creek Natural History Area (CCNHA) in east-central Minnesota (45°25'N, 93°10'W) is on a gently rolling sand plain comprised of fine and medium sands of the Sartell and Zimmerman series. Both soils are relatively nutrient poor and have low water content at field capacity; Zimmerman soils (Alfic Udipsamments) have greater nutrient content deeper in the soil profile (> 1 m) and a slightly higher water content than do the Sartell soils (Typic Udipsamments) (Grigal et al. 1974; Tester 1989). Both soils can be further subdivided based on slope inclination into a B (0–6%) or C (6–15%) group.

Elevation in the study area ranges from approximately 280 m to 286 m. The water table is essentially flat at Cedar Creek (M. Basiletti, *pers. comm.*). Fluctuations during the 1984–1989 period are not known. The water level in one part of the study area rose 1 m, from 278.6 m elevation to 279.6 m from August 4, 1989 to July 15, 1991. An approximate depth to water table in 1989 can be calculated by determining the mean elevation of a site or plot from available topographic maps of CCNHA.

Quercus ellipsoidalis E. J. Hill (northern pin oak) and *Quercus macrocarpa* Michx. (bur oak) are the most common tree species in the savanna area. Oak wilt disease, which can kill *Q. ellipsoidalis*, has become an increasing concern in the area (Gibbs and French 1980) and occurs sporadically at CCNHA (see *Methods*).

Prior to European settlement, fires in the region were frequent, perhaps every one to four years, and due almost entirely to native American Indians (Grimm 1984, 1985). No local fire history is available, but fires occurred as recently as the 1930's (Pierce 1954; D. Lawrence and M.

Heinselman, *pers. comm.*). Parts of Cedar Creek have also been disturbed by grazing, woodcutting, and farming (Pierce 1954; Tester 1989). As of 1964 savannas at Cedar Creek have been managed using a variety of prescribed burn frequencies, at intervals of 1–8 yr.

CLIMATE. Annual rainfall averages 726 mm (1950–1980, max = 1037, min = 327) (Tester and Greenland 1987). Rainfall during the period under study was as follows (in mm): 1983, 858; 1984, 882; 1985, 884; 1986, 819; 1987, 523; 1988, 604; 1989, 744; 1990, 959 (NOAA 1983–1990). Thus two years of below normal rainfall in 1987 and 1988 were preceded by three years of above normal rainfall. The Palmer Drought Severity Index (Palmer 1965), which has been calculated since 1895 for a 12 county area in east-central Minnesota that includes Cedar Creek, was used to determine the severity of the drought. The index uses precipitation, temperature, evapotranspiration, and regional constants for water capacity of the soil to calculate soil moisture content at both surface and lower soil levels. Values near 0 are “near normal,” those greater than +4.0 are “extremely moist” and those less than –4.0 are “extreme drought” (Haines et al. 1976). Changes in the Palmer index have been correlated with changes in woody plant water status (Jacquart et al. 1992).

In east-central Minnesota, there have been only six periods since 1895 when the Palmer index dropped below –4.0 for more than two consecutive months. One such six month period in 1923–1924 occurred from October to April and thus did not greatly affect the growing season. In 1910–1911 the index was < –4.0 for 12 consecutive months starting in July. In 1933–1934 the index was < –4.0 for 13 months, starting in August, then again in 1936–1937 for 8 months starting in August. In 1976–1977 the index was < –4.0 for 10 months, starting in September. Finally in 1988, the index was < –4.0 for 6 months starting in May (Fig. 1). The earlier drought periods correspond to those observed elsewhere in the prairie-forest border of Minnesota (Clark 1989). An unusual feature of the 1984–1989 period was that in September 1986, prior to the drought, the index reached a record high of +6.0.

Methods. FIELD PROCEDURES. In 1964, eight savanna sites (compartments), ranging from 2.4 to 27.5 ha in size, were established within a 320 ha block in the southeast corner of CCNHA and randomly assigned a prescribed burn frequency

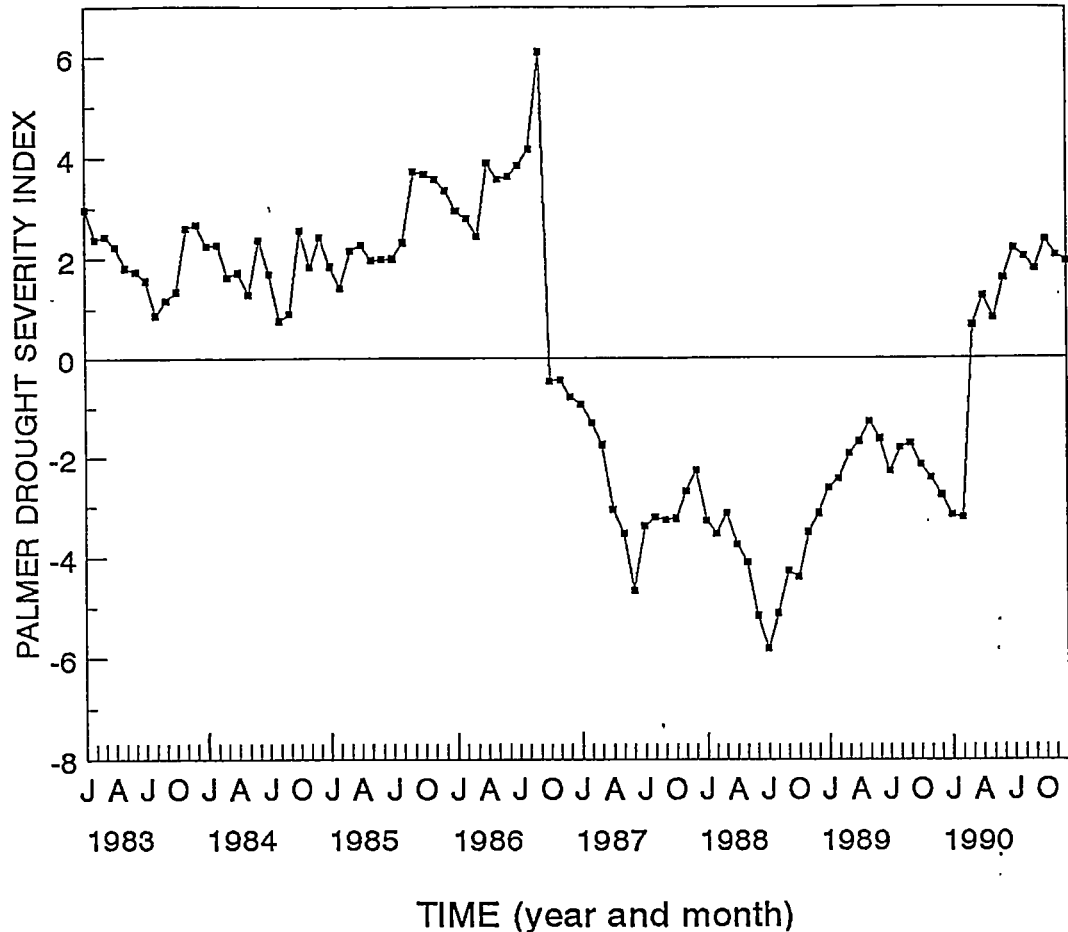


Fig. 1. Changes in the Palmer Drought Severity Index from January, 1983 to December, 1990. The Index is calculated from weather stations in a 12 county area of east-central Minnesota. Values greater than +4.0 "extremely moist" and less than -4.0 are "extreme drought."

(Table 1). Three additional compartments were left unburned. As of 1989, 98 of the 100 scheduled burns had been conducted in spring between April 3 and May 25. The average interval between burns for the eight compartments varied from 1.2 yr (21 burns/2 yr) to 8.3 yr (3 burns/25 yr) (Table 1). The management history of all compartments is similar except that one compartment (No. 16) had been used as a pasture for domestic livestock during the 1940's (Tester 1989).

In September 1984, a 50 m × 75 m (0.375 ha) plot was established near the center of each compartment. Each plot was gridded into six 25 × 25 m sections, and the outer corners of each section were marked with metal stakes. Basal area of all live and standing dead trees >5 cm diameter at breast height (dbh) was recorded

(Tester 1989). Only information on trees ≥10 cm dbh was used in this study. In September 1989 basal area and height of all live and dead trees ≥10 cm dbh were measured in each plot. All fallen dead trees were also measured, since these may have been standing in 1984. Condition of the fallen trees was not assessed. The number of fallen trees per plot averaged 3 ± 3 for *Q. ellipsoidalis* and <1 for *Q. macrocarpa*. Also, in 1989, sapling (1.0–9.9 cm dbh) density was measured in a 10 m × 10 m subplot located within each of the six sections of each plot.

MORTALITY ANALYSIS. An indirect approach was used to estimate percent mortality because live trees were not tagged in 1984. To be relatively conservative, we assumed that all but one of the dead fallen trees in 1989 had already fallen

Table 1. Vegetation and environmental features of 11 savanna plots at Cedar Creek Natural History Area. Tree density and basal area (B.A.) were measured for trees ≥ 10 cm dbh in 1984. The compartment area includes both savanna and non-savanna habitat. Plots are ordered by 1984 stand density.

No. ^a	Compartment		Plot				Soil type ^b	Depth to water table (m) ^c
	Area (ha)	No. burns 1985–1989	Density (#/ha)		B.A. (m ² /ha)			
			1984	1989	1984	1989		
5	16.2	2	77	51	4.5	3.3	SarB	4.84
11	12.1	1	112	61	11.8	5.9	SarB	3.32
4	18.2	2	160	101	13.8	9.7	SarC	4.54
10	11.0	0	163	195	15.9	15.3	SarC	5.45
9	10.0	0	171	157	17.3	11.2	SarC	2.41
1	13.4	1	197	147	14.8	10.5	ZimB	3.32
16	2.4	2	219	163	15.6	12.9	ZimB	2.41
8	27.5	1	269	299	14.2	15.3	SarB	5.15
7	2.8	2	293	227	13.4	12.0	SarB	3.62
3	10.9	3	389	328	13.6	12.1	ZimC	5.15
15	30.0	0	587	475	27.7	26.4	ZimB	3.32

^a Compartments have been renumbered from Tester (1989, Table 3) as follows: Tester's 16 = 9, Tester's 17 = 15, Tester's 15 = 16. Note that Tester's plot 13 was not relocated in 1989.

^b From Grigal et al. (1974).

^c Based on a water table elevation in August 1989 of 278.62 m (see text for further details).

in 1984. The number of new standing dead stems in 1989 and dead stems considered to have fallen since 1984 were totalled and are referred to as the number dying in the five year time period. The five year mortality rate was calculated by taking the number of live stems in 1984 and dividing by the number of stems dying during the 1984–1989 period. Annual mortality rates were calculated using the equation of Hamilton and Edwards (1976), in which mortality rates are treated as negative compound interest rates.

The remaining live stems in 1989 (that is those that survived from 1984–1989) was obtained by subtracting the number of stems dying from the number of live stems in 1984. Net recruitment into the tree category was the difference between remaining live stems in 1989 and actual stems counted in 1989 (see Tables 2, 3). The overall sampling error in these calculations is evident here, since both positive and negative values could occur. These errors were probably caused both by differences in measuring the minimum dbh (10 cm) and determining whether or not stems near or on the plot lines should be included.

Effects of mortality on stand structure were tested by comparing diameter distributions in 1984 with those in 1989 using the Kolmogorov-Smirnov (K-S) test. The effect of soil type and burn frequency on mortality rates were tested using a non-parametric Kruskal-Wallis test. All analyses, including regressions, were completed

with SAS statistical programs (SAS Institute Inc. 1988).

OAK WILT ASSESSMENT. All sites were surveyed with D. French (Dept. of Plant Pathology, University of Minnesota) for the presence of oak wilt in mid-July of 1990 and in June and July of 1992. In both years trees near but not in plots 9 and 11 were suspected of having oak wilt. Four trees showing signs of oak wilt were sampled on August 7, 1990, and five different trees on July 24, 1992. A section 1–2 cm thick and 15 cm long was collected from two branches of each tree. Samples were kept in closed envelopes to prevent excessive drying and were sent to the Forest Pathology Department, University of Minnesota. Tissue under the bark was cultured in petri dishes on malt agar at room temperature (D. French, pers. comm.). All trees in 1990 tested negative, but four of five trees in 1992 tested positive; thus, although oak wilt does not appear to have contributed to tree mortality in our plots at the time of survey, it does occur sporadically within Cedar Creek.

Results and Discussion. SPECIES COMPOSITION. Mean live stem density in 1984 was 241 stems/ha (90 stems/plot), and ranged from 77 to 587 stems (Table 1). In 1989, mean live stem density had declined to 200 stems/ha, and ranged from 51 to 475. Of the 988 live tree stems in 1984, 83.1% belonged to *Quercus ellipsoidalis*, followed by *Quercus macrocarpa* (14.9%) and

Table 2. Population changes and mortality rates for *Q. ellipsoidalis* in 11 permanent plots (0.375 ha) at Cedar Creek Natural History Area, 1984–1989. The number of dead fallen trees in 1984 was assumed to be only one less than in 1989 (see Methods for further details). Estimated (Est.) deaths equals the total number of dead stems in 1984 subtracted from those in 1989. Dead st. = dead standing; Dead fa. = dead fallen. Live = remaining live.

Plot	Condition	Actual 1984	Est. deaths	Live	Est. recruits	Actual 1989	Mortality rate	
							5-yr	1-yr
1	Live	69	12	57	0	49	0.174	0.038
	Dead st.	20				31		
	Dead fa.	(4)				5		
3	Live	142	20	122	0	120	0.141	0.030
	Dead st.	18				37		
	Dead fa.	(2)				3		
4	Live	55	22	33	0	32	0.400	0.097
	Dead st.	3				24		
	Dead fa.	(1)				2		
5	Live	15	9	6	0	6	0.600	0.167
	Dead st.	2				10		
	Dead fa.	(0)				1		
7	Live	95	14	81	0	70	0.147	0.031
	Dead st.	17				30		
	Dead fa.	(3)				4		
8	Live	41	0	41	12	53	0.000	0.000
	Dead st.	5				3		
	Dead fa.	(1)				2		
9	Live	50	12	38	0	37	0.240	0.053
	Dead st.	5				16		
	Dead fa.	(0)				1		
10	Live	47	4	43	13	56	0.085	0.018
	Dead st.	3				6		
	Dead fa.	(0)				1		
11	Live	36	8	28	0	20	0.222	0.049
	Dead st.	12				19		
	Dead fa.	(6)				7		
15	Live	191	28	163	0	155	0.147	0.031
	Dead st.	19				46		
	Dead fa.	(2)				3		
16	Live	80	16	64	0	59	0.200	0.044
	Dead st.	16				31		
	Dead fa.	(9)				10		

Table 3. Population changes and mortality rates for *Q. macrocarpa* in 11 permanent plots (0.375 ha) at Cedar Creek Natural History Area, 1984–1989. See Table 2 for details. Dead st. = dead standing; Dead fa. = dead fallen; Live = remaining live from 1984.

Plot	Condition	Actual 1984	Est. deaths	Live	Est. ingrowth	Actual 1989	Mortality rate	
							5-yr	1-yr
1	Live	5	0	5	1	6	0.000	0.000
3	Live	4	0	4	0	3	0.000	0.000
4	Live	5	0	5	1	6	0.000	0.000
5	Live	14	1	13	0	13	0.071	0.015
7	Live	15	0	15	0	15	0.000	0.000
8	Live	53	0	53	0	52	0.000	0.000
9	Live	10	0	10	1	11	0.000	0.000
10	Live	9	0	9	1	10	0.000	0.000
11	Live	6	2	4	0	3	0.333	0.078
	Dead st.	1				2		
	Dead fa.	(0)				1		
15	Live	25	4	21	0	18	0.160	0.034
	Dead st.	1				4		
	Dead fa.	(2)				3		
16	Live	1	0	1	0	1	0.000	0.000

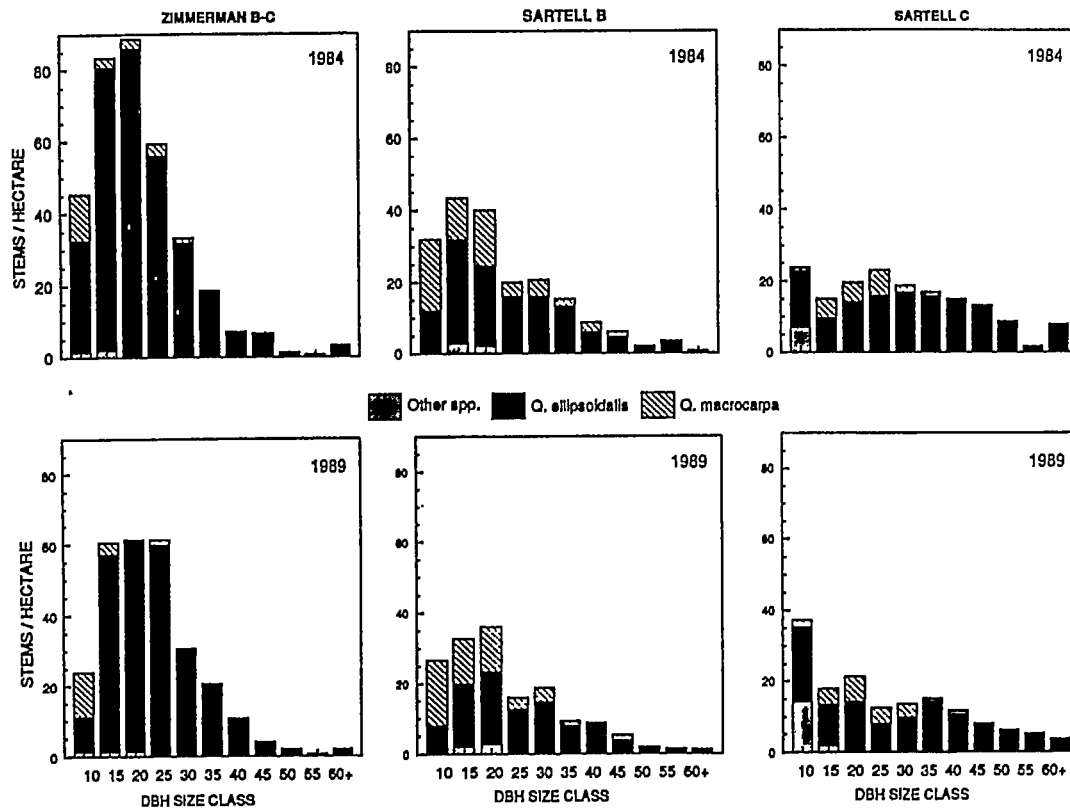


Fig. 2. Size class distribution of oak savanna plots at Cedar Creek by soil type in 1984 and 1989. The two species of oak, *Quercus ellipsoidalis* and *Quercus macrocarpa*, are shown; other species are primarily *Prunus serotina* and *Prunus virginiana*.

Prunus serotina Ehrh. (black cherry) (1.0%). In 1989, these proportions were similar (*Q. ellipsoidalis* = 79.5%, *Q. macrocarpa* = 16.6%, and *P. serotina* = 2.3% of the 826 live stems). The sapling size class (available for 1989 only) was dominated by *Q. ellipsoidalis* (53.4% of the 1380 live saplings), followed by *Q. macrocarpa* (28.6%). The majority (89%) of all saplings occurred in unburned plots. Saplings of *P. serotina* and *Prunus virginiana* L. (choke-cherry) occurred only in the unburned plots.

Q. ellipsoidalis dominated on most sites, containing at least 80% of all stems on nine of the plots. Oak percentages were significantly associated with soil type ($\chi^2 = 96.44$, $P < 0.0001$) with Zimmerman soils having an average of 93% *Q. ellipsoidalis* stems and Sartell soils having between 51 and 84% (Fig. 2).

STAND STRUCTURE. Diameter distributions between burned and unburned plots differed significantly in 1984 (K-S test, $P < 0.0001$). Unburned plots in 1984 had a larger percentage of

stems in the 10–25 cm dbh class (58%) compared to burned plots (45%). These differences persisted in 1989 ($P < 0.001$). In 1984, diameter distributions were also significantly different among different soil types ($P < 0.0001$); these differences were retained in 1989 ($P < 0.0001$ for Zimmerman vs. Sartells, $P < 0.05$ for Sartell B vs. C) (Fig. 2). Differences between the Sartells may have occurred because two of the three unburned plots were on Sartell C soils.

Tree mortality had little effect on average tree diameter distributions in individual plots between 1984 and 1989. Comparisons of live stem distribution between 1984 and 1989 were significantly different only for unburned plots 9 and 15 (K-S test, $P < 0.05$). These differences occurred in the smaller diameter classes (20–25 cm) but were in opposite directions. Plot 9 had relatively low densities in 1984 and showed a large increase within this size class in 1989. Plot 15, the most dense stand, showed a large decrease in the same size class, an indication that self-thinning may be occurring. The general absence

of change in diameter distribution suggests that stem mortality was proportional to stem density within each diameter class, and preexisting differences in stand structure associated with burn frequency and soil type were retained.

RECRUITMENT. Recruitment levels into the tree layer (> 10 cm dbh) were essentially zero for all but one of the eight plots that had been burned. The one exception was plot 8, which showed a large increase in *Q. ellipsoidalis* (Table 2). Unburned plots (9, 10, 15) showed variable recruitment, ranging from 5–45 stems/ha. Most of these stems, however, were *P. serotina* and *P. virginiana*. The higher level of recruitment by *Q. ellipsoidalis* in unburned plots offset its higher mortality rate over all plots, and the net result was only a slight increase in the proportion of *Q. macrocarpa* in these savannas.

MORTALITY RATES. Five-year mortality rates during the 1984–1989 period averaged 18.2% for all species, and ranged from 1.0% to 36.7% among plots. *Q. ellipsoidalis* varied from 0.0 to 60.0% (Table 2); *Q. macrocarpa* varied from 0.0 to 33.3% among plots (Table 3). The average five-year mortality rate of *Q. ellipsoidalis* ($21.4\% \pm 16.2\%$) was significantly different from *Q. macrocarpa* ($6.1\% \pm 10.6\%$) ($t = 2.614$, $P < 0.05$). Average annual mortality rates for the two oak species were 5.1% and 1.4% for *Q. ellipsoidalis* and *Q. macrocarpa*, respectively. The mortality rates of these two species were not correlated among plots. The differences in mortality rates led to a proportionately higher representation of *Q. macrocarpa* in several burned plots. For example, in 1984, both oak species had equal percentages of stems in plot 5; by 1989, 70% of the stems were *Q. macrocarpa*. Mortality rates were not significantly different between plots burned at different frequencies (0×, 1× or 2–3× in 5 years; $P > 0.05$, $df = 2$, Kruskal-Wallis test) or between the three soil types ($P > 0.05$, $df = 2$, Kruskal-Wallis test).

The average 5 yr mortality rates for *Q. ellipsoidalis* is higher than normal for oak stands in the eastern deciduous forest region, where rates are typically on the order of <1%–4%. *Q. macrocarpa* (and *Q. alba*) usually has a lower mortality rate than *Q. ellipsoidalis* (and *Q. rubra*) (Parker et al. 1985; Harcombe 1987). The lower mortality rate for *Q. macrocarpa* is consistent with its greater tolerance to water stress than members of the red-black oak group (*Q. ellipsoidalis* or *Q. rubra*) (Crow 1988). This tolerance is due in part to its thicker bark and extensive rooting system

which, in prairie soils, can extend downward over 5 m and laterally over 13 m (Albertson and Weaver 1945).

Oak mortality in the eastern deciduous forest is normally associated with small gap disturbances. In the Midwest, oak wilt disease can increase 5 yr mortality rates in the red-black oak group to 20% or more (McCune and Cottam 1985). Disturbances such as fire or windstorm can yet further increase the rates to over 50% annually (Glitzenstein and Harcombe 1988); droughts appear to have effects on mortality comparable to these disturbances, as suggested by data from this study. Similarly, Albertson and Weaver (1945) found that upland *Q. macrocarpa* forests experienced widespread canopy die-back and up to 50% mortality during the droughts of 1934–1935 in eastern Nebraska. Other species, such as *Q. rubra*, had even higher mortality rates. Rice and Penfound (1959) also reported 2 yr mortality rates of 42.3% in stands of *Q. marilandica* (blackjack oak) and *Q. stellata* (post oak) in 1956–1957, which they attributed to an extended drought from 1952–1956. They noted that, although *Q. marilandica* (red-black oak group) was more often found on less favorable sites, it was not as drought resistant as *Q. stellata* (white oak group). *Quercus ellipsoidalis* and *Q. macrocarpa* appear to have analogous responses in the upper Midwest.

A number of site variables, including fire frequency, elevation, soil type, organic matter, total live stem density in 1984, and total live basal area in 1984 were analyzed to see if they influenced differences in mortality rates between plots. Only total basal area in 1984 was a significant predictor of mortality rate for *Q. ellipsoidalis* using linear regression ($r = -0.53$, $P = 0.092$, $N = 11$), showing that, as total basal area increased, mortality rate decreased. Total stem density in 1984 was a poor predictor of mortality rate for *Q. ellipsoidalis* using linear regression ($r = -0.49$, $P > 0.1$, $N = 11$), but was a better predictor using a negative exponential model, with a total R^2 of 52% (Fig. 3). A stepwise regression using either total stem density in 1984 or total basal area in 1984 and the four abiotic factors (with soil type as a dummy variable) showed no significant improvement in explaining mortality rates. Density and basal area were used separately since they were highly correlated (Pearson $r = 0.7635$, $P < 0.01$). Mortality rates of *Q. macrocarpa* showed no significant relation to the factors analyzed here.

The declining mortality rates of *Q. ellipsoidalis*

with total live stem density in 1984 (Fig. 3) may seem unusual, but could reflect an interaction between soil moisture and tree stem density as reflected in canopy cover. Tree canopy cover in woodlands and savannas can reduce soil moisture losses in the upper 0–30 cm soil profile during dry periods by lowering evapotranspiration (Hanson 1922). Kucera (1952) found that soil moisture losses in the summer months in open grassland areas can be greater than under woodland canopy. These findings suggest that the resilience of stems in open areas to fire disturbance in savanna may be offset by a higher probability of mortality during drought. Transeau (1935) reported that in Illinois, “thousands of oaks bordering the prairie died by the close of the 1913–1914 drought.” Therefore, savannas may be more stable than woodlands with respect to fire disturbance (Anderson and Brown 1986), but less stable with respect to drought.

Because differences in structure and species composition were significantly related to soil type, it may be that soil conditions, such as soil texture and water holding capacity, are indirectly responsible for the differences in mortality rates among plots. In addition, vegetation structure has been altered to some degree by ongoing fires, complicating the overall interactions.

Although the relatively short-lived drought immediately preceded our 1989 sampling, it was in turn preceded by a very wet period. It's possible that the change from very high moisture levels in 1984–1986 to low levels in 1988 may have added to the stress on the trees. This may also explain why depth to water table *per se* did not correlate with mortality rates.

Finally, the role of drought is somewhat simplified in prescribed fire systems such as at Cedar Creek because the interaction between drought and fires is greatly reduced. Fires that normally do not spread into woodlands, except as low intensity ground fires, could cause widespread mortality during a drought, thereby reversing the pattern of mortality rates observed here. For example, Anderson (1990) found that fires starting during dry periods often destabilize woodlands on sandy soils because fuel loads there can be higher than in adjacent sand prairies. The interactions between fire and drought are not easily observed in prescribed burns at Cedar Creek because burns are controlled independent of drought conditions.

In conclusion our data suggest that episodic climatic events affecting moisture can kill well-established oak trees, depending on stand struc-

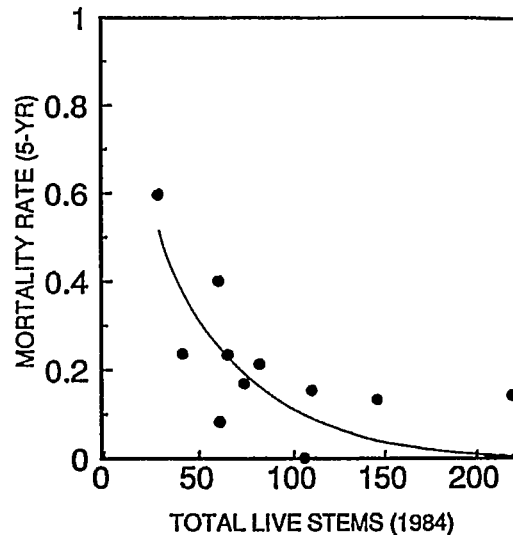


Fig. 3. Mortality rate of *Quercus ellipsoidalis* as a function of stem density in 1984. The equation for the negative exponential regression is $y = 0.965e^{-0.022x}$, where y is mortality rate and x = stem density. $R^2 = 52\%$.

ture. Stand structure itself depended on both soil type and prior burning history; burning all but eliminated recruitment. *Quercus ellipsoidalis* had much higher mortality rates than *Q. macrocarpa*; these differences produced significant shifts in tree species composition, particularly on burned sites. These observations emphasize the role of climate in maintaining sand savannas in the prairie-forest border region.

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