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Oak Tree Effects on Soil and Herbaceous Vegetation in Savannas and Pastures in Wisconsin

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ABSTRACT.—To study tree/nontree interactions, soil characteristics, aboveground biomass and plant composition were compared in areas under and adjacent to canopies of open grown bur oaks (*Quercus macrocarpa*) and northern pin oak × black oak hybrids (*Q. ellipsoidalis* × *velutina*) in two savannas and two pastures in S-central Wisconsin. One savanna and one pasture were paired on loam soils, the other sites were on sandy soils. In general, soil moisture was higher below tree canopies than outside canopies during a drying trend and was similar between areas after a period of rain. Soil organic matter and potassium (K) decreased with increasing distance from tree boles on all sites, while phosphorus (P) showed a similar trend only on the pastures. Pastures had greater soil organic matter and P than savannas of similar soil texture, while the loam soil sites had higher soil pH, organic matter, K, Ca and Mg than sandy sites of similar disturbance history. Areas below canopies received 67% of the ambient rainfall and 27–48% of the ambient photosynthetically active radiation and had 2.3–5.2 C lower soil temperatures compared to areas outside the canopies. Although soil moisture, nutrient and organic matter levels seemed more favorable for plant growth under the canopies, aboveground biomass was lower below canopies compared to open areas at the two savannas, while biomass was equal between canopy and open areas on the one pasture that was measured. This indicates that other factors, such as light, were more important in determining plant biomass. For all sites, plant composition under tree canopies differed from that outside the canopies. Savanna plant species were predominantly perennial and native while pasture species were mostly perennial and exotic. Grazing, fire and previous introductions of prairie species may have been major factors in determining the prevalent species (>5% cover) for a given site. *Poa* spp. were more prevalent below canopies compared to open areas on all sites, despite their different disturbance histories.

INTRODUCTION

Oak savanna in Wisconsin provides an unusual opportunity to study the tree/grass system in the midwestern United States. Curtis (1959) defined savanna as grassland having more than 2.5 trees per ha, but less than 50% cover and ". . . as the rarest community in Wisconsin today." While oak savanna was once a common plant community in the midwest, European settlers converted savanna into cropland, pastures or forests with the cessation of fire (Auclair, 1976). Savanna remnants can still be seen in pastures, abandoned fields and oak woodlots. Efforts to restore oak savannas by prescribed burning and seedling establishment have taken place in many midwestern states (White, 1983; Nuzzo, 1985; Packard, 1988).

Little is known, however, about the basic tree/nontree interaction in these midwestern systems. The University of Wisconsin–Madison Arboretum and surrounding pastures provided an opportunity to study such interactions. In these areas, plant distributions under oaks appeared visually different from the adjacent open areas and suggested a natural experiment to study soil and vegetation patterns under two types of disturbance: restoration

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and grazing. We therefore selected isolated oak trees in two restored savannas and two pastures, addressing the following questions:

(1) Are there differences in soil moisture, organic matter, pH and nutrients below tree canopies as compared to adjacent open areas in pastures and savanna systems?

(2) How do species composition, cover and biomass vary below tree canopies as compared to adjacent open areas in these systems and

(3) Do pastures differ from restored savannas in any of the above patterns?

METHODS AND MATERIALS

Site descriptions.—In Dane County, Wisconsin, two savanna sites and two pasture sites were selected for their management and soil texture characteristics and studied during the 1989 growing season. The savanna and pasture sites had similar restoration or grazing histories, respectively. Each restored savanna was paired with a pasture of similar soil texture and slope (Glocker and Patzer, 1978). Selection of an equal number of trees for the four sites was constrained by the limited number of open grown individuals. We selected a total of 18 oak trees whose canopies were free of overlap on at least three of the four cardinal directions.

The climate of the study area is continental, with long cold winters and humid warm summers. The mean January and July temperatures are −9 C and 21 C, respectively, while average annual precipitation is 78 cm with 54% falling from May to September, A total of 59 to 64 cm of precipitation fell in 1989 at weather stations near the four sites (NOAA, 1989).

Savanna Site 1 is a 4-ha savanna on the West Grady Knoll in the UW-Madison Arboretum (T6N, R9E, S4), restored since 1943 with plant introductions and burns occurring in each of the 4 yr before the study and periodically before then (V. Kline, pers. comm. 1990). Three bur oaks (*Quercus macrocarpa*) (mean height = 12 ± 1 m; mean dbh = 48 ± 8 cm; mean canopy radius = 5 ± 1 m) and four black oak hybrids (*Q. ellipsoidalis* × *velutina*) (mean height = 13 ± 2 m; mean dbh = 51 ± 7 cm; mean canopy radius = 6 ± 1 m) were studied in the savanna. The soils are Boyer sandy loam (Typic Hapludalf) and Spinks and Plainfield loamy sands (Psammentic Hapludalf, Typic Udipsamment) with 6–12% slopes (Glocker and Patzer, 1978).

Savanna Site 2 is located on the S edge of Curtis Prairie in the UW–Madison Arboretum (T7N, R9E, S33). The 26-ha prairie has been restored with plant introductions and prescribed burning since 1935. Burns occurred in 2 of the 4 yr previous to the study (V. Kline, pers. communication, 1990). Three open-grown bur oaks (mean height = 14 ± 1 m; mean dbh = 50 ± 9 cm; mean canopy radius = 6 ± 1 m) were studied at this site. The soil is Grays silt loam (Mollic Hapludalf) with 2–6% slopes (Glocker and Patzer, 1978).

Pasture Site 1 is a 5-ha pasture (T8N, R6E, S3) annually grazed by cattle in the previous 50 yr with the exception of the study yr 1989. In 1978, birdsfoot trefoil (*Lotus tenuis*) was no-tilled directly into the pasture (L. Lichte, pers. comm., 1989). Isolated bur oak and black oak hybrids are scattered throughout the pasture. We selected three bur oaks (mean height = 11 ± 1 m; mean dbh = 59 ± 5 cm; mean canopy radius = 7 ± 1 m) and two hybrids (mean height = 15 ± 1 m; mean dbh = 99 ± 6 cm; mean canopy radius = 8 ± 2 m) for study. The soils are Boyer sandy loam (Typic Hapludalf) and Spinks and Plainfield loamy sands (Psammentic Hapludalf) with 6–12% slopes (Glocker and Patzer, 1978).

Pasture Site 2 is a 5-ha pasture (T8N, R12E, S2) annually grazed in the previous 70 yr. With the exception of a narrow strip of sweet corn planted in the middle of the pasture during the 1960s, the pasture has not been planted or commercially fertilized (L. Benesch, pers. comm., 1989). Open grown bur oaks are scattered throughout the pasture. We selected three of these for study (mean height = 15 ± 1 m; mean dbh = 63 ± 10 cm; mean canopy radius = 7 ± 1 m). The soil is St. Charles silt loam (Typic Hapludalf) with 2–6% slopes (Glocker and Patzer, 1978).

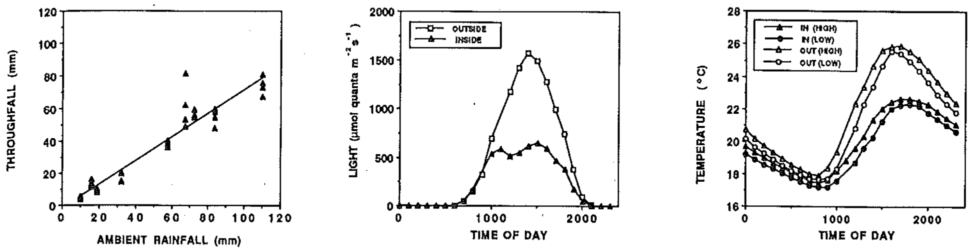

FIG. 1.—The left graph shows throughfall beneath four trees on Savanna Site 1. Each triangle represents the average throughfall per tree during nine rainfall events. Throughfall (mm) = −1.28 + 0.73·(rainfall, mm); $r^2 = 0.91$, $P < 0.01$. The middle and right hand graphs show photosynthetically active radiation (LIGHT, μmol m^{-2} s^{-1}) and soil temperatures, respectively, beneath and beyond a bur oak canopy at the same site on a representative day, 1 August 1989. Each "inside" symbol represents the average PAR over four sensors at midcanopy, while each "outside" symbol stands for a single sensor beyond the canopy. "IN (HIGH)" represents the highest temperature and "IN (LOW)" the lowest temperature averaged over two thermocouples inside the canopy during an hour. "OUT(HIGH)" and "OUT(LOW)" follow the same designations, but outside of the canopy

Microclimate measurements.—Rainfall, light and soil temperatures were taken to characterize conditions under and adjacent to two bur oaks and two black oak hybrids on Savanna 1. From 25 July to 1 September 1989, we measured throughfall (precipitation that passed through the canopy) and rainfall during nine rainfalls. We systematically placed eight collectors at midcanopy at approximately even spacing around each tree and one collector outside the canopy at a distance at least twice the height of the tree. The collectors were bottles with 63-mm diam funnels and were placed at a height of 1.2 m. Throughfall and rainfall were measured volumetrically within 12 h of each rainfall event. Simple linear regression was used to relate ambient rainfall to canopy throughfall (Fig. 1).

We measured photosynthetically active radiation (PAR) using gallium arsenide photodiodes (calibrated with quantum sensors). Four sensors were placed at midcanopy and one sensor beyond the canopy to the S at a height of 1.2 m. Soil temperature was measured by placing two thermocouples in midcanopy and two sensors adjacent to the canopy at a depth of 15 cm. From 22 July to 5 August, each tree was monitored for 5 days. Readings were taken every 5 min and the high, low and average measurements were recorded at each hour.

Soil moisture.—Soil moisture was measured on 20 June, 3 July and 28 July 1989, with the first measurements taken during a drying trend after 5 cm rain fell in June and the third after 12.8 cm rain fell in July. We measured soil moisture gravimetrically in the four cardinal directions inside and outside the canopy at 5–30 cm and 30–50 cm depth at two trees per species per site using a 2.5-cm soil probe. To detect differences within trees, we used paired "t" tests, with trees as replicates and pairs within trees, to measure soil moisture differences of samples taken between depths and inside and outside canopy areas.

Soil chemical analyses.—In September 1989, soil samples were collected beneath and beyond the canopies of two trees per species per site. For each tree, eight samples were taken with a 2.5-cm soil probe along a randomly chosen azimuth from the tree bole to 9 m outside the canopy. Five samples were taken at equidistant intervals from the tree bole to the canopy edge, while the remaining samples were taken 3, 6 and 9 m beyond the canopy edge. At each sample location, we made a composite from five randomly selected soil subsamples taken from 0 to 10 cm depth. The visible duff layer of each subsample was removed.

The samples were analyzed for pH, organic matter, calcium, potassium, magnesium and phosphorus by the UW–Madison Soil and Plant Analysis Laboratory. Soil pH was determined using a glass electrode pH meter. Organic matter was determined by dichromate-sulfuric acid digestion using the Schulte method. Available phosphorus was determined by the Bray P-1 method, while available potassium and exchangeable calcium and magnesium were determined by flame photometry (Liegel *et al.,* 1980).

Because soil sampling distances were proportional to tree canopy radii, it was not possible to compare absolute distance values between trees. To detect soil gradients from beneath to beyond the canopies for each site, we assigned rank values to sample distances and tested for soil trends using the Spearman Rank Correlation.

Aboveground biomass measurements.—To estimate aboveground biomass, samples from herbaceous vegetation were collected inside and outside canopy areas of all trees, except at Pasture Site 2 where active cattle-grazing was a confounding factor. Samples were taken on 22 July and 23 September 1989, with the latter date chosen to reflect the maximum accumulation for the season.

Aboveground vegetation within a 0.25 m^2 frame was harvested at midcanopy and 3 m beyond the canopy in each of the four cardinal directions for a total of eight sample plots per tree, for all trees on the three sites measured (15 trees). Forbs and grasses were separated and oven-dried to a constant weight at 80 C. To measure differences within trees rather than between trees, we used paired "t" tests (with trees as replicates and pairs within trees) to analyze biomass differences between dates, grass and forb components and areas inside and outside canopies.

Herbaceous composition sampling.—Plant cover was sampled beneath and beyond the canopies of all trees during August when most understory species are present (V. Kline, pers. comm., 1989). Using the same azimuth as for soil chemical sampling, we placed seven contiguous 1-m^2 quadrats from the bole to an area beyond the canopy edge and three quadrats at 3, 6 and 9 m outside of the canopy for a total of 10 sample plots per tree for the 18 trees. Quadrats were assigned to either beneath or outside of canopy classes. To aid cover estimations, the 1-m^2 frame was divided into nine sections and the percent cover was visually estimated by section for each species rooted within the frame. Cover was defined as the percentage of ground area obscured by the plant species using a scale of 0–1%, 1–5%, 6–25%, 26–50%, 51–75% and 76–100%. To expedite the sampling process, some species were grouped such as *Poa* spp. and *Andropogon* spp. The percent cover of plant species at each site was ordinated using Detrended Correspondence Analysis (Gauch, 1982). Raw data were relativized by samples, without downweighting rare species or eliminating stands.

At each site, species were grouped by plant form (grass, forb or woody), by life form (annual and biennial or perennial) and as native or exotic. Plant species located from the bole to the canopy edge were identified as "inside canopy" and those found outside were identified as "outside." Various groups and relationships were compared using the paired t-test, with trees as replicates and pairs within trees.

RESULTS AND DISCUSSION

Differences in microclimate characteristics.—Oak canopies reduced throughfall, light and soil temperature compared to open areas (Fig. 1). Throughfall under oak canopies ranged from 46 to 92% of ambient rainfall with an average of 67% over nine rainfalls. During rainfalls <50 mm and >50 mm, throughfall averaged 59% and 74% of ambient rainfall, respectively. Over the 20 measurement days (5 days for each of four trees), tree canopies reduced photosynthetically active radiation (PAR) by 52 to 83% during the peak of PAR at 1400 h (data not shown). During a typical sunny day (1 August 1989), PAR beneath and beyond a bur oak was 543 and 703 μmol quanta m^{-2} sec^{-1} at 1000 h; 521 and 1191 μmol quanta m^{-2} sec^{-1} at 1200 h; and 625 and 1598 μmol quanta m^{-2} sec^{-1} at 1400 h. Over all trees and measurement days, soil temperatures inside canopies ranged from 17.1 to 24.9 C (averaging 20.4 ± 0.1 C) and outside canopies ranged from 17.7 to 28.6 C (averaging 22.7 ± 0.1 C). At 1600 h, soil temperatures under oak canopies were reduced by 2.3 to 5.2 C relative to open areas, while temperatures differed by 0.7 to 1.8 C at 0800 h (Fig. 1 and data not shown).

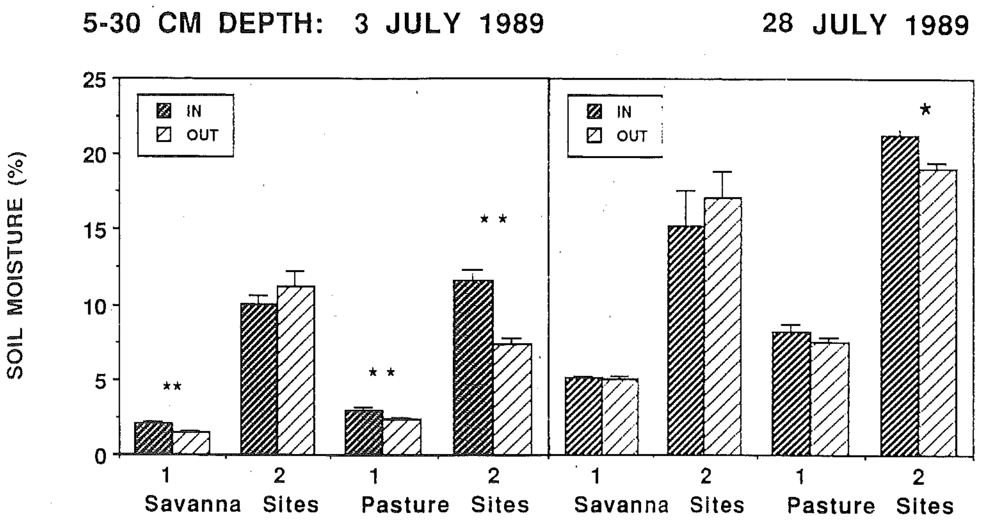

FIG. 2.—Soil moisture (%) at 5–30 cm depth (±1 SE) at two dates inside and outside tree canopies in two savannas and two pastures. Within sites and dates, significant differences between inside and outside canopy areas ($P < 0.01$ and 0.05) are noted by ** and *, respectively and no significance ($P > 0.05$) is designated by the absence of letters

Differences in soil characteristics.—Although less rain reached the areas below oak canopies, higher soil moisture was found in these areas on 3 July following a dry period (Fig. 2). At this date, soil water content at 5–30 cm depth was significantly higher inside than outside canopies ($P < 0.01$) on all sites with the exception of Savanna Site 2. On 28 July, after a rainy period, only Pasture Site 2 had significantly higher soil water content at 5–30 cm depth inside than outside canopies ($P < 0.05$) (Fig. 2). This trend can be explained by the combination of lower solar radiation and soil temperature levels found under trees which reduce understory evapotranspiration (Johnsen, 1962; Eastham and Rose, 1988). No consistent differences were found at the 30–50 cm depth between inside and outside zones (data not shown).

Soil organic matter and K were both lower beyond than beneath tree canopies on all sites, despite different disturbances and soil textures at each site. Using the Spearman Rank Correlation, organic matter (Fig. 3) and K (Fig. 4) decreased by roughly a third with increasing distance from the tree trunk on all sites ($P < 0.05$, $P < 0.01$). We suggest that the organic matter and soil K gradients were due to increased leaf litter, decreased decomposition from cooler temperatures and lower leaching rates compared to open areas. Others

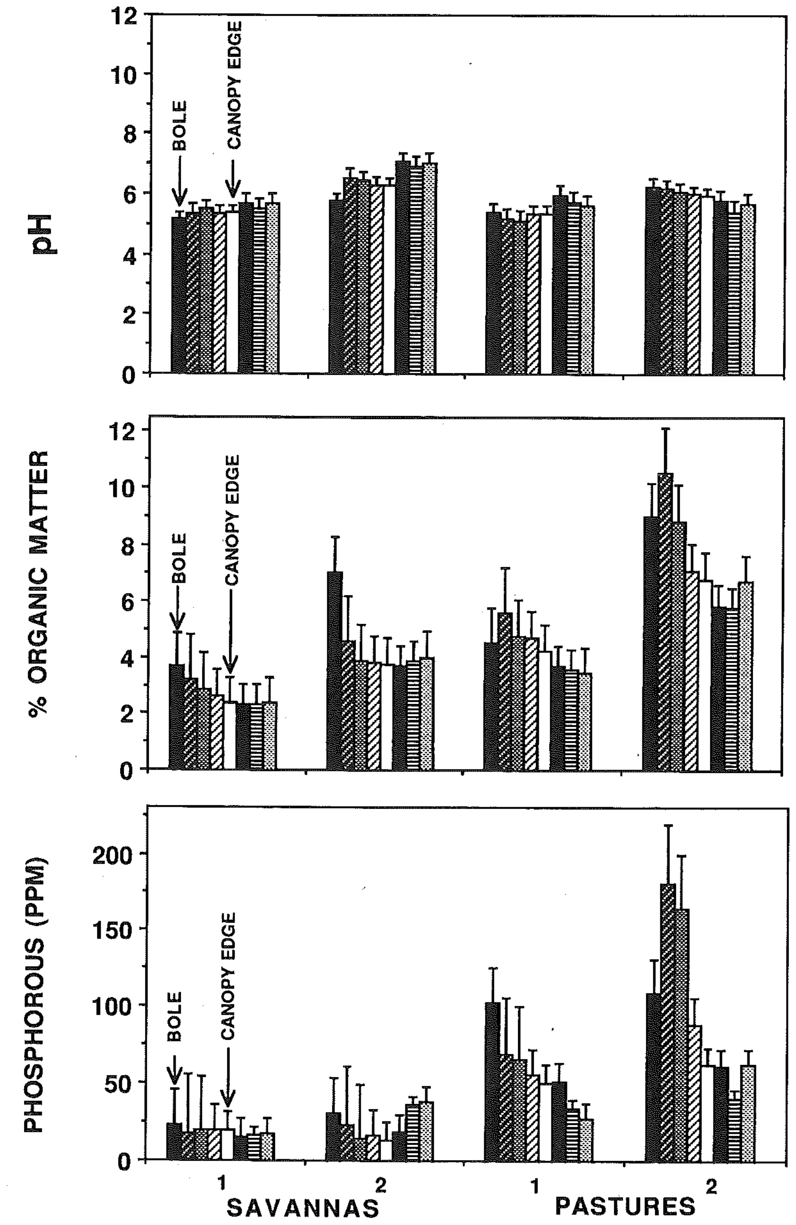

FIG. 3.—Soil pH, organic matter and phosphorus (±1 SE) measured along relativized gradients from oak boles to 9 m outside the canopy (*see* Methods section for sampling regimes). Using the Spearman Rank Correlation, soil pH increased with increasing distance from bole on the savanna sites ($P < 0.05$), while the opposite was true on the Pasture Site 2. Organic matter decreased with increasing distance on all sites ($P < 0.05$), and phosphorus showed the same trend only on the pasture sites ($P < 0.01$). Eight soil samples were taken at each tree, with the black far left bar representing the average bole sample and the clear bar the canopy edge sample within each site

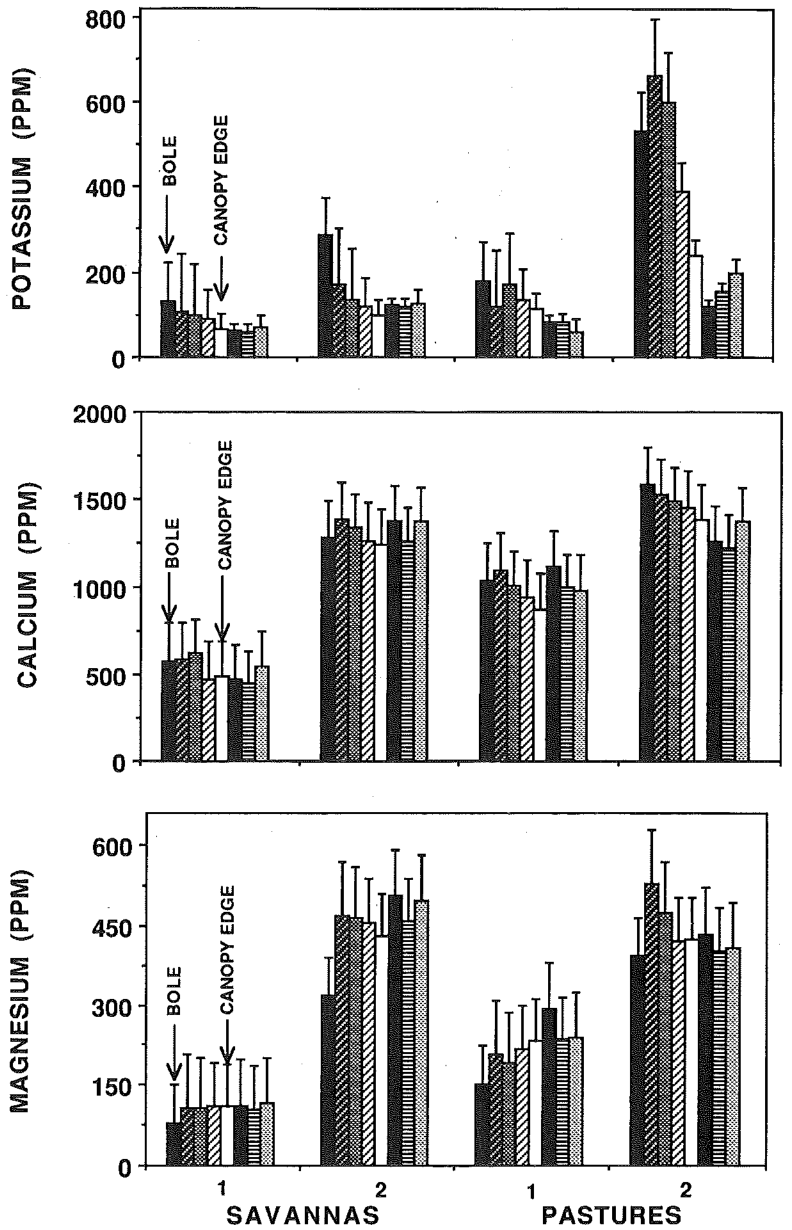

FIG. 4.—Soil potassium, calcium and magnesium gradients (±1 SE) measured from the bole to 9 m outside the canopy. K decreased with increasing distance from the bole ($P < 0.05$) and Mg was lower at the boles than other inside samples on all sites ($P < 0.05$)

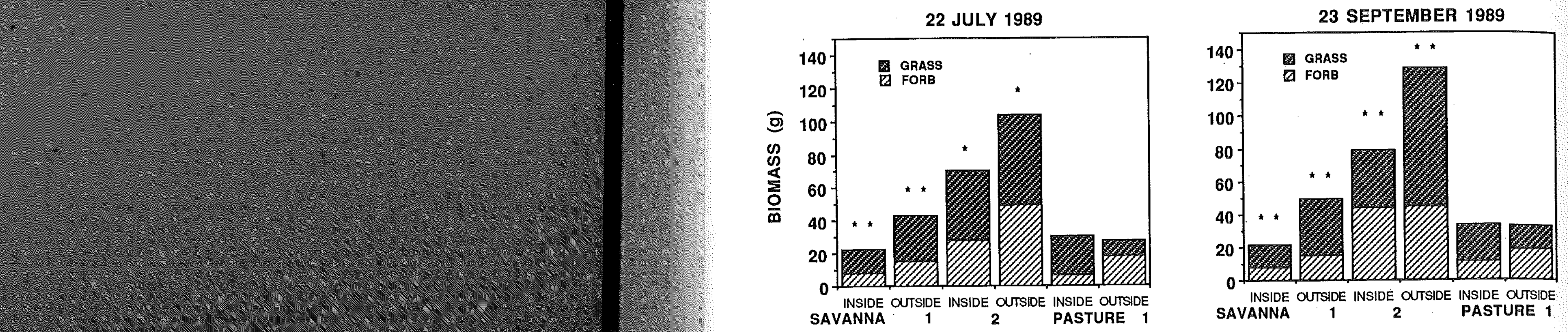

FIG. 5.—Total aboveground biomass (g/m^2) on two savannas and one pasture taken on 22 July 1989 and 23 September 1989. Within sites, significant differences between inside and outside canopy areas ($P < 0.05$ and 0.10) are noted by ** and *, respectively and no significance is designated by the absence of letters. Standard errors of the total and component biomass were roughly 5–10% of the mean values

have found the same trend in shore pine (*Pinus contorta*) and mesquite (*Prosopis juliflora*) (Zinke, 1962; Tiedemann and Klemmedson, 1973).

Phosphorus decreased with increasing distance from tree trunks on the two pastures ($P < 0.01$) but not on the savannas (Fig. 3). Microsite differences in P input from leaf litter may not have been significant in savannas, whereas the addition of P from cow manure contributed to the differences found at the pasture sites. Cows seemed to "lounge" more often in the shelter of oaks than in the open (pers. observ.). In a similar situation, Klopatek (1987) found higher extractable P under canopies at a grazed site than under trees at a burned site in Arizona.

Soil pH increased with increasing distance from the trunk on the savannas ($P < 0.05$), while the opposite was true on Pasture Site 2 ($P < 0.05$) (Fig. 3). The low savanna soil pH found below canopies may have originated from organic acids from leaf litter and acidic stemflow and throughfall as found in other tree systems (Lodhi, 1978; Riha *et al.*, 1986). However, Barth and Klemmedson (1978) and McBain (1983) found higher soil pH under palo verde (*Cercidium floridum*) and eastern redcedar, respectively and ascribed this difference to high base content and Ca in leaf litter. Cow manure contributes high base and calcium inputs that could account for the greater pH found in canopy zones at Pasture Site 2 ($P < 0.05$), and there was a trend ($P < 0.10$) for soil Ca to be higher beneath than beyond tree canopies at this site (Fig. 4). On all sites, soil Mg was significantly lower at the boles compared to other inside canopy samples ($P < 0.05$) (Fig. 4), but otherwise was not different beneath vs. outside tree canopies. Because cations readily leach at lower pH (Lodhi, 1977), acidic stemflow could account for the lower Mg found at the bole. In comparing management histories and soil type, both pasture soils had greater organic matter and P than the savanna soils of similar texture, while each loam soil had higher pH, organic matter, K, Ca and Mg than the sandy site of similar management history.

Differences in biomass.—Grass and total aboveground biomass were roughly 50 to 100% greater outside than inside the canopy for the two savanna sites (Fig. 5). However, on Pasture Site 1 grass biomass was lower outside than inside the canopy ($P < 0.01$) and total biomass was not significantly different. Pasture Site 2 had active grazing and was not measured. Mean herbaceous biomass ranged from a high of approximately 129 g/m^2 outside canopies on Savanna Site 2 to a low of 22 g/m^2 below canopies on Savanna Site 1. Results from the two sampling dates were similar (Fig. 5). Despite more favorable nutrient and moisture conditions, biomass was generally lower or equal beneath trees compared to open areas, indicating that other factors such as light or allelopathic chemicals from oak leaf litter may have inhibited vegetative productivity.

TABLE 1.—The number of species inside (beneath) and outside of oak canopies, categorized by plant form, perennial vs. annual and native vs. exotic groups. Species with double designations were not counted (*e.g.*, *Plantago major* is both annual and perennial, *Poa* spp. is both native and exotic). Categories are those of Gray (1908) and Wax *et al.* (1981)

Site	Position	Grass	Forb	Woody	Annual	Perennial	Native	Exotic
Savanna	Inside	9	31	8	2	44	41	4
1	Outside	10	31	6	3	42	39	6
Savanna	Inside	4	33	5	1	38	33	7
2	Outside	4	31	1	0	33	32	5
Pasture	Inside	9	29	4	18	19	9	30
1	Outside	10	24	2	16	15	7	26
Pasture	Inside	6	17	0	8	13	3	19
2	Outside	7	13	0	9	10	3	16

Differences in plant composition.—There were 55, 48, 55 and 27 species on Savanna Site 1, Savanna Site 2, Pasture Site 1 and Pasture Site 2, respectively. On all sites, similar numbers of species were noted beneath and outside of canopies. Savanna sites were made up of 90 to 93% perennial and 80 to 81% native species. In contrast, pasture sites comprised

TABLE 2.—Mean percent cover of prevalent plant species ($\geq \approx 5\%$ cover), of all other species combined, and bare soil inside and outside oak canopies at two savannas and two pastures

	Savanna 1		Savanna 2		Pasture 1		Pasture 2	
Species	Inside	Out	Inside	Out	Inside	Out	Inside	Out
Poa spp.	13.4		14.8		28.1	24.5	28.9	46.0
Andropogon spp.	4.8	12.6	11.1	28.6				
Taraxacum officinale					17.0	26.8	19.5	16.5
Agropyron repens					25.2		5.1	11.1
Bromus inermis					8.4		5.3	18.5
Cacalia atriplicifolia			12.1	5.0				
Solidago altissima			11.2					
Melilotus alba			7.5	6.7				
Berteroa incana						7.1		
Arctium minus							6.9	
Carex spp.	6.1	5.7						
Atriplex patula							5.7	
Helianthus strumosus			5.3					
All other species	17.2	29.8	22.2	36.7	12.9	26.4	5.8	7.0
Other cover[a]	58.5	51.9	15.8	23.0	8.4	15.2	22.8	0.9

[a] Other cover includes bare soil and litter.

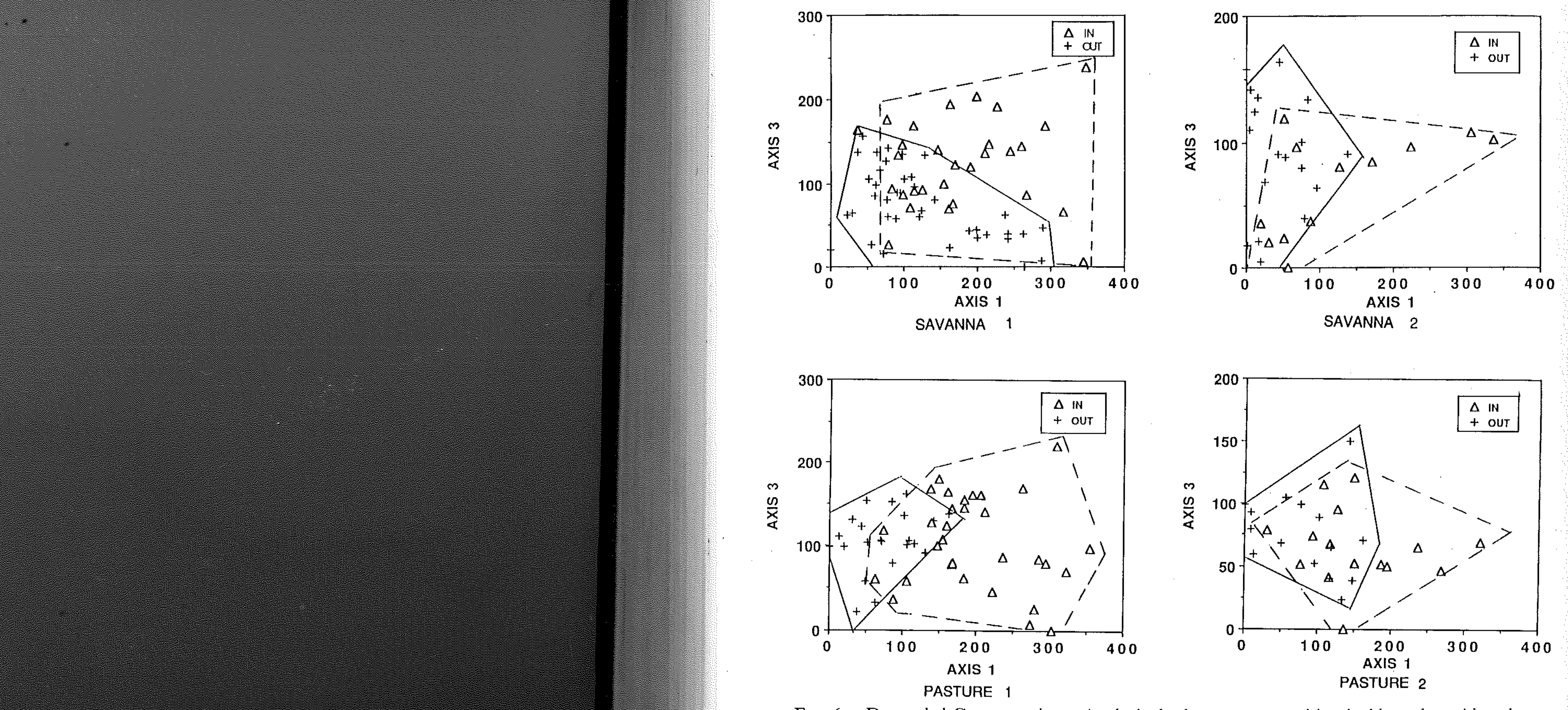

FIG. 6.—Detrended Correspondence Analysis, herbaceous composition inside and outside oak canopies on two savannas and two pastures using a species mode ordination

54 to 58% perennial and 15 to 20% native species. No differences were seen for these groups between inside and outside canopy areas (Table 1). Data for all species and their locations by canopy position and site are available in Ko (1990).

It is not surprising that the restored savannas were dominated by native species, whereas the pastures were dominated by exotics. In grazed prairies, researchers have reported sharp reductions in native species in terms of frequency and diversity (Curtis, 1959; Weaver, 1968). Dix (1959) noted that both *Poa* spp. and *Taraxacum officinale* have low growth form characteristics that resist grazing pressures, which explains the dominance of these species at the pasture sites. Plant introductions and disturbance from grazing and fire appear to be major factors in determining species at these sites.

Detrended Correspondence Analysis (DCA) indicated that plant composition inside the canopy differed from outside the canopy, although with considerable overlap (Fig. 6). Eleven of 12 species that were frequent (>5% cover) outside the canopy were also frequent inside (Table 2). However the reverse was not true; almost half of the species frequent inside were infrequent outside. Grazing disturbance may have provided the opportunity for more species to thrive in pastures beneath canopies than beyond. At Pasture Site 2, cattle trampling and

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cool temperatures under oak trees accounted for the common presence of *Arctium minus* and *Atriplex patula,* two weedy species which prefer disturbed moist soils (Wax *et al.,* 1981).

Poa spp. had the highest percent cover below the canopy, averaging from 13 to 15% and 28 to 29% on the savanna and pasture sites, respectively. Beyond the canopies, *Poa* spp. never reached 1% cover at the savanna sites, but it had the first an second highest average plant cover at 46 and 25% at Pastures 2 and 1, respectively (Table 2). *Poa pratensis* and *P. compressa* were the two species grouped under *Poa* spp. during percent cover estimations. Both are cool season grasses that grow well in moist soils during the spring and tolerate shade, which were two conditions present under canopies in this study. The dominance of *P. pratensis* under eastern red cedar (*Juniperus virginiana*) in undisturbed bluestem prairie was also reported by Gehring and Bragg (1992) and reinforces the idea that *Poa* spp. is widely adapted to canopied areas in a diverse group of tree/non-tree systems in the midwestern states.

Results presented in this study clearly show significant influences of tree canopies on soil nutrient and water relations, and on vegetation composition and productivity. This research reinforces the idea that savannas are not merely prairies with trees, but have their own unique attributes. Differences observed between savannas and pastures point out the important interactions that can occur as a result of alternative management.

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Distribution of Seven Native and Two Exotic Plants in a Tallgrass Prairie in Southeastern Wisconsin: The Importance of Human Disturbance

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ABSTRACT.—Invasion by exotic plant species is a serious threat to the integrity of natural communities. The distribution of an exotic species depends upon environmental conditions, the structure of the native community, patterns of disturbance and ecological features of the species itself. This study identifies (1) associations between two exotic and seven native species in a tallgrass prairie in southeastern Wisconsin and (2) factors underlying the distribution of these species, with special regard to the effects of human disturbance. The distribution of two exotic species, *Melilotus alba* (white sweetclover) and *Daucus carota* (Queen Anne's lace), and seven native species, *Potentilla arguta* (prairie cinquefoil), *Pedicularis canadensis* (Canada lousewort), *Dodecatheon meadia* (Mead's shooting star), *Equisetum laevigatum* (scouring rush), *Pycnanthemum virginianum* (Virginia mountain mint), *Phlox glaberrima* (smooth phlox) and *Solidago graminifolia* (bushy goldenrod), were studied in 100, 4 m^2 quadrats on five transects. Plant densities and soil characteristics were recorded for each quadrat and analyzed using nonparametric comparison of means and Spearman correlation analysis. Densities of the two exotic species were positively correlated with each other and negatively correlated with those of five of the seven natives. Most species exhibited a clear segregation between disturbed and undisturbed transects; *Melilotus* and *Daucus* dominated the disturbed transects, and native species dominated the undisturbed transects. Edaphic conditions appear to be the most important factor driving this habitat segregation between exotics and natives. Our finding is instructive for prairie restoration, because it suggests that in some cases, soil restoration may be desirable even if it results in additional mechanical disturbance. Although the prairie in its undisturbed state seems to resist invasion of these two exotic species, *Daucus* is able to escape disturbed microhabitats more extensively than is *Melilotus*.

INTRODUCTION

The introduction of exotic plant species into native communities is an increasingly important issue in ecology and conservation (Temple, 1990). Invasive exotics function as a "biological pollution" in natural areas (Thomas, 1980); many have special characteristics that allow them to compete vigorously with native plants (Baker, 1965, 1974; Bazzaz, 1986), as well as the ability to exploit human-generated disturbances (Orians, 1986; Macdonald *et al.,* 1989; Hobbs and Huenneke, 1992). Exotic invaders may expand their range rapidly into unoccupied areas and are often aided, intentionally or unintentionally, by humans. Some theoretical work suggests that the impact of a species introduction may depend on the stability and diversity of the invaded community (Elton, 1958; Moulton and Pimm, 1983; Case, 1990). Understanding the distribution of native species surviving in an area of exotic invasion is central to assessing the community-level impact of an invasion. In addition, the

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