Scott E. Nielsen and Alan Haney

Gradient Responses for Understory Species in a Bracken Grassland and Northern Dry Forest Ecosystem of Northeast Wisconsin

Abstract *Spread Eagle Barrens, located in Northeastern Wisconsin, occupies an area of pitted outwash created during the late Wisconsin glaciation. This irregular topography forms a heterogeneous landscape influencing both site characteristics and associated plant communities. Today the dominant plant communities, which often occur in a mosaic pattern, consist of both bracken-grasslands and northern dry forests. It is in this landscape that we investigated the distribution and position of 35 groundlayer species along six environmental gradients and one competitive gradient. These include slope position, site severity index, canopy, soil nutrient index, organic matter, pH, and bracken fern frond densities. The presence or absence of each species, along with environmental data, were recorded in random 1 m^2 quadrats placed throughout the Sand Lake Region. Probability responses of individual species along measured gradients were then determined through logistic regression. Response shapes of species across gradients were often non-linear, with both quadratic and cubic functions being common. Results indicate that topoedaphic factors, canopy and bracken fern all influence species distributions. Overall, however, canopy was the single most important gradient examined. Bracken fern frond densities also showed strong significance for many species indicating the important role it plays on the landscape. Additionally, as predicted by competition theory, bracken fern was also found in the center of environmental gradients where the strongest competitors are thought to dominate.*

Savannas are one of the most extensive and socioeconomically important ecosystems on the planet, covering over 18 million km^2 or 14% of the earth's surface (Botkin et al. 1984, Perry 1994). In Wisconsin one type of savanna, called pine barrens, once occupied a large portion of the state covering over 947,000 ha at the time of European settlement (Curtis 1959). Today, however, many of our native Midwestern savanna communities are rare (Nuzzo 1986) due to fire suppression and associated woody encroachment (Abrams 1992). The situation for pine barrens in Wisconsin is no different. Only about 20,000 ha currently remain of both oak and pine barrens (Mossman et al. 1991).

Two distinct forms of pine barrens can be recognized based on the groundlayer composition, perhaps reflecting soils, topography, and location to tension zone (Vogl 1970). The first type, prairie-like barrens, tend to occur in coarse sands, gentle topography, and are geographically close to prairies. The second type, non-prairie barrens, tend to occur in loamy sands and sandy loams, have more topographic variability, and are relatively isolated from prairies or the tension zone. The latter community, which rarely has received attention, also includes that which has been referred to as depauperate bracken-grasslands (Vogl 1964*a*). These bracken-grasslands were initially assumed to be secondary communities in Wisconsin resulting from logging and fire. However, based on both ecological studies of northern Wisconsin (Curtis 1959, Vogl 1964*a*) and European records, it appears that the bracken-grassland community was indeed part of the state prior to settlement, although in relatively small coverage. It since has expanded due to anthropogenic causes.

Today, these bracken-grassland communities are often integrated into a mosaic of other communities in northern Wisconsin, particularly northern dry forests. In some instances, many can even attain the appearance of an aspen parkland, with the dominant woody species being aspen (*Populus tremuloides* and *P. grandidentata*). Once bracken-grasslands are established, they are fairly resilient and do not appear to require fire for their maintenance (Vogl 1964*a*), unlike other savanna communities of the Midwest (Bray 1955; Curtis 1959; Vogl 1964*b*, 1970; Kline and Cottam 1979; Grimm 1984; Haney and Apfelbaum 1990; Leitner et al. 1991; Abrams 1992). Possible mechanisms responsible for this maintenance are competition and microclimate.

Competition between tree seedlings and bracken fern may inhibit or limit succession (Curtis 1959, Vogl 1964*a*). Bracken fern (*Pteridium aquilinum* L. Kuhn), which is the most widely distributed plant in the world (Page 1982), has an excellent ability to compete for moisture, nutrients, and light. In addition to direct competition for resources, bracken fern can also inhibit plant establishment and growth through allelopathy (Ferguson and Boyd 1988). Bracken fern rhizomes also quickly invade or re-establish following disturbance (Conway 1952). Many of the bracken-dominated systems of the world today are associated with disturbances such as fire, timber harvesting, or grazing. In Finland, Oinonen (1967) was able to positively correlate clone sizes of bracken fern to time of last fire, with ages of clones going back to the years of 1300 (old fortress at Sulkava) and 1318 (Turku raided) and clone sizes exceeding 200 m in diameter.

The second factor potentially influencing the stability of bracken-grasslands, at least in Wisconsin, is the microclimate (Curtis 1959, Vogl 1964*a*). In many areas where bracken-grasslands dominate, the landscape (pitted outwash) promotes drastic changes in temperature, including the frequent frost formation as a result of cold air drainage and re-radiation (Figure 1, Table 1). These frosts

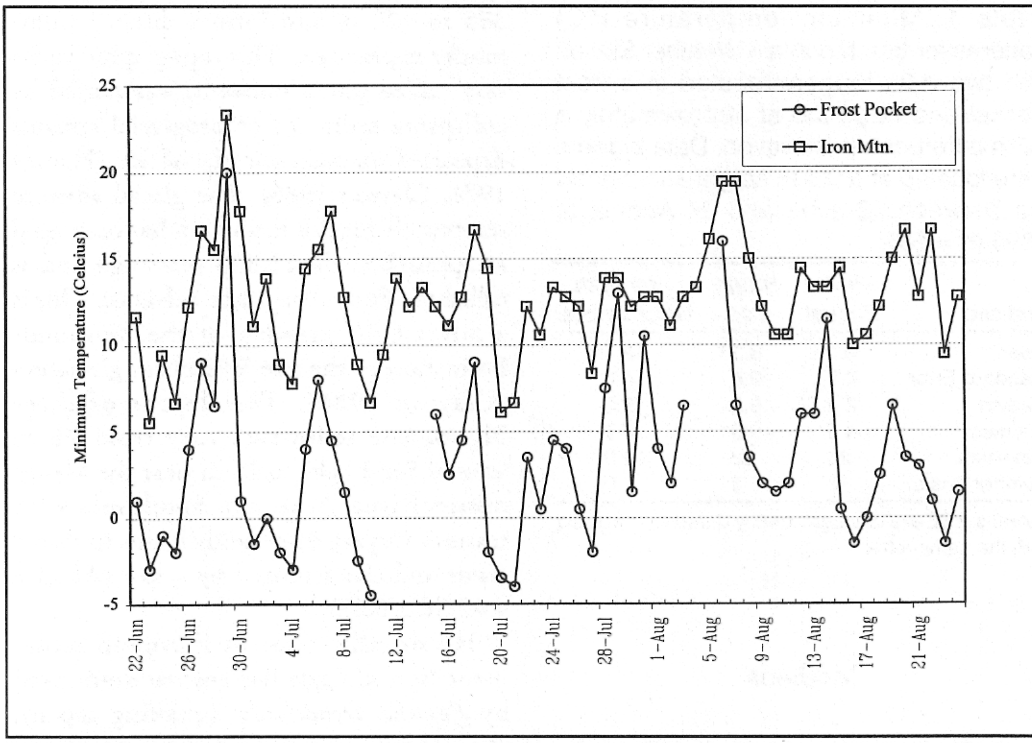

Figure 1. Minimum temperature patterns between a kettle (frost pocket) at the study site and nearest (*c.* 6 km) weather station (Iron Mountain) for the summer of 1996.

may then be referred to as a form of disturbance, which restricts recruitment of woody species in low areas of the landscape. Interestingly, bracken fern is also frost sensitive and restricted from the low kettles and valleys (Nielsen 1997). Therefore, bracken fern itself cannot influence the relative openness and stability of frost pockets (Vogl 1964*a*). It is likely that both competition and extremes in temperature exert an influence, with bracken fern competition acting according to an inhibition model of succession (Connell and Slayter 1977) and the microclimate functioning as a factor influencing recruitment based on frost sensitivity.

Because bracken-grasslands have rarely been studied (however, see Vogl 1964*a*), particularly in relations to the surrounding communities, first understanding which species are present to an area and why, may prove essential in understanding the communities' origins, ecology, and possible future management. In other Midwest savannas, variables such as soils, topography, and canopy have been found to be important determinants of species distributions (Bray 1958, Ware et al. 1992, Leach 1994, Pruka 1994, Hujik 1995). It is our objective here to determine patterns of plant species distributions along the major environmental gradients of canopy, soil organic matter, pH, soil nutrient index, slope position, and site severity index. Additionally, since the importance of bracken fern in this system may be quite substantial, responses of plants to densities of bracken fern fronds are examined.

Table 1. Minimum temperature (°C) patterns for Iron Mountain Weather Station and two data loggers located in a frost pocket and ridge top at approximately a 30 m difference in elevation. Data loggers were located at a 0.5 m height and placed out between 22 June and 24 August of 1996 (n = 58).

Statistic	*Frost Pocket*	*Ridge Top*	*Iron Mtn. Weather Sta.*
Mean*	3.1 [a]	8.3 [b]	12.7 [c]
Standard Error	0.7	0.6	0.6
Median	2.3	8.5	12.8
Minimum	- 4.5	- 0.5	5.6
Maximum	20	22	23.3
Number frosts	16	3	0

*Means ±SE are not significantly different if labeled with the same letter

Methods

Study Site

Field research was conducted at Spread Eagle Barrens State Natural Area, located c. 7 km southeast of Florence, Wisconsin (45°52′N, 85°10′W). This landscape size Natural Area occupies 3,580 ha, being bordered by the Menominee River to the east and approximately dissected in half by the Pine River. An ecological classification of the site in *Ecoregions of North America* (Bailey and Cushwa 1981) identifies Spread Eagle Barrens as a humid temperate domain, humid warm-summer continental division, and Laurentian mixed-forest province. The climate of the area is intermediate between lake moderated and continental, with a mean annual temperature of 5.2°C and a median frost-free period of 113 days. Mean annual precipitation is 739 mm with an average annual snowfall of 1,595 mm.

Elevations of the study area range from 385 to 320 m and form a distinct hummocky appearance. This topographic variation, called pitted outwash, was caused by collapsing sediment of proglacial streams deposited on stagnant glacial ice (Hadley 1976, Clayton 1986). The glacial advance responsible for this formation has been aged at approximately 12,300 years ago and is called the Early Athelstane Advance. This is a Silver Cliff member of the Kewaunee Formation of the late Wisconsin glaciation (Clayton 1986). The depths of these Pleistocene sediments vary from 76 m around Sand Lake to 16 m near the Menominee River. Soils are Spodosols with textures varying from sandy loams to loamy sands and characterized by a low pH (μ = 4.87 SE ± 0.02).

Historically, prior to European settlement, Spread Eagle Barrens was dominated by *Populus tremuloides* (quaking aspen), *Pinus banksiana* (jack pine), and *Betula papyrifera* (white birch) (Table 2) (Nielsen 1997). Today, however, many of the sites have been converted through management (logging and prescribed burning) to large homogenous bracken-grasslands, originally intended to optimize habitat for sharp-tail grouse. One region that escaped much of this management is the area surrounding Sand Lake. This area still maintains a rich mosaic of northern dry forests and bracken grasslands, perhaps because a wildfire swept the area in the late 40s or early 50s. Research was concentrated in the area surrounding Sand Lake because the existence of bracken-grasslands was not a function of management and because of the large variability there in site characteristics and competition across the landscape. In that vicinity we could investigate species responses to the landscape variables without having to account for recent management related effects.

Table 2. Numbers and frequencies of witness trees for Spread Eagle Barrens, listed by common names and Linnaean taxanomic equivalents.

Common Name	Scientific Name	Total Witness Trees	# Survey Points	Survey Point Frequency[a]
Aspen	*Populus tremuloides* or *Populus grandidentata*	40	25	44.6
White birch	*Betula paperifera*	26	17	30.4
Jack pine	*Pinus banksiana*	28	16	28.6
Red pine	*Pinus resinosa*	9	8	14.3
White pine	*Pinus strobus*	9	6	10.7
Spruce[b]	*Picea glauca* or *Picea mariana*	8	3	5.4
Maple[c]	*Acer saccharum* or *Acer rubrum*	1	1	1.8
White cedar	*Thuja occidentalis*	1	1	1.8
Oak	*Quercus ellipsoidalis*	1	1	1.8
Total		**123**		

[a] Survey point frequency represents the frequency of tree species to survey point. Since the survey points had between 2 and 4 witness trees, the sum of the frequencies exceed 100%.
[b] It appears that the surveyor did not distinguish between *Picea glauca* and *Picea mariana*.
[c] It appears that the surveyor did not distinguish between *Acer saccharum* and *Acer rubrum*.

Field Methods

In investigations dealing with distribution patterns of populations, a systematic grid design may allow for greater precision in analyses (Brown and Ruthery 1993). Therefore, in the summer of 1996, within the Sand Lake region of Spread Eagle Barrens, six 250 m^2 cells were randomly selected from an overlaying grid on a United States Geological Service 7.5 minute quadrangle. Within each of these six cells, 50 random observation points were chosen for sampling, producing a sample size of 300. Sites were sampled once between the dates of July 10th and August 20th of 1996. Each sample consists of a 1 m^2 circular herbaceous quadrat centered over the random position previously determined. Within this quadrat all living ground-layer plant species (<1 m height) were recorded for presence or absence based on taxonomy following E. G. Voss (1972, 1985, 1996). Along with plant presence or absence, the number of live bracken fern fronds was counted within each quadrat. To determine canopy coverage of a site, the line intercept method was used over a 10 m transect, which was centered over each quadrat (Haney and Apfelbaum 1994). In this method, a vertical plane was projected from the transect with the starting and stopping positions of tree species recorded.

Soil characteristics of each sample point were based on a composite soil sample from around each quadrat by combining four soil cores, each being 2 cm x 15 cm in size, from the major cardinal sectors of the quadrat. Samples were analyzed by the University of Wisconsin-Marshfield Soil and Forage Analysis Laboratory for organic matter, pH, P, K, Ca, and Mg. For the cations (P, K, Ca, and Mg), an index (nutrient index, NI) was created in order to reduce both the number of variables and the multi-collinearity between variables. This was done by ranking (ascending) each soil variable and summing the rank values.

The influence of topography was addressed by two complex gradients. The first is an index relating aspect and slope to incoming solar radiation. In both temperate and boreal zones, both aspect and slope combine to influence vegetation patterns caused by differences in solar radiation. Solar radiation has not only been found to influence vegetation patterns (Haase 1970, Fralish 1988, Bonan and Shugart 1989), but also soil moisture and forest productivity (Beers et al. 1966). Therefore, an index was created for this study called "site severity index" (SSI), which takes into consideration both aspect and slope, thereby representing the amount of direct solar radiation and heating of a site in relation to flat surface.

This index was modified from one created by Beers et al. (1966), which is based on a sine wave varying according to aspect. This gave maximum values for northeast slopes (productive forests) and minimum values for southwest slopes (unproductive forests). Other studies within the Midwest (Ware et al. 1992, Thomas and Anderson 1993) have used this function to investigate the influence of aspect on vegetation. In this study, however, the Beers' equation was modified so that a southwest slope received the highest value and a northeast slope the lowest, while being scaled between +1 and -1, representing xeric to mesic sites respectively. In addition, the function was scaled to take into account the amount of slope. As slope decreases from a high of 45%, the wave dampens toward zero, representing a flat surface. In the field, slope was recorded with a clinometer, while aspect was determined with a compass. Using these values, the site severity index was determined through the equation SSI = sin(A + 225) x (% slope/45), where A represents degrees from polar north and % slope from horizontal.

The second topographic variable examined was slope position. For this, each sample location was placed into one of six slope positions based on a visual inspection of the landscape. Slope position categories were as follows: frost pockets and valley bottoms (5), lower one third of slopes (4), middle one third of slopes (3), upper one third of slopes (2), narrow ridge (< 50 m wide) (1), and lastly a broad ridge or plain (> 50 m wide) (0).

Statistical Analyses

To determine species responses along examined gradients, logistic regression was used on presence/absence data of common (>10% frequency) ground-layer species in 1 m^2 quadrats (Appendix A). The logistic regression statistic is similar to linear regression except that the dependent variable (Y) is binary (1 or 0, hence present or absent) instead of continuous (Sokal and Rohlf 1995). Logistic regression then relates the proportions of a dependent variable to an independent variable. This independent variable can be continuous or discontinuous. Significance was considered at the level of $P < 0.10$ for the chi-square statistic. The modeling technique used here is one variant of GLM (general linear modeling) and is similar to analyses of *Eucalyptus* species in Australia by Austin et al. (1990).

For logistic regression modeling, a total of 34 species were tested in order across all six gradients of interest (canopy, NI, soil organic matter, pH, slope position, and SSI). In addition to the standard linear responses, which represent an increase or decrease in probability of that species across a variable, additional combinations were tested by adding quadratic and cubic functions. The quadratic function would indicate a Gaussian or Normal distribution, which is expected in ordination analyses. This type of response has been called Gaussian logistic

Table 3. Gradient partitions used for determining patterns of species optimal responses across examined gradients of topoedaphic factors, bracken fern (a), and canopy (b).

[a] Gradient Variable	Low	Mid	High	[b] Community Classification	Canopy Interval (%)
Soil O.M.	<2.6	2.6–4.0	>4.0	Forest	>85
Soil pH	<4.9	4.9–5.6	>5.6	Woodland	<85–>50
NI	<28	28–46	>46	Savanna	<50–>1
SSI	<-0.34	-0.34–0.34	>0.34	Grassland	<1
Slope position	4,5	2,3	0,1		
Bracken density	<9	9–18	>18		

regression (GLR) by ter Braak (et al. 1986). The cubic function would verify a more complex response, such as bimodal distributions. All gradients were examined for each species in histograms, in order to determine if these higher order functions were appropriate in the logistic model.

After modeling, probability responses for every significant species were plotted across the selected gradient. These gradients were then subjectively divided into sections to determine guilds of species (Table 3a). For these divisions, canopy was the only variable that was not segmented into equal proportions, in order to correspond to existing abstract community definitions based on canopy amounts (Table 3b). Since species are responding across gradients in a continuum fashion, these segmented divisions are to be used only for generalizations.

Results

Canopy

The canopy variable examined was the most important gradient overall, as determined by chi-square significance tests. All 34 species examined showed significant responses to this inferred light gradient. The majority of species response models were linear, followed by quadratic, and finally cubic functions (Table 4, Figure 2a). Along this gradient, four main segments were arbitrarily stratified for determination of optimal position according to community classifications following canopy amounts. Most species modeled were forest species, followed by the grassland guild, woodland guild, and savanna guild. The species that optimized their probabilities in the canopy range associated with the savanna classification include *Apocynum androsaemifolium, Comandra umbellata, Comptonia peregrina, Prunus pumila,* and *Vaccinium pallidum* (Table 5).

Nutrient Index (NI)

Nutrient Index represents the combinations of the relative ranks of available nutrients P, K, Ca, and Mg. This was the least predictive gradient in describing species responses; only 14 species were significantly related to it (Table 4). Of the significant models, most were linear, followed by a few quadratic, and only one cubic function (Figure 2b). Optimal positions tended to occur at the high end of the nutrient index, with a few in the middle and a few at the low end (Table 5). One of the species that optimized low nutrient sites, *Comptonia peregrina,* is a non-Leguminosae nitrogen fixer and perhaps an important early

Table 4. Functions used in logistic regression analyses of species along each gradient. Significance of each model is indicated as a subscript in each function.

Species	*Canopy*	*Nutrient Index*	*Organic Matter*	*pH*	*Topographic Position*	*Severity Index*	*Bracken Densities*
Acer rubrum	^{c}C	^{a}N		$^{a}P+P^2$	$^{c}T+T^2$		$^{c}B+B^2+B^3$
Agropyron trachycaulum	^{c}C			^{c}P	$^{c}T+T^2$		$^{c}B+B^2+B^3$
Amelanchier spp.	^{a}C	$^{a}N+N^2$					
Anemone quinquefolia	^{c}C		$^{b}O+O^2$		$^{b}T+T^2$	^{a}S	^{b}B
Apocynum androsaemifolium	$^{c}C+C^2+C^3$			^{b}P	$^{b}T+T^2+T^3$	^{a}S	^{c}B
Aster ciliolatous	^{c}C	^{a}N	$^{a}O+O^2$	^{c}P	$^{b}T+T^2$	^{a}S	
Aster macrophyllus	^{c}C	^{c}N	^{a}O	$^{a}P+P^2$	$^{c}T+T^2$		$^{b}B+B^2+B^3$
Bromus kalmii	^{c}C		$^{a}O+O^2$	^{c}P	^{c}T		$^{c}B+B^2+B^3$
Calystegia spithamaea	^{c}C				$^{b}T+T^2+T^3$	$^{b}S+S^2+S^3$	^{b}B
Campanula rotundifolia	^{c}C		^{a}O	^{c}P	$^{c}T+T^2+T^3$	$^{a}S+S^2+S^3$	$^{c}B+B^2+B^3$
Carex pensylvanica	$^{a}C+C^2+C^3$			^{b}P			
Comandra umbellata	$^{c}C+C^2$			^{a}P		^{a}S	$^{b}B+B^2+B^3$
Comptonia peregrina	$^{c}C+C^2$	^{c}N			$^{a}T+T^2+T^3$	^{a}S	^{c}B
Corylus cornuta	^{c}C		^{c}O	$^{b}P+P^2$	$^{c}T+T^2$	$^{c}S+S^2$	$^{b}B+B^2+B^3$
Danthonia spicata	^{c}C		^{a}O	$^{b}P+P^2+P^3$	^{c}T	^{c}S	^{c}B
Diervilla lonicera	^{a}C				$^{c}T+T^2$		$^{b}B+B^2$
Gaultheria procumbens	$^{c}C+C^2$		$^{a}O+O^2$	$^{b}P+P^2+P^3$	$^{c}T+T^2$	$^{b}S+S^2$	$^{c}B+B^2+B^3$
Hieracium aurantiacum	^{c}C		$^{a}O+O^2$	^{c}P	^{c}T	$^{a}S+S^2+S^3$	$^{c}B+B^2+B^3$
Lysimachia quadrifolia	$^{a}C+C^2$				$^{a}T+T^2$	$^{a}S+S^2+S^3$	
Maianthemum canadense	^{c}C	$^{b}N+N^2$	^{a}O	$^{a}P+P^2$	^{c}T	^{b}S	$^{b}B+B^2+B^3$
Melampyrum lineare	$^{c}C+C^2$			$^{a}P+P^2$			
Oryzopsis asperifolia	^{c}C	^{a}N	$^{b}O+O^2$	$^{c}P+P^2$	^{c}T	$^{b}S+S^2$	$^{b}B+B^2$
Poa spp.	$^{c}C+C^2$	^{a}N		^{c}P	$^{c}T+T^2+T^3$		$^{a}B+B^2+B^3$
Polygala paucifolia	$^{c}C+C^2$				$^{b}T+T^2$	^{a}S	$^{b}B+B^2+B^3$
Prunus pumila	$^{b}C+C^2$		^{b}O	^{c}P	$^{c}T+T^2$	$^{c}S+S^2$	$^{c}B+B^2$
Pteridium aquilinum	^{c}C	$^{a}N+N^2$	$^{c}O+O^2$	$^{c}P+P^2$	^{c}T	$^{a}S+S^2+S^3$	
Rubus allegheniensis	^{b}C	^{a}N			$^{a}T+T^2$	$^{a}S+S^2+S^3$	
Schizachne purpurascens	^{c}C		$^{a}O+O^2+O^3$	$^{b}P+P^2+P^3$	^{a}T		$^{c}B+B^2+B^3$
Trientalis borealis	^{c}C		^{a}O	^{b}P	$^{a}T+T^2$	$^{c}S+S^2$	$^{a}B+B^2$
Vaccinium angustifolium	$^{b}C+C^2$	^{a}N		$^{a}P+P^2$	^{c}T		$^{c}B+B^2$
Vaccinium myrtilloides	$^{a}C+C^2$		$^{b}O+O^2$	$^{a}P+P^2$			
Vaccinium pallidum	$^{c}C+C^2$	^{c}N					
Viola adunca	^{c}C	$^{a}N+N^2+N^3$		^{c}P	^{b}T	$^{a}S+S^2+S^3$	$^{c}B+B^2+B^3$
Waldsteinia fragarioides	^{c}C	^{a}N	$^{b}O+O^2$	$^{c}P+P^2$	^{c}T	^{b}S	$^{b}B+B^2$

Model chi-square = $^{a}P<0.10$, $^{b}P<0.01$, $^{c}P<0.001$

Table 5. Optimal positions for significant species as determined from logistic regression models.

Species	*Canopy*	*Nutrient Index*	*Organic Matter*	*pH*	*Slope Position*	*Severity Index*	*Bracken Densities*
Acer rubrum	100	62		4.8	1		28
Agropyron trachycaulum	0			6.3	5		21
Amelanchier spp.	100	35					
Anemone quinquefolia	100		2.1		3	-1	0
Apocynum androsaemifolium	34			4.2	0	-1	28
Aster ciliolatous	0	62	2.4	6.3	5	-1	
Aster macrophyllus	100	62	5.5	4.7	1		28
Bromus kalmii	0		5.5	6.3	5		0
Calystegia spithamaea	0				0	-1	28
Campanula rotundifolia	0		1.1	6.3	4	-1	0
Carex pensylvanica	69			6.3			
Comandra umbellata	33			6.3		-1	18
Comptonia peregrina	12	12			0	1	28
Corylus cornuta	100		5.5	4.6	1	-0.4	5
Danthonia spicata	0		1.1	6.3	5	1	0
Diervilla lonicera	100				1		28
Gaultheria procumbens	83		3	4.7	0	-0.37	7
Hieracium aurantiacum	0		5.5	6.3	5	-1	11
Lysimachia quadrifolia	100				3	1	
Maianthemum canadense	100	41	5.5	4.7	0	-1	28
Melampyrum lineare	56			4.7			
Oryzopsis asperifolia	100	62	3.5	4.7	0	-0.16	28
Poa spp.	0	62		6.3	5		21
Polygala paucifolia	54				4	-1	9
Prunus pumila	36		5.5	6.3	3	1	0
Pteridium aquilinum	100	35	3	4.5	0	0.04	
Rubus allegheniensis	100	62			2	1	
Schizachne purpurascens	0		5.5	5.2	5		19
Trientalis borealis	100		1.1	4.2	3	-0.59	28
Vaccinium angustifolium	52	12		4.6	0		28
Vaccinium myrtilloides	53		3.4	4.8			
Vaccinium pallidum	28	12					
Viola adunca	0	12		6.3	5	-1	0
Waldsteinia fragarioides	100	62	3.3	4.7	0	-1	28

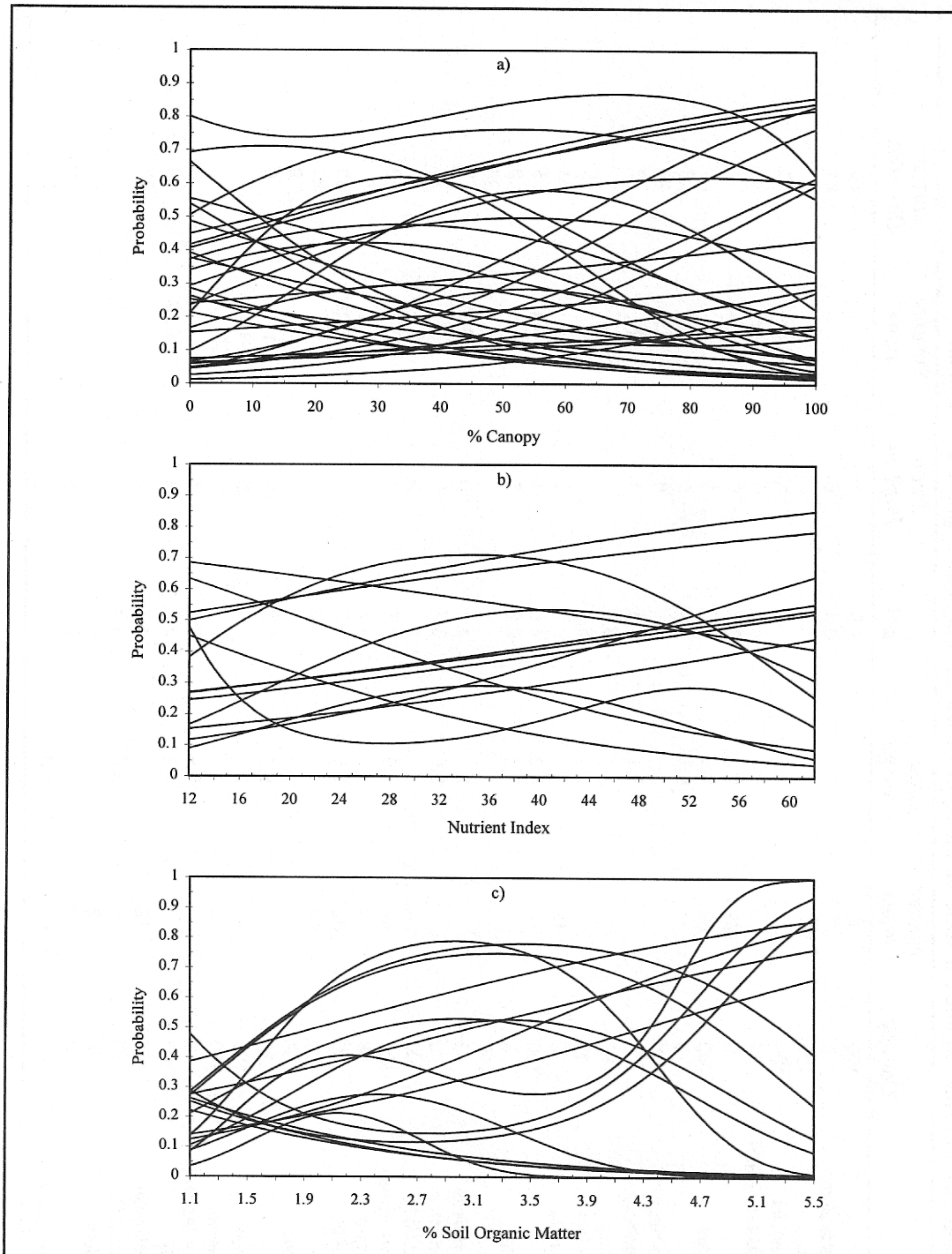

Figure 2. Responses of significant species, as determined by logistic regression, showing shape, optimal position, and distribution patterns of species across the gradients of canopy (a), nutrient index (b), soil organic matter (c), pH (d), slope position (e), site severity index (f), and bracken frond densities (g).

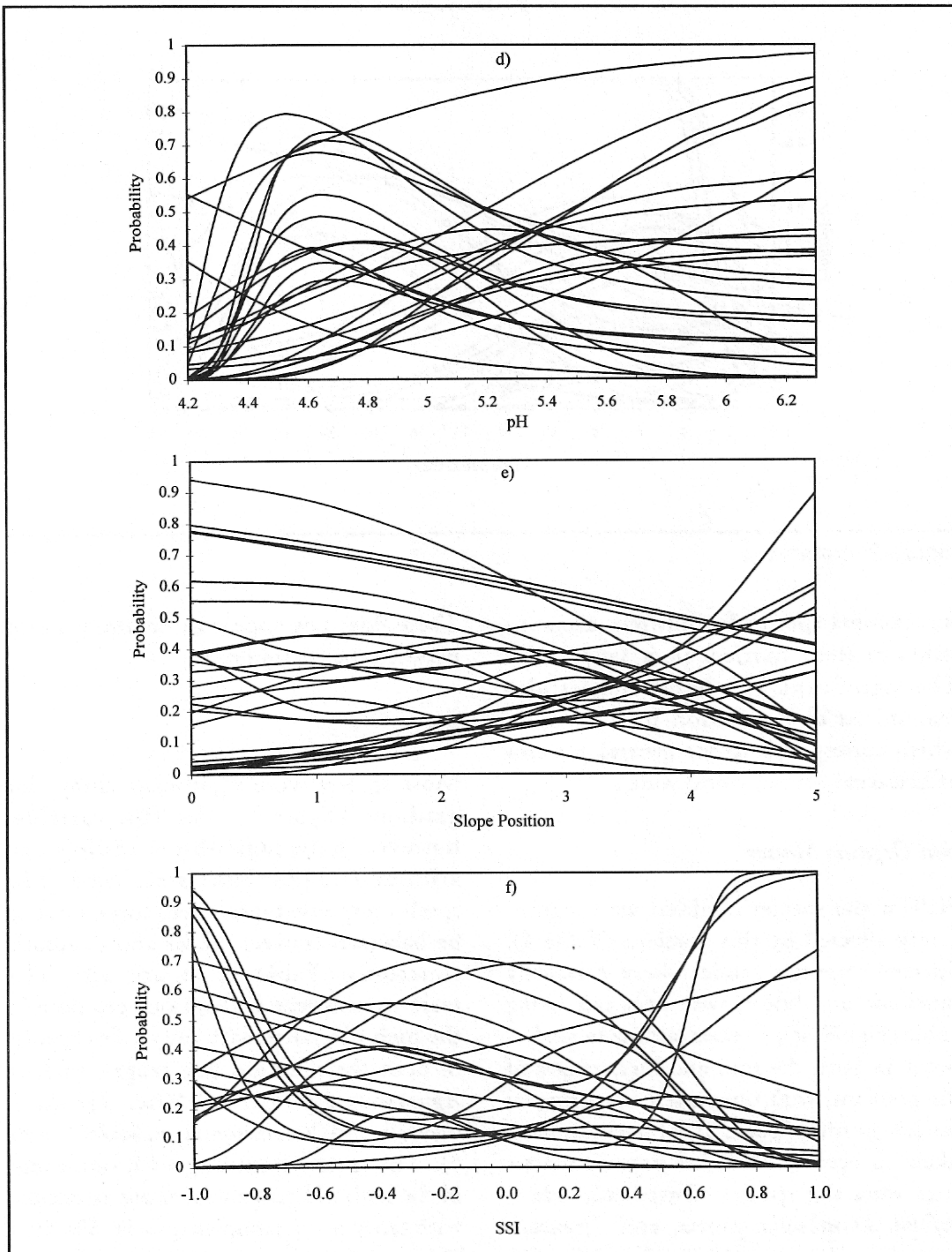

Figure 2, continued.

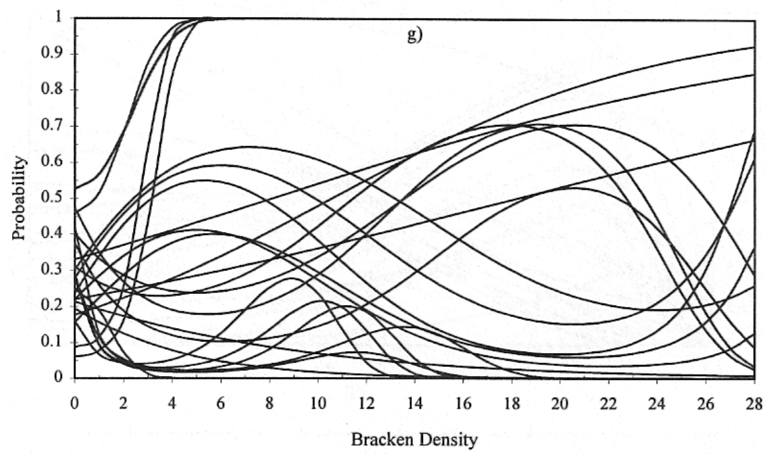

Figure 2, continued.

successional species for nutrient accumulation in these nutrient poor sandy soils. The significant *Vaccinium* species also maximized their position in these sites, which corresponds to the general patterns of Ericaceae species world wide.

Soil Organic Matter

Half of the species modeled were significantly affected by this gradient (Table 4). Species response models were primarily quadratic and linear, with only one being cubic (Figure 2c). Species optima tended to occur in both the mid and high ranges of the gradient, with only a few occurring in the low portion (Table 5). The species most likely to occur in low soil organic matter sites were the species *Campanula rotundifolia, Danthonia spicata,* and *Trientalis borealis,* while species such as *Corylus cornuta, Hieracium aurantiacum, Maianthemum canadense, Prunus pumila,* and *Schizachne purpurascens* tended to optimize probabilities in high soil organic matter. There does not appear to be any patterns between the two guilds.

pH

Most species were significant along this gradient (Table 4). For this variable, however, both logarithmic scaling and arithmetic equivalents were used. The species response types, then, turned out to be balanced between linear and quadratic functions (Table 4, Figure 2d). The majority of species had optimal positions in the high pH range with only a few species in both the mid and low ranges, such as *Apocynum androsaemifolium, Trientalis borealis,* and *Vaccinium myrtilloides* (Table 5). The species occurring with optimums in the high pH range were those associated with fairly open canopies (μ = 10.5% SE ± 7.4, n = 10) representing savanna communities, while species associated with low and mid pH ranges occurred in higher canopies (μ = 82.9% SE ± 7.4, n = 12) associated with forest communities.

Slope Position

This variable contained a high majority of significant models, indicating the importance of topography (Table 4). The response functions were again primarily quadratic and linear, with some complex cubic responses (Table 4, Figure 2e). Interestingly, most of the species had optimal positions in either the frost pocket/valley bottom or upland plains (Table 5). The upland plains' guild includes species such as *Apocynum androsaemifolium, Calystegia spithamaea, Comptonia peregrina, Gaultheria procumbens, Maianthemum canadense, Oryzopsis asperifolia, Pteridium aquilinum, Vaccinium angustifolium,* and *Waldsteinia fragarioides.* The frost pocket guild included such species as *Agropyron trachycaulum, Aster ciliatous, Bromus kalmii, Danthonia spicata, Hieracium aurantiacum, Poa* spp., *Schizachne purpurascens,* and *Viola adunca.*

The apparent difference between these two guilds is that the first guild (upland) is characterized by species typically found in northern dry forest and boreal communities (77.8%), while the second guild of species (frost pockets) are representative of a bracken-grassland communities (100%). This would point to the possibility that the topography variable of slope position may be critical in determining which community will occupy a site. Bracken-grasslands are found primarily in the kettles and valleys of pitted outwash, while forests tend to occupy the more upland positions.

Site Severity Index (SSI)

Site Severity Index was significant in explaining distribution patterns for many of the species (Table 4). A fairly balanced distribution of linear, quadratic, and cubic model functions were used (Table 4, Figure 2f). Optimal response patterns revealed that most species occurred on the mesic end of the gradient (SSI = -1), while a few species used the xeric (SSI = 1) and mid portions (Table 5). The xeric guild included the species *Comptonia peregrina, Danthonia spicata, Lysimachia quadrifolia, Prunus pumila,* and *Rubus allegheniensis,* which are common species to pine barrens and bracken-grasslands. The mesic guild contains species common to boreal forests, northern dry mesic forests, northern dry forests, and bracken-grasslands.

Bracken Fern

The change in bracken fern frond densities proved to play an important role in determining species distributions, with most species being significant (Table 4). Species responses were primarily cubic, with a fair number of both quadratic and linear functions (Table 4, Figure 2g). The cubic response may point to the complex interaction bracken fern may present to other species, with a set of interactions including allelopathy, nutrient competition, and light interception. Another possibility that may promote the unusually complex responses of species are that bracken clones are not at an equilibrium with the landscape. The clones are constantly invading outward with underground rhizomes at least 1 m in advance of emergent fronds (Watt 1940).

Regardless of bracken fern dynamics, a few species seem to respond positively to increasing bracken densities, which is interesting since bracken fern is thought to be an effective competitor and inhibitor (allelopathy). Most of the species showing positive responses to bracken densities (Table 5, Figure 2g), were also species that tended to have optima in high canopy conditions (μ = 72.5% SE ± 12.1, n = 11), while those that were negatively associated with increasing bracken densities tended to have optima in low canopy conditions (μ = 22.7% SE $\pm$ 16.6, n = 6). Thus, many typical forest species (northern dry forest) are located in the open bracken-grasslands. This distribution may partially be a function of bracken fern densities, with interception of light acting as a type of canopy. This, then, may infer advantages for species that can photosynthesize under low light conditions and hence may able to out compete species normally associated with the grasslands.

Discussion

Results indicate that canopy, topoedaphic variables, and bracken fern are all significant factors accountable for distribution patterns of plant species at Spread Eagle Barrens. Canopy appeared to be the most influential predictor for many species. Since canopy is also the easiest of the gradients to manipulate, a potential exists for management of desired species under certain conditions. Based on other environmental conditions, responses of species should be able to be predicted from logistic regression equations.

Topographic variables (slope position and site severity index) are often ignored. We found them to be key factors in determining both plant and community distributions. For instance, slope position influenced both community species patterns and individual species distributions. In particular, bracken fern, a keystone species, was most significantly related to slope position, presumably due to its frost sensitivity. Of the edaphic variables examined, both soil pH and % organic matter were influential for a number of species. However, the nutrient index created for the study was not related to the distribution of a majority of species.

Bracken fern had a cubic response in distribution models for many species. These responses suggest a complex relationship between bracken fern and other species, with the interactions of allelopathy, nutrient competition, and light interception being important. It was initially assumed that both allelopathy and competition would result in negative responses for many species, but our results indicate that the reverse was true. This may be explained by the fact that most positively associated species were those that would be classified as "forest" species, perhaps pointing to the importance of light interception by bracken fern.

According to Austin and Gaywood (1994), the ecological responses of species will be increasingly skewed toward the far ends of a gradient, representing the increasing role of physiological tolerance, while the center of the gradient will be dominated by responses of species occurring due to the increasing role of competition. The more superior competitors should then be found in the center of a gradient, resulting in high dominance and low diversity (Austin and Smith 1989). If this were the case, bracken fern, a noted competitor with high dominance, should be found in the center of direct gradients. This seems to be occurring for the variables of nutrient index, organic matter, pH, and site severity index at Spread Eagle Barrens. Removing or controlling bracken fern might produce an associated shift in species composition due to the releasing of competitive interactions. Bracken fern influence on species responses, including factors that influence bracken fern, are important considerations in the management of Midwestern Savannas. In fact, by selectively harvesting the woody species based on site characteristics that promote domination by bracken fern or within a frost pocket, maintenance may occur through competitive inhibition or the microclimate, instead of intensive management.

Appendix A. Species selected for logistic regression modeling based on frequency of occurrence (> 10%) within 1 m^2 herbaceous quadrats at Spread Eagle Barrens. Curtis fidelity represents the number of native communities, out of 34 identified, in which the species was found. The community maximum describes which plant community a species achieved maximum presence (Curtis 1959).

Genus	*Species*	*Family*	*Common Name*	*Curtis Fidelity*	*Community Maximum*
Acer	*rubrum*	Aceraceae	red maple	12	NDM
Agropyron	*trachycaulum*	Gramineae	wheatgrass	9	BG
Amelanchier	spp.	Rosaceae	serviceberry		
Anemone	*quinquefolia*	Ranunculaceae	wood anemone	18	NDM
Apocynum	*androsaemifolium*	Apocynaceae	spreading dogbane	18	ND
Aster	*ciliolatus*	Asteraceae	Lindley's aster	9	BG
Aster	*macrophyllus*	Asteraceae	large leaved aster	14	BF
Bromus	*kalmii*	Gramineae	Kalm's brome	10	BG
Calystegia	*spithamaea*	Convolvulaceae	low bindweed	11	ND
Campanula	*rotundifolia*	Campanulaceae	bluebell; harebell	14	CG
Carex	*pensylvanica*	Cyperaceae	Pensylvania Sedge	16	SDM
Comandra	*umbellata*	Santalaceae	bastard toadflax	21	OB
Comptonia	*peregrina*	Myricaceae	sweetfern	8	BG
Corylus	*cornuta*	Betulaceae	beaked hazlenut	9	BF
Danthonia	*spicata*	Gramineae	poverty oatgrass	5	BG
Diervilla	*lonicera*	Carpifoliaceae	bush-honeysuckle	17	BF
Gaultheria	*procumbens*	Ericaceae	wintergreen	13	ND
Hieracium	*aurantiacum*	Asteraceae	orange hawkweed	5	BG
Lysimachia	*quadrifolia*	Primulaceae	whorled loosestrife	8	PB
Maianthemum	*canadense*	Liliaceae	Canada mayflower	18	BF
Melampyrum	*lineare*	Scrophulariaceae	cow-wheat	4	ND
Oryzopsis	*asperifolia*	Gramineae	rice-grass	9	BF
Poa	spp.	Gramineae	bluegrass	10	BG
Polygala	*paucifolia*	Polygalaceae	gay-wings	6	ND
Prunus	*pumila*	Rosaceae	sand cherry		
Pteridium	*aquilinum*	Polypodiaceae	bracken fern	22	BG
Rubus	*allegheniensis*	Rosaceae	common blackberry	14	SD
Schizachne	*purpurascens*	Gramineae	false melic	8	BG
Trientalis	*borealis*	Primulaceae	star-flower	15	BF
Vaccinium	*angustifolium*	Ericaceae	low sweet blueberry	16	ND
Vaccinium	*myrtilloides*	Ericaceae	velvetleaf blueberry	11	NW
Vaccinium	*pallidum*	Ericaceae	hillside blueberry		
Viola	*adunca*	Violaceae	sand violet	8	BG
Waldsteinia	*fragarioides*	Rosaceae	barren-strawberry	8	ND

Acknowledgments

This research was supported by the Department of Defense Legacy Resource Management Program and the Sand County Foundation. We would like to thank the UW-Stevens Point Oak Savanna Legacy crew, in particular Angela Collada, for both field and logistical support. In addition, guidance by Mark Boyce, James Cook, and Evelyn Merrill was much appreciated in the analytical phases of this project.

Literature Cited

Abrams, M. D. 1992. Fire and the development of oak forests. *Bioscience* 42:346–53.

Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83:35–47.

Austin, M. P., and M. J. Gaywood. 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. *Journal of Vegetation Science* 5:473–82.

Bailey, R. G., and C. T. Cushwa. 1981. Ecoregions of North America. Washington, DC: U.S. Geological Survey. 1 map (1: 12,000,000).

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64:691–92.

Bonan, G. B., and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics* 20:1–28.

Botkin, D. B., J. E. Estes, R. M. MacDonald, and M. V. Wilson. 1984. Studying the Earth's vegetation from space. *Bioscience* 34:508–14.

Bray, J. R. 1955. The savanna vegetation of Wisconsin and an application of the concepts order and complexity to the field of ecology. Ph.D. Dissertation. University of Wisconsin-Madison, Madison.

Bray, J. R. 1958. The distribution of savanna species in relation to light intensity. *Canadian Journal of Botany* 36:671–81.

Brown, D., and P. Ruthery. 1993. *Models in biology: mathematics, statistics, and computing.* John Wiley & Sons, Chichester, England. 688 pp.

Clayton, L. 1986. Pleistocene geology of Florence County, Wisconsin. University of Wisconsin Extension, Wisconsin Geological and Natural History Survey. Information Circular 51. Madison, Wisconsin.

Connell, J. H., and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–44.

Conway, E. 1952. Bracken-the problem plant, a review of recent conclusions about its spread and dominance. *Scottish Agriculture* 31:181–84.

Curtis, J. T. 1959. *The vegetation of Wisconsin.* The University of Wisconsin Press, Madison, Wisconsin. 657 pp.

Ferguson, D. E., and R. J. Boyd. 1988. Bracken fern inhibition of conifer regeneration in northern Idaho. U.S. Department of Agriculture Forest Service. Research Paper: INT-388. 11 pp.

Fralish, J. S. 1988. Predicting potential stand composition from site characteristics in the Shawnee Hills Forest of Illinois. *American Midland Naturalist* 120:79–101.

Grimm, E. C. 1984. Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* 54:291–311.

Hadley, D. W. 1976. Glacial deposits of Wisconsin: sand and gravel resource potential. Wisconsin Geological and Natural History Survey, Map 10. Madison, Wisconsin.

Haney, A., and S. I. Apfelbaum. 1990. Structure and dynamics of Midwest oak savannas. Pp. 20-30 *in Management of Dynamic Ecosystems.* North Central Section, The Wildlife Society, West Lafayette, Indiana.

Haney, A,. and S. I. Apfelbaum. 1994. Measuring changes in oak savannas: a review and recommendations for a monitoring protocol. Pp. 253–57 *in* J. S. Fralish, R. C. Anderson, J. E. Ebinger, and R. Szafoni, eds. *Proceedings of the North American Conference on Savannas and Barrens.* Illinois State University, Normal.

Haase, E. F. 1970. Environmental fluctuations on south-facing slopes in the Santa Catalina Mountains of Arizona. *Ecology* 51:959–74.

Hujik, P. M. 1995. Lowland savannas: groundlayer composition and distribution in relation to elevation and light. M.S. Thesis. University of Wisconsin-Madison, Madison, Wisconsin.

Kline, V. M., and G. Cottam. 1979. Vegetation response to climate and fire in the driftless area of Wisconsin. *Ecology* 60:861–68.

Leach, M. K. 1994. Savanna plant species distributions along gradients of sun-shade and soils. Pp. 223–27 *in* J. S. Fralish, R. C. Anderson, J. E. Ebinger, and R. Szafoni, eds. *Proceedings of the North American Conference on Savannas and Barrens.* Illinois State University, Normal.

Leitner, L. A., C. P. Dunn, G. R. Guntenspergen, F. Stearns, and D. M. Sharpe. 1991. Effects of site, landscape features, and fire regime on vegetation patterns in presettlement southern Wisconsin. *Landscape Ecology* 5:203–17.

Mossman, M. J., E. Epstein, and R. M. Hoffman. 1991. Birds of Wisconsin pine and oak barrens. *The Passenger Pigeon* 53:137–63.

Nielsen, S. E. 1997. The influence of topoedaphic factors, canopy, and bracken fern on distributional patterns of plant species at Spread Eagle Barrens. M.S. Thesis. University of Wisconsin-Stevens Point, Stevens Point, Wisconsin.

Nuzzo, V. 1986. Extent and status of Midwest oak savanna: Presettlement and 1985. *Natural Areas Journal* 6:6–36.

Oinonen, E. 1967. The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn) clones and certain periods of site history. *Acta Forestalia Fennica* 83:1–51.

Page, C. N. 1982. The history and spread of bracken in Britain. *Proceedings of the Royal Society of Edinburgh* 81B:3-10.

Perry, D. A. 1994. *Forest ecosystems.* The John Hopkins University Press, Baltimore, Maryland. 649 pp.

Pruka, B. W. 1994. Distribution of understory plant species along light and soil depth gradients in an upland oak savanna remnant in southern Wisconsin. Pp. 213–15 *in* J. S. Fralish, R. C. Anderson, J. E. Ebinger, and R. Szafoni, eds. *Proceedings of the North American Conference on Savannas and Barrens.* Illinois State University, Normal.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research.* 3rd Edition. W. H. Freeman and Company. New York, NY. 887 pp.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–79.

Thomas, R. L., and R. C. Anderson. 1993. Influence of topography on stand composition in a Midwestern ravine forest. *American Midland Naturalist* 130:1–12.

Vogl, R. J. 1964*a*. The effects of fire on the vegetational composition of bracken grasslands. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 53:67–82.

Vogl, R. J. 1964*b*. Vegetational history of Crex Meadow, a prairie savanna in Northwestern Wisconsin. *American Midland Naturalist* 72:157–75.

Vogl, R. J. 1970. Fire and the northern

Wisconsin pine barrens. Pp. 175–209 *in Proceedings of the Annual Tall Timbers Fire Ecology Conference.* No. 10.

Voss, E. G. 1972. *Michigan flora: Part I gymnosperms and monocots.* Cranbrook Institute of Science. Broomfield Hills, Michigan. 488 pp.

Voss, E. G. 1985. *Michigan flora: Part II dicots.* Cranbrook Institute of Science. Ann Arbor, Michigan. 724 pp.

Voss, E. G. 1996. *Michigan flora: Part III dicots.* Cranbrook Institute of Science. Ann Arbor, Michigan. 622 pp.

Ware, S., P. L. Redfearn Jr., G. L. Pyrah, and W. R. Weber. 1992. Soil pH, topography and forest vegetation in the Central Ozarks. *American Midland Naturalist* 128:40–52.

Watt, A. S. 1940. Contributions to the ecology of bracken *(Pteridium aquilinum).* 1. the rhizome. *New Phytologist* 39: 401–22.

Scott E. Nielsen is currently an ecologist for the Sand County Foundation. He has been studying pine barrens and savannas within the Midwest since 1994, when he began working for the Oak Savanna Legacy Project. He has both a B.S. and M.S. from the University of Wisconsin-Stevens Point in biology and forest ecology. ***Address:*** *Sand County Foundation, 201 Waubesa Street, Madison, WI 53704.*

Alan Haney is a Professor of Forestry at the University of Wisconsin-Stevens Point. An ecologist, he has published widely on community structure. He is a leading authority on Midwest oak savannas. His recent book (1997) on ecosystem management, edited with Mark Boyce, was published by Yale University Press. ***Address:*** *College of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, WI 54481.*