DOI: 10.1007/s00267-003-0055-9

Vegetation Composition, Dynamics, and Management of a Bracken–Grassland and Northern-Dry Forest Ecosystem

SCOTT E. NIELSEN*
Department of Biological Sciences
University of Alberta
Edmonton, Alberta, Canada T6G 2E9

ALAN HANEY
College of Natural Resources
University of Wisconsin-Stevens Point,
Stevens Point, Wisconsin, USA 54481

ABSTRACT / We investigated differences in vegetation composition and dynamics for two globally rare ecosystems, bracken–grasslands and northern–dry forests of northern Wisconsin. These ecosystems commonly have been viewed as degraded pine barrens. Bracken–grasslands contained a high dominance of exotic species, low native richness, and no obvious prairie species, suggesting logging-era anthropogenic origins. Differences in cover for common plants among ecosystems were examined using Mann-Whitney U tests of equivalence. Cover of all 8 graminoid species, 4 of 5 Ericaceae and Myricaceae species, and 10 of 17 species of forbs were significantly different between ecosystems. Vegetation changes over a 4-year period were examined through detrended correspondence analysis (DCA) and analysis of variance (ANOVA) repeated measures. DCA analyses of community composition failed to detect significant temporal trends within individual management units, although differences were apparent between ecosystems, regardless of sample year. In addition, no apparent patterns could be detected between years when comparing dominant individual species to management history (prescribed fire). This is contrary to what would be expected for a degraded pine barrens and questions the efficacy of using repeated prescribed fire as a management tool in bracken–grasslands. Methods for conservation and restoration of xeric ecosystems of northern Wisconsin have historically relied heavily on single species (e.g., sharp-tailed grouse) wildlife models, without full consideration of other factors. We suggest that stakeholders involved in these restoration projects examine historic processes and reference conditions prior to formulating management goals. Greater attention to the differentiation and individual management needs of pine barrens, northern–dry forests, and bracken–grasslands is needed.

Despite climatic predisposition for forest vegetation in the Upper Great Lakes, a number of grassland and savanna ecosystems, often called barrens, prevail. While fire is generally thought to be the primary disturbance maintaining this open stature (Abrams 1992), select locations appear in arrested succession. In northern Wisconsin, many of these openings are best described as bracken–grasslands (Curtis 1959). Floristically, bracken–grasslands are unlike the surrounding forests or nearby pine barrens (Curtis 1959). Two characteristics that best differentiate bracken-grasslands from surrounding plant communities are: (1) a lack of prairie species typical of pine barrens vegetation, and (2) a domination by exotic species (Curtis 1959).

KEY WORDS: Bracken–grasslands; Natural areas; Northern–dry forests; Pine barrens; Prescribed fire; Vegetation dynamics; Wisconsin

Published online May 13, 2003.
*Author to whom correspondence should be addressed; *email:* scottn@ualberta.ca

Historic evidence suggests that bracken–grasslands developed after the early logging era and within areas of severe slash fires on glacial, pitted outwash deposits or well-drained sandy loam soils (Curtis 1959). Once established, bracken–grasslands were resistant to short-term successional changes. Many locations, for instance, have been stable enough to even resist reforestation attempts (Stoeckeler and Limstrom 1942). Possible mechanisms for this stability included both physical and biological phenomena. Physical factors include the reduction of soil moisture-holding capacity, organic matter, nitrogen, and soil fauna and flora following intense forest fires of the logging era, coupled with temperature extremes, lower relative humidity, and the frequent formation of frosts in topographic depressions (Vogl 1964b, Levy 1970, Nielsen 1997, Nielsen and Haney 1998). Biological factors include competition, especially resulting from allelopathy of bracken fern [*Pteridium aquilinum* (L.) Kuhn], and a thick grass sod (Vogl 1964b, Levy 1970, Ferguson and Boyd 1988, Nielsen 1997, Nielsen and Haney 1998).

Despite apparent anthropogenic origins, bracken–grasslands are classified as imperiled for Wisconsin (S2) and globally rare and local (G3) (Henderson 1995, WIDNR 2000). No estimates of historic or current extents of these ecosystems are available.

Closely associated with bracken–grasslands are northern–dry forests (Curtis 1959). These forests are often found among bracken–grasslands in a landscape mosaic locally determined by the interaction of topography, soils, and site history (Nielsen and Haney 1998). It is apparent that most bracken–grasslands historically were northern–dry forest communities prior to settlement, although some open frost pockets were present (Nielsen 1997). The presettlement (ca. 1840) extent of northern–dry forests has been estimated at 1380 km^2 for Wisconsin, although it was not clearly differentiated from that of pine barrens (Curtis 1959). Misclassification of fire-regenerated northern–dry forests as pine barrens has likely occurred during interpretation of general land office (GLO) notes (Radeloff and others 1999), thus representing a conservative estimate. Fire is the primary natural process leading to the persistence of northern–dry forests. Without fire, northern–dry forests succeed to northern–dry mesic or northern–mesic forests (Curtis 1959). Edaphically, northern–dry forests are similar to bracken–grasslands, occupying patchy environmental mosaics (topoedaphic sequences) associated with rolling pitted outwash terrain and sandy loam or loamy sand soils. Both bracken–grasslands and northern–dry forests are limited to areas north of the tension zone (Curtis 1959), with some of the best examples appearing in northeast Wisconsin (Vogl 1964b). Currently, high-quality northern–dry forests, especially those dominated by jack pine, cover only a small fraction of their original extent. Much of these losses can be attributed to fire suppression and conversion to red pine plantations. Today, northern–dry forests are considered globally rare and local (G3) and rare within Wisconsin (S3) (Henderson 1995, WIDNR 2000).

To date, little information is available regarding vegetation composition, dynamics, and history for bracken–grasslands and northern–dry forest ecosystems (see, however, Vogl 1964b). Furthermore, little regard has been given to the differences between these two ecosystems and pine barrens, a globally imperiled ecosystem (G2) (WIDNR 2000) often mistakenly interpreted when in bracken–grassland habitats. Given the globally imperiled classification of pine barrens, recent management goals for many landscapes have called for an increase of pine barrens habitats without full consideration of local historic composition or structure that distinguishes bracken–grasslands and northern–dry forests from pine barrens.

In this paper, we summarize the composition and short-term dynamics of vegetation for a bracken–grassland and northern–dry forest site in northeast Wisconsin (Spread Eagle Barrens State Natural Area). Our objectives were: (1) to document the differences in vegetation for bracken–grasslands and northern–dry forests relating to native and exotic species; (2) understand short-term changes in vegetation among management activities (prescribed fires); and (3) evaluate the efficacy of prescribed fire for bracken–grassland management. We hypothesized that: (1) bracken–grasslands vegetation was different from northern–dry forests, being dominated by exotics and having fewer native species; and (2) compositional changes following fire would be negligible. Although the study site is interpreted as barrens, conferring a prairie component or pine barrens habitat, we evaluate whether it should be considered a pine barrens, bracken–grassland or northern–dry forest for purposes of management and restoration.

Study Site

Fieldwork was conducted at Spread Eagle Barrens (SEB) State Natural Area in eastern Florence County, Wisconsin (45°51'N, 88°11'W; Figure 1). This 3488-ha Natural Area is cooperatively managed by the Wisconsin Department of Natural Resources (WI-DNR), Wisconsin Electric and Power Company, and Florence County. Prior to Natural Area designation in October 1995, the WI-DNR leased 1726 ha from Florence County for wildlife management. Prescribed burning has been widely applied since 1979, primarily for upland wildlife management, especially sharp-tailed grouse (*Tympanuchus phasianellus*). Climatically, the area is intermediate between lake moderated and continental, with an average annual precipitation of 739 mm and an annual average temperature of 5.2°C.

Hummocky topography formed from ice-stagnation and out-wash materials, varying in depth from 0 to 100 m, were deposited during the Early Athelstane Advance of the Wisconsin Glaciation (Clayton 1986). Soils consisted of Sayner and Vilas loamy sands, Pence sandy loams, and Pence-Vilas Complex (unpublished soil survey). Upland vegetation consisted of bracken–grasslands, northern–dry forests and northern dry–mesic forests (Figure 1). Dominant woody species across SEB included quaking aspen (*Populus tremuloides* Michx.), big-tooth aspen (*Populus gradidentata* Michx.), white birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lambert), red pine (*Pinus resinosa* Aiton.),

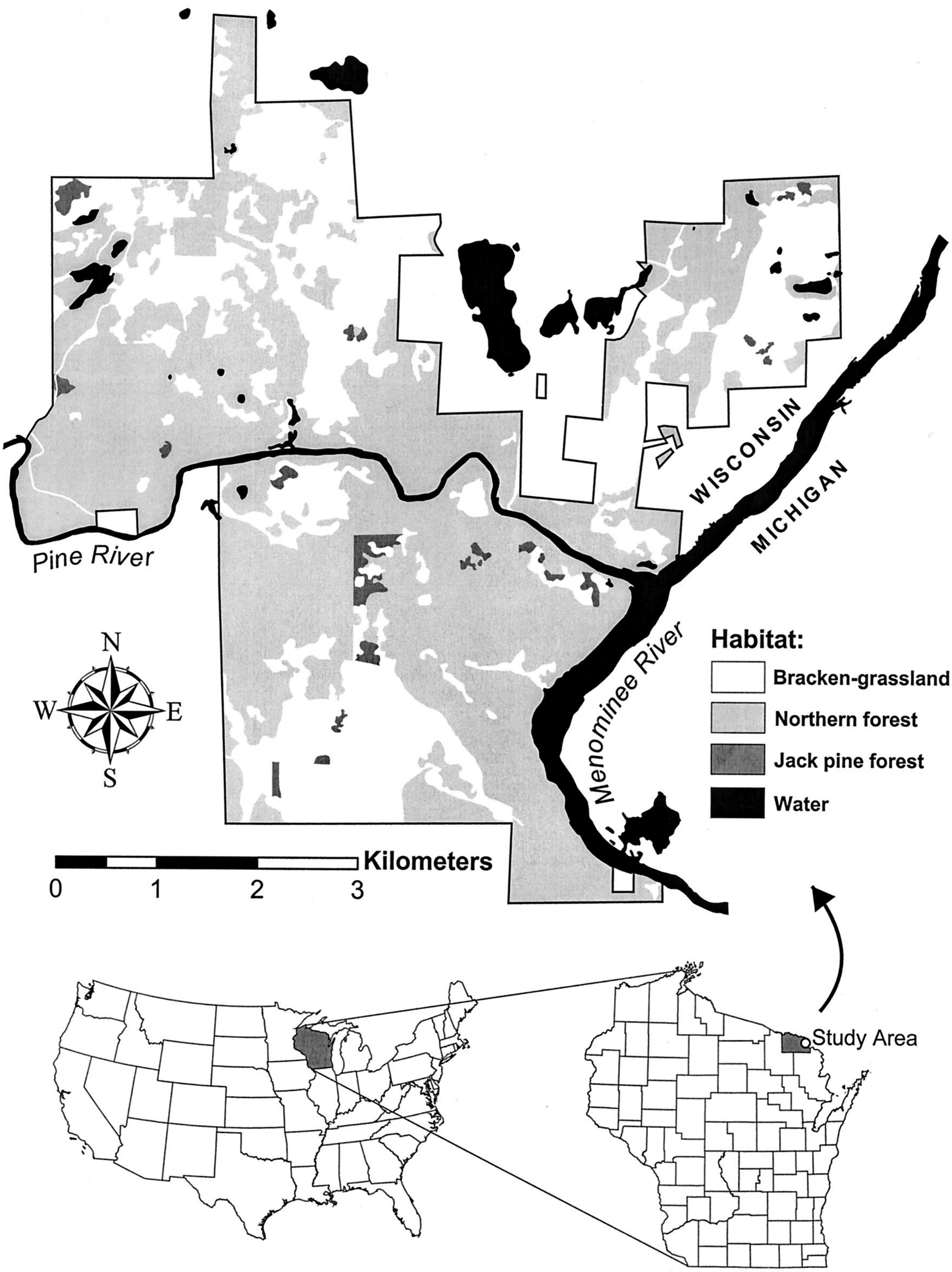

Figure 1. Location of Spread Eagle Barrens State Natural Area (study area) in Florence, County Wisconsin, USA (45°51'N, 88°11'W). General vegetation and water (lakes and rivers) are depicted. Location of study area with respect to Wisconsin in lower right of figure, while the location of Wisconsin with the respect to the United States is provided in the lower left of figure.

juneberry (*Amelanchier* spp.), and wild black cherry (*Prunus serotina* Ehrh.). Northern–dry forests dominated the landscape prior to European settlement, although small open frost pockets were present (Nielsen 1997, Nielsen and Haney 1998).

Methods

Field Methods

In 1995, 67 long-term vegetation monitoring transects, 50 m in length, were established among 18 management units using a stratified random approach. Management areas were defined as areas with consistent vegetation and treatment (prescribed fire or timber harvest) history. Stratification was based on geographic information system maps of relevant management units and randomly chosen field locations for sampling. Along each transect, trees (dbh ≥5 cm), shrubs (dbh < 5 cm), groundlayer vegetation (< 1 m height), and site characteristics (slope, aspect, and landscape position) were measured. Cover of groundlayer vegetation was estimated within 1-m^2 circular quadrats centered at the 5-, 15-, 25-, 35-, and 45-m positions. In 1999, 42 of 67 transects were remonitored with an additional 12 transects established, providing a management unit sample size of 22. Taxonomic nomenclature follows that of Voss (1972, 1985, 1996).

Analytical Methods

Vegetation composition. For each management unit by plant community, relative frequency and relative cover for each groundlayer species was calculated and used for deriving importance values. Importance values were used to qualitatively compare differences in floristic composition for management units and plant communities. We further stratified northern–dry forests into one of two associations based on tree composition. Sites dominated by jack pine were assigned northern–dry forest jack pine stands, while those dominated by aspen were considered northern–dry forest aspen stands. Native and exotic species richness and cover were estimated and compared among plant communities using parametric (*t* test) and nonparametric (Mann-Whitney U) comparison tests. All significance levels were reported at the $P < 0.05$ level. For individual species, cover differences among plant communities were examined using a Mann-Whitney U two-tailed test of equivalence. We tested all common (≥5% frequency) groundlayer species from the following four families and functional groups: Gramineae, Ericaceae, Myricaceae, and forbs/ferns. Rare species were excluded, as they likely had little influence on local community structure and dynamics.

Vegetation dynamics. Detrended correspondence analysis (DCA) (Hill 1979) was used to explore compositional community interrelationships between management units and plant communities and intrarelationships across sample years (1995 and 1999) within management units. All transects within management units were pooled and used as the unit of replicate with importance values of individual species used as the response. Rare species were down-weighted. Following ordination, we used management unit DCA scores to examine community trends. We compared DCA scores between years and plant communities using repeated-measures analysis of variance (ANOVA) and post-priori Tukey-Kramer multiple comparison tests.

To investigate vegetation dynamics at the species level, repeated-measures ANOVA and post-priori Tukey-Kramer multiple comparison tests were used. We based the analysis on relative cover estimates for specific common species and across sample years for each management unit. Each species was tested sequentially against ANOVA factors of management unit, transect (nested), and sample year. Because we were interested in how species were responding to management (prescribed fire), we used the significant interaction between management unit and year of sample to indicate management effect. Spearman rank correlations were used for examining patterns and relationships between the number of significant species within a management unit across sample periods and the number of burns or years since burn. We did not consider sequential Bonferroni corrections for our analyses, instead relying on common sense and biological significance to guide interpretations (Yoccoz 1991, Cabin and Mitchell 2000).

Results

Vegetation Composition

Bracken–grasslands were dominated by sweet fern [*Comptonia peregrina* (L.) Coulter], Pennsylvania sedge (*Carex pensylvanica* Lam.), bluegrass (*Poa pratensis* L. and *P. compressa* L.), low sweet blueberry (*Vaccinium angustifolium* Aiton) and bracken fern (Table 1). Compositionally, the groundlayer of northern–dry forests was separated from bracken–grasslands by the absence of three modal bracken–grassland graminoids: slender wheatgrass [*Agropyron trachycaulum* (Link) Malte.], *Muhlenbergia racemosa* [(Michx.) BSP], and Kalm's brome (*Bromus kalmii* Gray). Although northern forests generally lacked these three grasses, they did contain *Oryzopsis pungens* (Sprengel) Hitchc. and a number of forbs not well represented in bracken–grassland samples.

Table 1. Importance values (relative cover + relative frequency), by ecosystem, for 48 common groundlayer species at Spread Eagle Barrens State Natural Area

Species	Bracken–grassland	Northern–dry forest: Aspen	Northern–dry forest: Jack pine
a. Gramineae/Cyperaceae			
Agropyron trachycaulum	6.6	—	—
Bromus kalmii	1.2	—	—
Carex pensylvanica	20.3	13.1	26.5
Carex spp.	—	1.7	—
Danthonia spicata	1.9	—	0.9
Muhlenbergia racemosa	2.5	—	—
Oryzopsis asperfolia	5.4	17.3	12
Oryzopsis pungens	—	1.2	6.5
Panicum spp.	—	1	—
Poa spp.	18.9	3.3	2.3
Schizachne purpurascens	5.6	3.5	9.2
b. Myricaceae/Ericaceae			
Comptonia peregrina	29.8	3	3.6
Gaultheria procumbens	1.2	9	8.6
Vaccinium angustifolium	24	10.9	20.1
Vaccinium myrtilloides	8.8	5.7	8.5
c. Forbs and ferns			
Anemone quinquefolia	—	0.7	—
Apocynum androsaemifolium	3.8	3.8	1.9
Aster ciliolatus	3.2	1.6	3
Aster macrophyllus	—	6.8	3.6
Calystegia spithamaea	7.1	0.9	2.5
Campanula rotundifolia	1.7	—	1.1
Comandra umbellata	2	0.8	1.3
Diervilla lonicera	2	3.1	2.5
Fragaria virginiana	1.6	—	—
Hieracium spp.	3.6	1	2.2
Lactuca canadensis	0.6	—	0.8
Linaria vulgaris	2.1	—	—
Lysimachia quadrifolia	1.1	3.9	4.4
Maianthemum canadense	—	3.6	5.4
Melampyrum lineare	—	1.7	5.4
Polygala paucifolia	—	—	2
Pteridium aquilinum	15.3	31.3	19.4
Solidago juncea	3	—	—
Solidago spp.	—	1.8	—
Trientalis borealis	—	1	—
Trillium grandiflorum	—	—	1.1
Viola adunca	1.2	1.5	1.3
Waldsteinia fragaroides	8.3	18.5	14.6
d. Trees and shrubs			
Acer rubrum	—	7.8	3.8
Amelanchier spp.	4.1	5.2	4.6
Corylus americana	—	5.1	1.3
Corylus cornuta	—	9.7	3.4
Populus tremuloides	—	2.6	—
Prunus pumila	2.9	—	1.3
Prunus serotina	0.6	2.3	3.2
Quercus ellipsoidalis	—	2.9	—
Quercus rubra	—	—	1.7
Rubus allegheniensis	9.1	12.6	10

Some of these preferential forbs included large-leaved aster (*Aster macrophyllus* L.), Canada mayflower (*Maianthemum canadense* Desf.), and cow-wheat (*Melampyrum lineare* L.) (Table 1). Analyses of native richness revealed that bracken–grasslands were significantly lower in native species with 8.8 (± 0.22 SE) species/m^2, compared with 10.1 (± 2.41 SE) and 11.2 (± 0.36 SE) species/m^2 for aspen- and jack pine-dominated northern–dry forest stands respectively (Table 2). Likewise, representation of exotic species was different between bracken–grassland and northern–dry forests. Exotic cover and richness was significantly higher in bracken–grasslands (Table 2).

Statistical differences between communities for eight common Gramineae species further supported compositional distinction (Table 3). All eight species were significantly different between at least two of three plant communities. Beyond higher cover for slender wheatgrass and Kalm's brome, bracken–grassland stands were also higher in cover for bluegrass and lower in cover for rough-leaved ricegrass (*Oryzopsis asperfolia* Michx.). Differences in graminoids and sedges among jack pine and aspen northern–dry forest associations were best distinguished by higher amounts of *Oryzopis pungens*, Pennsylvania sedge, and false melic [*Schizachne purpurascens* (Torrey) Swallen] within jack pine stands.

Of four Ericaceae and Myricaceae species examined (Table 3), only Canada blueberry (*Vaccinium myrtilloides* Michx.) failed to show significant differences between plant communities. Wintergreen (*Gaultheria procumbens* L.) showed higher cover for northern–dry forest associations, while low sweet blueberry (*V. angustifolium* Aiton) was higher in bracken–grasslands (Table 3). Sweetfern [*Comptonia peregrina* (L.) Coulter] obtained its highest importance value and cover within bracken–grasslands.

Ten of 17 forb species showed significant differences in cover between plant communities (Table 3). Large-leaved aster (*Aster macrophyllus* L.), whorled loosestrife (*Lysimachia quadrifolia* L.), Canada mayflower (*Maianthemum canadense* Desf.), and barren strawberry (*Waldsteinia fragarioides* (Michaux) Tratt.) were all lower in cover for bracken–grassland stands than either northern–dry forest association. In contrast, low bindweed [*Calystegia spithamaea* (L.) Pursh] and early goldenrod (*Solidago juncea* Aiton) showed higher cover in bracken–grasslands than northern–dry forests, while wild strawberry (*Fragaria virginiana* Miller) and hawkweed (*Hieracium* spp.) were more dominant in bracken–grasslands than in the northern–dry forest aspen stands, but not in northern–dry forest jack pine stands. As expected, the exotic butter-and-eggs (*Linaria vulgaris* Miller) was more dominant in bracken–grass-

Table 2. Native and exotic species cover and richness (means and standard errors) by plant community[a]

Variable	Bracken–grassland (mean ± SE)	Northern–dry forest Aspen (mean ± SE)	Northern–dry forest Jack pine (mean ± SE)
Native richness	8.80a±0.22	10.13b±2.41	11.21b±0.36
Exotic richness[b]	1.23a±0.07	0.36b±0.09	0.44b±0.09
Native cover	149.28a±3.68	114.47b±5.88	113.35b±7.78
Exotic cover[b]	23.78a±2.11	1.44b±0.49	1.81b±0.54

[a]Means followed by the same letter are not significantly ($P \le 0.05$) different from one another in parametric and nonparametric *t* tests.
[b]Nonparametric equivalent.

Table 3. Comparison of mean cover (± standard errors in parentheses) for common (frequency > 5%) species by plant community at Spread Eagle Barrens State Natural Area[a]

Species	Bracken–grassland	Northern–dry forest aspen	Northern–dry forest jack pine
a. Gramineae/Cyperaceae			
Agropyron trachycaulum	3.86a (0.78)	0.07b (0.05)	0.04b (0.04)
Carex pensylvanica	19.81a (1.72)	6.73b (1.64)	20.33a (3.06)
Danthonia spicata	0.98a (0.41)	0.00b (0.00)	0.15ab (0.08)
Muhlenbergia racemosa	0.64a (0.14)	0.13b (0.11)	0.02b (0.02)
Oryzopsis asperfolia	3.89a (0.67)	9.62b (1.88)	7.19b (1.36)
Oryzopsis pungens	0.08a (0.05)	0.29b (0.16)	4.52c (1.63)
Poa spp.	18.92a (1.85)	0.89b (0.35)	0.94b (0.42)
Schizachne purpurascens	2.47a (0.32)	1.42b (0.56)	3.40c (0.58)
b. Myricaceae/Ericaceae			
Comptonia peregrina	34.92a (2.18)	2.13b (1.38)	1.29b (0.56)
Gaultheria procumbens	0.47a (0.17)	3.02b (0.75)	4.42b (1.69)
Vaccinium angustifolium	19.01a (1.91)	5.71b (1.32)	12.17a (2.70)
Vaccinium myrtilloides	8.24a (1.37)	3.69b (1.66)	5.35ab (1.68)
c. Forbs and Ferns			
Apocynum androsaemifolium	1.46 (0.27)	1.24 (0.42)	0.46 (0.17)
Aster ciliolatus	1.14 (0.22)	0.33 (0.16)	0.65 (0.19)
Aster macrophyllus	0.13a (0.09)	3.11b (0.93)	1.68b (0.83)
Calystegia spithamaea	1.74a (0.20)	0.22b (0.18)	0.67b (0.23)
Campanula rotundifolia	0.22 (0.05)	0.04 (0.03)	0.13 (0.06)
Comandra umbellata	0.38 (0.10)	0.09 (0.05)	0.15 (0.06)
Diervilla lonicera	1.19 (0.35)	1.22 (0.52)	0.96 (0.31)
Fragaria virginiana	0.38a (0.10)	0.04b (0.04)	0.19ab (0.13)
Hieracium spp.	2.64a (0.74)	0.33b (0.19)	0.79ab (0.38)
Lactuca canadensis	0.11 (0.04)	0.07 (0.07)	0.10 (0.05)
Linaria vulgaris	1.68a (0.53)	0.18ab (0.18)	0.00b (0.00)
Lysimachia quadrifolia	0.25a (0.08)	1.64b (0.58)	1.15b (0.31)
Maianthemum canadense	0.05a (0.03)	0.78b (0.35)	1.81b (0.64)
Melampyrum lineare	0.03a (0.01)	0.38b (0.18)	1.19c (0.31)
Pteridium aquilinum	16.66a (1.91)	27.49b (3.67)	16.52a (3.56)
Solidago juncea	1.65a (0.52)	0.11b (0.08)	0.04b (0.03)
Viola adunca	0.12 (0.03)	0.02 (0.02)	0.08 (0.04)
Waldsteinia fragaroides	6.40a (1.24)	11.58b (2.44)	9.25b (1.98)

[a]Means followed by the same letter are not significantly ($P < 0.05$) different from one according to Mann-Whitney U tests.

lands. Finally, cow-wheat (*Melampyrum lineare* Desr.) was significantly different for all three ecosystems, showing a high fidelity for northern–dry forest jack pine stands. Seven species that lacked differentiation included spreading dogbane (*Apocynum androsaemifolium* L.), Lindley's aster (*Aster ciliolatus*), harebell (*Campanula rotundifolia* L.), bastard toadflax [*Comandra umbellata* (L.) Nutt.], bush honeysuckle (*Diervilla lonicera* Miller), wild lettuce (*Lactuca canadensis* L.), and sand violet (*Viola adunca* J. E. Smith).

Vegetation Dynamics

Detrended correspondence analysis (DCA) separated bracken–grasslands, northern–dry forests, and

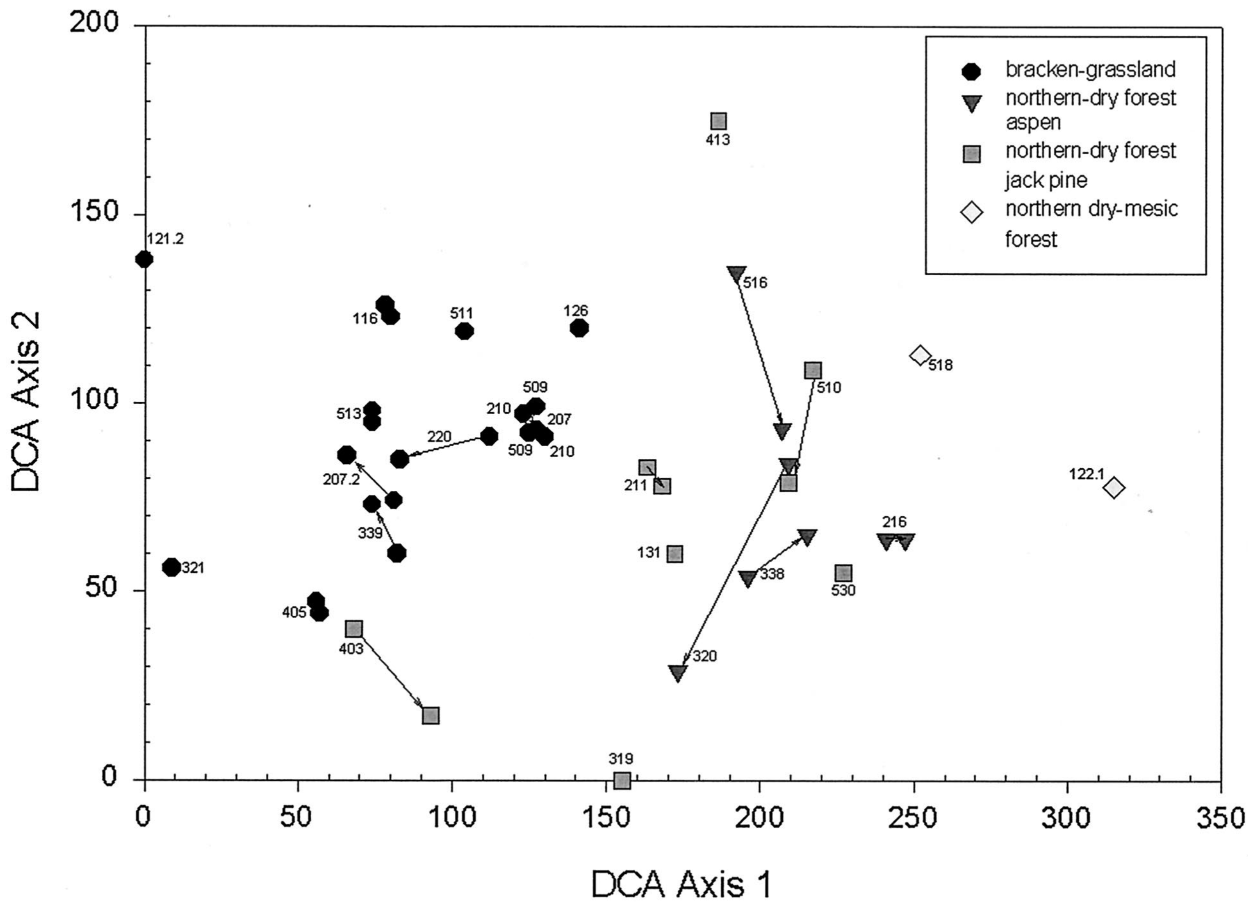

Figure 2. Detrended correspondence analysis (DCA) of management unit vegetation composition across plant communities and year of sample (DCA axis 1, E = 0.35; DCA axis 2, E = 0.11). Axis 1 describes samples along a canopy and vegetation community gradient. Vectors describe the vegetation dynamics between 1995 and 1999 among management unit.

northern dry–mesic forests along the first axis (Figure 2). Bracken–grassland management units were represented by low axis 1 values, while northern–dry forest stands of jack pine and aspen were associated with high axis 1 scores. Two northern dry–mesic management stands included in the analysis were found to have the highest axis 1 scores. Axis 1 therefore represented a canopy and soil moisture gradient that ranged from xeric, open canopy conditions (bracken–grasslands) to relatively mesic, closed canopy conditions (northern dry–mesic forests). Although plant communities were significantly different from one another across axis 1 DCA scores using ANOVA, no significant changes for management stands were observed across sample years (Table 4). Thus, community ordination scores for management units did not change across the 4-year sampling period regardless of management. Bracken–grassland management units appeared particularly stable when examining temporal vectors (Figure 2).

For species-specific analyses of plant dynamics among the 14 paired (temporally) management units, 25 significant interactions by stand and year were revealed (Table 5). In bracken–grasslands, four species increased within three management units, while eight species decreased within six management units. For aspen, two species increased within two management units, while a single species decreased within a single management unit. And finally, within jack pine stands, three species increased and three species decreased within two management units (Table 5). There was a lack of change between sample periods for four of 14 management units (220, 513, 338, and 211). Units 220 and 513 were bracken–grasslands that were intensively managed (three and two prescribed burns, respectively), and thus may be exhibiting strong stability in the

Table 4. Average (± SE) detrended correspondence analysis (DCA) value by ecosystem and year of sample[a]

	Bracken–grassland		Northern–dry forest aspen		Northern–dry forest jack pine	
Axis	1995	1999	1995	1999	1995	1999
One	92.5a (9.6)	85.3a (8.9)	213.3b (9.7)	206.8b (15.9)	149.3c (43.6)	156.7c (34.0)
Two	85.8 (8.8)	86.9 (8.0)	73.8 (9.0)	73.3 (22.2)	77.3 (20.1)	58.0 (20.5)
Three	77.1 (5.5)	82.1 (6.9)	83.0 (6.7)	79.5 (21.3)	63.7 (18.9)	64.3 (10.0)

[a]Means followed by the same letter are not significantly ($P \leq 0.05$) different according to ANOVA Tukey-Kramer multiple comparison tests.

Table 5. Repeated measures ANOVA results for significant ($P < 0.05$) interactions (Tukey-Kramer multiple comparison tests) between management unit (number) and year of sample (1995 versus 1999) by species[a]

Species	Increasing management unit	Decreasing management unit
Acer rubrum		210-BG
Aster ciliolatus		510-JP
Calystegia spithamaea		509-BG
Campanula rotundifolia	403-JP	207.2-BG, 339-BG
Comandra umbellata		207.2-BG, 339-BG
Comptonia peregrina	207.2-BG	
Corylus americana		339-BG
Diervilla lonicera	116-BG	
Fragaria virginiana		339-BG
Hieracium spp.		403-JP
Lysimachia quadrifolia	516-A	116-BG, 405-BG
Maianthemum canadense		216.1-A
Oryzopsis asperfolia	216.1-A	
Poa spp.		403-JP
Prunus pumila		207.2-BG
Prunus serotina	510-JP	
Pteridium aquilinum	116-BG, 516-A	
Schizachne purpurascens	403-JP	
Solidago juncea	339-BG	

[a]Only significant species are presented with the management unit (e.g., 210) indicated and associated abbreviated plant community (BG, bracken–grassland; A, aspen-dominated northern–dry forest; JP, jack pine dominated northern–dry forest). See Appendix 1 for details on management unit characteristics.

vegetation community. The remaining management units (338 and 211) were northern–dry forest stands where management had only recently begun. Overall, we witnessed a lack of the restoration (appearance) for "barren-like" prairie species with prescribed fire. Moreover, no statistical correlation was observed for the number of significant groundlayer species against the number of prescribed fires ($r_s = -0.254$, $P > 0.20$, $df = 13$) or years since burned ($r_s = -0.199$, $P > 0.20$, $df = 13$). Apparently, the observed changes across the 4-year study period were less attributable to management history than either observational or natural environmental noise.

Discussion

We found differences in vegetation composition among bracken–grasslands and northern–dry forests ecosystems at Spread Eagle Barrens (SEB). Bracken–grasslands were dominated by exotics, low in native species richness, and lacked a prairie barrens flora, therefore supporting our first hypothesis. Although rare in extent at SEB, northern–dry forest jack pine stands showed the highest richness of native species, suggesting that preservation of these stands should be a priority. Currently, many of these stands are slated for "barrens" conversion through timber harvest and/or prescribed fire. In agreement with our second hypothesis and conclusions by Vogl (1964b), prescribed fire lacked directional compositional responses that would be expected for degraded pine barrens. Bracken–grasslands therefore exhibited a strong stable composition, only varying slightly from year to year, but not in a successional direction typical for most open or barren vegetation devoid of fire for an extensive period or following the reintroduction of fire after extended suppression. Stability of bracken–grasslands appears to instead result from competition, edaphic factors, and microclimates (Curtis 1959, Vogl 1964b, Nielsen 1997, Nielsen and Haney 1998). In the short-term, maintenance of bracken–grasslands with fire appears to be unnecessary. With respect to exotics, management of bracken–grasslands did not appear to influence exotic cover in an already exotic-rich groundlayer, although some exotics appeared to be increasing in cover within native-rich jack pine stands. Given their anthropogenic origins, a lack of prairie flora or rare and unusual natives, and domination by exotic species, we question the efficacy of managing for bracken–grasslands, especially in a state natural area.

In contrast to bracken–grasslands, fire suppression has resulted in the disappearance of many historic pine barrens. Consequent with this loss has been decline in

Table 6. Characteristics useful for differentiating pine barrens, bracken–grasslands, and northern–dry forest ecosystems of northern Wisconsin (based on Curtis 1959, this research, and authors' observations)

Characteristic or variable	Pine barrens	Bracken–grasslands	Northern–dry forest
C4 grasses	common	absent	absent
Total grass cover	medium (~50%)	high (> 75%)	low (< 35%)
Schizachne purpurascens	rare	common	common
Agropyron trachycaulum	rare	common	absent
Bromus kalmii	common to rare	common	absent
Oryzopsis pungens	common	rare	common
Euphorbia corollata	common	absent	absent
Helianthemum canadense	common	absent	absent
Lupinus perennis	common	absent	absent
Lithospermum canescens	common	absent	absent
Liatris spp.	common	absent	absent
Comptonia peregrina	common	common	uncommon
Polygala paucifolia	uncommon	absent	common
Melanpyrum lineare	uncommon	absent	common
Aster macrophyllus	uncommon	uncommon	common
Epigaea repens	present	absent	common
Pteridium aquilinum	present	common	common
Vaccinium spp.	common	common	common
Exotic species	low	high	low
No. modal species	5	36	17
Allelopathy	medium	high	low
Total tree cover (%)	1–50	< 1	> 50
Pinus banksiana overstory	common	absent	common
Pinus resinosa overstory	rare to common	rare	common
Populus spp. overstory	rare	absent	common
Quercus spp. overstory	common	absent	rare to common
Soils	sands	sandy loams	sandy loams
pH	5.2	4.9	4.9
Catena position	top	middle to low	top
Pleistocene feature	outwash plains	pitted outwash	pitted outwash
Growing season frosts	rare to common	common	rare
Original area (acres)	2,340,000	< 100,000?	340,000
Stability	low	high	low
Mosaic type	remnant, spot, envir.	environmental resource	spot disturbance
Fire return interval (yr)	~10–55	~30–80	~50–120
Period of origin	~3500 yr BP	since 1850	~3,500 yr BP

populations of area sensitive species, such as *Tympanuchus phasianellus* (sharp-tailed grouse). Given these changes, land managers and conservationists have recently begun preserving, managing, and restoring "barren-like" landscapes throughout the region. However, there appears to be much confusion regarding fire management and ecology of open ecosystems in northern Wisconsin. The term pine barrens, where fire management is essential, has often been applied to all xeric, barren-like ecosystems of the region, including bracken–grasslands and northern–dry forests. Shively and Temple (1994) pointed out these problems, saying, "This narrow definition has obscured the diverse character of the communities that were likely present." Given the globally imperiled nature of pine barrens (G2) (WIDNR 2000) and rarity of both bracken–grasslands and northern–dry forests (G3), it is important that we recognize individual ecosystems, the dynamics associated with each, and multiple management strategies. In general, management strategies have been homogenous among ecosystems, being based on wildlife management models (e.g., sharp-tailed grouse) that strive for large (> 40-km^2) static openings (Hamerstrom and others 1952, Hamerstrom 1963, Vogl 1967, Temple 1992). Based on these models, isolated patches of red pine and/or jack pine are thought to preclude viability of area-sensitive species (Mossman and others 1991, Temple 1992, Neimuth 1993) and further provide potential predatory perch sites for sharp-tailed grouse (Savage 1993, Shively and Temple 1994). Such models, however, are inconsistent with ideas of dynamic mosaic landscapes and the concept of an ecosystem's natural range of variability, where landscape elements (e.g., northern–dry forests and pine barrens) are flexible in both space and time (Forman 1998, Radeloff and others 1999). Current management suppresses these landscape dynamics through the stabilization and maintenance of open patches, within a matrix of fire-suppressed forest stands or alternative land use. When few natural openings exist, and associated game and nongame species continue to decline, it is often hard to justify dynamic management of patches. However, despite possible negative impacts of area-sensitive species, we feel innovative strategies for incorporating and managing mosaic elements of northern–dry forests within pine barrens are important for species diversity and ecological processes. Reaching a balance between management of open or closed stands within an area using a dynamic mosaic approach may facilitate sustainable populations of some area sensitive species, while allowing for natural patterning of northern–dry forests and associated species.

Management Implications and Recommendations

With caution to extrapolation beyond Spread Eagle Barrens, it appears that management of bracken–grasslands with prescribed fire is unnecessary for short-term maintenance. Further conversion of native ecosystems, especially rare northern–dry forests, to exotic-rich bracken–grasslands is inconsistent with conservation and science-based management. Conservation time and money may be better allocated toward restoration of historic diverse barrens with prescribed fire and timber harvests, where such methods have largely been shown to be successful (Vogl 1964a, 1967, 1970). Proper identification of bracken–grasslands, northern–dry forests and closely associated pine barrens is therefore necessary. In Table 6 we present a working list of ecological characteristics to facilitate differentiation of these ecosystems. For some variables, fuzzy boundaries exist, as they represent differences along a continuum. Caution should be exercised when using traditional pine barren indicators, such as the presence of sweet fern and blueberry, as these species are also present and, in some cases, modal to bracken–grasslands (Curtis 1959). In addition to variables listed in Table 6, we suggest using the presence of the following forbs and legumes, absent in bracken–grasslands but prevalent in pine barrens, to differentiate these ecosystems: flowering spurge (*Euphorbia corollata* L.), frostweed (*Helianthemum canadense* (L.) Michx.), hoary puccoon (*Lithospermum canescens* (Michx.) Lehm.), and wild lupine (*Lupinus perennis* L.), the obligate host of the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis*).

It is important that prior to restoration or management, stakeholders develop a conceptual model of the system, including a historical profile, to understand processes and reference conditions (Walker and others 2002). Without reconstructing the past, it is difficult to formulate an objective vision of the future, especially when there is a tendency to perceive the landscape in a biased manner. Sound adaptive management is one strategy that is consistent with these ideas (Haney and Power 1996, Power and Haney 1998). (Brown and Curtis 1952, Canham and Loucks 1984, Haney and Apfelbaum 1994, Kent and Coker 1992, Murphy 1931, Vora 1993) Acknowledgments Special thanks go to B. Jessen, the coordinator and program director of the Savanna Partnership at the Sand County Foundation (SCF) during this project. Other personnel from SCF that have helped in ways too numerous to mention include R. Coleman, B. Haglund, L. Kearney, K. McAleese, A. Miller, and J. Scott. B. Haglund provided numerous stimulating conversations during analysis. Field help in 1995 was provided by A. Collada, M. Grover, M. Sheehan, and D. Taylor. A. Collada, B. Jessen, R. Power, and M. Sheehan helped during the second field season (1999). N. Cutright and Wisconsin Electric Power Company provided lodging and GIS data through Stagerwalt Land Services, Inc. S. Borren provided logistical support and background on management history. This project was made possible through the Wisconsin Savanna Partnership with funds from the Department of Defense Legacy Project (1995), the Sand County Foundation (1995 and 1999), and MacIntire-Stennis grant number WIS04325 (1999).

Literature Cited

Abrams, M. D. 1992. Fire and the development of oak forests. *BioScience* 42:346–353.

Brown, R. T., and J. T. Curtis. 1952. The upland conifer-hardwood forests of northern Wisconsin. *Ecological Monographs* 22:217–234.

Cabin, R. J., and R. J. Mitchell. 2000. To Bonferroni or not to Bonferroni: when and how are the questions. *ESA Bulletin* 81:246–248.

Canham, C. D., and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* 65:803–809.

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

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

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

Forman, R. T. 1998. The pine barrens of New Jersey: an ecological mosaic. Pages 569–585 *in* R. T. Forman (ed.), Pine barrens: ecosystems and landscape. Rutgers University Press, New Brunswick, New Jersey.

Hamerstrom, F., F. N. Hamerstrom, and O. E. Mattson. 1952. Sharptails into the shadows? Wisconsin Wildlife No. 1. Wisconsin Conservation Department, Madison, Wisconsin.

Hamerstrom, F. N., Jr. 1963. Sharptail brood habitat in Wisconsin's northern pine barrens. *Journal of Wildlife Management* 27:792–802.

Haney, A., and S. I. Apfelbaum. 1994. Measuring changes in oak savannas: a review and recommendations for a monitoring protocol. Pages 253–257 *in* Proceedings of the North American Conference on Savannas and Barrens, 15–16 October 1994. Illinois State University, Normal, Illinois.

Haney, A., and R. L. Power. 1996. Adaptive management for sound ecosystem management. *Environmental Management* 20:879–886.

Henderson, R. 1995. Overview of Wisconsin's Biological Communities. Pages 40–49 *in*Wisconsin's biodiversity as a management issue: a report to Department of Natural Resource Managers. PUB-RS-915 95. Madison, Wisconsin.

Hill, M. O. 1979. DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Page 30 *in* Ecology and Systematics. Cornell University, Ithaca, New York.

Kent, M., and P. Coker. 1992. Vegetation description and analysis: a practical approach. John Wiley & Sons, Chichester, England 363.

Levy, G. F. 1970. The phytosociology of northern Wisconsin upland openings. *The American Midland Naturalist* 83:213–237.

Mossman, M. J., E. Epstein, and R. M. Hoffman. 1991. Birds of Wisconsin pine and oak barrens. *The Passenger Pigeon* 52:153–168.

Murphy, R. E. 1931. The geography of the northwestern pine barrens of Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 26:69–120.

Neimuth, N. 1993. Response of grassland/savanna birds to pine barrens savanna patch size, origin, and structure: preliminary investigations. Page 23 *in*The future of pine barrens in northwest Wisconsin: a workshop summary, 21–23 September 1993. Solon Springs, Wisconsin.

Nielsen, S. E. 1997. The influence of topoedaphic factors, canopy, and bracken fern on distributional patterns of plant species at Spread Eagle Barrens. MS thesis. University of Wisconsin, Stevens Point, Stevens Point, Wisconsin, 162 pp.

Nielsen, S. E., and A. Haney. 1998. Gradient responses for understory species in a bracken grassland and northern dry forest ecosystem of northeast Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 86:149–166.

Power, R. L., and A. Haney. 1998. Adaptive management: a solution to restoration uncertainties. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 86:177–188.

Radeloff, V. C., D. J. Mladenoff, H. S. He, and M. S. Boyce. 1999. Forest landscape change: The northwest Wisconsin pine barrens before European settlement and Today. *Canadian Journal of Forest Research* 29:1649–1659.

Shively, M. M., and S. A. Temple. 1994. An ecosystem recovery plan for Wisconsin pine–shrub–grassland ecosystems (pine barrens). University of Wisconsin-Madison, Department of Wildlife Ecology, Madison, Wisconsin 82.

Stoeckeler, J. H., and G. A. Limstrom. 1942. Site classifications for reforestation on the national forest of Wisconsin. *Journal of Forestry* 40:308–315.

Temple, S. A. 1992. Population viability analysis of a sharp-tail grouse metapopulation in Wisconsin. Pages 750–758 *in* D. R. McCullough, and R. H. Barrett (eds.)., Wildlife 2001: Populations. Elsevier Applied Science, London.

Vogl, R. J. 1964a. Vegetation history of Crex Meadows, a prairie savanna in northwestern Wisconsin. *The American Midland Naturalist* 72:157–175.

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

Vogl, R. J. 1967. Controlled burning for wildlife in Wisconsin. *Tall Timbers Annual Fire Ecology Conference* 6:47–96.

Vogl, R. J. 1970. Fire and the northern Wisconsin pine barrens. *Tall Timbers Annual Fire Ecology Conference* 10:175–209.

Vora, R. S. 1993. Moquah Barrens: Pine barrens restoration experiment initiated in Chequamegon National Forest. *Restoration Management Notes* 11:39–44.

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

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

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

Walker, B., S. Carpenter, J. Anderies, N. Abel, G. Cumming, M. Janssen, L. Lebel, J. Norberg, G. D. Peterson, and R. Pritchard. 2002. Resilience management in social-ecological systems: a working hypothesis for a participatory approach. *Conservation Ecology* 6(1):14 [online].

WIDNR The working list: natural communitieshttp://www.dnr.state.wi.us/org/land/er/workinglists/taxalists/00list12.htm..

Yoccoz, N. G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *ESA Bulletin* 72:106–111.

Appendix I. Sampling history, management, and vegetation characteristics by management unit (unit no.) and year of sample[a]

Unit no.	Year	Plant community	Years since burn	No. of burns	Area (ha)	Sample size (*N*)	Forbs		Grasses/ sedges		Trees/ shrubs		Ferns		Mean richness		Mean cover	
							C	R	C	R	C	R	C	R	N	E	N	E
116	1995	BG	1	2	16.1	25	66.5	21	95	9	119.4	8	32.7	3	8.7	1.6	154	47
116	1999	BG	5	2	—	25	25.4	21	51.5	10	85.2	10	33.5	1	9.8	1.7	256	57
121.2	1999	BG	>40	0	23.5	5	42.8	6	54.4	5	37.0	1	0	0	4.4	2.2	80	54
126	1995	BG	3	3	50.4	25	44.6	24	65.1	7	90.0	12	60.4	2	12.2	0.9	250	11
207	1995	BG	>40	0	36.9	25	44.8	19	84.1	8	91.5	8	28.2	1	9.2	0.9	217	31
207.2	1995	BG	>40	0	3.9	7	15.3	8	97.9	6	109.4	6	38.6	1	7.3	0.7	240	21
207.2	1999	BG	1	1	—	7	5.3	7	52.9	7	76.1	5	18.3	1	6.9	0.9	130	23
210	1995	BG	>40	0	65.5	13	22.2	20	41.0	6	92.1	12	43.2	2	11.2	1	176	23
210	1999	BG	1	1	—	13	29.7	21	52.6	9	88.2	11	40.8	1	12.2	1.5	181	30
220	1995	BG	0	3	72.3	25	35.5	24	65.6	10	113.9	14	35.4	1	10.6	0.9	239	12
220	1999	BG	5	3	—	25	17.5	13	39.6	10	115.9	9	13.8	1	7.9	0.8	167	19
321	1999	BG	>40	0	56.3	5	4.6	2	46.8	6	103.6	4	0	0	5.8	1	146	9
339	1995	BG	>40	0	6.9	12	40.8	17	83.7	9	94.3	7	25.0	1	11.3	1.5	222	22
339	1999	BG	1	1	—	12	41.9	17	47.8	9	76.2	8	11.8	1	11.1	1.4	161	16
405	1995	BG	>40	0	44.8	25	12.6	16	62.8	7	81.1	12	12.6	1	8	0.8	152	17
405	1999	BG	2	1	—	20	10.4	16	47.7	8	60.7	10	10.9	1	7.7	0.8	121	9
509	1995	BG	4	3	42.0	25	32.4	18	72.1	9	138.4	8	22.0	1	11.6	1	250	15
509	1999	BG	3	3	—	25	14.3	17	53.9	7	93.1	8	16.2	1	10.7	1.1	165	13
511	1995	BG	16	2	67.9	25	26.6	21	71.1	8	65.2	9	29.4	1	10.2	1.1	159	33
513	1995	BG	5	2	33.4	25	22.6	25	84.6	10	104.1	8	9.6	1	8.6	1.1	193	28
513	1999	BG	9	2	—	25	19.4	21	61.8	9	69.9	9	7	1	8.2	1.6	124	34
216.1	1995	NDF-A	>40	0	9.8	12	12.0	10	20.3	5	37.2	14	20.9	1	10.1	0.1	90	0
216.1	1999	NDF-A	1	1	—	12	19.3	10	30	5	59.2	11	13.9	1	10.5	0.2	121	1
320	1995	NDF-A	>40	0	43.1	5	53.8	24	76.0	7	35.2	17	34.5	2	11.4	0.4	193	6
320	1999	NDF-A	>40	0	—	5	49.2	11	44.6	8	42.8	8	3.4	1	12.6	1	134	6
338	1995	NDF-A	>40	0	1.5	13	12.3	11	28.4	5	80.9	13	39.2	2	10.5	0	161	0
338	1999	NDF-A	1	1	—	13	7.8	9	10.2	2	48.5	12	29.7	1	8.7	0	96	0
413.1	1999	NDF-A	>40	0	14.4	5	44.8	10	22.8	6	12	4	24.4	1	8.8	0.8	102	2
516	1995	NDF-A	>40	0	11.2	10	25.3	15	30.7	6	39.8	11	28.8	1	10.9	0.4	120	5
516	1999	NDF-A	3	1	—	10	24.2	15	9	7	40	11	54.5	1	11	0.5	126	1
131	1999	NDF-PJ	1	1	1.5	5	34.6	7	42	3	65.7	8	41.4	1	9.2	0.2	180	1
211	1995	NDF-PJ	>40	0	1.1	13	37.2	15	64.5	7	81.2	14	48.7	2	13.5	0.7	221	10
211	1999	NDF-PJ	1	1	—	13	25.2	16	39.8	7	41.2	14	31.4	2	13.5	0.5	134	3
319	1999	NDF-PJ	>40	0	2.4	15	21.1	15	59.4	3	65.7	15	1	1	11.2	0.2	161	1
510	1995	NDF-PJ	4	2	2.4	5	21.6	10	24.6	2	15.6	4	37.2	1	11.2	0	99	0
510	1999	NDF-PJ	3	3	—	10	21.4	10	20.8	4	36	6	23.8	1	9.2	0.4	78	0
403	1995	NDF-PJ	>40	0	2.7	5	28.6	13	71.6	5	25.6	6	2.0	1	9.6	1.6	96	32
403	1999	NDF-PJ	2	1	—	5	10.6	8	30.2	6	15.6	5	10.4	1	8.6	1.4	61	6
530	1999	NDF-PJ	>40	0	2.5	5	9.4	11	21.4	3	17.8	9	0	0	10.6	0.2	48	0
122.1	1999	NDMF	>40	0	10.5	5	16.6	9	2.4	2	8.8	4	5.4	2	8.6	0.2	33	0
518	1999	NDMF	>40	0	43.7	4	40	12	10.8	3	17	6	23.8	1	10.8	0	92	0

[a]Plant communities include bracken–grassland (BG), northern–dry forest aspen (NDF-A), and northern–dry forest jack pine (NDF-JP). For each vegetation group we list the average cover (C) and richness (R) by management unit and present total mean richness and cover for native (N) and exotic (E) species.