VEGETATION-SITE RELATIONSHIPS AND FIRE HISTORY OF A SAVANNA-GLADE-WOODLAND MOSAIC IN THE OZARKS

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Abstract: There is a growing interest in reconstructing past disturbance regimes and how they influenced plant composition, structure and landscape pattern. Such information is useful to resource managers for determining the effects of fire suppression on vegetation or tailoring prescribed fires to restore community and landscape diversity. In the spring of 1995, the National Park Service reintroduced landscape-scale prescribed fire to an extensive oak/pine woodland-savanna-glade complex on Turkey Mountain, Buffalo National River, Arkansas. We took advantage of this opportunity to: (1) reconstruct the fire history of Turkey Mountain from fire scars and (2) determine how plant composition, forest structure, and past fire intensity varied along topoedaphic gradients before the site was burned. A fire history was derived from wedges or cross-sections of one dead and eight live shortleaf pines. Woody and herbaceous vegetation were sampled in 18, 20 by 25-m plots systematically spaced along transects running upslope. The percentage of trees scarred was determined in 80, 20 by 20- or 20 by 40-m plots located along transects running upslope. Highest plant diversity occurred on shallow, calcareous soils (limestone glades). Lowest diversity was associated with deeper, acidic soils and high woody basal area. Vegetation composition changed gradually along environmental gradients, but the most distinct flora was associated with: (1) limestone glades, (2) deeper acid soils, (3) high basal area sites, and (4) sandstone glades. Savanna herbaceous species were characteristic of sites with intermediate soil depth and fertility. Black hickory, post oak, eastern red cedar, and chinquapin oak were overstory dominants. Encroachment of cedar (on circumneutral soils), black jack oak, and black hickory (on acidic soils) may pose a serious threat to the diverse flora. For the 223-year fire record, the mean return interval was 5.7 years. The longest fire-free interval was 34 years (1770-1804) and the shortest was 1 year. No fire scars were documented between 1972 and 1993. The number of trees scarred per plot increased with fetch (distance from the bottom of the mountain), proximity to south-southwest slope aspects (especially on steeper slopes), and distance from the Buffalo River. Past variation in fire frequency and intensity may have acted synergistically with topoedaphic gradients to maintain a mosaic of plant communities.

INTRODUCTION

Oak ecosystems in Eastern North America have evolved under the influence of fire for thousands of years (Abrams 1992). Savannas, glades, and woodlands in the Ozarks remained open in the past due to fire but were distributed in complex mosaics subtly integrated along continua relating to soil depth and bedrock type. In the Ozarks, glades are treeless or sparsely wooded openings in woodlands, with bedrock at or near the surface (Logan 1992). Glades are often concentrated on, but not limited to, south and west aspects of hillsides, with savanna above and below. Savannas and woodlands are usually defined physiognomically, with the former having less canopy cover (10 to 50%) and more herbaceous groundcover (especially graminoids, composites, and legumes). Savannas and glades are also strongly influenced by the frequency, intensity, and seasonal variation in the occurrence of fire (Ladd 1991).

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Since implementation of fire suppression in the Ozarks and other parts of the Midwest, savannas and glades have undergone rapid succession to more closed conditions (Anderson and Schwegman 1991, Apfelbaum and Haney 1990, Beilmann and Brenner 1951, Guyette and McGinnes 1982, Kucera and Martin 1957, and many others). Ozark savannas have become overgrown with black hickory (*Carya texana* Buckl.), black jack oak (*Quercus marilandica* Muenchh.), and a variety of fire-sensitive hardwoods (e.g., shadbush (*Amelanchier arborea* (Michx. f.) Fern.)). Glades have become fragmented by invasion of eastern red cedar (*Juniperus virginiana* L.), black jack oak, winged elm (*Ulmus alata* Michx.), and winged sumac (*Rhus copallina* L.) (Reiter 1991). Fire, cutting, and herbicide application are often recommended to reduce woody density and promote herbaceous diversity, but there is often no explicit rationale for where and how intensively these restoration techniques should be applied across the landscape.

Savannas and glades contain some of the richest floras in North America. For instance, Ver Hoef and others (1991) recorded 365 glade species in the vicinity of the Current River, Missouri, and over 300 species were found in one small restored savanna in central Missouri (Ken McCarty, Missouri Department of Natural Resources, personal communication). Several endangered species, such as Mead's Milkweed (*Asclepias meadii* Torr.), have been recorded in Ozark savannas (Tim Nigh, Missouri Department of Conservation, personal communication). Savannas or "barrens" have widely scattered trees and extremely diverse groundcover vegetation that combines the floristic characteristics of both grasslands and woodlands (Nuzzo 1986). However, research seldom targets transitional areas, and therefore many species remain undetected. Furthermore, glades and savannas provide some of the most striking patch diversity across the Ozark landscape, and the distribution of these communities modifies disturbance regimes, nutrient dynamics, and habitat use of many wildlife species. These communities often represent islands of high diversity (herbaceous plants, insects, and other groups) in a matrix of low diversity, even-aged, closed-canopy forest. Yet, management activities continue to homogenize the landscape through fire suppression and logging without regard to the underlying vegetation patterns.

In the Spring of 1995, the National Park Service reintroduced landscape-scale prescribed fire to an extensive oak/pine woodland-savanna-glade complex on Turkey Mountain, Buffalo National River, Arkansas. The present study was undertaken to provide a better understanding of both the presettlement fire regime and the effects of fire suppression on vegetation. The objectives of this study were to: (1) reconstruct the fire history of Turkey Mountain from fire scars and (2) determine trends in plant composition and past fire intensity along topoedaphic gradients. We were particularly interested in understanding the more subtle variation in vegetation composition across several community types, and how vegetation and fire regimes vary along the same topoedaphic gradients.

METHODS

Study Area

Turkey Mountain is located at the junction of the Buffalo and White rivers, Hathaway Wilderness Area, Buffalo National River. A several hundred-hectare oak/shortleaf pine (*Pinus echinata* Mill.) woodland-savanna-glade complex covers the south aspect of Turkey Mountain and north aspect of Granite Mountain. The stratigraphy is complex, consisting of various layers of Ordovician limestone and sandstone. The sandstone "caps" of Turkey Mountain appear to be part of the massive St. Peter formation (Craig 1988, Craig and Deliz 1988). The majority of limestone glades on mid-slopes probably are found on dolomitic limestones of the Powell and Cotter formations. Topography is very steep, with 100-150 m of local relief.

Vegetative Sampling

Eighteen 500-m^2 (20 by 25-m) plots were established in 1993 and permanently marked with rebar on Turkey Mountain and adjoining Granite Mountain. Plots were located 100 m apart along 5 transects running upslope. Transects were subjectively located to cover representative vegetation assemblages, soil types, and slope aspects within the proposed burn unit (Table 1). Herbaceous vegetation was surveyed in June and again in early September. Some pre-vernal species may have already become senescent by late June, but most species were probably detected in these two periods. Cover class values between 0 and 5 (20% cover-scale increments) were assigned to all herbaceous and woody ground cover species (<1 m tall) in each plot. In addition, all trees ≥ 5 cm dbh (diameter at

Table 1. Site and soil characteristics of Turkey Mountain (TM) and Granite mountain (GM), Buffalo National River, Arkansas

Plot	Slope Pos.	Substrate	Dominant Trees/Community	Elev. (m)	Aspect (°)	Slope (°)	Moisture Index 0 = dry	Soil Depth (cm±SD)	Salt pH	CEC (meq/100g)
1 (TM)	upper	chert/sandstone	black oak-black hickory	311	150 SE	22	19	5.90 ± 2.6	5.10	10.45
2 (TM)	mid	limestone	blackjack oak-black hickory	253	176 S	26	15	14.10 ± 9.3	5.00	5.90
3 (TM)	lower	limestone	post oak, gladey	201	179 S	18	24	10.80 ± 8.3	6.75	14.65
4 (TM)	upper	limestone	chinquapin oak, gladey	262	170 S	20	21	2.90 ± 4.6	7.30	11.45
5 (TM)	mid	limestone	chinquapin oak, gladey	213	175 S	19	19	7.90 ± 7.5	6.90	13.00
6 (TM)	lower	limestone	eastern red cedar, gladey	184	185 S	19	26	4.40 ± 3.7	6.85	22.65
7 (TM)	ridge	sandstone	black hickory-blackjack oak, gladey	275	115 E	8	20	30.40 ± 24.9	5.00	8.40
8 (TM)	ridge	sandstone	black hickory	301	82 E	8	23	13.60 ± 7.6	6.05	36.25
9 (TM)	ridge	sandstone	blackjack oak-post oak, gladey	283	230 SW	4	11	18.40 ± 12.8	4.85	8.70
10 (TM)	saddle	limestone/sandstone colluvium	black hickory-chinquapin oak, open glade	267	115 E	8	23	5.00 ± 6.5	6.60	10.10
11 (TM)	lower	limestone	eastern red cedar, gladey	173	125 ESE	11	36	15.90 ± 16.1	6.75	16.50
12 (TM)	upper	limestone	post oak-northern red oak	250	290 WNW	21	23	8.30 ± 8.3	6.45	28.35
13 (GM)	upper	limestone	post oak	263	242 WSW	20	15	4.20 ± 3.8	6.45	15.40
14 (GM)	lower	limestone	black hickory-eastern red cedar	197	20 NNE	12	46	13.40 ± 16.1	6.55	18.15
15 (GM)	mid	limestone	eastern red cedar, gladey	218	325 NW	12	32	9.80 ± 12.2	7.15	32.10
16 (GM)	upper	limestone	chinquapin oak, gladey	251	331 NW	18	25	5.40 ± 5.4	6.85	19.30
17 (GM)	ridge	chert/sandstone	white oak-southern red oak	288	349 NW	4	30	40.10 ± 9.7	4.60	3.10
18 (TM)	lower	chert	shortleaf pine	155	163 SSE	24	26	22.10 ± 7.8	4.45	6.90

breast height) were tallied and dbhs were recorded. Tree cores were taken at 0.4 m aboveground from about 10 trees in each plot. Trees were subjectively chosen to represent the range of sizes for each species and past periods of recruitment. Saplings ($2.5 \leq$ dbh < 5 cm), large seedlings (>0.5 m tall; < 2.5 cm dbh), and small seedlings (<0.5 m tall) were tallied in 100-m^2, 10-m^2, and 1-m^2 circular subplots, respectively. Two subplots of each size were located in each main plot. The total area sampled for small seedlings, 36 m^2, was insufficient to provide good density estimates for most species; thus, these data should be interpreted with caution.

Soil depths were measured with a steel rod at 16 points located at 4-m intervals along the plot diagonals. Soil samples were taken from the upper 15 cm from the center of each quarter of the plot. The two upper and two lower quarters were pooled separately. Samples were frozen for several months, sieved, and analyzed by the Soil Characterization Lab at the University of Missouri. In general, the within-plot variation in soil properties was very small, so only plot averages are presented in the results. Elevation, slope aspect, slope steepness, topographic position, and slope shape were recorded at each plot and used to compute a topographic relative moisture index (TRMI; Parker 1982). The TRMI is lowest for steep, upper, convex, southwest-facing slopes, and highest for valley bottoms or lower, northeast-facing slopes.

Fire History

Tree-ring analysis of fire scar dates was used to document the fire history of Turkey Mountain. Wedges or cross-sections were cut from eight living shortleaf pines and one well-preserved shortleaf pine snag. The snag, located on an upper slope, had 31 fire scars and recorded most of the fire years. Scars were cross-dated by comparison with cores from Turkey Mountain and chronologies from Leatherwood Creek and the Current River and Piney River watersheds in Missouri.

We examined variation in past fire intensity along topographic gradients by counting the number of trees scarred in 80, 20 by 20-m plots, systematically spaced every 15 m in vertical relief along eight transects running from the base to the summit of Turkey Mountain. Where trees were sparse (e.g., near glades), 20 by 40-m plots were used. As a general rule, only trees ≥ 15 cm dbh were included. At each plot we also recorded aspect, slope, elevation (by altimeter, 0.9-m resolution), estimated range of tree diameters, and tree species. Fetch (vertical relief from the bottom of the mountain) and the distance of each plot to the Buffalo River were determined from a USGS topographic map. We suspected that the Buffalo River would be a major anthropogenic ignition source, so we measured distance to the point on the river where Cook Creek enters, following the most likely path that fire would burn into the area.

Numerical Analyses

Multiple regression analysis (PROC GLM; SAS 1988) was used to model the percentage of trees scarred with respect to aspect, slope steepness, fetch, distance to the Buffalo River, and interactions among these variables. We transformed aspect, a circular variable, to a linear scale by treating all azimuths as deviations from 205°, approximately the most xeric aspect in terms of solar radiation and moisture demand (Parker 1982).

We used ordination by Canonical Correspondence Analysis (CCA) to examine trends in vegetation composition along environmental gradients. Ordination objectively arranges plots and (or) species together based on their degree of similarity. CCA uses measured environmental variables to constrain plots and species ordinations. The computer program CANOCO (Ter Braak 1988) was used for all analyses. Untransformed cover values were used for groundcover vegetation. Plot importance values (relative density + relative basal area + relative frequency /3) were used for trees ≥ 5 cm dbh. A square root transformation was used for tree data to reduce the effects of dominant species. For the understory stratum, we used relative densities that were weighted by size class: 1 for saplings, 0.1 for large seedlings, and 0.01 for seedlings. Rare species were down-weighted and scaling was symmetric; otherwise, all defaults in CCA were used. Environmental variables used in the ordination included: elevation, a topographic moisture index or TRMI, salt (0.01 M $CaCl_2$) pH, cation exchange capacity (CEC), total bases, percent organic matter, percent sand, total plot basal area, importance values of major overstory species, and the predicted percent trees scarred. Soil, topographic, and overstory variables were initially screened separately; then, "forward selection" techniques within CANOCO were used to identify a final subset of variables that were most correlated with the vegetation data sets. Monte Carlo permutation tests were used to determine the significance of the first canonical axis for overall significance of the species-environmental relationship.

RESULTS

Fire Regime

We cross-dated 54 scars on the 9 pines, and for the 223 years of record the mean fire interval was 5.7 years (Figure 1). The longest fire-free interval was 34 years (1770-1804) and the shortest was 1 year. During the 1950s, Turkey Mountain burned almost annually. Only one fire year, 1953, was found on more then one tree during that decade. No fire scars were documented between 1972 and 1993. Our fire history provides only minimum estimates for return intervals; the small sample size probably underestimated the frequency of fire on Turkey Mountain.

Figure 1. Fire-year chronology for Turkey Mountain, Arkansas.

The percentage of trees scarred (not dated) in the plots was significantly related to fetch (FETCH, in feet), the interaction of slope steepness and aspect (*SLP x ASP*), and distance from the Buffalo River (DIST, in miles):

% scarred = -0.58+(0.098**FETCH*)+(0.0069**SLP x ASP*)+(11.65**DIST*); r^2=0.75, $F^{3,76}$=45.45, P<0.001.

The percent of tree scarred increased with fetch and on steeper south- and west-facing slopes (Figure 2). The mean percent of trees scarred ranked by aspect were as follows: south (52%), west (47%), east (43%), and north (37%). The interaction of slope steepness and aspect contributed more to the regression model than either variable alone: the percent of trees scarred increased with greater slope steepness on south and west aspects, but steepness had little effect on north and east aspects (Figure 2).

Age Structure

The age structures of hardwood tree species on Turkey Mountain were distinctly multimodal, with even-aged cohorts establishing in the 1910s, 1940s and 1960s (Figure 3). The oldest tree was a 188-year-old post oak (*Quercus stellata* Wang.), but most of the large trees were hollow and could not be dated. The majority of eastern red cedar and shortleaf pine trees on the lower slopes established c. 1925-1940, a period when the mountain was burned relatively frequently (see Figure 1), although the extent of the burns is unknown. It should be cautioned that this was not a random sample of tree ages and that coverage was fairly limited. Also, <50% of the cores were sound enough to estimate complete ages.

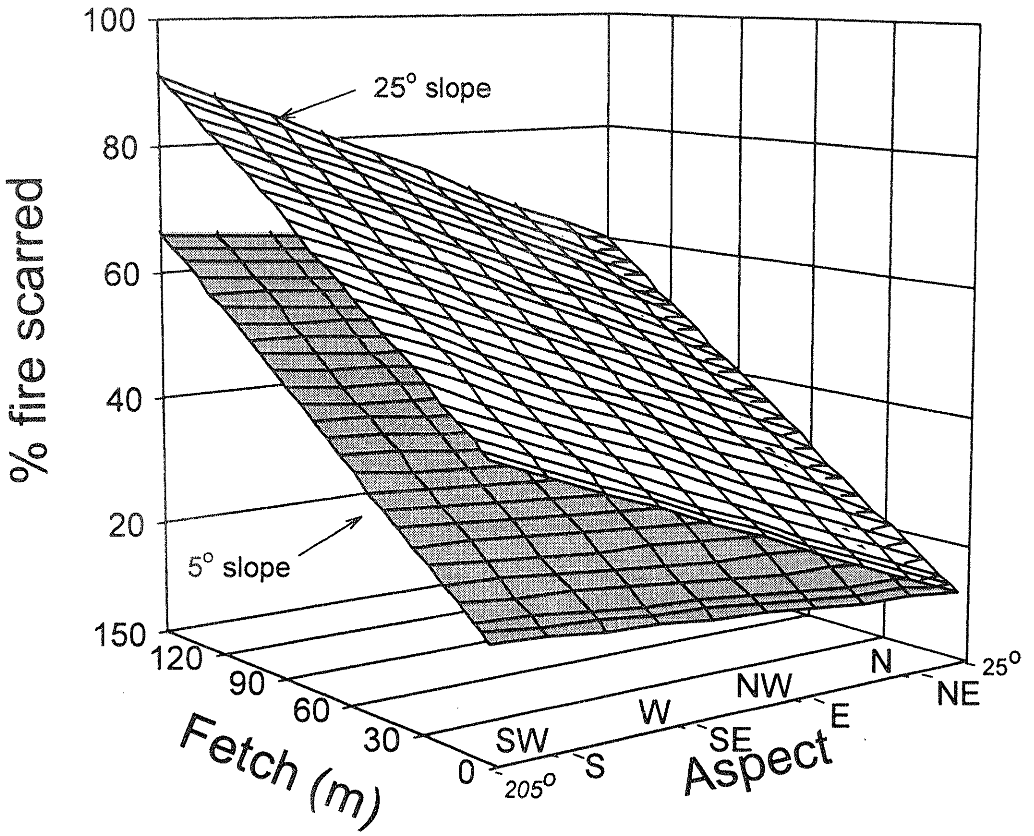

Figure 2. Percentage of trees scarred as a function of fetch (distance from bottom of mountain), aspect, and slope steepness. Aspect is given as degrees deviation from 205° azimuth. Two levels of slope steepness are shown.

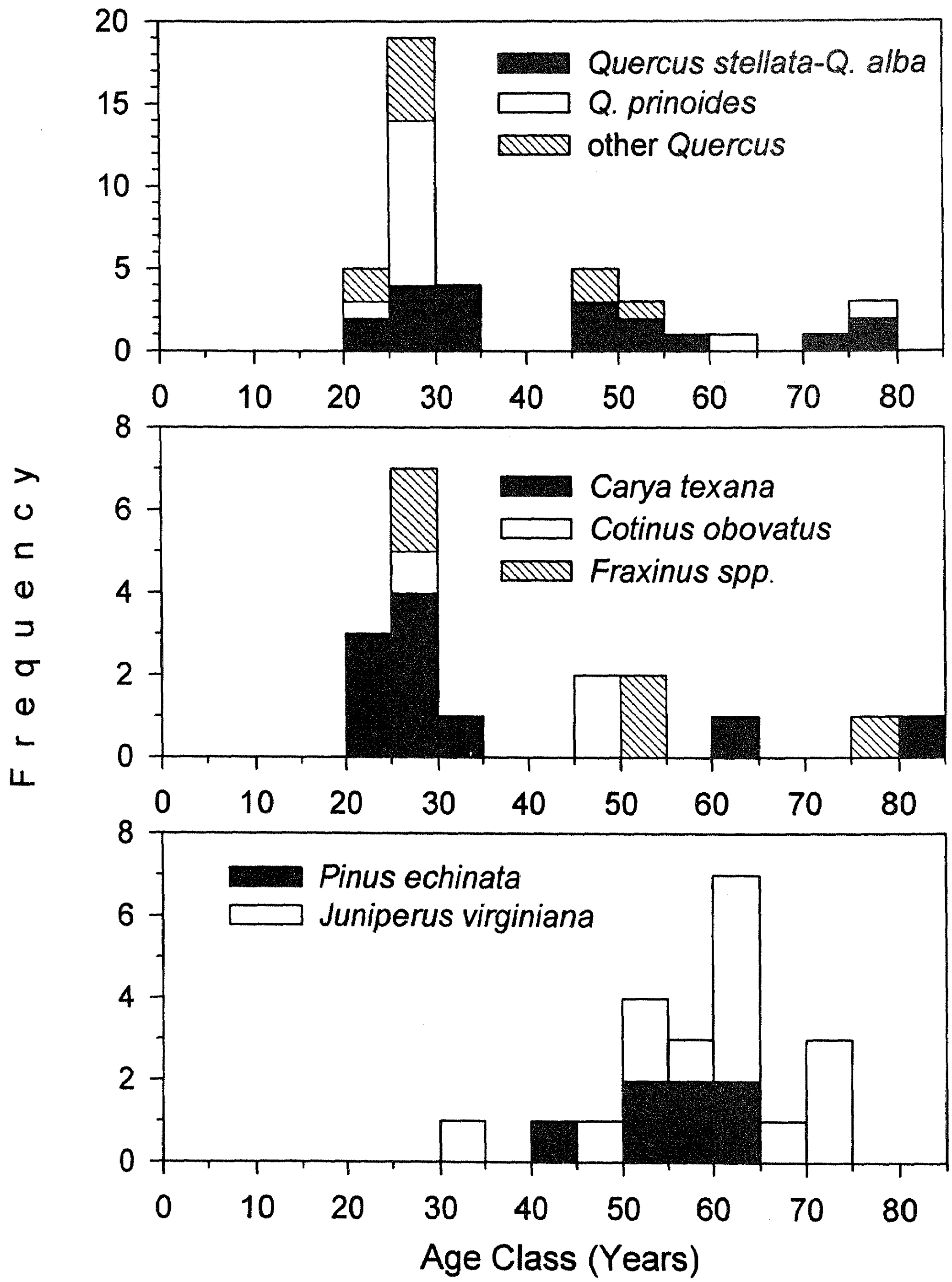

Figure 3. Age distribution of trees on Turkey Mountain. Trees > the 85 years are not shown.

Vegetation

There were 26 tree and tall shrub species (≥ 5 cm dbh) found on Turkey Mountain, with black hickory, eastern red cedar, post oak, and chinquapin oak (*Quercus prinoides* Willd.) having the highest importance values (Table 1). Tree compositional patterns were strongly related to environmental variables (Figure 4). The first two ordination axes accounted for 36% of the variance in species data and 59% of the variance in the species-environment relation (see Ter Braak 1988). The first canonical axis and overall species-environmental relationship were both highly significant (Monte carlo tests, P=0.01). Plot 18 was the most distinct, characterized by pine and sassafras on deeper soil with low pH, CEC, and total bases (Figure 4). Plots 1, 2, 7, 9, and 17 were also on deeper, more acid soils overlying sandstone or chert; with indicator species such as black jack oak, black locust (*Robinia pseudo-acacia* L.), southern red oak (*Quercus falcata* Michx.), white oak (*Q. alba* L.), and black oak (*Q. velutina* Lam.). White oak was apparently restricted more by soil depth than pH. The rest of the plots were on shallow soils overlying limestone. Indicator species included typical calcicoles: blue ash (*Fraxinus quadrangulata* Michx.), eastern red cedar, gum bumelia (*Bumelia lanuginosa* (Michx.) Pers.), chinquapin oak, and American smoke tree (*Cotinus obovatus* Raf.). Chinquapin oak importance values were also highly correlated with magnesium levels (not shown on ordination). Post oak, persimmon (*Diospyros virginiana* L.), and northern red oak (*Quercus rubra* L.) were the most widespread, but were slightly more abundant on circumneutral soils.

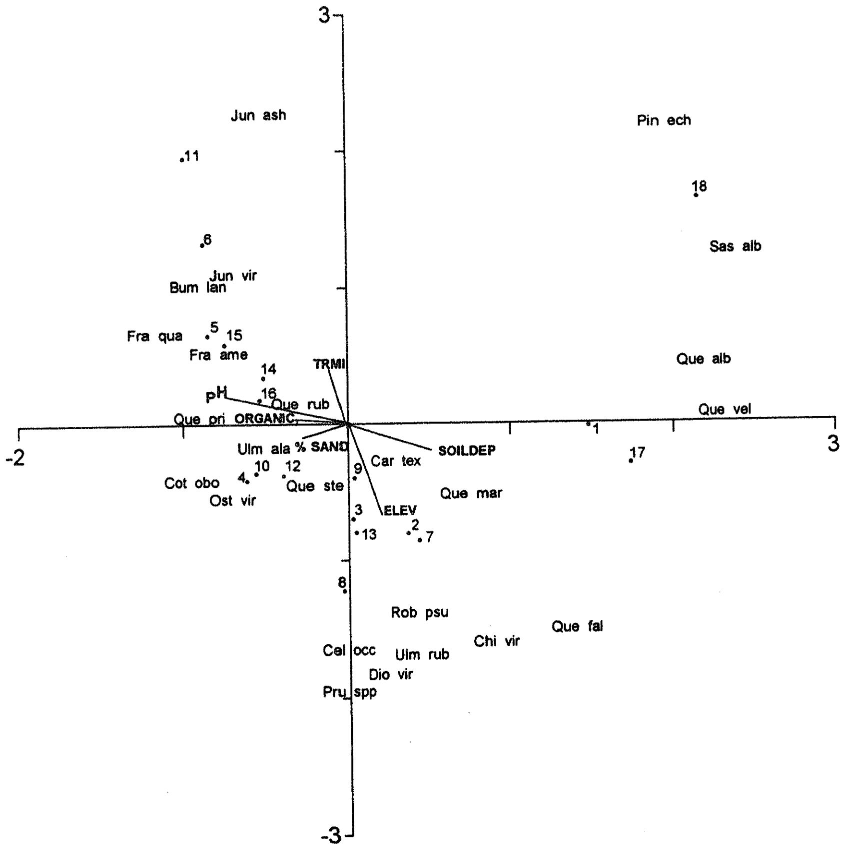

Figure 4. CCA ordination triplot of tree and tall shrub species (≥ 5 cm dbh) on Turkey Mountain. The environmental vectors point in the direction of maximum correlation and vector length is proportional to the strength of the correlation. Numbers represent plots and species codes include the first three letters of the genus and specific epithet (see Appendix 1).

The understory stratum was dominated by black jack oak, black hickory, post oak, and eastern red cedar (Table 1). Black jack oak and black hickory pose the greatest threat to sandstone glade and savanna vegetation; their abundance was clearly correlated with lower groundcover diversity (see Figure 6). Savanna species, such as post oak, are still reasonably abundant in the understory strata. The woody understory vegetation was less strongly related to measured environmental gradients than the overstory (data not shown). The first and second ordination axes accounted for 27% of the variance in species data and 56% of the variance in the species-environment relation. The first canonical axis was significant ($P = 0.01$), and the overall species-environmental relationship was also significant ($P = 0.01$). Plots on deeper and/or acid soils were characterized by fringe tree, winged sumac, black oak, white oak, sassafras, and black jack oak. Basic soils were characterized by the same calcicoles as in the overstory plots (see above); as well as winged elm, southern rusty blackhaw (*Viburnum rufidulum* Raf.), and rough-leaf dogwood (*Cornus drummondii* Meyer). Persimmon, post oak, and shadbush displayed a wide range of occurrence.

The composition of ground cover vegetation was highly variable with respect to topoedaphic gradients. The first and second ordination axes only accounted for 23% of the variance in species data and 42% of the variance in the species-environment relation. The first canonical axis was marginally signifcant ($P = 0.06$), but the overall species-environmental relationship was highly significant ($P = 0.01$). Vegetation composition tended to change gradually along environmental gradients (Figure 5). Plots 2, 7, 9, and 17—all on acid soils—were characterized by a tick trefoil (*Desmodium pauciflora* (Nutt.) DC.), two sedges (*Carex muhlenbergii* Schk., *C. retroflexa* Muhl.), a nut sedge (*Cyperus filiculmis* Vahl.), several grasses (*Sphenobolis intermedia* Rydb., *Elymus virginicus* L., *Sporobolus asper* (Michx.) Kunth., *Aristida dichotoma* Michx., *Panicum linearifolium* Scribn.), hairy lip fern (*Cheilanthes lanosa* (Michx.) D.C. Eaton), dwarf dandelion (*Krigia dandelion* (L.) Nutt.), purple cudweed (*Gnaphalium purpureum* L.), butterfly pea (*Clitoria mariana* L.), pellitory (*Parietaria pensylvanica* Muhl.), St. Andrew's cross (*Ascryum hypericoides* L.), forked chickweed (*Parinychia fastigata* (Raf.) Fern.), a sunflower (*Helianthus hirsutus* Raf.), a rushfoil (*Crotonopsis linearis* Michx.), and others (Figure 5).

Plots 7 and 9 are partly on sandstone glade (soil depth ranged from 0 cm on the exposed bedrock ledge to 50-80 cm further upslope). Indicator species on these shallow, acidic soils included stonecrop (*Sedum nuttallianum* Raf.), a brome grass (*Bromus racemosus* L.), and many of the same species listed for acidic soils above.

Plots 1, 8, and 18 were associated with high basal area (closed woodland canopy) and soils with low sand (high silt) content. Indicator species included *Vaccinium* spp., summer grape (*Vitis aestivalis* Michx.), and wild yam (*Dioscorea quaternata* (Walt.) J.F. Gmel.); in addition to more shade-tolerant woodland herbs, such as three-lobed violet (*Viola triloba* Schwein.), alum root (*Heuchera americana* L.), and wild bergamot (*Monarda fistulosa* L.) (Figure 5b and c).

Most of the plots on basic soils grouped very closely together, floristically (plots 3, 4, 5, 6, 10, 11, 12, 13, 14, 16). Characteristic species for these plots included purple prairie clover (*Petalostemon purpureum* (Vent.) Rydb.), false boneset (*Kuhnia eupatorioides* L.), two bluets (*Houstonia nigricans* (Lam.) Fern., *H. tenuifolia* Nuttall.), prairie acacia (*Acacia angustissima* (Mill.), two tick trefoils (*Desmodium sessifolium* (Torr.) T. & G., *D. illinoense* Gray), blue-eyed grass (*Sisyrhinchium campestre* Bickn.), squaw-weed (*Senecio obovatus* Muhl.), a coreopsis (*Coreopsis palmata* Nutt.), side-oats grama (*Bouteloua curitipendula* (Michx.) Torr.), a rock pink (*Talinum calycinum* Engelm.), and dwarf hackberry (*Celtis tenuifolia* Nutt.) (Figure 5b and c).

Physiographically, plot 14 is the most mesic site (lower slope, north aspect) and it had several distinct species: wild yam, agrimony (*Agrimonia rostellata* Wallr.), lyre-leaved sage (*Salvia lyrata* L.), a morning glory species (*Ipomoea* sp. L.), and a crown-beard (*Verbesina helianthoides* Michx.) (Figure 5 b and c).

A total of 251 species (154 genera, 62 families; 202 herbaceous/semi-woody and 49 woody species) were recorded on Turkey Mountain; 240 were recorded in plots (Appendix 1). Species richness was highest in plots on limestone glades (Figure 6). Low diversity was correlated with acid soils and high basal area (closed canopy). Relatively low diversity was also correlated with high importance values of black jack oak (also on acidic soil), where thickets were heavily shaded. The high density of black jack oak stems was probably a result of fire suppression starting in the 1970's after the area became part of the Buffalo National River. High basal area was also correlated with the deeper

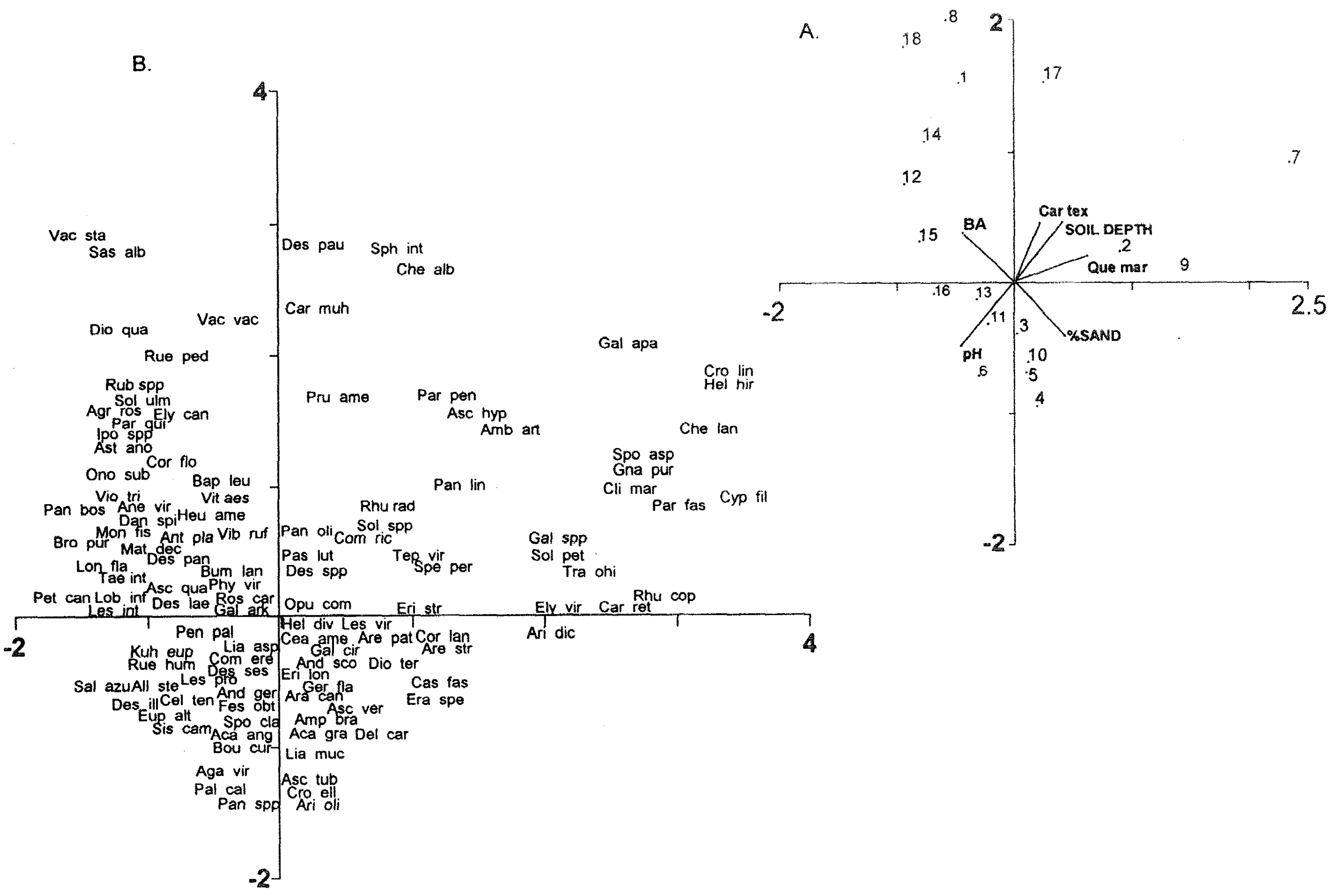

Figure 5. CCA ordination of plots (A) and groundcover species (B and C). Figure 5C shows species locations in the vicinity of the origin, where not all species were labeled in Figure 5B. See Figure 4 for further explanation of ordination diagrams.

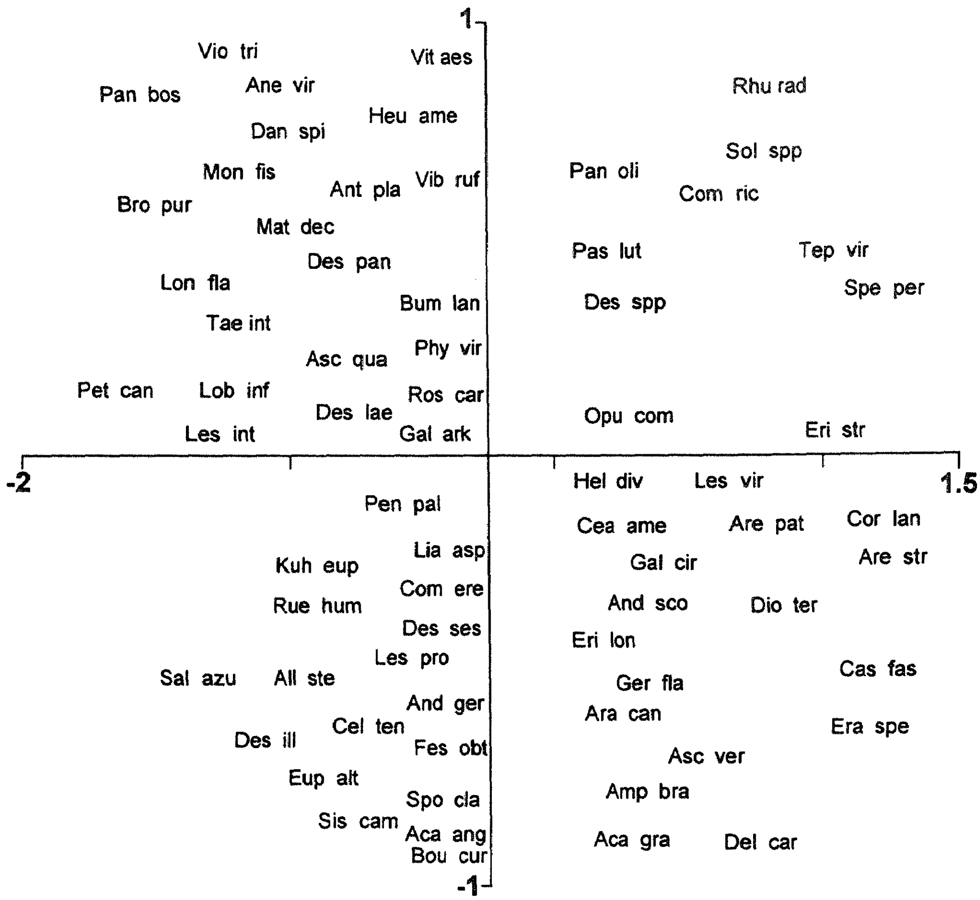
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Figure 5c.

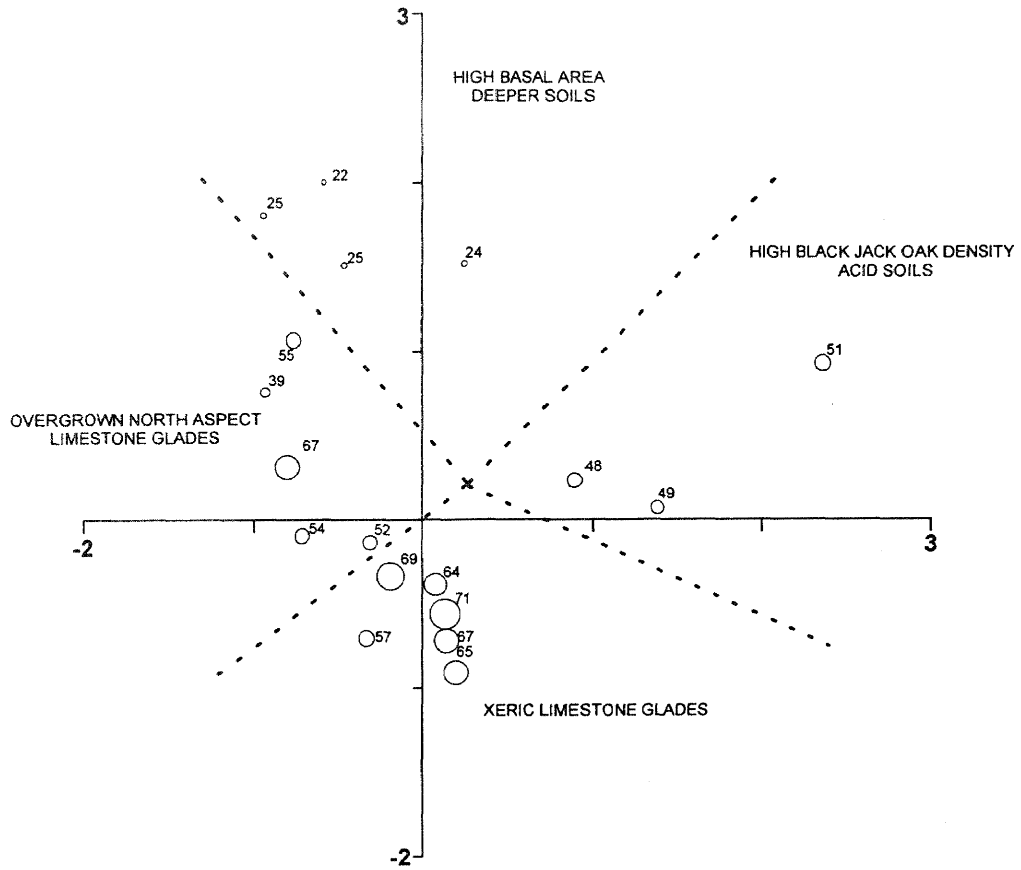

Figure 6. Species richness (number of species) of plots on Turkey Mountain. Plots are positioned in CCA ordination space and the environmental vectors are the same as those in Figure 5a. Circle size is proportional to species richness.

acidic soils located on the upper (shoulder) slopes and summits of knobs (Table 2), where more rapid invasion of black jack oak and black hickories has occurred.

DISCUSSION

Fire has influenced vegetation in the area for at least the past two centuries. The mean fire return interval, 5.7 years, is very similar to fire frequencies documented for oak and oak-pine sites in the Missouri Ozarks (Guyette and Cutter 1991, Cutter and Guyette 1994). Fire frequency in the Ozarks is highly dependent on ignitions from human populations because of the rarity of lightning caused fires (Guyette and Cutter 1991). The absence of fire scars in the early period, 1770-1804, is weak evidence for the absence of fire in the area because the older part of this record is based on only one tree, and the first fire scar generally requires more heat than subsequent scars (Gutsell and Johnson 1996). Alternatively, 1804 may indicate the beginning of frequent burning by the Cherokee, who migrated into the area during the period 1785-1828 (Pitcaithley 1987). The Cherokee began to leave Arkansas by treaty in 1828. The few fire scars between 1815 and 1840 may indicate a true reduction in fire frequency despite the data being from only one tree. Fire scar data from a post oak savanna 50 km to the north showed a similar reduction in fire frequency between 1810 and 1850 (Guyette and Cutter 1991).

Table 2. Summary of woody vegetation on Turkey mountain. Sap = saplings, LS = large seedlings, SS= small seedlings, IV = importance value. For overstory trees IV = ((relative + relative basal area + relative frequency/3)*100). For woody regeneration IV = ((relative density + relative frequency/2)*100).

Species	TREES Frequency (% of plots)	TREES Basal Area (m^2)/ha	TREES Density (stems/ha)	TREES I.V.	REGENERATION Frequency (% of plots)	REGENERATION Sap/ha	REGENERATION LS/ha	REGENERATION SS/ha	REGENERATION I.V.
Carya texana	94.4	2.37	256	16.62	77.8	267	170	1700	12.1
Juniperus virginiana	44.4	3.14	239	15.28	55.6	139	250	3100	0.0
Quercus stellata	83.3	2.70	159	14.11	50.0	211	360	9400	11.1
Q. prinoides	66.7	1.83	117	10.32	44.4	17	250	3100	4.7
Q. marilandica	44.4	0.81	141	7.75	38.9	425	190	1900	13.0
Pinus echinata	22.2	1.90	33	5.96	5.6	3	0	0	0.5
Quercus rubra	55.6	0.55	46	5.16	44.4	31	190	800	4.4
Q. velutina	16.7	0.60	66	3.88	16.7	83	30	300	3.1
Ulmus alata	50.0	0.34	19	3.71	55.6	44	170	800	5.4
Quercus falcata	11.1	0.68	9	2.21	0.0	0	0	0	0.0
Cotinus obovatus	22.2	0.11	27	2.07	38.9	33	60	1900	4.0
Quercus alba	11.1	0.43	20	1.99	11.1	14	0	0	1.1
Bumelia lanuginosa	27.8	0.05	12	1.81	27.8	8	60	300	2.3
Fraxinus americana	22.2	0.07	11	1.55	44.4	44	170	300	4.5
Sassfras albidum	16.7	0.04	14	1.29	27.8	97	280	2800	5.3
Robinia pseudoacacia	16.7	0.04	13	1.27	22.2	33	0	0	2.3
Diospyros virginiana	11.1	0.05	14	1.04	27.8	22	30	0	2.5
Fraxinus	5.6	0.09	9	0.71	5.6	6	30	300	0.7
Ulmus rubra	11.1	0.04	2	0.69	0.0	0	0	0	0.0
Juniperus ashei	5.6	0.12	2	0.58	0.0	0	0	0	0.0
Prunus sp.	5.6	0.01	3	0.38	16.7	6	30	0	1.4
Chionanthus	5.6	0.01	2	0.35	11.1	36	110	0	1.8
Celtis occidentalis	5.6	0.01	1	0.33	5.6	3	0	10000	2.7
Rhus copallina	5.6	0.003	1	0.31	5.6	0	110	0	0.6
Acer saccharum	5.6	0.002	1	0.31	0.0	0	0	0	0.0
Ostrya virginiana	5.6	0.002	1	0.31	0.0	0	0	0	0.0
Amelanchier arborea	0.0	0.00	0	0.00	16.7	6	60	600	1.6
Cornus drummondii	0.0	0.00	0	0.00	5.6	3	140	0	0.8
Viburnum rufidulum	0.0	0.00	0	0.00	11.1	19	80	0	1.4
Carpinus caroliniana	0.0	0.00	0	0.00	5.6	11	0	0	0.6
Cornus florida	0.0	0.00	0	0.00	5.6	3	0	0	0.5
Crataegus sp.	0.0	0.00	0	0.00	5.6	8	0	0	0.6
Rhus glabra	0.0	0.00	0	0.00	5.6	3	0	0	0.5
Vaccinium spp	0.0	0.00	0	0.00	5.6	3	110	300	0.7
Celtis tenuifolia	0.0	0.00	0	0.00	16.7	3	0	0	1.5

The age structures of overstory trees appear to reflect recent variation in fire history. A major even-aged cohort 20-35 years old, for example, corresponds to the cessation of frequent burning; in particular, dating back to extensive burns in 1960 and 1963. Multimodal age structures of oak savannas have been described by Apfelbaum and Haney (1990) in the Upper Midwest and by Jenkins and Rebertus (1994) in the Missouri Ozarks. Distinct even-aged cohorts are thought to originate during fire-free periods that allow stems to grow tall enough to survive the next fire. Jenkins and Rebertus (1994) also found that near-annual burning reduced fuel loads and resulted in very mild, patchy fires that encouraged sporadic regeneration of oaks. Livestock grazing, which was once pervasive in the Ozarks, could also cause very patchy, mild burns by trampling and reducing fine matrix fuels. The establishment of a cedar cohort 50-65 years ago, a period of frequent burning, may illustrate the combined effect of frequent burning and grazing in reducing fuel loads and exposing bare mineral soil for conifer seed germination.

The distribution of fire-scarred trees aptly illustrates the influence of landscape features on fire intensity. Fetch is important because fires tend to burn upslope and gain momentum by convective pre-heating of fuels and the generation of thermal winds (Pyne 1984). Slope aspect and steepness determine the amount of solar radiation received, and also influence temperature, wind exposure, and relative humidity—all factors that influence fire intensity. Steep south- and west-facing slopes at mid to upper slope positions had the highest percentage of trees scarred (Figure 2), and these also tended to be the most xeric sites (Parker 1982). We also found a 22% increase in fire scarring from the mouth of Cook Creek to its upper reaches (about 3.2 km), which may indicate that fires were more frequent, but less intense near a major ignition source (Buffalo River), or simply that fires gained momentum as they travelled upslope from the river. Describing variation in scarring across topographic gradients is potentially confounded by parallel changes in species composition and tree size, two factors known to affect probability of scarring (Gutsell and Johnson 1996). However, the results of our model are consistent with known fire behavior in hilly topography.

One of the major roles fire plays in maintaining species diversity in savannas and grasslands is the control of woody plant invasion (Huston 1994). However, it is difficult to separate the effects of fire regime and topoedaphic gradients on vegetation composition because all these factors are interrelated. For example, the predicted percent of trees scarred in the vegetation plots on Turkey Mountain was highly correlated with elevation ($r=0.83$, $P<0.001$, $n=18$) and the topographic moisture index ($r=-0.77$, $P<0.001$, $n=18$), two variables that also defined a major gradient in woody overstory composition and accompanying fuels (Figure 4). Fertility is also known to influence burning probability: low fertility tends to promote highly pyrogenic, non-woody species (Kellman 1984). With continued fire suppression, there will probably be a continued reduction in herbaceous diversity in the high basal area sites and a slower, but inevitable encroachment of cedar into the very shallow soils on mid and upper-slopes. Continued woody encroachment would result in the continued loss of diversity (reviewed by Heikens and Robertson 1994). In addition, the dramatic changes in light and litter on glades and savannas may result in less distinct flora on these sites. Besides black jack oak and cedar, Reiter (1991) identified winged elm, winged sumac, and aromatic sumac as invaders of glades in southern Missouri. Both winged elm and aromatic sumac are relatively abundant on Turkey Mountain.

The overriding environmental factors controlling the distribution of both woody and herbaceous species on Turkey Mountain are bedrock type; which influences soil pH, CEC, total bases, percent sand, soil depth and topographic position (elevation, TRMI). These variables, in turn, are also interrelated to bedrock stratigraphy. Glades occur on limestone exposed at mid to lower slope positions on both south and west aspects. Chert savanna and sandstone glades are located on upper slope positions and summits. However, subsurface chert and colluvial processes on the steep slopes probably blur some of the floristic types on Turkey Mountain, producing more of a vegetation continuum (see Figure 6). The complex stratigraphy and colluvial processes also increase resource heterogeneity in these generally infertile soils, a situation known to foster high species diversity (Tilman 1982). The high diversity of the limestone glades is probably due to several interacting factors including: (1) low moisture and soil infertility (Tilman 1982), (2) drier, windier conditions conducive to export of herb-smothering litter, (3) periodic disturbances (fire, frost heaving, and erosion) preventing single species dominance (Huston 1994), and (4) slower woody encroachment on shallow soils (Pallardy and others 1991).

Turkey Mountain presents a rare opportunity for using landscape-scale prescribed burns to restore a mosaic of savannas, glades, and woodlands. Topographic variation and its control of fire intensity will reestablish gradients in tree structure and community composition (particularly sun versus shade herbs). Overall species richness remains high at Turkey Mountain because of slow woody encroachment on its shallow soils; however, fire should increase the abundance of many species and promote flowering. Many savanna species can persist under a closed canopy but in a very low state of vigor (McCarty and Hassein 1984). Burning of this landscape not only has historical precedent but will help maintain diversity at multiple scales.

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Appendix 1. Species list and codes for Turkey Mountain. Scientific names follow Steyermark (1955).

Genus/species	Code	Genus/species	Code	Genus/species	Code
Acacia angustissima (Mill.)	Aca ang	*Carex sp.* L.	Car spp	*Erigeron annus* (L.) Pers.	Eri ann
Acalypha gracilens Gray	Aca gra	*Carpinus caroliniana* Walt.	Car car	*Erigeron strigosus* Muhl.	Eri str
Acer saccharum Marsh	Ace sac	*Carya texana* Buckl.	Car tex	*Eriogonum longifolium* Nutt.	Eri lon
Agave virginica L.	Aga vir	*Cassia fasciculata* Michx.	Cas fas	*Eupatorium altissimum* L.	Eup alt
Agrimonia pubescens Wallr.	Agr pub	*Ceanothus americanus* L.	Cea ame	*Euphorbia corollata* L.	Eup cor
Agrimonia rostellata Wallr.	Agr ros	*Celtis occidentalis* L.	Cel occ	*Euphorbia dentata* Michx.	Eup den
Allium stellatum Fraser	All ste	*Celtis tenuifolia* Nutt.	Cel ten	*Festuca obtusa* Biehler.	Fes obt
Ambrosia artemisiifolia L.	Amb art	*Cheilanthes lanosa* (Michx.) D.C. Eaton	Che lan	*Festuca octoflora* Walt.	Fes oct
Amelanchier arborea (Michx. f.) Fern.	Ame arb	*Chenopodium album* L.	Che alb	*Fraxinus americana* L.	Fra ame
Amphicarpa bracteata (L.) Fern.	Amp bra	*Chionanthus virginica* L.	Chi vir	*Fraxinus quadrangulata* Michx.	Fra qua
Andropogon gerardi Vitm.	And ger	*Clitoria mariana* L.	Cli mar	*Galactica volubilis* (L.) Britt.	Gal vol
Andropogon scoparius Michx.	And sco	*Comandra richardsiana* Fern.	Com ric	*Galium aparine* L.	Gal apa
Anemone virginiana L.	Ane vir	*Commelina erecta* L.	Com ere	*Galium arkansanum* Gray	Gal ark
Antennaria plantaginifolia (L.) Hook.	Ant pla	*Coreoposis lanceolata* L.	Cor lan	*Galium circaezans* Michx.	Gal cir
Arabidopsis thaliana (L.) Heyn.	Ara tha	*Coreopsis palmata* Nutt.	Cor pal	*Galium sp.* L.	Gal spp
Arabis canadensis L.	Ara can	*Cornus drummondii* Meyer	Cor dru	*Galium virgatum* Nutt.	Gal vir
Arenaria patula Michx.	Are pat	*Cornus florida* L.	Cor flo	*Geranium carolinianum* L.	Ger car
Arenaria stricta Michx.	Are str	*Cotinus obovatus* Raf.	Cot obo	*Gerardia flava* L.	Ger fla
Aristida dichotoma Michx.	Ari dic	*Crataegus sp.* L.	Cra spp	*Gerardia tenuifolia* Vahl	Ger ten
Aristida oligantha Michx.	Ari oli	*Crotonopsis elliptica* Willd.	Cro ell	*Gnaphalium purpureum* L.	Gna pur
Aristida purpurascens Poir.	Ari pur	*Crotonopsis linearis* Michx.	Cro lin	*Helianthus divaricatus* L.	Hel div
Asclepias quadrifolia Jacq.	Asc qua	*Cunila origanoides* (L.) Britt.	Cun ori	*Helianthus hirsutus* Raf.	Hel hir
Asclepias tuberosa L.	Asc tub	*Cyperus filiculmis* Vahl.	Cyp fil	*Helianthus maximiliani* Schrad.	Hel max
Asclepias verticillata L.	Asc ver	*Danthonia sericea* Nutt.	Dan ser	*Heliotropium tenellum* (Nutt.) Torr.	Hel ten
Ascryum hypericoides L.	Asc hyp	*Danthonia spicata* (L.) Beauv.	Dan spi	*Heuchera americana* L.	Heu ame
Asplenium platyneuron (L.) Oakes.	Asp pla	*Delphinium carolinianum* Walt.	Del car	*Houstonia longifolia* Gaery.	Hou lon
Aster anomalus Engel.	Ast ano	*Desmodium cuspidatum* (Muhl.) Loud.	Des cus	*Houstonia nigricans* (Lam.) Fern.	Hou nig
Aster drummondii Lindl.	Ast dru	*Desmodium glutinosum* (Muhl.) Wood	Des glu	*Houstonia purpurea* L.	Hou pur
Aster patens Ait.	Ast pat	*Desmodium illinoense* Gray	Des ill	*Houstonia tenuifolia* Nuttall.	Hou ten
Aster sp. L.	Ast spp	*Desmodium laevigatum* (Nutt.) DC.	Des lae	*Hypericum punctatum* L.	Hyp pun
Astragalus canadensis L.	Ast can	*Desmodium nuttallii* (Schindl.) Schub.	Des nut	*Hypericum spathulatum* (Spach) Steud.	Hyp spa
Baptisia leucophaea Nutt.	Bap leu	*Desmodium paniculatum* (L.) DC.	Des pan	*Hypericum sphaerocarpum* Michx.	Hyp sph
Botrychium dissectum Spreng.	Bot dis	*Desmodium pauciflorum* (Nutt.) DC.	Des pau	*Ipomoea sp.* L.	Ipo spp
Bouteloua curtipendula (Michx.)Torr.	Bou cur	*Desmodium sessilifolium* (Torr.) T. & G.	Des ses	*Juniperus ashei* Buchholz	Jun ash
Bromus purgans L.	Bro pur	*Desmodium sp.* Desv.	Des spp	*Juniperus virginiana* L.	Jun vir
Bromus racemosus L.	Bro rac	*Diodia teres* Walt.	Dio ter	*Krigia dandelion* (L.) Nutt.	Kri dan
Bumelia lanuginosa (Michx.) Pers.	Bum lan	*Dioscorea quaternata* (Walt.) J.F. Gmel.	Dio qua	*Kuhnia eupatorioides* L.	Kuh eup
Carex arctitecta Mackenz.	Car arc	*Diospyros virginiana* L.	Dio vir	*Lactuca scariola* L.	Lac sca
Carex cephalophora Muhl.	Car cep	*Echinacea pallida* Nutt.	Ech pal	*Lechea tenuifolia* Michx.	Lec ten
Carex lanuginosa Michx.	Car lan	*Elymus canadensis* L.	Ely can	*Lepidium virginicum* L.	Lep vir
Carex muhlenbergii Schk.	Car muh	*Elymus virginicus* L.	Ely vir	*Lespedeza capitata* Michx.	Les cap
Carex retroflexa Muhl.	Car ret	*Eragrostis spectabilis* (Push) Steud.	Era spe	*Lespedeza hirta* (L.) Hornem.	Les hir

Appendix 1. Continued

Genus species	Code	Genus species	Code	Genus species	Code
Lespedeza intermedia (S. Wats.) Britt.	Les int	*Petalostemon candidum* (Willd.) Michx.	Pet can	*Solidago arguta* Ait.	Sol arg
Lespedeza procumbens Michx.	Les pro	*Petalostemon purpureum* (Vent.) Rydb.	Pet pur	*Solidago nemoralis* Ait.	Sol nem
Lespedeza sp. Michx.	Les spp	*Phlox pilosa* L.	Phl pil	*Solidago petiolaris* Ait.	Sol pet
Lespedeza virginica L.	Les vir	*Physalis virginiana* Mill.	Phy vir	*Solidago radula* Nutt.	Sol rad
Liatris aspera Michx.	Lia asp	*Physostegia virginiana* (L.) Benth.	Phi vir	*Solidago sp.* L.	Sol spp
Liatris cylindracea Michx.	Lia cyl	*Pinus echinata* Mill.	Pin ech	*Solidago ulmifolia* Muhl.	Sol ulm
Liatris mucronata DC.	Lia muc	*Plantago virginica* L.	Pla vir	*Sorghastrum nutans* (L.) Nash.	Sor nut
Liatris scabra (Greene) K. Schum.	Lia sca	*Polygonum convolvulus* L.	Pol con	*Specularia perfoliata* (L.) A. DC.	Spe per
Liatris squarrosa (L.) Michx.	Lia squ	*Prunus sp.* L.	Pru spp	*Sphenobolis intermedia* Rydb.	Sph int
Linaria canadensis (L.) Dumort.	Lin can	*Quercus alba* L.	Que alb	*Sphenobolis obtusata* (Michx.) Scribn.	Sph obt
Lithospermum canescens (Michx.) Lehm.	Lit can	*Quercus falcata* Michx.	Que fal	*Spiranthes gracilis* (Bigel.) Beck	Spi gra
Lithospermum incisum Lehm.	Lit inc	*Quercus marilandica* Muenchh.	Que mar	*Sporobolus asper* (Michx.) Kunth.	Spo asp
Lobelia inflata L.	Lob inf	*Quercus prinoides* Willd.	Que pri	*Sporobolus clandestinus* (Biehler) Hitchc.	Spo cla
Lonicera flava Sims	Lon fla	*Quercus rubra* L.	Que rub	*Strophostyles helvola* (L.) Ell.	Str hel
Matelea decipiens (Alex.) Woodson	Mat dec	*Quercus stellata* Wang.	Que ste	*Strophostyles leiosperma* (T. & G.) Piper	Str lei
Melica nitens Nutt.	Mel nit	*Quercus velutina* Lam.	Que vel	*Stylosanthes biflora* (L.) BSP.	Sty bif
Mirabilis albida (Walt.) Heimerl	Mir alb	*Rhus aromatica* Ait.	Rhu aro	*Symphoricarpos orbiculatus* Moench	Sym orb
Monarda fistulosa L.	Mon fis	*Rhus copallina* L.	Rhu cop	*Taenidia integerrima* (L.) Drude	Tae int
Muhlenbergia capillaris (Lam.) Trin.	Muh cap	*Rhus glabra* L.	Rhu gla	*Talinum calycinum* Engelm.	Tal cal
Muhlenbergia sobolifera (Muhl.) Trin.	Muh sob	*Rhus radicans* L.	Rhu rad	*Talinum parviflorum* Nutt.	Tal par
Myosotis virginica (L.) BSP.	Myo vir	*Robinia pseudo-acacia* L.	Rob pse	*Tephrosia virginiana* (L.) Pers.	Tep vir
Onosmodium subsetosum Mackenz. & Bush	Ono sub	*Rosa carolina* (L.)	Ros car	*Tradescantia ohiensis* Raf.	Tra ohi
Opuntia compressa (Salisb.) Macbr.	Opu com	*Rubus sp.* L.	Rub spp	*Tragia urticifolia* Michx.	Tra urt
Ostrya virginiana (Mill.) K. Koch	Ost vir	*Rudbeckia hirta* L.	Rud hir	*Tridens flavus* (L.) Hitchc.	Tri fla
Oxalis stricta L.	Oxa str	*Ruellia humilis* Nutt.	Rue hum	*Ulmus alata* Michx.	Ulm ala
Oxalis violacea L.	Oxa vio	*Ruellia pedunculata* Torr.	Rue ped	*Ulmus rubra* Muhl.	Ulm rub
Palafoxia callosa (Nutt.) T. & G.	Pal cal	*Ruellia strepens* L.	Rue str	*Vaccinium stamineum* L.	Vac sta
Panicum boscii Poir.	Pan bos	*Salvia azurea* Lam.	Sal azu	*Vaccinium vacillans* Torr.	Vac vac
Panicum clandestinum L.	Pan cla	*Salvia lyrata* L.	Sal lyr	*Verbena bracteata* Lag. & Rodr.	Ver bra
Panicum lanuginosum Ell.	Pan lan	*Salvia sp.* L.	Sal spp	*Verbena canadensis* (L.) Britt.	Ver can
Panicum latifolium L.	pan lat	*Sanicula gregaria* Bicknell	San gre	*Verbesina helianthoides* Michx.	Ver hel
Panicum laxiflorum Lam.	Pan lax	*Sassafras albidum* (Nutt.) Nees	Sas alb	*Verbesina virginica* L.	Ver vir
Panicum linearifolium Scribn.	Pan lin	*Satureja arkansana* (Nutt.) Briq.	Sat ark	*Vernonia baldwini* Torr.	Ver bal
Panicum oligosanthes Schult.	Pan oli	*Schrankia uncinata* Wild.	Sch unc	*Viburnum rufidulum* Raf.	Vib ruf
Panicum sp. L.	Pan spp	*Scleria oligantha* Michx.	Scl oli	*Viola triloba* Schwein.	Vio tri
Panicum virgatum L.	Pan vir	*Scutellaria ovata* Hill	Scu ova	*Vitis aestivalis* Michx.	Vit aes
Parietaria pensylvanica Muhl.	Par pen	*Sedum nuttallianum* Raf.	Sed nut		
Parinychia fastigata (Raf.) Fern.	Par fas	*Sedum pulchellum* Michx.	Sed pul		
Parthenocissus quinquefolia (L.) Planch.	Par qui	*Senecio obovatus* Muhl.	Sen obo		
Passiflora lutea L.	Pas lut	*Silene virginica* L.	Sil vir		
Pellaea atropurpurea (L.) Link	Pel atr	*Silphium laciniatum* L.	Sil lac		
Penstemon cobaea Nutt.	Pen cob	*Sisyrhinchium campestre* Bickn.	Sis cam		
Penstemon pallidus Small	Pen pal	*Smilax bona-nox* L.	Smi bon		