Journal of Vegetation Science 14: 25-34, 2003

The importance of environment vs. disturbance in the vegetation mosaic of Central Arizona

Huebner, Cynthia D.[1,2]* & Vankat, John L.[1]

*[1]Department of Botany, Miami University, Oxford, OH 45056, USA; [2]Current address: Northeastern Research Station, USDAFS, Morgantown, WV 26505, USA; *Author for correspondence; Fax +13042851505; E-mail chuebner@fs.fed.us*

Abstract. The vegetation of central Arizona is a mosaic of four vegetation types: chaparral, chaparral grassland, woodland, and woodland grassland. We analysed ten environmental variables, three disturbance variables, and five disturbance indicators to answer the question: What is the relative importance of environment and disturbance in explaining the vegetation pattern of our study area? We found that chaparral, chaparral grassland, and woodland are differentiated primarily by environmental factors and have high stability in the landscape. In contrast, woodland grassland is differentiated primarily by disturbance and is likely an early-successional stage of woodlands. Although other researchers have indicated that semi-arid vegetation is generally unstable, the vegetation of central Arizona is composed of two systems: those with a more stable landscape position determined primarily by environmental factors and those with a less stable landscape position determined primarily by disturbance factors.

Keywords: Canonical Correspondence Analysis; Chaparral; Conversion; Fire; Grassland; Grazing; Multi-Response Permutation Procedure; Stability; Succession; Woodland.

Nomenclature: Kearney & Peebles (1960) and McDougall (1973).

Abbreviations: A = Grazing allotment size and chance corrected within-agreement; C = Number of permitted domestic grazing animals; CCA = Canonical Correspondence Analysis; DCA = Detrended Correspondence Analysis; MRPP = Multi-Response Permutation Procedure; NMS = Non-Metric Multidimensional Scaling; S = Fire size class; T = Grazing period; W = Probability that fire burned a stand or a conversion event took place.

Introduction

Vegetation science has a long history of studies on the influence of environmental variables and disturbance on vegetation pattern (Pickett & White 1985). Many studies have sought to examine the relative importance of environment and disturbance, focusing on individual plant communities (O'Connor & Roux 1995; Miller & Halpern 1998; Leach & Givnish 1999; White et al. 2001) or a mosaic of plant communities across a landscape (Naveh 1967; Harmon et al. 1983; Brosofske et al. 2000; Woods 2000). We compare environment vs. disturbance in the semi-arid landscape of central Arizona, which is a mosaic of chaparral shrubland, woodland and grassland. The disturbances we studied are common to semi-arid vegetation throughout the world (e.g. Noy-Meir et al. 1989; Pickup & Stafford Smith 1993; Dodd 1994; Milton et al. 1994).

The environmental determinants of the vegetation of central Arizona are not well known. In general, chaparral is bordered by woodlands at higher elevations and grasslands at lower elevations (Lowe 1977; Carmichael et al. 1978), but these vegetation types commonly occur outside their typical elevation zones and on various soil types, slope aspects, and slope inclinations (Lowe 1977; Saunier & Wagle 1967; Bedell 1987). Water and nitrogen have been considered the most important limiting resources for each of these vegetation types (Woodmansee 1979; Klopatek & Klopatek 1987; Ellis & Kummerow 1989; Vankat 1989; Stephens & Whitford 1993; Weber et al. 1999) and may help explain the patchy mosaic. Water needs are 230-500 mm.yr^{-1} for grasslands, 300-500 mm.yr^{-1} for woodlands, and 330-630 mm.yr^{-1} for chaparral (Bolander 1981). Total soil nitrogen (10 cm depth) has been estimated to be 6600 kg.ha^{-1} in woodlands (Neary et al. 1996), 1313 kg.ha^{-1} in chaparral (Wienhold & Klemmedson 1992), and likely intermediate in grassland (Emmerich 1999).

The disturbance factors likely to have affected the current distribution of vegetation in central Arizona are livestock grazing, fire, and conversion (removal of woody plants to produce grassland). Livestock grazing became important in Arizona about 200 yr BP and coincided with increases of woodlands (Johnson 1962; O. Davis 1987) that may be ongoing (Bahre 1991). Little is known about the past role of fire in central Arizona; however, Leopold (1924) speculated that fire had maintained Arizona grasslands and restricted woodlands to areas of rocky soils and rough topography. Fire prevention and suppression were common in the 20th century until at least 1980, when prescribed burning became common (Wright & Bailey 1982; Bahre 1985; Miller 1999). Conversion occurred since at least 1960 (Aro 1971; Sheridan 1995) and usually involved changing woodland to grassland, with tree removal followed by repeated prescribed burning (Johnson 1999). Conversion of chaparral to grassland has been less common (Longstreth & Patten 1975; E. Davis 1987).

We address the question: What is the relative importance of environment and disturbance in explaining the vegetation pattern of our study area? If the types occur in similar environments, they may represent alternative stable states or different successional stages of a developmental sequence (Clements 1936; Holling 1973; Sutherland 1990). Regardless of their stability, they may be best explained by past disturbance (Connell & Sousa 1983; Johnson & Mayeux 1992; Sullivan 1996).

Material and Methods

Study area

We conducted our study within ca. 1500 km^2 of the Chino Valley and Verde Ranger Districts of Prescott National Forest in Yavapai County, Arizona (Huebner et al. 1999). This area is located in the Tonto Transition Section of the Colorado Plateau Semi-Desert Province in the Dry Domain (Bailey et al. 1994). The topography is variable, with slopes ranging from flat plains to steep hillsides and elevations ranging from approximately 1100 to 2500 m (Huebner 1996). Mean annual precipitation is 250-650 mm and is concentrated in two seasons, late-summer and winter (Cross et al. 1960; Bailey et al. 1994). The soil is generally low in organic matter, which along with relatively high volatilization rates results in low levels of nitrogen (Cross et al. 1960).

Central Arizona is characterized by four vegetation types: chaparral, woodland, chaparral grassland (grassland patch within a chaparral matrix), and woodland grassland (grassland patch within a woodland matrix). Chaparral is a broad-sclerophyll shrubland usually dominated by *Quercus turbinella* and often including *Rhus trilobata*, *Arctostaphylos pungens*, and *Cercocarpus montanus* (Huebner 1996). Woodlands in this region are more widespread (Spang 1987; Evans 1988) and tend to be dominated by small trees of *Juniperus osteosperma* or *J. monosperma*, with some *Pinus edulis*. Both grassland types are extensive, with chaparral grassland dominated by *Hilaria belangeri* and woodland grassland dominated by an exotic annual, *Bromus tectorum* (Huebner 1996).

Sampling design

We focused on grassland patches within chaparral and woodland vegetation. Therefore, we sampled 30 stands of chaparral paired with 30 stands of grassland, and 30 of woodland paired with 30 of grassland (total of 120 paired stands; Huebner 1996). These stands were selected from recent aerial photographs, followed by a site visit, such that (1) the paired stands were adjacent to one another and (2) each stand was ≥ 0.4 ha (although variable in shape). We sampled nearly all stands that met these two criteria.

Within each stand, we determined the cover of woody species using the line intercept method (Bonham 1989) along a 50 m line transect placed parallel to the topographic contour and at least 20 m from stand edges. One end of the transect was permanently marked with a 0.5-m metal stake. We visually estimated the cover of each herbaceous and suffrutescent species (to ca. 5% accuracy) in 10 quadrats (0.5 m $\times$ 0.5 m) randomly located along each transect.

Environmental variables

We recorded slope aspect, inclination, and elevation at the midpoint of each transect (values were generally uniform along transects). The north-south coordinates (herein referred to as latitude) were determined in meters using the Universal Transverse Mercator projection. Angular data for aspect (°) were linearized according to the following equation: SIN(°–135) + 1 (modified from Huebner et al. 1995), where larger values represent drier slopes (west and south-facing) and smaller values represent more mesic slopes (east and north-facing).

We collected a soil sample of 3 cm diameter and 10 cm depth from the interspace between woody plants that was nearest each quadrat (sampling in interspaces reduces sample variability caused by removal of nutrients by woody plants; Klopatek & Klopatek 1987). All 10 samples from each stand were combined, mixed, passed through a 2 mm mesh sieve, and dried immediately in a forced-air oven at 40 °C overnight.

Subsamples of each soil sample were passed through a 0.5-mm sieve. Those used for nitrogen and carbon analyses were kept frozen (to reduce nitrification and denitrification) until immediately before analysis. Total nitrogen (organic and inorganic) and carbon were determined using a LECO CNS-2000 Carbon, Nitrogen and

Sulfur Analyzer, which measures percent nitrogen and carbon (converted to N_2 and CO_2, respectively) for a given mass of soil via thermal conductivity of the gases. Analyses were conducted by IAS Laboratories of Phoenix, AZ. We determined soil texture by the hydrometer technique (Bouyoucos 1927) and estimated soil water-holding capacity as mass loss from a sample weighed when saturated and again when dried at 110 °C for 24 h (Stock & Lewis 1986). Although soil structure is important to water-holding capacity, we used sieved soils to avoid variation in soil structure introduced by our sampling and transporting of soils.

Disturbance factors

We considered livestock grazing between 1930 (when records were first kept for our entire study area) and 1993 using records of the two Ranger Districts. Grazing records included the number of livestock allowed for each of the 16 grazing allotments (sectors). The number of permitted livestock was likely slightly higher than the actual number, but actual numbers were available for most years after 1950. In addition, the grazing records noted the length of the grazing period and the area of each grazing allotment. Records on type of livestock and season of grazing were inconsistent, and no records were kept on native grazing animals such as deer, elk, and other herbivores.

For each grazing allotment, we calculated an annual grazing index in animal months per ha using the following formula: $(C \times T)/A$, where C is number of permitted domestic grazing animals, T is the grazing period (months), and A is the size (ha) of the grazing allotment. The annual grazing index was averaged for 1930-1993. Grazing allotments were much larger than a single stand, so we were forced to treat all stands within a given allotment as having the same grazing pressure. Therefore, differences in grazing between paired stands (i.e., a chaparral stand and its adjacent grassland stand) usually could not be estimated.

We obtained fire records from both Ranger Districts and the Prescott Fire Center (at the Henry Y.H. Kim Aviation Facility). Consistent record keeping began in 1946. Fire locations were estimated from fire maps for 1946-1965, from written descriptions for 1965 and 1972-1993, and from fire names (based on geographic features) for 1966-1971. Fire size was recorded by class: 1 if < 0.1 ha, 2 if 0.1-4.0 ha, 3 if 4.1-40 ha, and 4 if 41-100 ha (no larger fires were recorded for our stands). Records also separated wild fires (lightning- and human-caused) from prescribed fires. Ratings of fire intensity were available after 1980; however, rating scales were inconsistent.

For each stand, we calculated a unitless annual fire index that reflected fire size and the probability of the stand being within the fire boundaries: $S(S \times W)$, where S is the size class of the fire and W approximates the probability that the fire burned the stand. We included fire size in our index because size is often correlated with fire intensity in our study area. Our estimates of W were 0.3 for fires from 1966-1971 when fire locations had to be estimated from fire names, 0.5 for fires whose centers were recorded within 1.6 km of the stand, and 1.0 for fires mapped as having covered the stand. We averaged the annual fire index for 1946-1993.

We examined conversion using records from both Ranger Districts. Record keeping began in 1946, and the records included only the date and location of conversions; size was recorded inconsistently. For each stand, we calculated an annual conversion index (rate) by summing the conversion attempts (usually 0 or 1). We averaged the annual conversion index for 1946-1993, but included in this calculation additional, undated, unrecorded conversion events. Evidence for these additional conversion events was our personal observation of stumps or slash in stands with no written record of conversions. Because the presence of stumps and slash could reflect only partial clearing of woody vegetation and not complete conversion and because some of these conversions may have occurred before 1946, we downweighted these unrecorded conversions by estimating the probability of the stand being subject to complete conversion: W. Our estimates of W were 0.3 if the stand had tree stumps but lacked slash and 0.5 if the stand had stumps and slash.

Disturbance indicators

Various limitations in the records of grazing, fire, and conversion restricted assessment of disturbance. Therefore, we also computed four disturbance indicators: vegetation stability, number of nearby vegetation types present, number of patches present, and fractal dimension.

For vegetation stability, we assumed an inverse relationship with disturbance because the half-century period (for which aerial photographs of our landscape are available) is likely too short to include significant climatic change and resultant vegetation shifts. To calculate vegetation stability, we constructed transition matrices for 1940-1989 based on aerial photograph overlays (cf. Huebner et al. 1999) for circular 1 km^2 areas surrounding the center point between each pair of stands. We defined stability of the dominant vegetation (hereafter 'dominant stability') as the probability of the vegetation of a stand remaining unchanged and stability of all vegetation (hereafter called 'overall stability') as the mean of the stabilities of all vegetation types within the 1 km^2 area. Therefore, paired stands can be differentiated from each other by dominant stability, but not by overall stability.

The relationship of number of vegetation types, number of patches, and fractal dimension to disturbance is likely landscape-specific (Turner 1989; Sughara & May 1990). For central Arizona, we assumed an inverse relationship between these three variables and disturbance because aerial photographs of our region indicated that areas known to have been disturbed had fewer patches and more linear vegetation boundaries than areas with less disturbance (Huebner 1996; Huebner et al. 1999).

Using a 1 km^2 circular area centered on each pair of stands, we summed the number of vegetation types, summed the number of patches, and calculated fractal dimension by regressing summed patch area against summed patch perimeter (measured with IDRISI 4, a raster-base GIS package) and multiplying by 2 (O'Neill et al. 1988). For each of these three disturbance indicators, we averaged values for the 1940-1989 time period. Unfortunately, these indicators do not differentiate between paired stands.

Data analysis

We expressed species composition using absolute cover values and calculated species richness as the number of species present and diversity as an inverted Simpson's index (the inversion allows expression of diversity in terms of species equivalents; Peet 1974). We evaluated differences in species composition among vegetation types using multi-response permutation procedure (MRPP; Biondini et al. 1985; Zimmerman et al. 1985; MJM Software PC-ORD v.4; Anon. 1999b).

We compared environmental and disturbance variables among vegetation types using two complementary analyses, Bonferroni t-tests (Anon. 1990; Anon. 1999a) and MRPP. We compared the importance of environment vs. disturbance in determining vegetation types using canonical correspondence analysis coupled with correlation analysis (CCA; ter Braak 1988; Anon. 1999b; Bonferroni t-tests were used to compare mean ordination scores of vegetation types). Other ordination methods, including Detrended Correspondence Analysis (DCA), indirect CCA (final scores derived from species scores instead of a linear combination of environmental variables), and Non-metric Multi-dimensional Scaling (NMS), produced similar results, so only CCA is presented here. We chose CCA because it gave easily repeatable results, did not appear to be affected by noisy data, and included a combined effect of all variables on the plot and axes ordination scores (Minchin 1987; Økland 1996; McCune 1997).

Results

A total of 169 taxa were sampled in the 120 stands (Huebner 1996). A multi-response permutation procedure (MRPP), with the plots grouped by vegetation type, documented that the four vegetation types were significantly different in species composition (p = 0.000; the chance corrected within-agreement (A) is 0.356).

Among the four vegetation types, woodland had the highest mean richness and diversity but the lowest mean plant cover (Table 1). Chaparral had the lowest mean richness and diversity and the highest total cover. The two types of grasslands were generally intermediate (Table 1).

Bonferroni t-test analysis of the means of the environmental variables showed that the four vegetation types had similar slope aspect, elevation, % clay, water holding capacity, nitrogen, and carbon (Table 2). In contrast, chaparral and chaparral grassland were generally associated with steeper slopes, southern latitudes, higher % sand, and lower % silt than woodland and woodland grassland; however, there were no statistically significant differences between grasslands and their associated woody vegetation type.

Analysis of the means of the disturbance variables showed that the four types of vegetation had similar grazing and fire indices (Table 2). The woodland grassland,

Table 1. A. Species with ≥ 2% mean cover in chaparral, chaparral grassland, woodland, and woodland grassland. Total cover averaged 76 %, 66 %, 57 % and 63 %, respectively. Dominant species in bold. **B.** Diversity and cover parameters.

A. Species	Chaparral	Chaparral Grassland	Woodland	Woodland Grassland
Quercus turbinella	35.6			
Gutierrezia sarothrae	5.2	6.8	2.4	5.2
Rhus trilobata	4.5			
Bouteloua curtipendula	3.8	4.0	2.7	2.5
Hilaria belangeri	3.2	11.1		
Eriogonum wrightii	2.6	7.9		
Bouteloua gracilis	2.5	3.3	2.6	5.5
Mimosa biuncifera	2.2			
Arctostaphylos pungens	2.2			
Ceanothus greggii	2.2			
Juniperus osteosperma			17.5	
Cordylanthus laxiflorus			2.3	
Aristida spec.			2.2	2.2
Bromus tectorum[1]				10.6
Hilaria mutica		3.7		3.9
Viguiera annua				5.9
Bromus rubens[1]		5.2		
Muhlenbergia repens				2.9
Plantago purshii		3.3		
Lotus humistratus		2.1		
Festuca octoflora				2.0
B.				
Mean richness[2]	16.1	14.2	14.8	15.8
Diversity[3]	5.4	3.9	4.9	5.4
Total cover (%)	76	66	57	63

[1]Exotic annual; [2]Number of species; [3]Species equivalents

Table 2. Means for environmental and disturbance variables. Different letters indicate statistically significant differences among vegetation types by Bonferroni t-tests (p-value < 0.05). Slope aspect was calculated using Sin (° – 135) +1.

	Chaparral	Chaparral Grassland	Woodland	Woodland Grassland
Environmental variables:				
Slope aspect	0.84 A	0.97 A	0.84 A	0.53 A
Slope inclination (%)	17.7 A	12.5 AB	9.0 BC	2.9 C
Elevation (m)	1451 A	1438 A	1432 A	1409 A
Latitude (m)	3827 B	3827 B	3854 A	3857 A
% Sand	52 A	44 AB	41 B	37 B
% Silt	30 BC	25 C	37 A	36 AB
% Clay	23 A	28 A	23 A	24 A
Water Holding Capacity (g)	31 A	34 A	34 A	34 A
% Total Nitrogen	0.145 A	0.138 A	0.127 A	0.117 A
% Carbon	1.87 A	1.57 A	2.38 A	2.19 A
Disturbance variables:				
Grazing index	0.17 A	0.17 A	0.17 A	0.16 A
Fire index	0.023 A	0.028 A	0.026 A	0.035 A
Conversion index	0.0002 B	0.0007 B	0.0022 B	0.018 A
Dominant stability (%)	0.82 A	0.77 AB	0.59 B	0.59 B
Overall stability (%)	0.62 A	0.68 A	0.46 B	0.49 B
Fractal dimension	1.067 A	1.056 A	1.049 A	1.035 A
Number of vegetation types	4.5 A	4.3 A	4.2 A	3.9 A
Number of patches	18 A	17 A	13 A	12 A

however, had higher rates of conversion than the other vegetation types.

Analysis of the means of disturbance indicators showed that the four types of vegetation had similar fractal dimensions, number of nearby vegetation types, and number of patches (Table 2). In contrast, chaparral had significantly higher stability (dominant and overall) than both woodland and woodland grassland, but had similar stability as its associated grassland. Chaparral grassland had higher overall stability than both woodland and woodland grassland.

Table 3. Multi-Response Permutation Procedure (MRPP) organized by vegetation type and variable. Vegetation types with different letters are significantly different from each other ($p < 0.01$). Because the T (observed-expected/standard deviation of expected) statistic and A (chance corrected within group agreement) values differ for each vegetation type paired comparison, the presentation of these data in a single, simple table is impossible. Only variables showing significant differences in one or more vegetation types are listed.

	Chaparral	Chaparral Grassland	Woodland	Woodland Grassland
Environmental variables				
Slope inclination	A	A	B	B
Elevation	A	A	B	B
Latitude	B	B	A	A
% Sand	A	B	B	B
% Silt	B	B	A	A
% Carbon	C	C	AB	AC
Disturbance variables				
Conversion index	C	C	B	A
Dominant stability	A	B	C	C
Overall stability	A	A	B	B
Fractal dimension	A	A	B	B

An MRPP indicated that, in comparison to woodland and woodland grassland, chaparral and chaparral grassland had significantly steeper slopes, higher elevation, lower % silt, lower latitude, lower conversion, higher dominant and overall stability, and higher fractal dimension ($p \leq 0.01$; Table 3). In addition, chaparral had higher percentages and and higher dominant stability than chaparral grassland, woodland grassland had higher conversion than woodland, and woodland had higher % carbon than either chaparral or chaparral grassland.

A CCA of our 120 stands using environmental variables but no disturbance variables resulted in a statistically significant separation along axis 1 of chaparral and chaparral grassland stands (right side of the ordination figure) from woodland and woodland grassland stands (left side), but did not separate either woody vegetation from its associated grassland along any of axes 1-3 (Fig. 1, Table 4). Axis 1 is most strongly correlated with latitude ($r = -0.883$), % silt (–0.659), and slope inclination (0.620; Table 5). Axis 2, which did not separate any of the vegetation types and therefore is related more to differences within vegetation types rather than among types, is most strongly correlated with % clay (0.782), water holding capacity (0.764), % sand (– 0.631) and % carbon (– 0.594).

A second CCA using disturbance variables but no environmental variables also resulted in a statistically significant separation of chaparral and chaparral grassland stands from woodland and woodland grassland stands along the first axis (Fig. 2, Table 4). In addition, this axis also separated woodlands from woodland grasslands. Axis 1 is most strongly correlated with overall stability (– 0.776), conversion (0.760), and dominant stability (– 0.631; Table 5). Axis 2, which also differentiates some of the vegetation types, is most strongly correlated with dominant stability (0.373) and conversion (0.566).

A third CCA using environmental and disturbance variables also resulted in a statistically significant sepa-

Table 4. Means axis scores of the vegetation types. Different letters indicate statistically significant differences among vegetation types as determined by Bonferroni t-tests ($p < 0.05$). Only axes showing significant differences between one or more vegetation types are shown; other axes are not significant.

Ordination	Chaparral	Chaparral Grassland	Woodland	Woodland Grassland
Environment				
Axis 1	0.5897A	0.4789A	– 0.5716B	– 0.5173B
Disturbance				
Axis 1	– 0.3804C	– 0.3462C	0.1392B	0.6190A
Axis 2	0.0461BA	– 0.0027BC	– 0.2616C	0.3120A
Environment and disturbance				
Axis 1	0.5984A	0.4797A	– 0.5694B	– 0.5197B
Axis 3	– 0.02533B	– 0.03385B	– 0.37008C	0.52056A

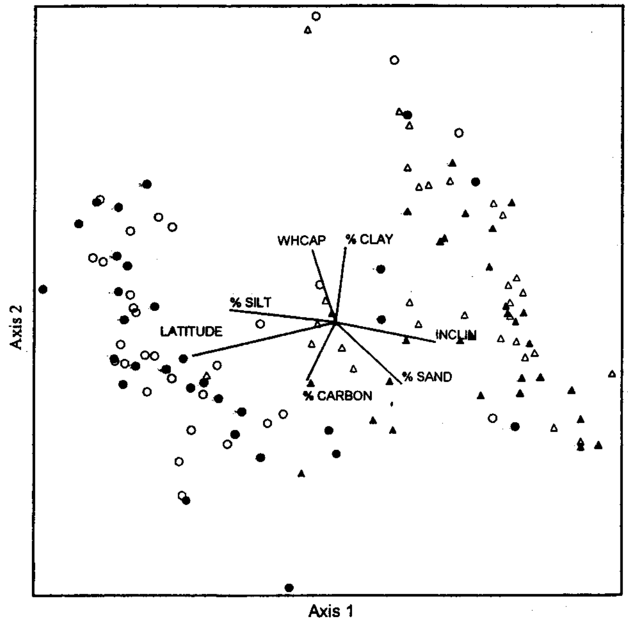

Fig. 1. CCA ordination on environmental variables only. Eigenvalues for axes 1-3 are 0.492, 0.297 and 0.171. Total variance in the species data is 10.4 and 9.2 % of this is explained by the environmental variables. INCLIN = slope inclination; WHCAP = water holding capacity. Woodland = ●; Woodland Grassland = ○; Chaparral = ▲; Chaparral Grassland = △.

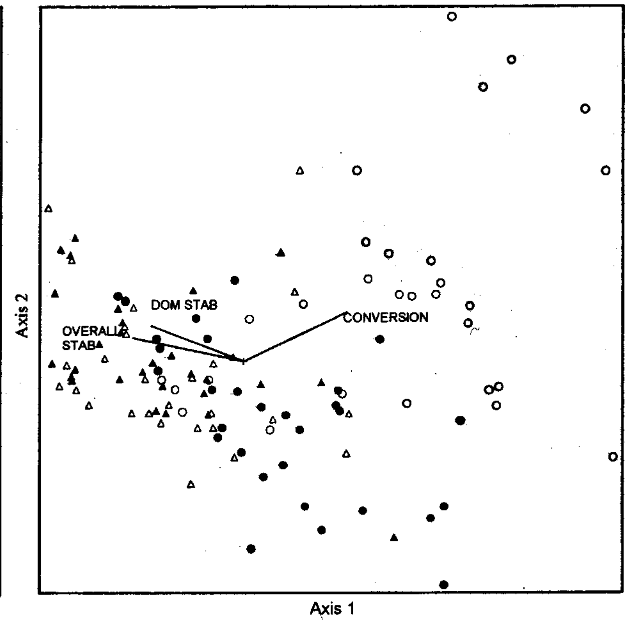

Fig. 2. CCA using only disturbance variables. Eigenvalues for axes 1-3 are 0.343, 0.185 and 0.164, respectively. Total variance is 10.4 and 6.6% of this is explained by the disturbance variables. DOM STAB = dominant stability; OVERALL STAB = overall stability. Woodland = ●; Woodland Grassland = ○; Chaparral = ▲; Chaparral Grassland = △.

ration of chaparral and chaparral grassland stands from woodland and woodland grassland stands along the first axis (Fig. 3, Table 4). Axis 1 is most strongly correlated with latitude (– 0.871), % silt (– 0.649), overall stability (0.609), and slope inclination (0.604; Table 5).

Axis 2 did not separate any of the vegetation types (Fig. 3, Table 4) and therefore is related more to differences within rather than among vegetation types. It is most strongly correlated with environmental variables: % clay (0.779), water holding capacity (0.755), % sand (– 0.604), and % carbon (– 0.578; Table 5). Axis 3 produced a statistically significant separation of woodland from woodland grassland (Fig. 4; Table 4) and is strongly correlated only with conversion (0.728; Table 5).

Discussion

Most analyses showed that environmental variables did not separate either chaparral or woodland from its associated grassland; however, it is possible that other, unmeasured environmental variables could provide this separation. For example, chaparral shrubs such as *Quercus turbinella* have deep roots that can penetrate rock fractures to ground water (Saunier & Wagle 1967; E. Davis & Pase 1977; E. Davis 1989), a potentially critical factor because periodic droughts characterize this region (Vankat 1989). Therefore, degree of bedrock fracturing may be important in separating chaparral from chaparral grassland. Also, although nitrogen is likely the most important limiting nutrient in Arizona, phosphorus and calcium, which were not measured, have been noted as important for some species and communities (Ellis & Kummerow 1989; Kramer 1999; Quideau 1999). However, if no important variables have been neglected, chaparral and chaparral grasslands as well as woodland and woodland grasslands may represent multiple stable states, depending on the role of disturbance.

Grazing and fire indices did not account for vegetation differences; however, our characterization of disturbance, especially grazing and fire, was limited by the fact that the records were incomplete and imprecise. For example, data on seasonal variation in grazing were lacking, yet this variation could be significant, especially for grassland vegetation (Valone 1999). Also, the scale of records was generally too broad to explain differences in vegetation of adjacent paired stands. For example, the grazing records are for areas several times larger than the areas of paired stands. Therefore, if grazers were concentrated in grassland patches, this preference would not have been detected with our estimate of grazing.

Despite statistical similarity in our fire index, there is evidence that fire, at least when restricted to one vegetation type in paired stands, is more frequent in

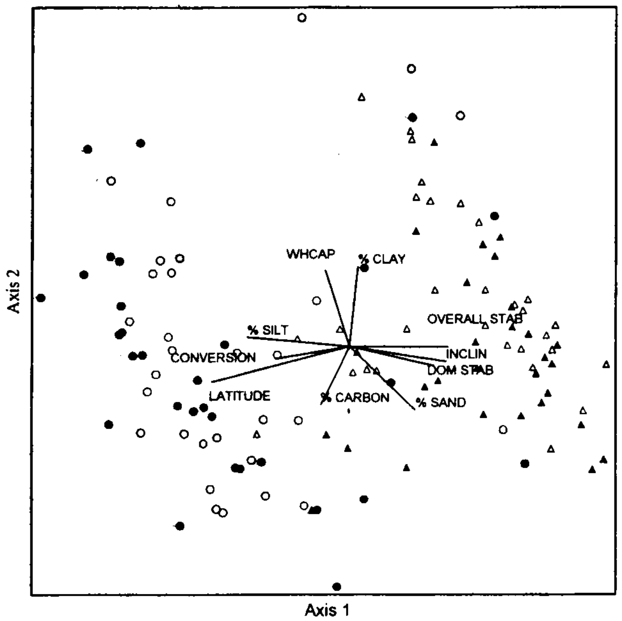

Fig. 3. CCA using all variables (axes 1 and 2). Eigenvalues for axes 1-3 are 0.500, 0.315 and 0.243. Total variance is 10.4 and 10.2% of this is explained by all variables. WHCAP = water holding capacity; INCLIN. = slope inclination; DOM STAB = dominant stability; OVERALL STAB = overall stability. Woodland = ●; Woodland Grassland = ○; Chaparral = ▲; Chaparral Grassland = △.

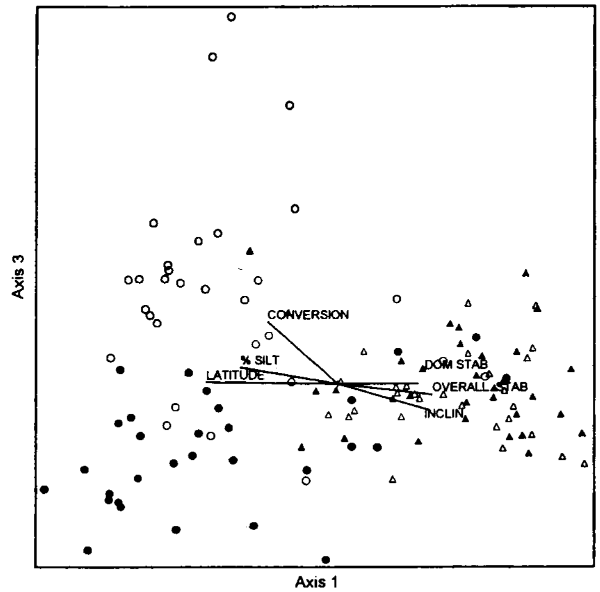

Fig. 4. CCA using all variables (axis 1 and 3). See Fig. 3 caption.

grassland, with 11 in woodland grassland, eight in chaparral grassland, six in woodland, and one in chaparral. The reason Arizona chaparral is so stable and does not appear to require fire for self perpetuation, unlike some California chaparral stands (Vogle 1981; Hilbert & Larigauderie 1990), may be that Arizona chaparral is typically less dense than California chaparral (Bolander 1981).

Our finding that woodland grassland had a higher conversion index than the other vegetation types was not surprising. Conversion has been used primarily to attempt to form grassland from woodland (cf. Arnold 1964).

The two stability measures and fractal dimension may be more sensitive indicators of disturbance in our study area than number of vegetation types and patches. Also, our finding of differences in disturbance indicator variables where there were no differences in grazing,

Table 5. Pearson correlations (r) of environmental and disturbance variables with ordination axes for CCAs with environmental, disturbance, and environmental+disturbance variables. The sign in front of each r-value indicates direction of correlation. In CCA, p-values are not provided for each variable, but a Monte Carlo test was used to determine the significance of each axis. The correlations for the Environmental and Environmental + Disturbance CCA are significant at the 0.01 level for all three axes. However, the correlations for the Disturbance CCA had p-values of 0.01 for axis 1, 0.06 for axis 2 and 0.13 for axis 3. Only variables with r-values of 0.5 or greater (i.e. the most important variables) for at least one axis of any of the three CCAs are shown.

	Environmental or Disturbance CCA			Environmental+Disturbance CCA		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Environmental variables						
Slope inclination	0.620	-0.195	0.187	0.604	-0.129	-0.326
Latitude	-0.883	-0.357	0.239	-0.871	-0.359	0.063
% Sand	0.401	-0.631	-0.318	0.404	-0.604	-0.037
% Silt	-0.659	0.071	0.020	-0.649	0.035	0.207
% Clay	0.076	0.782	0.409	0.062	0.779	-0.143
Water holding capacity	-0.117	0.764	0.278	-0.132	0.755	-0.176
% Carbon	-0.207	-0.594	-0.542	-0.203	-0.578	-0.132
Disturbance variables						
Fire index	0.015	0.266	0.643	0.000	0.232	0.145
Conversion index	0.760	0.566	-0.102	-0.487	-0.174	0.728
Dominant stability	-0.631	0.373	-0.340	0.503	-0.173	0.015
Overall stability	-0.776	0.248	0.023	0.609	0.001	-0.133

fire, and conversion reaffirms the shortcomings in the disturbance records or indicates that other disturbances may be important. Fine-scale disturbances are important in some arid and semi-arid areas, but were not examined in this study. For example, small mammals and ants affect the distribution of species by moving seeds, promoting seed germination with soil disturbance, and enhancing plant growth with increased nutrients around nests (Huntly 1991; MacMahon 1997). Where these plant species provide favorable forage for the animals, positive feedback among populations may occur (Wiens 1985), thereby reinforcing vegetation differences.

In general, environment is more important than disturbance in the central Arizona landscape (both among and within vegetation types). For example, environment separates chaparral from the other vegetation types, with chaparral occurring on lower latitudes, coarser soils, and steeper slopes than woodland and woodland grassland and on coarser soils than chaparral grassland. The high stability of chaparral also indicates that disturbance is relatively unimportant. Chaparral's stability results from the resprouting of shrubs such as *Quercus turbinella* and *Arctostaphylos pungens*, something recognized by land managers who only infrequently attempt to convert chaparral to grassland (Longstreth & Patten 1975; E. Davis 1987).

Only in the case of woodland grassland is disturbance more important than environment. Here conversion is the key factor and instability also evidences the importance of disturbance. There are many examples of disturbance-dependent grasslands, some of which represent successional stages of associated woody vegetation (cf. Weaver & Fitzpatrick 1934; Cusick 1981; Bock & Bock 1992). Formerly, naturally-occurring woodland grassland in central Arizona was likely maintained by fires which curtailed tree invasion. However, since the beginnings of overgrazing in the late 1800s (Cable 1975) and fire suppression in the 20th century, the rate of tree invasion has increased (Bahre 1991) and is countered primarily by conversion. In contrast, chaparral grassland does not appear to be a successional stage of chaparral, because where invasion occurs it is not by chaparral shrubs but rather by *Juniperus osteosperma*, *J. monosperma*, *Prosopis juliflora* and *Acacia greggii* (Huebner 1996; Huebner et al. 1999).

Our finding that most vegetation types are defined primarily by environment and are stable conflicts with the assumption that semi-arid systems are generally unstable (Johnson & Mayeux 1992; Sullivan 1996; Walker & Wilson 2002). However, we did not evaluate stability in the sense of recovery of species composition to equilibrium after disturbance (Holling 1973; DeAngelis & Waterhouse 1987). Instead we examined stability in the sense of persistence of a vegetation type in its geographic position in the landscape. At least in this sense, we conclude that the semi-arid vegetation of central Arizona is composed of two systems: those whose landscape position is more stable and determined primarily by environmental variables and those whose landscape position is less stable and determined primarily by disturbance.

Acknowledgements. This research would have been impossible without support and funding from the staff of the Verde and Chino Ranger Districts of Prescott National Forest and funding from Miami University's Academic Challenge and William Sherman Turrell Herbarium Fund grant programs. We particularly thank Doug MacPhee, District Ranger of the Verde District.

References

Anon. 1990. *SAS/STAT User's Guide*, Version 6, 4th ed. SAS Institute Inc., Cary, NC.

Anon. 1999a. SYSTAT v. 9. SPSS Science Marketing Department. Chicago, IL.

Anon. 1999b. *PC-ORD: Multivariate analysis of ecological data*, v. 4. MjM Software Design, Gleneden Beach, OR.

Arnold, J.E. 1964. *The Pinyon-Juniper type of Arizona: Effects of grazing, fire, and tree control.* USDA For. Serv. Production Research Report No. 84, Washington, DC.

Aro, R.S. 1971. Evaluation of pinyon-juniper conversion to grassland. *J. Range Manage.* 24: 188-197.

Bahre, C.J. 1985. Wildfire in southeastern Arizona between 1859 and 1890. *Desert Plants* 7: 190-194.

Bahre, C.J. 1991. *Legacy of change: Historic human impact on vegetation in the Arizona borderlands.* University of Arizona Press, Tucson, AZ.

Bailey, R.G., Avers, P.E., King, T. & McNab, W.H. 1994. *Ecoregions and subregions of the United States* (map). USDA For. Serv., Washington, DC.

Bedell, T.E. 1987. Range management concerns on juniper woodlands. In: Everett, R.L. (ed.) *Proceedings Pinyon-Juniper Conference*, pp. 436-440. USDA For. Serv. Gen. Tech. Rep. INT-215, Ft. Collins, CO.

Biondini, M.E., Bonham, C.D. & Redente, E.F. 1985. Secondary successional patterns in a sagebrush (*Artemisia tridentate*) community as they relate to soil disturbance and soil biological activity. *Vegetatio* 60: 25-36.

Bock, J.H. & Bock, C.E. 1992. Vegetation responses to wildfire in native versus exotic Arizona grassland. *J. Veg. Sci.* 3: 439-446.

Bolander, D.H. 1981. Chaparral in Arizona. In: Conrad, C.E. & Oechel, W.C. (eds.) *Proceedings of the Symposium on Dynamics and Management of Mediterranean-Type Ecosystems*, pp. 60-63. USDA For. Serv. Gen. Tech. Rep. PSW-58, San Diego, CA.

Bonham, C.D. 1989. *Measurements for terrestrial vegetation.* Wiley, New York, NY.

Bouyoucos, G.J. 1927. The hydrometer as a method for the mechanical analysis of soils. *Soil Sci* 23: 343-353.

Brosofske, K.D., Chen, J. & Crow, T.R. 2001. Understory vegetation and site factors: implications for a managed Wisconsin landscape. *For. Ecol. Manage.* 146: 75-87.

Cable, D.R. 1975. *Range management in the chaparral type and its ecological basis: The status of our knowledge.* USDA For. Serv. Gen. Tech. Rep. RM-155, Ft. Collins, CO.

Carmichael, R.S., Knipe, O.D., Pase, C.P. & Brady, W.W. 1978. *Arizona chaparral: Plant associations and ecology.* USDA For. Serv. Gen. Tech. Rep. RM-202, Ft. Collins, CO.

Clements, F.E. 1936. Nature and structure of climax. *J. Ecol.* 24: 252-284.

Connell, J.H. & Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121: 789-824.

Cross, J.L., Shaw, E.H. & Scheifele, K. (eds.) 1960. *Arizona: Its people and resources.* The University of Arizona Press, Tucson, AZ.

Cusick, A.W. 1981. The prairies of Adams County, Ohio: 50 years after the studies of Lucy Braun. In: Stuckey, R.L. & Reese, K.J. (eds.) *The prairie peninsula - in the 'shadow' of Transeau*: Proc. North American Prairie Conference, pp. 56-60. Ohio Biol. Surv. Biol. Notes 15.

Davis, E.A. 1987. Chaparral conversion to increase streamflow in Arizona: Sequential treatments extend duration of nitrate loss to stream water. *Forest Sci.* 33: 89-103.

Davis, E.A. 1989. Patterns in mixed chaparral stands differential water status and seedling survival during summer drought. In: Keeley, S.C. (ed) *The California chaparral: Paradigms reexamined,* pp. 97-105. No. 34 Science Series, Natural History Museum of L.A. County, Los Angeles, CA.

Davis, E.A. & Pase, C.P. 1977. Root system of shrub live oak: implications for water yield in Arizona chaparral. *J. Soil Water Conserv.* July-August 1977: 174-179.

Davis, O.K. 1987. Palynological evidence for historic juniper invasion in central Arizona: A late-Quaternary perspective. In: Everett, R.L. (ed). *Proc. Pinyon-Juniper Conference*, pp. 12-124. USDA For. Serv. Gen.Tech. Rep. INT-215, Ft. Collins, CO.

DeAngelis, D.L. & Waterhouse, J.C. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* 57: 1-21.

Dodd, J.L. 1994. Desertification and degradation in Sub-Saharan Africa: the role of livestock. *BioScience* 44: 28-34.

Ellis, B.A. & Kummerow, J. 1989. The importance of N_2 fixation in *Ceanothus* seedlings in early postfire chaparral. In: Keeley, S.C. (ed) *The California chaparral: Paradigms reexamined,* pp. 115-117. No. 34 Science Series, Natural History Museum of L.A. County, Los Angeles, CA.

Emmerich, W.E. 1999. Nutrient dynamics of rangeland burns in Southeastern Arizona. *J. Range Manage.* 52: 606-614.

Evans, R.A. 1988. *Management of pinyon-juniper woodlands.* USDA For. Serv. Gen. Tech. Rep. INT-249, Ft. Collins, CO.

Harmon, M.E., Bratton, S.P. & White, P.S. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetatio* 55: 129-139.

Hilbert, D.W. & Larigauderie, A. 1990. The concept of stand senescence in chaparral and other Mediterranean type ecosystems. *Acta Oecol.* 11: 181-190.

Holling, S. 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol.Syst.* 4: 1-23.

Huebner, C.D., Randolph, J.C. & Parker, G.R. 1995. Environmental factors affecting understory diversity in second-growth deciduous forests. *Am. Midl. Nat.* 134: 155-165.

Huebner, C.D. 1996. *Effects of disturbance and environment on the chaparral-woodland-grassland landscape mosaic of Central Arizona.* Dissertation, Miami University, Oxford, OH.

Huebner, C.D., Vankat, J.L. & Renwick, W.H. 1999. Change in the vegetation mosaic of central Arizona USA between 1940 and 1989. *Plant Ecol.* 144: 83-91.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annu. Rev. Ecol. Syst.* 22: 477-503.

Johnson, H.B. & Mayeux, H.S. 1992. Viewpoint: A view on species additions and deletions and the balance of nature. *J. Range Manage.* 45: 322-333.

Johnson, P. 1999. Economics of redberry juniper control in the Texas Rolling Plains. *J. Range Manage.* 52: 569-574.

Johnson, T.N. 1962. One-seed juniper invasion of northern Arizona grasslands. *Ecol. Monogr.* 32: 187-207.

Kearney, T.H. & Peebles, R.H. 1960. *Arizona Flora.* University of California Press, Berkeley, CA.

Klopatek, C.C. & Klopatek, J.M. 1987. Mycorrhizae, microbes and nutrient cycling processes in pinyon-juniper systems. In: Everett, R.L. (ed). *Proc. Pinyon-Juniper Conference*, pp. 360-364. USDA For. Serv. Gen. Tech. Rep. INT-215, Ft. Collins, Co.

Kramer, S. 1999. Phosphorus pools in tree and intercanopy microsites of a juniper-grass ecosystem. *Soil Sci. Soc. Am. J.* 63: 1901-1905.

Leach, M.K. & Givnish, T.J. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecol. Monogr.* 69: 353-374.

Leopold, A. 1924. Grass, brush, timber, and fire in southern Arizona. *J. Forest.* 22: 1-10.

Longstreth, D.J. & Patten, D.T. 1975. Conversion of chaparral to grass in central Arizona: Effects on selected ions in watershed runoff. *Am. Midl. Nat.* 93: 25-34.

Lowe, C.H. 1977. *Arizona's natural environment.* The University of Arizona Press, Tucson, AZ.

MacMahon, J.A. 1997. Ecological restoration. In: Meffe, G.K. & Carroll, C.R. (eds.) *Principles of conservation biology,* 2nd ed., pp. 479-511. Sinauer, Sunderland, MA.

McCune, B. 1997. Influence of noisy environmental data on canonical correspondence analysis. *Ecology* 78: 2617-2623.

McDougall, W.B. 1973. *Seed plants of Northern Arizona.* The Museum of Northern Arizona, Flagstaff, AZ.

Miller, E.A. & Halpern, C.B. 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *J. Veg. Sci.* 9: 265-282.

Miller, R.F. 1999. Fire history and western juniper encroachment in sagebrush steppe. *J. Range Manage.* 52: 550-559.

Milton, S.J., Dean, W.R.J., du Plessis, M.A. & Siegfried, W.R. 1994. A conceptual model of arid rangeland degradation: the escalating cost of declining productivity. *BioScience* 44: 70-76.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 71: 145-156.

Naveh, Z. 1967. Mediterranean ecosystems and vegetation types in California and Israel. *Ecology* 48: 445-459.

Neary, D.G., Overby, S.A., Gottfried, G.J. & Perry, H.M. 1996.

Nutrients in fire-dominated ecoystems. In: Ffolliott, P.F., DeBano, L.F., Baker Jr., M.B., Gottfried, G.J., Solis-Garza, G., Edminster, C.B., Neary, D.G., Allen, L.S. & Hamre, R.H. (eds.) *Effects of fire on Madrean Province ecosystems*, pp. 207-117. USDA For. Serv. Gen. Tech. Rep. RM-289, Ft. Collins, CO.

Noy-Meir, I., Gutman, M. & Kaplan, Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. *J. Ecol.* 77: 290-310.

O'Connor, T.G. & Roux, P.W. 1995. Vegetation changes (1949-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *J. Appl. Ecol.* 32: 612-626.

Økland, R.H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *J. Veg. Sci.* 7: 289-292.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H. & Graham, R.L. 1988. Indices of landscape pattern. *Landscape Ecol.* 1: 153-162.

Peet, R.K. 1974. The measurement of species diversity. *Annu. Rev. Ecol. Syst.* 5: 285-307.

Pickett, S.T.A. & White, P.S. (eds) 1985. *The ecology of natural disturbance and patch dynamics.* Academic Press, San Diego, CA.

Pickup, G. & Stafford Smith, D.M. 1993. Problems, prospects and procedures for assessing the sustainability of pastoral land management in arid Australia. *J. Biogeogr.* 20: 471-487.

Quideau, S.A. 1999. Biogeochemical cycling of calcium and magnesium by *Ceanothus* and chamise. *Soil Sci. Soc. Am. J.* 63: 1880-1888.

Saunier, R.E. & Wagle, R.F. 1967. Factors affecting the distribution of shrub live oak (*Quercus turbinella* Greene). *Ecology* 48: 35-41.

Sheridan, T.E. 1995. *Arizona: A history*. The University of Arizona Press, Tucson, AZ.

Spang, E.F. 1987. Juniper from a Bureau of Land Management perspective. In: Everett, R.L. (ed.) *Proceedings of the Pinyon-Juniper Conference*, pp.489-493. USDA For. Serv. Gen.Tech. Rep. INT-215, Ft. Collins, CO.

Stephens, G. & Whitford, W.G. 1993. Responses of *Bouteloua eriopoda* to irrigation and nitrogen fertilization in a Chihuahuan desert grassland. *J. Arid Environ.* 24: 415-421.

Stock, W.D. & Lewis, O.A.M. 1986. Soil nitrogen and the role of fire as a mineralization agent in a South African coastal fynbos ecosystem. *J. Ecol.* 74: 317-328.

Sughara, G. & May, R.M. 1990. Applications of fractals in ecology. *Trends Ecol. Evol.* 5: 79-86.

Sullivan, S. 1996. Towards a non-equilibrium ecology: perspectives from an arid land. *J. Biogeogr.* 23: 1-5.

Sutherland, J.P. 1990. Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. *Am. Nat.* 136: 270-275.

ter Braak, C.J.F. 1988. *CANOCO – a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis* (version 2.1). Center for Biometry, Wageningen, NL.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20: 171-197.

Valone, T.J. 1999. Fire and grazing in a shrub-invaded arid grassland community: independent or interactive ecological effects? *J. Arid Environ.* 42: 15-28.

Vankat, J.L. 1989. Water stress in chaparral shrubs in summer-rain versus summer-drought climates: Whither the Mediterranean-type climate paradigm? In: Keeley, S.C., (ed) *The California chaparral: Paradigms reexamined*, pp. 117-124. No. 34 Science Series, Natural History Museum of L.A. County, Los Angeles, CA.

Vogl, R. 1981. Chaparral succession. In: Conrad, C.E. & Oechel, W.C. (eds) *Proceedings of the Symposium on Dynamics and Management of Mediterranean-Type Ecosystems*, pp. 81-85. USDA For. Serv. Gen. Tech. Rep. PSW-58, San Diego, CA.

Walker, S. & Wilson, J.B. 2002. Tests for nonequilibrium, instability, and stabilizing processes in semiarid plant communities. *Ecology* 83: 809-822.

Weaver, J.E. & Fitzpatrick, T.J. 1934. The prairie. *Ecol. Monogr.* 4: 109-295.

Weber, D.J., Bunderson, E.D., Davis, J.N, Nelson, D.L. & Hreha, A. 1999. Diseases and Environmental factors of the pinyon-juniper communities. In: Monsen, S.B. & Stevens R. (eds) *Proceedings: Ecology and Management of Pinyon-Juniper Communities within the Interior West*, pp. 118-120. USDA For. Serv. Gen. Tech. Rep. RMRS-P-9, Ogden, UT.

White, P.S., Wilds, S.P. & Stratton, D.A. 2001. The distribution of heath balds in the Great Smokey Mountains, North Carolina and Tennessee. *J. Veg. Sci.* 12: 453-466.

Wienhold, B.J. & Klemmedson, J.O. 1992. Effect of prescribed fire on nitrogen and phosphorus in Arizona chaparral soil-plant systems. *Arid Soil Res. Rehabil.* 6: 285-296.

Wiens, J.A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. In: Pickett, S.T.A. and White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics*, pp.180-189. Academic Press, San Diego, CA.

Woodmansee, R.G. 1979. Factors influencing input and output of nitrogen in grasslands. In: French, N. (ed) *Perspectives in grassland ecology*, pp. 117-129. Springer-Verlag, New York, NY.

Woods, K.D. 2000. Long-term change and spatial pattern in a late-successional hemlock-northern hardwood forest. *J. Ecol.* 88: 267-282.

Wright, H.A. & Bailey, A.W. 1982. *Fire ecology: United States and Southern Canada*. Wiley, New York, NY.

Zimmerman, G.M., Goetz, H. & Mielke, Jr., P.W. 1985. Use of an improved statistical method for group comparison to fire effects of prairie fire. *Ecology* 66: 606-611.

Received 15 December 2000;
Revision received 28 July 2002;
Accepted 11 September 2002.
Coordinating Editor: P.S. White.