

Spatial patterns in leaf area and plant functional type cover across chronosequences of sagebrush ecosystems

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Abstract Since most studies of ecosystem dynamics after disturbance require longer durations of study than the life span of most research careers, many studies rely on chronosequence approaches to substitute space for time. We tested the chronosequence approach for assessing the change in plant functional type cover and leaf area index (L) using three replicated mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* (Rydb.) Boivin) dominated ecosystems in southern Wyoming. We further tested our broader inferences of mountain big sagebrush ecosystem chronosequences by assessing whether dynamics in spatial patterning of plant functional type cover and leaf area index would compromise the chronosequence approach. We hypothesized that (1) L and total cover increase with age at similar rates across replicated chronosequences, (2) spatial autocorrelation is greatest with shrub cover, and (3) spatial autocorrelation increases with age. We failed to reject all three hypotheses. Our analyses showed that mean shrub cover, total cover, and L all increased linearly with time since disturbance across all three replicated chronosequences. While neither graminoid nor forb cover was correlated with time since disturbance,

graminoid cover did show an inverse relationship with shrub cover and L . Semivariogram analysis showed that spatial patterning increased with shrub cover and time since disturbance. Thus, while we cannot yet provide a process to fit the spatial patterns, the chronosequence approach for sagebrush ecosystems recovering from disturbance has survived a rigorous test because the mean changes in shrub cover, total cover, and L were replicable across three different sites.

Keywords Geostatistics · Rangelands · Fire · Disturbance · Prescribed burn · Shrub islands

Introduction

Emphasis is often placed on the role of climate (temperature and precipitation) in the distribution of major world biomes (Whittaker 1975). However, disturbance has increasingly been acknowledged as a driver of ecosystem dynamics, although broad relationships are more difficult to discern due to the mismatch between the slow rate of ecosystem change and the short life span of most research projects (Powers and Van Cleave 1991). In fire prone ecosystems that cover approximately 40% of the world land surface (Chapin et al. 2002), fire fundamentally alters the type, structure, and function of vegetation that exists within a given climate (Bond et al. 2005).

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While a chronosequence approach (holding all variables but time since disturbance constant; Jenny 1941) is one of the best methods to overcome the mismatch of long-term ecosystem response to disturbance and short-term research studies, chronosequence approaches may suffer from assumptions regarding substituting space for time (Yanai et al. 2000) and that succession follows a single pathway (Fastie 1995). The assumption that space can be substituted for time can be difficult to test for long time-scale chronosequences (e.g., more than 10 years Bond-Lamberty et al. 2004).

Another untested assumption is that measurements at particular spatial locations within an age in a chronosequence are spatially independent of each other. This assumption requires that there be no spatial autocorrelation between points in space, an assumption rarely met when rigorously tested (Legendre 1993). Traditional sampling designs such as random samples (Muller and Zimmerman 1999; Bogaert and Russo 1999) and stratified random sampling schemes (Fassnacht et al. 1997) have recently been supplemented with sampling strategies designed to explicitly quantify spatial autocorrelation more efficiently (Burrows et al. 2002; Ferreyra et al. 2002; Fagroud and Van Meirvenne 2002; Di Zio et al. 2004). Such sampling designs acknowledge that processes at small, patch scales may play a role in both variability and ecological processes (Legendre 1993) at larger scales of interest. Spatial autocorrelation occurs at scales ranging from centimeters in microbial communities (Franklin et al. 2002), meters to hundreds of meters in vegetation stands (Burrows et al. 2002), and thousands of meters in landforms (Bishop et al. 2003). Across all of these spatial scales most processes that occur near one another in space are more similar than those that occur far apart. The autocorrelation depends on the environment and nature of observation (Curran and Atkinson 1998) illustrating that changes in spatial autocorrelation indicate changes in ecosystem function (Legendre 1993). Thus, changes in ecosystem structure and function throughout a chronosequence may lead to changes in spatial autocorrelation.

Burning and recovery from burning have important effects on patterns of plant distribu-

tion, cover, and leaf area index (L) in sagebrush ecosystems. Sagebrush steppe is the largest semi-arid vegetation type in North America, historically covering at least 630,000 km² in the western US (West 1983). Sagebrush steppe ecosystems are characterized by an overstory of one of several woody species of *Artemisia*, and an important understory component of perennial bunch grasses (Beetle and Johnson 1982). Mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* (Rydb.) Boivin) communities are found at the higher elevation limit for *A. tridentata* (~2,000–2,900 m), in deep and well-drained soils (Beetle 1961; Beetle and Johnson 1982). Prior to European settlement, natural fire is thought to have burned these systems at 20 to 35-year intervals (Burkhardt and Tisdale 1976), with recovery to pre-burn density and canopy cover after 15–50 years (Harniss and Murray 1973; Bunting et al. 1987; Hironaka et al. 1983; Miller et al. 2000; Wambolt et al. 2001). Lower elevation, Wyoming big sagebrush (*A. tridentata* var. *wyomingensis*) communities had comparatively longer natural burn intervals, 110 years or more, and took at least 40 years to recover to 20% canopy cover (Young and Evans 1981; Windward 1991). Due to the potentially bidirectional impact of arid land shrubs on edaphic conditions (Caldwell et al. 1985; Schlesinger et al. 1990; Bolling and Walker 2002), spatial autocorrelation may increase with shrub cover as stands recover from disturbance.

The existence of predictable pathways of succession in sagebrush ecosystems has been debated, and over the last decade, multiple stable states have been recognized (Laycock 1991). Management practices play a strong role in pathways of sagebrush succession across Western US rangelands (e.g., McLendon and Redente 1990; McLendon and Redente 1992; McLendon and Redente 1991; West and Yorks 2002). In many regions, sagebrush ecosystems have become degraded by a combination of overgrazing by domestic livestock, drought, invasion by exotic annual grasses, and fire suppression (West and Young 2000). In areas without significant exotic annual grasses and fire suppression, sagebrush recovery after burning may be predictable (Harniss and Murray 1973; Wambolt et al. 2001). Such an increase in sagebrush cover into early succes-

sional grass and forb dominated stands provides direct connections to work on ecosystem consequences of woody plant invasions into grasslands (Brown and Archer 1999). Sagebrush stand productivity may decline over time due to dominance by senescent shrubs with a concurrent loss of herbaceous production; this represents a stable state that resists changes in grazing practices (Laycock 1991). An alternative stable state may occur in the case of cheat grass (*Bromus tectorum*) invasion, which is associated with a loss of most woody species and most native perennial grasses (Booth et al. 2003), altered ecosystem properties (Norton et al. 2004; Ogle et al. 2003), and loss of wildlife habitat (Crawford et al. 2004).

The goal of this project was to test the chronosequence approach to evaluating ecosystem response to disturbance in replicated mountain big sagebrush steppe ecosystems. We chose a sampling design that would efficiently quantify

spatial autocorrelation and mean values of *L* and plant functional type cover to test for changes following disturbance. Our specific hypotheses were (1) *L* and total cover increase with age at similar rates across replicated chronosequences, (2) spatial autocorrelation is greatest with shrub cover, and (3) spatial autocorrelation increases with age.

Material and methods

Field site descriptions

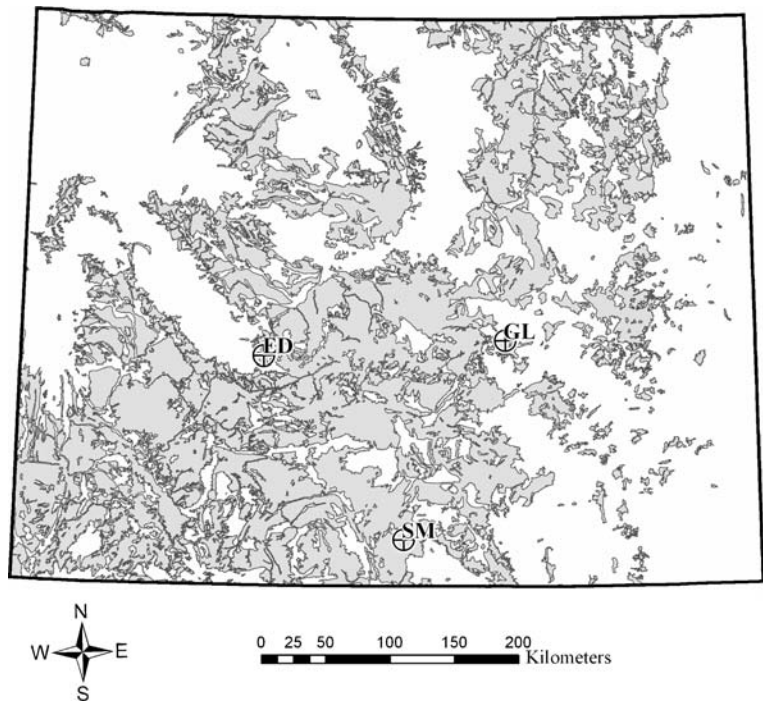
Three sites were selected for study that each encompassed a range of ages (Table 1) of mountain big sagebrush recovering from disturbance (Fig. 1). The vegetation type is sagebrush steppe (West and Young 2000), and all sites are relatively pristine, not having been subjected to

Table 1 General characteristics of three chronosequences of *A. tridentata* var. *vaseyana* dominated sites at Ed Young, Glades, and Sierra Madre (ED, GL, SM, respectively, see Fig. 1 for locations)

Site	Age (years)	Latitude, longitude	Elevation (m)	Depth (cm)	USDA texture	pH	%C	%N	C:N
ED	2	42°36'59", 108°43'51"	2310	0–5	Sandy loam	7.3	5.6	0.5	11.1
				5–15	Sandy loam	7.4	2.1	0.2	9.7
				15–30	Sandy clay loam	7.5	2.3	0.2	9.6
	27	42°38'2", 108°43'30"	2280	0–5	Loam	7.5	5.0	0.4	11.8
				5–15	Loam	7.8	4.1	0.3	13.1
				15–30	Loam	7.7	3.8	0.3	12.7
	67	42°36'48", 108°43'42"	2300	0–5	Sandy loam	6.9	3.2	0.3	10.5
				5–15	Sandy loam	7.1	3.0	0.3	10.7
				15–30	Loam	7.2	3.2	0.3	10.9
GL	3	42°43'52", 106°26'37"	1940	0–5	Loam	6.6	5.5	0.5	11.8
				5–15	Loam	6.5	2.4	0.2	10.0
				15–30	Sandy loam	6.4	1.7	0.2	8.9
	19	42°43'22", 106°25'10"	1980	0–5	Loam	6.6	5.2	0.4	11.8
				5–15	Loam	6.6	2.1	0.2	9.1
				15–30	Loam	6.8	2.0	0.2	9.2
	38	42°43'32", 106°25'37"	1960	0–5	Loam	6.9	3.1	0.3	10.8
				5–15	Loam	6.7	1.7	0.2	9.2
				15–30	Loam	6.6	1.3	0.2	8.0
SM	4	41°20'14", 107°23'46"	2270	0–5	Sandy loam	6.5	3.3	0.3	11.6
				5–15	Sandy loam	6.8	2.5	0.2	11.2
				15–30	Sandy clay loam	7.2	1.8	0.2	9.9
	18	41°21'44", 107°21'4"	2260	0–5	Sandy loam	6.4	3.2	0.3	12.2
				5–15	Loamy sand	6.8	1.8	0.2	10.3
				15–30	Loamy sand	6.9	1.4	0.1	9.8
	37	41°20'23", 107°23'33"	2270	0–5	Sandy loam	6.7	2.7	0.2	10.8
				5–15	Sandy loam	6.8	2.2	0.2	10.1
				15–30	Sandy loam	7.0	1.8	0.2	9.9

Ages are from 2003. Soil depths properties include soil texture from United States Department of Agriculture classification, pH, the carbon and nitrogen (C and N, respectively) % of the total soil, and the ratio of soil C:N

Fig. 1 Digital elevation map (30 m) of the state of Wyoming (United State) showing the location of the three study sites, Ed Young (ED) southeast of the Wind River Mountain Range, Glades (GL) northwest of the Laramie Mountain Range, and Sierra Madre (SM) northwest of the Sierra Madre Mountain Range



degradation by overgrazing or cheat grass (*B. tectorum*) invasion. Elevation of the sites ranged from ~1,960 m at the Glades (GL) to ~2,270 m at Sierra Madres (SM), and ~2,300 m at Ed Young (ED; Table 1). Soil properties in the top 30 cm were similar across all sites, with sandy loam to loam textures, near neutral pH, 2–5% C content, and C/N ratios of 9 to 11 (Table 1). Soils at all sites formed in alluvium dominated by sedimentary rocks, with limestone and dolomite prevalent at ED, sandstones and shale at GL, and sandstone and tuffaceous sandstone at SM (Case et al. 1996). While each site is located near substantial mountain ranges, all of the measurements were taken in areas with slopes less than 1%. The climate of the region can be characterized as semi-arid, with cold winters and warm summers. Mean annual temperatures are ~7.2°C in Lander (closest meteorological station to ED) and Casper (closest meteorological station to GL), and ~6.2°C at Baggs, WY (closest meteorological station to SM). Mean annual precipitation is 341 mm in Casper, 331 mm in Lander, and 259 mm in Baggs; about 40% of the annual precipitation at all sites occurs in April, May, and June.

The sites are all managed for moderate grazing, and cattle are generally present from June to September (C. Newberry, BLM, Rawlins, WY, personal communication 2004). Prescribed burning has become a commonly applied management tool over the last 30 years in these ecosystems to reduce the shrub cover and stimulate forb and grass production (Sapsis and Kauffman 1991; Bastian et al. 1995; Wambolt et al. 2001). Burning may be done in the spring or autumn when temperatures are low. Prescribed burning took place at ED in 2001 and 1976; at GL in 2000 and 1984; and at SM in 1999 and 1985. Prior to the 1970s herbicide treatment was more common than burning, and the GL and SM sites received applications of 2,4-D (2,4-dichlorophenoxy acetic acid) in the mid-1960s to reduce the shrub cover. The ED site never received herbicide but rather experienced a natural fire disturbance in the mid-1930s (historical records, Shoshone National Forest, Washakie Ranger District, Lander, WY).

Spatially explicit field sampling

All sites were sampled for plant functional type cover and *L* during the growing season of 2003.

We used the spatially explicit cyclic sampling procedure of Burrows et al. (2002) which improves on earlier spatial measurement schemes by efficiently sampling pairs of points at all distances throughout the spatial sampling grid (Fig. 2). Burrows et al. (2002) provide a complete treatment of the a priori analysis and selection of a suitable cyclic sampling design. The original Burrows et al. (2002) a priori analysis utilized remote sensing imagery to establish a sampling design. In this study, we conducted an a priori analysis across all three chronosequences in June 2003 by measuring vegetation cover of plant functional type in four transects that were 20 m long and 5 m apart using the line intercept method for percent cover (Canfield 1941). Each cover value was determined from adjacent 50-cm segments of the full transects because this was the shortest length segment that when averaged together yielded the same mean cover values as the full 20 m transect. By finding the shortest, usable segment, we were able to maximize the spatial variability available in the data. Using these data, we established the approximate range of spatial autocorrelation for each plant functional type assuming isotropy. From these data,

we established a 3/7 cyclic sampling design that encompassed more than 30 sample point pairs at twice the spatial range (Burrows et al. 2002) found in the a priori sampling repeated in each direction four times (Fig. 2). This sampling design resulted in 144, 50-cm cover transects within a 12 m × 12 m grid at each age within all three chronosequences.

Plant cover and leaf area index measurements

Field sampling for the full spatially explicit dataset took place in the last week of August, 2003 at GL and SM, and during the first week of September, 2003 at ED. Total percent covers could be over 100 due to overlapping vegetation strata. Standard field measurement methods were used to quantify *L* using optical sensors (LAI-2000; LiCor Lincoln, Neb. USA; Gower and Norman 1991; Fassnacht et al. 1994; Chen et al. 1997; Gower et al. 1999) at the same points. We recorded one above-canopy measurement of incoming light and one below-canopy (ground-level) measurement of attenuated light for each plot to calculate *L*. We used a 15° open cap to prevent the measurements from overlapping with

Fig. 2 Depiction of one quarter of the 3/7 cyclic sampling method used for all cover and leaf area index measurements. The 3/7 cycle is shown repeated only twice in both directions; the actual sampling design repeated the 3/7 cycle four times out to 12 m distance in each direction resulting in 144, 50 cm cover transects at each age within all three chronosequences

		Distance (m)													
		0.0	0.5	1.5	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5
Distance (m)	0.0	A1	B1		C1				D1	E1		F1			
	0.5	A2	B2		C2				D2	E2		F2			
	1.0														
	1.5	A3	B3		C3				D3	E3		F3			
	2.0														
	2.5														
	3.0														
	3.5	A4	B4		C4				D4	E4		F4			
	4.0	A5	B5		C5				D5	E5		F5			
	4.5														
	5.0	A6	B6		C6				D6	E6		F6			
	5.5														
	6.0														
	6.5														

plots adjacent to the measured point. The actual viewing area of each measurement changed depending upon the canopy height at any individual plot, so some overlap between points in a forward direction was possible. Such overlap may contribute to higher nuggets in the semivariogram (see below).

Statistical analyses

To investigate spatial patterns across sites and ages, we applied a semivariogram analysis to all of our spatially collected data. The semivariogram examines the relationship between distance between pairs of points, also known as lags (h), and the semivariance for each distance (γ) calculated as

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \{z(x_i + h) - z(x_i)\}^2 \quad (1)$$

where N is the number of observations at lag distance h , x_i is the i th location, and z is data value (Cressie 1993). Interpretation of the measured, or experimental semivariograms requires a fitted model through the γ values at all h 's. We fit three types of relationships. The first was an exponential model:

$$\gamma = y_0 + b \left[1 - e^{(-3h/c)} \right] \quad (2)$$

where y_0 is the nugget, b is the sill, and c is the range; the second was a linear model

$$\gamma = y_0 + bh \quad (3)$$

and the third was a nugget model

$$\gamma = y_0 \quad (4)$$

The nugget is the amount of variation found at distance zero and indicates variance that exists at a scale finer than the field samples, inherently high variability, or sampling error. The sill is the amount of variance that occurs at the distance beyond which samples are independent. The range is the distance between point pairs at which the sill occurs and provides an index of the scale of spatial pattern in the variable of interest. A

linear model (Eq. 3) indicates that the sampling did not find a range at which a sill was reached. The nugget model (Eq. 4) indicates no significant spatial autocorrelation at the scales measured and that all points are independent. Ninety five percent confidence intervals for the experimental (measured) semivariogram were calculated as (Cressie 1993; Burrows et al. 2002):

$$CI_{95} = 1.96 \frac{\sqrt{2}\gamma}{\sqrt{N}} \quad (5)$$

symbols are the same as Eq. 1.

Kriging is a linear interpolation that allows predictions of unknown values in the study area based on information from measurements made at sample locations. It incorporates the model of spatial variance (range, sill, and nugget estimates; Eqs. 2–4) derived from those observations, as well as the individual measurements, to produce a map that predicts the values across the sampling domain. Kriged maps are especially useful for interpreting the semivariograms and visually verifying isotropy and lack of drift (Isaaks and Srivastava 1989). For additional information on Kriging, see Cressie (1993), Kaluzny et al. (1998), and Pinheiro and Bates (2000).

Statistical analyses were performed in SAS (version 8.0, SAS Institute, Cary, NC, USA) and GS+ (version 7.0; Gamma Design Software, Plainwell, MI, USA). Since our measurements were collected to explicitly quantify spatial autocorrelation, we used the MIXED procedure to account for the effect of spatial autocorrelation on standard errors of means using a repeated measures analysis in space (Burrows et al. 2002). Experimental semivariograms constructed from the original data were quantified using Proc Variogram of SAS. Experimental semivariograms were restricted to h values that were greater than or equal to 30-point pairs (Legendre and Legendre 1998). Visualization of spatial patterns through Kriging and tests of anisotropy and drift were performed in GS+. We determined the appropriate number of parameters and variance structure in repeated measures analysis that minimized the Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC; Littell et al. 1996; Ewers et al. 2002). Both of

these criteria are log likelihood values penalized for the number of parameters used. Modeled semivariograms (Eqs. 2–4) were fitted to the experimental semivariograms using Sigmaplot (version 8.0, SPSS Inc., Chicago, IL, USA).

Results

Spatial patterns

The strongest spatial patterns detected were for percent shrub cover, and these patterns increased with time since burning (Tables 2, 3, 4, 5, 6; Fig. 3). Percent graminoid and forb cover spatial patterns generally had lower correlation coefficients, and thus displayed less spatial structure, than did percent shrub cover, percent total cover or *L*. Based on the experimental semivariogram, we found it necessary to use all three types of modeled semivariograms (Eqs. 2–4). Linear relationships were only found in percent graminoid basal cover at the GL site (Table 2). Percent graminoid cover linear relationships indicate that our sampling grid was not large enough to quantify the range in either case. Nugget models were found in portions of all plant functional type covers across all ages (Tables 2–6). A general trend towards increasing spatial patterning with increasing age in all quantities was found; in particular, shrub cover had significant spatial pattern in all three sites in the oldest stands (Fig. 3). Neither anisotropy nor drift was found in any measured quantity.

The three components of the semivariogram (nugget, sill, and range) were highly variable. The exponential model generally fit the experimental semivariogram well except for shrub cover at old ED (Fig. 3C). In this case, a second, increasing semivariance with lag distance was detected beyond 8 m lags. The widest variability in spatial range was found in forb cover (0.9–7.1 m) and the least in shrub cover (1.6–3.2 m) across ages and sites. Nuggets were present in the 18-year-old SM graminoids basal cover (Table 2), forb cover (Table 3), shrub cover (Table 5), and *L* (Table 6). Additional nuggets appeared in the middle ages of ED and GL for *L* (Table 6). The nugget was between 8% and 65% of the sills.

We show two different point Kriged maps (Fig. 4) of shrub cover as a sample visualization of the spatial analyses conducted. Figure 4A represents a sagebrush stand with a spatial autocorrelation range more than double that in Fig. 4B (3.2 and 1.3 m, respectively). The decreasing spatial autocorrelation in Fig. 4B can be seen by the greater variability in shrub cover % compared to Fig. 4. Our confidence in these maps is high because the cross validation (Isaaks and Srivastava 1989) of the maps revealed a correlation coefficient above 0.8 for each with no bias (slope not significantly different from 1.0; $P > 0.2$; and intercept not significantly different from zero; $P > 0.3$). In all other significant spatial patterns (Tables 2–6) the correlation coefficients ranged between 0.5 and 0.9 with no bias. Two main patterns emerge from the maps. First, much of the

Table 2 Statistical information for percent graminoid basal cover semivariograms based on site (see Fig. 1), age of stand, and equation types with lin being $\gamma = y_0 + b$

(Eq. 3) and exp being $\gamma = y_0 + b(1 - \exp(-3x/c))$ (Eq. 2) where γ is spatial variance, y_0 is the nugget, b is the sill, and c is the range

Site	Age (years)	Eq.	y_0 (%) ²	b (%) ²	c (m)	R^2	P
ED	2	exp	–	300 (10)	1.2 (0.2)	0.30	**
	27	–	–	–	–	–	ns
	60	–	–	–	–	–	ns
GL	3	lin	60 (9)	6 (7)	–	0.80	***
	19	–	–	–	–	–	ns
	38	lin	30 (10)	1 (3)	–	0.72	***
SM	4	–	–	–	–	–	ns
	18	exp	–	80 (1)	1.6(0.5)	0.15	*
	37	–	–	–	–	–	ns

A value of (–) for the nugget indicates that the nugget was not significant at $\alpha = 0.05$. The R^2 are reported fit of the two equation types and significance of the regressions (P) are *, **, or *** for $P < 0.05, 0.01, \text{ and } 0.001$, respectively

Table 3 Statistical information for percent forb cover semivariograms based on site (see Fig. 1), age of stand, and equation types with lin being $\gamma = y_0 + b$ (Eq. 3) andexp being $\gamma = y_0 + b(1 - \exp(-3x/c))$ (Eq. 2) where γ is spatial variance, y_0 is the nugget, b is the sill, and c is the range

Site	Age (years)	Eq.	y_0 (%) ²	b (%) ²	c (m)	R^2	P
ED	2	exp	–	400 (50)	0.9 (0.2)	0.26	*
	27	exp	–	300 (70)	1.0 (0.3)	0.13	*
	60	–	–	–	–	–	ns
GL	3	–	–	–	–	–	ns
	19	–	–	–	–	–	ns
	38	exp	–	200 (40)	2.0 (0.4)	0.54	***
SM	4	exp	–	1 (0.1)	2.0 (0.8)	0.22	*
	18	exp	250 (40)	300 (70)	7.1 (5.1)	0.38	**
	37	exp	–	100 (10)	2.2 (1.4)	0.16	*

A value of (–) for the nugget indicates that the nugget was not significant at $\alpha = 0.05$. The R^2 are reported fit of the two equation types and significance of the regressions (P) are *, **, or *** for $P < 0.05$, 0.01, and 0.001, respectively

Table 4 Statistical information for percent shrub semivariograms based on site (see Fig. 3), age of stand, and equation types with lin being $\gamma = y_0 + b$ (Eq. 3) and expbeing $\gamma = y_0 + b(1 - \exp(-3x/c))$ (Eq. 2) where γ is spatial variance, y_0 is the nugget, b is the sill, and c is the range

Site	Age (years)	Eq.	y_0 (%) ²	b (%) ²	c (m)	R^2	P
ED	2	–	–	–	–	–	ns
	27	exp	–	2000 (30)	2.1 (0.2)	0.74	***
	60	exp	–	1000 (40)	1.9 (0.5)	0.32	**
GL	3	–	–	–	–	–	ns
	19	–	–	–	–	–	ns
	38	exp	–	2000 (40)	1.6 (0.3)	0.34	**
SM	4	exp	–	200 (8)	1.7 (0.6)	0.31	**
	18	exp	560 (22)	1000 (20)	3.2 (2.1)	0.32	*
	37	exp	–	1500 (30)	1.3 (0.2)	0.45	***

A value of (–) for the nugget indicates that the nugget was not significant at $\alpha = 0.05$. The R^2 are reported fit of the two equation types and significance of the regressions (P) are *, **, or *** for $P < 0.05$, 0.01, and 0.001, respectively

Table 5 Statistical information for percent total cover semivariograms based on site (see Fig. 1), age of stand, and equation types with lin being $\gamma = y_0 + b$ (Eq. 3) andexp being $\gamma = y_0 + b(1 - \exp(-3x/c))$ (Eq. 2) where γ is spatial variance, y_0 is the nugget, b is the sill, and c is the range

Site	Age	Eq.	y_0 (%) ²	b (%) ²	c (m)	R^2	P
ED	2	exp	–	400 (6)	0.9 (0.2)	0.20	*
	27	exp	–	2000 (30)	1.7 (0.2)	0.52	***
	60	exp	–	1000 (40)	1.7 (0.5)	0.22	*
GL	3	–	–	–	–	–	ns
	19	–	–	–	–	–	ns
	38	exp	–	1000 (30)	1.4 (0.2)	0.39	**
SM	4	exp	–	200 (7)	1.2 (0.4)	0.16	**
	18	exp	0.079 (0.036)	1000 (40)	3.8 (3.0)	0.23	*
	37	exp	–	2000 (30)	1.1 (0.2)	0.42	***

A value of (–) for the nugget indicates that the nugget was not significant at $\alpha = 0.05$. The R^2 are reported fit of the two equation types and significance of the regressions (P) are *, **, or *** for $P < 0.05$, 0.01, and 0.001, respectively

sampled areas have very low shrub cover. The resulting contrast between areas with low shrub cover and the high cover shrub islands creates the

relatively high nugget values (Table 4) in Fig. 4A. Second, the shrub islands are prominent and drive much of the spatial patterning.

Table 6 Statistical information for percent leaf area index (L) semivariograms based on site (see Fig. 1), age of stand, and equation types with lin being $\gamma = y_0 + b$ (Eq. 3) andexp being $\gamma = y_0 + b(1 - \exp(-3x/c))$ (Eq. 2) where γ is spatial variance, y_0 is the nugget, b is the sill, and c is the range

Site	Age	Eq.	y_0 (%) ²	b (%) ²	c (m)	R^2	P
ED	2	–	–	–	–	–	ns
	27	exp	0.8 (0.3)	1.2 (0.03)	3.5 (2.7)	0.24	*
	60	–	–	–	–	–	ns
GL	3	–	–	–	–	–	ns
	19	exp	0.2 (0.1)	0.4 (0.01)	3.4 (1.8)	0.45	**
	38	exp	–	0.7 (0.02)	3.6 (0.5)	0.71	***
SM	4	–	–	–	–	–	ns
	18	exp	–	0.5 (0.01)	1.3 (0.3)	0.30	**
	37	–	–	–	–	–	ns

A value of (–) for the nugget indicates that the nugget was not significant at $\alpha = 0.05$. The R^2 are reported fit of the two equation types and significance of the regressions (P) are *, **, or *** for $P < 0.05$, 0.01, and 0.001, respectively

Trends in plant functional type cover and L with age

Despite the variability in spatial patterning, we found consistent relationships between percent total cover, percent shrub cover, and L with age across all three chronosequences (Fig. 5). All three chronosequence showed a maximum measured percent shrub cover, percent total cover, and L at approximately age 40. Across all three quantities, the ED old data consistently showed a decline, although there were no stands of similar ages in the other two sites for comparison. Thus, regression equations for Fig. 5 exclude ED old data. Positive intercepts were found in L and cover ($P < 0.001$); there was no significant intercept for shrub cover ($P > 0.2$). In contrast, we found no significant trend with age for percent graminoid basal or forb cover ($P > 0.4$; Fig. 6). Much less variation was found across the three ages in graminoid basal and forb cover in ED compared to GL and SM.

Trends in cover between plant functional types

The importance of shrubs, especially *A. tridentata* var. *vaseyana*, across the sites is illustrated by the tight relationship between percent shrub cover and L (Fig. 7A). However, there was a positive intercept ($P < 0.01$) in the relationship depicting the role of the other plant functional types in the young stands with low shrub cover. The relationship between percent total cover and L was also

tight, but had a negative intercept ($P < 0.01$; Fig. 7B). These effects are further illustrated in Fig. 8; percent graminoid basal cover was inversely correlated with both percent shrub cover and L . However, the amount of variability explained was much less than other relationships previously described (Figs. 6–8).

Discussion

Our results, based on careful site selection controlling for big sagebrush subspecies and environment, demonstrate the utility of the chronosequence approach in response to disturbance in sagebrush steppe. Across three replicated chronosequences, we found the same increase in average percent total cover, percent shrub cover and L for ~40 years following disturbance. The chronosequence approach was further confirmed because changes in spatial pattern did not alter the fundamental relationships between vegetation structure and age. We failed to reject all of our hypotheses (1) L and total cover increase with age at similar rates across replicated chronosequences, (2) spatial autocorrelation is greatest with shrub cover, and (3) spatial autocorrelation increases with age.

Trends in vegetation structure

The similarity in the rates of shrub cover expansion following disturbance at our three mountain big sagebrush steppe chronosequence sites

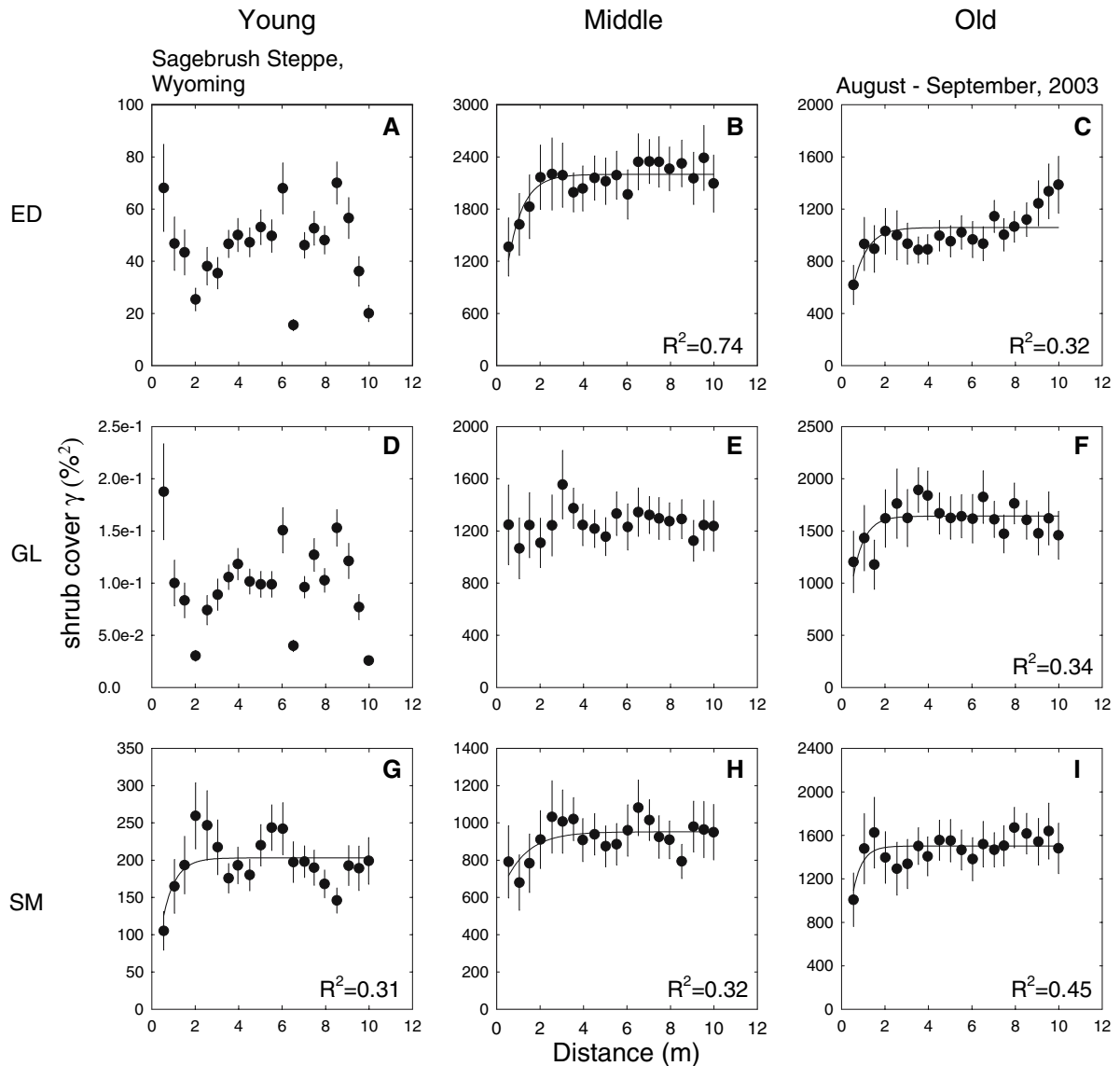


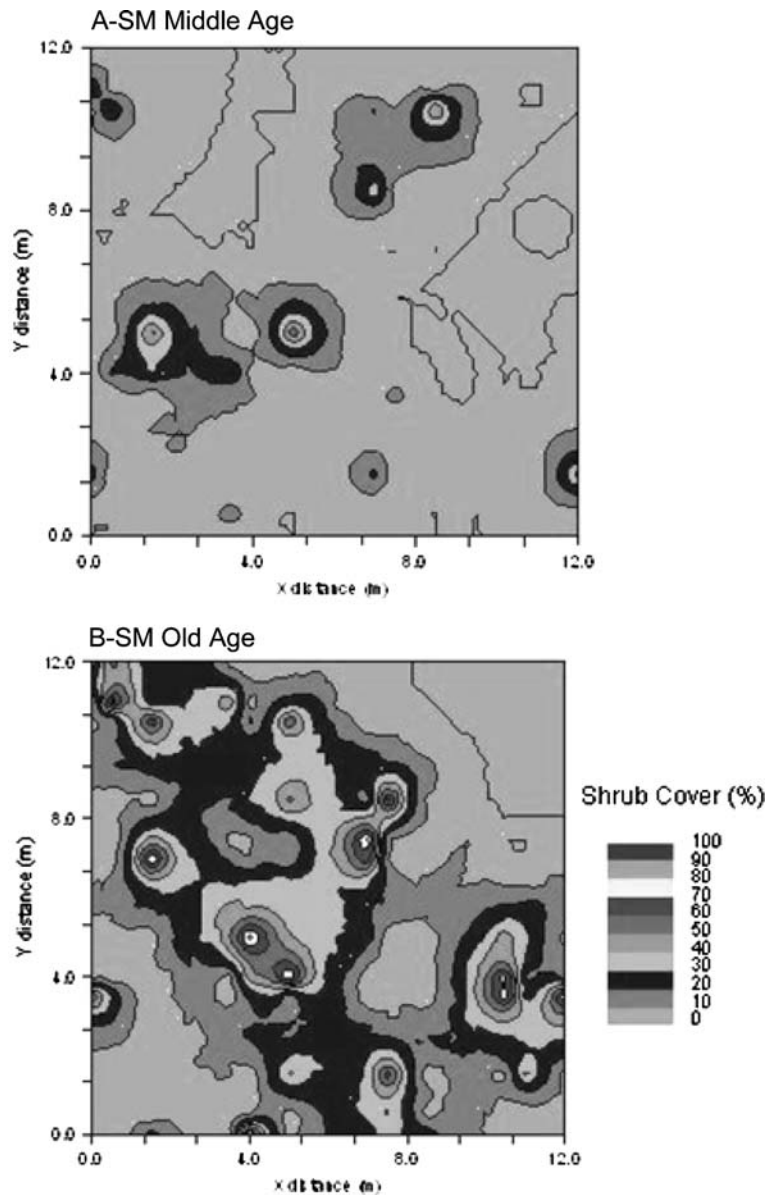
Fig. 3 Semivariogram of percent shrub cover spatial variance (γ) vs. distance of *Artemisia tridentata* at the ED site for ages 2 (**A**), 27 (**B**), and 60 years old (**C**); at the GL site for ages 3 (**D**), 19 (**E**), and 38 years old (**F**); and at the SM site for ages 4 (**G**), 18 (**H**), and 37 years old (**I**).

Each point has a sample size of at least 30 and bars represent 95% CI calculated from Eq. 5. Nonlinear regressions are from fits of Eqs. 2–4 to the data. Parameters for the nonlinear regression are in Table 4

(Fig. 5) suggests that a predictable pathway of succession, from perennial grasses and forbs to dominance by a single species (*A. tridentata* var. *vaseyana*), can be found in mountain big sagebrush plant communities. The patterns of relatively rapid sagebrush establishment and increase to cover values of ~40% are consistent with Miller

et al. (2000), Miller and Rose (1999), and Harniss and Murray (1973), and suggest that this plant community is adapted to burning on decadal time scales (Burkhardt and Tisdale 1976). Although we lack replicated data on temporal changes in vegetation structure and functional group cover in old sagebrush stands (>40 years; Fig. 5), perma-

Fig. 4 Point Kriged maps of (A) SM middle age shrub cover using semivariogram in Fig. 3H and parameters in Table 4 and (B) SM old age shrub cover using semivariogram in Fig. 3I and parameters in Table 4



ment plots in sagebrush steppe in Idaho showed that over 45 years of recovery from heavy grazing, cover of big sagebrush increased, then decreased (Anderson and Inouye 2001). Big sagebrush appeared to progress to a decadent phase during the last 20 years of the Idaho study, and perennial grass cover increased during this period, although shrub and grass cover were also found to be related to precipitation patterns with lags of 2–4 years (Anderson and Inouye 2001).

We found that increasing shrub cover was the main driver of total plant cover and L for all three

chronosequences (Fig. 7). Further, graminoid basal cover was inversely correlated with shrub cover (Fig. 8). An inverse relationship was also found in Idaho sagebrush steppe during years when total cover was relatively high (Anderson and Inouye 2001). This suggests that some competitive interactions may occur between these functional groups. In contrast, Wambolt et al. (2001) found that dominant herbaceous species Idaho fescue (*Festuca idahoensis* Elmer) actually decreased with burning in four of 13 sites in Montana suggesting caution when attempting to

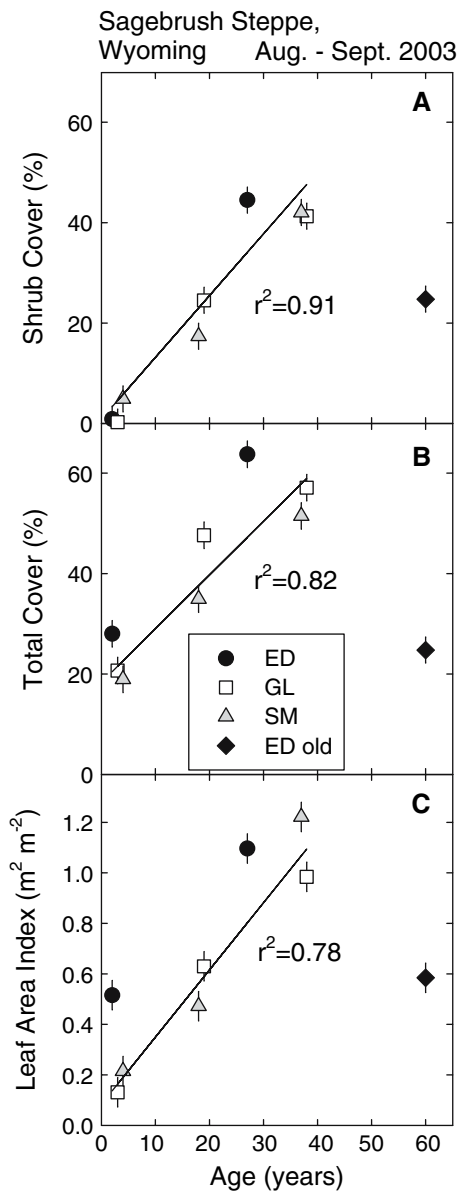


Fig. 5 Relationship between age of stand and percent shrub cover (**A**; $y = 1.2x$), percent total cover (**B**; $y = 18.3 + 1.1x$), and leaf area index (**C**; $y = 0.1 + 0.03x$). Regression lines do not include the oldest ED measurements; see text for details

extrapolate results across the entire sagebrush region. Increased shrub cover was correlated with higher biodiversity and reduced cover of invasive species, although the rarity of cheatgrass was cited as a factor in low overall cover of exotic species (Anderson and Inouye 2001). By contrast, over a gradient of decreasing grazing disturbance,

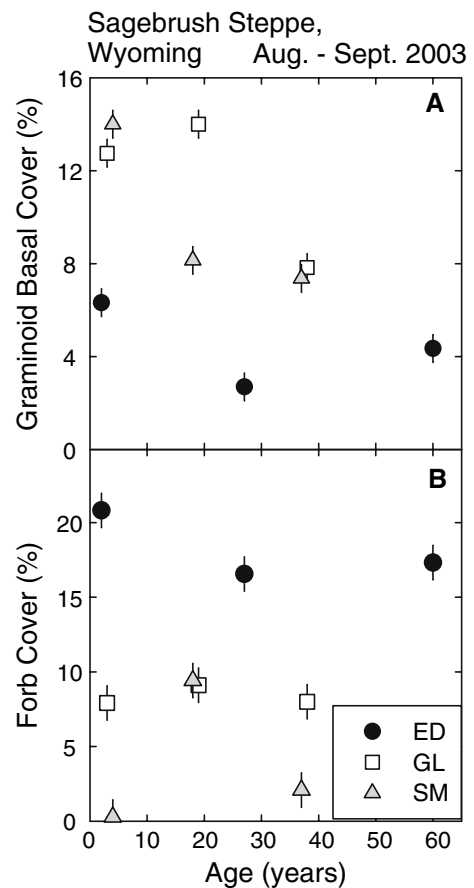


Fig. 6 Relationship between age of stand and percent graminoid basal cover (**A**) and percent forb cover (**B**)

cheatgrass cover drove changes in total plant cover in northern Nevada, with highest total cover at the most disturbed sites (Tueller and Platou 1991). Cheatgrass abundance at our sites in Wyoming is low, and this may be one factor in the progression of succession, cover and L that we observed.

One caveat to broad interpretation of our replicable trends in percent total cover, shrub cover, and L is that our data are one snapshot within the growing season. Percent shrub cover changes very little over a growing season. However, percent forb cover would be much higher immediately after snowmelt at all three of our sites. Our August/September measurements very likely underestimate the peak forb cover. This underestimation probably hides real interactions between shrub cover and forb cover and likely led

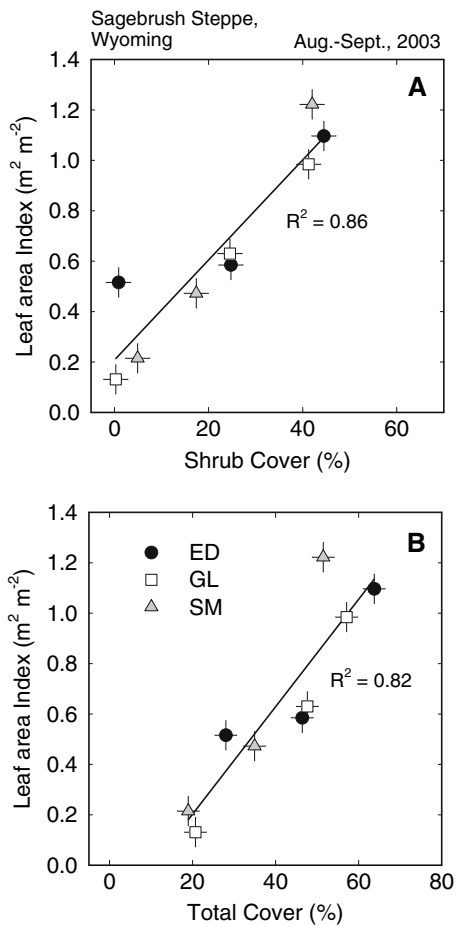


Fig. 7 Relationship between percent shrub cover (A; $y = 0.2 + 0.02x$), percent total cover (B; $y = -0.2 + 0.02x$), and leaf area index

to the null result (Fig. 6). While graminoid basal cover is also unlikely to change within a growing season, graminoid basal cover may not be as important as total plant size or canopy cover for comparisons with other plant functional types (Haase et al. 1999).

Spatial patterns in plant functional type cover with time since disturbance

Using semivariogram analyses, we found nugget models (Eq. 4), exponential saturations (Eq. 2) and linear models (Eq. 3). Nugget models indicate no spatial patterning in the quantity measured and that all points can be treated as independent. The exponential saturation type

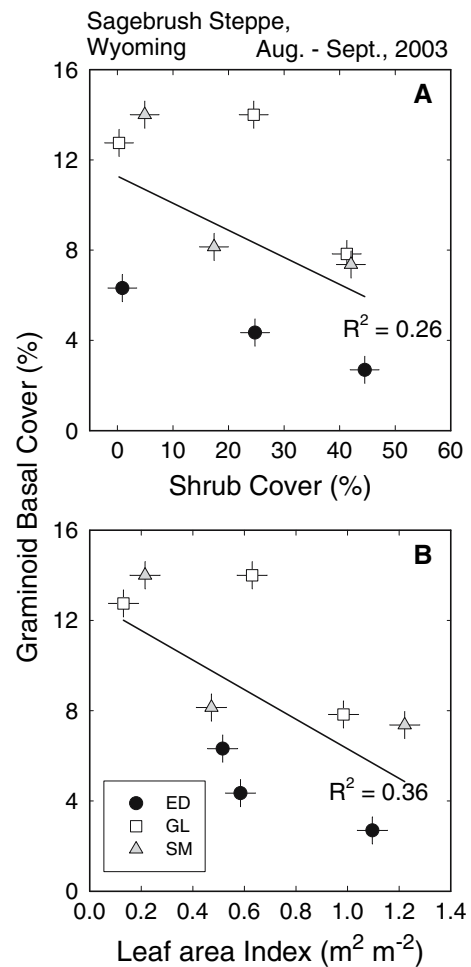


Fig. 8 Relationship between percent shrub cover (A; $y = 11.3 - 0.12x$), leaf area index (B; $y = 12.9 - 6.6x$), and percent graminoid basal cover

model indicates that distances between measured points smaller than the range are autocorrelated while those larger are independent. A linear model was found in graminoid basal cover at GL indicating no range within our sampling grid and that autocorrelation was found at all spatial lags. Linear relationships in graminoid basal cover have been found in grasslands of Serengenti national park (Anderson et al. 2004), Yellowstone National Park (Frank and Groffman 1998), and the Santa Monica Mountains of California (Rahman et al. 2003).

Two different analyses can be used to evaluate the degree of spatial patterning. Testing the statistical fit of modeled semivariograms (Eqs. 2

and 3) against the experimental semivariograms provides one means of formal testing. Another method is to compare the nugget (y_0) to the sill (b). This relative method splits the ratio of the two into three categories: strong, ratio between 0 and 0.25, moderate, 0.26 and 0.75, and weak, greater than 0.75 (Lopez-Granados et al. 2004). Most of our fits were considered moderate (Tables 2–6). However, all of the fits in which the nugget was not significant could not be evaluated with this method and indicate a very strong spatial dependence. In one case, the old site at ED (Fig. 3C), we found evidence of a potential second range. Second ranges could indicate nested ranges due to multiple spatial aggregation scales (Aukema 2004). Such nested ranges indicate that our study results cannot simply be aggregated to larger scales; spatial patterning must also be quantified at the larger scales.

Various studies have attempted to explain spatial patterns in plant properties because spatial patterning indicates important ecological mechanisms and not just random, noise-generating processes (Legendre 1993). Cross-variogram analysis has been used to show that soil properties such as clay content, phosphorus content, and pH may be negatively or positively cross correlated with weedy species density (Walter et al. 2002). The spatial patterning of soil nutrients in desert ecosystems known as “islands of fertility” reflects the spatial distribution of shrubs (Schlesinger et al. 1996; Jackson and Caldwell 1993), which drives patterns of nitrogen cycling, soil respiration (Robertson et al. 1988) and other soil properties (Saetre 1999). Spatial patterns in soil nutrients may depend on the degree of biological control over the nutrients (Gallardo 2003). Long-lived woody species may also influence microclimate (Xu et al. 2004); these interactions may be species dependent (Chen et al. 2003). Fertile islands and nurse plant effects suggest that feedbacks likely exist between past edaphic conditions and spatial patterning (Caldwell et al. 1985). The spatial patterning of biomass correlates with spatial patterning in fire intensity in shrubland systems (Gimeno-Garcia et al. 2004). Spatial patterns in plant cover may also be related to spatial patterns in genotypes (Stratton 1994; Bjornsad et al. 1995).

Since different arid land shrubs may control or be controlled by soil heterogeneity (Bolling and Walker 2002) future research should address what drives spatial heterogeneity in both plant and soil components of the ecosystem.

Confirmation of the chronosequence approach

In addition to the implication of explicit tests of spatial patterning at scales less than or equal to 10 m, our results also have implication for larger scale spatial patterns. The use of a chronosequence approach to disturbance and succession assumes that space substitutes for time. Thus, our relationships between stand age and percent shrub cover, percent total cover, and L (Fig. 5) show that there are consistent, replicable spatial patterns that occur due to disturbance in mountain big sagebrush steppe of Wyoming. However, our results must be tested in disturbance regimes that may change the edaphic factors more drastically than fire or herbicide such as road construction or natural gas well drilling which are becoming more common in these ecosystems.

Our confidence in the chronosequence is well founded in these sagebrush ecosystems because (1) large variation in spatial autocorrelation (Fig. 3, Tables 2–6) of plant functional type cover or leaf area index did not change the patterns in the spatial mean with age (Fig. 5) and (2) the trends were consistent despite climatic variability during the development of each stand. Our confirmation of the chronosequence approach in this sagebrush steppe ecosystem agrees with replicated chronosequence approaches in other shrublands (Keeley et al. 2005; Vandvik et al. 2005), and in boreal forests where trends in L were found at the same approximate age since fire across disparate sites (Bond-Lamberty et al. 2004). Our study thus adds to chronosequence tests in arid shrublands that investigate the interaction between time since disturbance and spatial patterning (Bolling and Walker 2002). Long-term work at these study sites will allow additional testing of the chronosequence approach using a vector analysis that follows individual stands through several years to quantitatively assess if the trajectories of each stand will eventually merge with the next older

stand measured in the chronosequence (Yanai et al. 2000).

If 2–4% of a given sagebrush management area is burned annually, the oldest sagebrush stands would be 25–50 years old, which may be fairly similar to pre-European conditions (Miller et al. 2000). During the four centuries prior to 1940, fires were thought to have burned about 4% of sagebrush steppe in the Columbia River basin annually (Barrett et al. 1997). In eastern Oregon prior to 1871, mountain big sagebrush burning intervals were about 15 years, but fires virtually ceased around 1900 owing to livestock introduction and fire suppression (Miller and Rose 1999). Both prescribed burns and wildfires have the potential to improve forage quality and quantity for grazing, especially if perennial grasses have been well established before the fires (West and Hassan 1985). Overall, prescribed burning in mountain big sagebrush communities is likely to improve ecosystem sustainability and rangeland health and provides predictable relationships between time since disturbance and plant functional type cover and leaf area index.

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