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LANDSCAPE-SCALE CHANGES IN PLANT SPECIES ABUNDANCE AND BIODIVERSITY OF A SAGEBRUSH STEPPE OVER 45 YEARS

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Abstract. Increasing demands on arid and semiarid ecosystems, which comprise one-third of Earth's terrestrial environment, create an urgent need to understand their biodiversity, function, and mechanisms of change. Sagebrush (*Artemisia*) steppe, the largest semiarid vegetation type in North America, is endangered because of losses to agriculture, excessive grazing, and invasive species. Establishment in 1950 of what is now designated as the Idaho National Engineering and Environmental Laboratory (southeastern Idaho, USA) created the largest existing reserve of this extensive vegetation type. We used cover, density, and frequency data for vascular plants sampled on 79 permanent plots nine times during 45 years to (1) assess long-term changes in abundance and distribution of major species and life forms, (2) assess changes in species richness and plot similarity, and (3) test the hypotheses that plant cover and stability of cover are positively associated with species richness and that invasibility is inversely related to native plant cover and richness.

From 1933 through 1957 the area was subject to severe drought, with annual precipitation exceeding the long-term mean only four times. Cover of shrubs plus perennial grasses was 18% in 1950, and the vegetation was heavily dominated by sagebrush. Perennial grass cover was only 0.5%. With elevated precipitation after 1957, shrub cover increased to 25% by 1965, and by 1975 cover of perennial grasses had increased 13-fold. Subsequent fluctuations in cover did not track precipitation closely. Cover and density of major species were often out of phase, and correlation analyses indicated lags of 2–5 yr in responses of species or functional groups to precipitation. Aggregate species richness of the area has not changed appreciably, but richness of shrubs, perennial grasses, and forbs per plot steadily increased from 1950 to 1995. Vegetative heterogeneity also increased, with mean similarity among plots declining from 72% to 40%. Plots having higher species richness tended to maintain higher levels of cover and to vary less in cover relative to their mean level, indicating links between species richness and function. Abundance of nonnative species was negatively correlated with cover, but not with richness of native species. Thus, adequate cover of native species can render these semiarid communities more resistant to invasion. Maintaining richness and cover of native species should be a high management priority for these ecosystems.

Key words: *Artemisia tridentata*; *Bromus tectorum*; ecosystem function and species diversity; Idaho (USA) INEEL; invasibility; landscape-scale long-term data set; livestock grazing; precipitation and vegetative cover; sagebrush steppe; species richness; stability; vegetation dynamics.

INTRODUCTION

Approximately one third of the Earth's land surface consists of arid and semiarid ecosystems (Schlesinger et al. 1990), the vast majority of which are utilized for livestock production. On all continents, heavy livestock use of these ecosystems has altered plant species composition and biodiversity and often has reduced secondary productivity and increased the proportions of non-palatable shrubs (Walker et al. 1981, West 1983a, 1999, Schlesinger et al. 1990, Dean and Macdonald 1994, Milton et al. 1994). In the past decade we have seen increasing concerns about habitat quality, sustainability, losses of biodiversity, and impacts of invasive species (Walker 1993, Milton et al. 1994, West

1996, 1999). These concerns, coupled with increased demands for recreation and, in many parts of the world, agricultural production, underscore the need for a better understanding of ecological processes, the nature of long-term variation in productivity and species composition, and the mechanisms driving change in semiarid lands.

In North America, sagebrush steppe occurs on some 4.48×10^5 km² of the Columbia and Snake River Plateaus, the northern edge of the Great Basin, and southwestern Wyoming (West 1983a). Similar sagebrush communities having a lower proportion of herbaceous species occupy another 1.8×10^5 km² of the Great Basin and Colorado Plateau (West 1983b). The two types constitute the largest temperate semidesert in North America (Miller et al. 1994). Despite their areal extent, however, sagebrush-dominated communities are among North America's critically endangered eco-

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systems as a consequence of losses to agriculture, conversions to exotic annual communities, or degradation due to excessive grazing by domestic livestock (Noss et al. 1995, Christensen et al. 1996, Knick 1999). Livestock were introduced to the region in the mid 1800s, and by the end of the century the grazing capacity of most sagebrush-dominated rangelands had been exceeded (West 1983a). The original grazing capacity of the sagebrush steppe was estimated as 0.83 animal unit months (AUM) per hectare, whereas the estimated capacity in 1970 was about 0.29 AUM/ha (West 1983a). Although stocking rates generally have been reduced since the 1930s, many areas have shown little recovery and may represent new steady states with reduced diversity, depleted populations of deep-rooted perennial grasses and forbs, and increased fire frequencies due to an abundance of fire-prone introduced annuals or short-lived perennials (Miller et al. 1994).

Numerous studies of semiarid ecosystems indicate that once woody species become dominant as a result of livestock grazing or alteration of natural-disturbance regimes (e.g., fire suppression) the resulting cohort of unpalatable woody plants may persist for long periods (e.g., Smeins et al. 1976, Rice and Westoby 1978, Anderson and Holte 1981, Holechek and Stephenson 1983, Sneva et al. 1984, West et al. 1984, Austin and Williams 1988, Westoby et al. 1989, Milton et al. 1994, Wiegand and Milton 1996). Dominance by woody species is often accompanied by loss of biodiversity and low productivity of palatable herbaceous plants (West 1993, 1999). The resistance to change in such communities is a consequence of the longevity of individuals of woody species, the usurping of resources by mature individuals of those species, and the relative paucity of propagules of herbaceous species. Contemporary models of vegetation dynamics in such systems postulate that the vegetation can exist in one of various relatively stable states and that transitions between states may require some biotic or abiotic force to drive the system over a threshold (Laycock 1991, Tausch et al. 1993, West 1999). Thus we might predict that, in the absence of a major disturbance, the vegetation of a shrub-steppe heavily dominated by a relatively long-lived woody species would be quite static.

To test that prediction, we analyzed data from permanent plots established in 1950 at the Idaho National Engineering and Environmental Laboratory (INEEL). We assessed changes in cover, species richness, and plot similarity through time. Our first objective was to describe and account for changes that occurred during a 45-yr period. We assumed that the major drivers of vegetative change in this ecosystem would be (1) annual or longer term variation in precipitation (Le Houerou et al. 1988, Wiegand and Milton 1996), (2) biotic and abiotic disturbances including herbivory, diseases, and fire, (3) the pool of species available for dispersal and establishment, and (4) competitive interactions (Pickett et al. 1987, Pickett and McDonnell

1989). Because livestock have been excluded from 49 permanent plots (see *Methods: Permanent vegetation plots*, below) and all of the permanent plots have been free from major abiotic disturbances such as fire since at least 1950 (except for two plots that burned in 1994), those factors could be eliminated as potential causes of change. Water is the major limiting factor in this ecosystem (Caldwell 1985, Toft et al. 1989), so we predicted that changes in abundance of plant species would be correlated with precipitation patterns, but potentially constrained by propagule availability.

Our second objective was to use the long-term data set from the permanent plots to test predictions concerning relationships between species richness and functional attributes of ecosystems. Numerous recent studies (Tilman and El Haddi 1992, Naeem et al. 1994, 1996, Tilman and Downing 1994, Tilman et al. 1996, 1997a, Hector et al. 1999) as well as theoretical analyses (McNaughton 1977, Tilman et al. 1997b, Loreau 1998) have shown or predicted positive relationships between species richness and plant cover or primary productivity and between species richness and the stability of cover or primary productivity. Exceptions to these patterns, particularly the positive relationship between productivity and species richness, have been reported (McNaughton 1968, 1985, Mellinger and McNaughton 1975, Hooper and Vitousek 1997, Wardle et al. 1997), and the design and interpretation of some studies have been challenged (Johnson et al. 1996, Grime 1997, Huston 1997). While some authors claim an emerging consensus that "on average" higher diversity *can* give rise to higher productivity and greater stability of ecosystem processes (McCann 2000, Purvis and Hector 2000), a lively debate continues (Hector et al. 2000, Huston et al. 2000, Naeem 2000, Wardle et al. 2000). Many studies addressing these predictions involved artificial communities grown in controlled-environment facilities (e.g., Naeem et al. 1994, 1996) or field experiments in which species composition was manipulated (e.g., Tilman and El Haddi 1992, Tilman and Downing 1994, Tilman et al. 1996, Hooper and Vitousek 1997, Hector et al. 1999). We reasoned that if such relationships were general and robust they should be apparent in the dynamics of long-term data from permanent plots. Therefore, we predicted that mean vegetative cover on the permanent plots would be positively correlated with species richness and that vegetative cover would tend to be more stable on plots having higher species richness.

The third objective of our study was to test two hypotheses concerning invasibility. Another prediction concerning the functional effects of biodiversity is that communities having more species are more resistant to invasion (Elton 1958, Fox and Fox 1986, Holdgate 1986). Conflicting results have come from studies of intact ecosystems (Lonsdale 1999, Chapin et al. 2000), but in experiments where diversity was manipulated, "communities with more species are often more resis-

tant to invasion" (Purvis and Hector 2000:217). We predicted that the abundance of introduced species would be inversely correlated with native-species richness on the permanent vegetation plots at the INEEL. Assuming that cover would reflect the resource space occupied on a plot, we also predicted that the abundance of introduced species would be inversely correlated with cover of native species.

Grime (1997:1261) speculated that high biodiversity might be "vitally important" in semiarid or other ecosystems that experience "drastic fluctuations" on seasonal or longer time scales. Demonstrating that any of the postulated relationships between biodiversity and ecosystem function hold for a natural sagebrush steppe could have important implications for sustainable management of semiarid ecosystems globally.

METHODS

Study area

In 1950 and 1957, 2315 km² of sagebrush steppe on the upper Snake River Plain (southeastern Idaho, USA) were purchased or withdrawn from the public domain to form what is now designated as the Idaho National Engineering and Environmental Laboratory (INEEL, Fig. 1). About 43% of the area has been closed to grazing by domestic stock since at least 1957. Most of that area has been closed to grazing since 1950, and, before that, grazing was restricted on much of the land when it was used as a Naval gunnery range during World War II. The absence of anthropogenic disturbances over most of the area coupled with data from permanent vegetation plots provides a unique opportunity to study landscape-scale vegetation dynamics in a large area of natural sagebrush steppe.

The INEEL is on the western edge of the upper Snake River Plain in southeastern Idaho, USA (43° N, 112° W) (Fig. 1). Average elevation of the areas covered by this study is ~1500 m (range: 1460–1620 m). Mean annual temperature is 5.6°C; the frost-free period averages ~90 d but has ranged from 68 to 123 d over 45 yr of record (U.S. National Oceanic and Atmospheric Administration [NOAA], *unpublished data*). Characterized by high-magnitude diurnal and seasonal temperature fluctuations, the climate is typical of that of the region occupied by sagebrush steppe (West 1983b, Caldwell 1985, Smith et al. 1997). During summer, low humidities and clear skies result in high temperatures and high evaporative demand during the day and relatively low temperatures at night due to rapid radiative cooling. Winters are cold, with several months having mean temperatures below freezing. Snow cover may persist for periods of a few weeks to >2 mo.

The INEEL lies in the rain shadow of the numerous mountain ranges of central Idaho. Average annual precipitation is 220 mm. Precipitation tends to be uniformly distributed throughout the year except for a peak early in the growing season (Fig. 2). On average, 37%

of the annual precipitation falls during April, May, and June; May and June are the wettest months (Fig. 2). Melting snow and spring rains account for most of the annual recharge of moisture in the soil profile (Caldwell 1985, Anderson et al. 1987). In a typical year, most of the water available to plants is depleted by early summer to midsummer (Anderson et al. 1987). The predictability of the annual cycle of moisture availability has apparently selected for similar patterns of water use among the dominant species (Caldwell 1985, Anderson et al. 1987).

Surface features at INEEL reflect a long history of volcanic activity (Nace et al. 1972). Most of the area is a relatively flat plain, but the terrain is frequently broken and undulating because of underlying Quaternary basalt flows. Most soils are of aeolian origin derived from older silicic volcanics and Paleozoic sedimentary rocks from the surrounding mountains (McBride et al. 1978). Soils are primarily orthidic Aridisols, with Calciorthids being the most common great group. Accumulations of sand on the lee sides of outcrops, in depressions, and on dunes result in abrupt gradients in soil texture that may influence plant species composition over relatively short distances (Shumar and Anderson 1986).

Vegetation at the INEEL typically is characterized by an overstory of big sagebrush (*Artemisia tridentata*); two subspecies, *A. t. wyomingensis* and *A. t. tridentata*, are common (Shumar and Anderson 1986). Other common shrubs include *Chrysothamnus viscidiflorus*, *Lepodactylon pungens*, *Grayia spinosa*, *Tetradymia canescens* and *Krascheninnikovia lanata* (Table 1). Perennial grasses, including *Stipa comata*, *Elymus elymoides*, *E. lanceolatus*, *Oryzopsis hymenoides*, and *Pseudoroegneria spicata*, are typically the most abundant herbaceous perennials, but the area also supports a diversity of forbs (Table 1). In 1995, total vascular plant cover was 38%. Shrubs contributed 52% of the cover, graminoids 15%, and perennial forbs 7.5%. Annuals and biennials accounted for 24% of the total cover, of which nearly half consisted of introduced species, primarily *Bromus tectorum* (Table 1). Anderson et al. (1996) provide a general description of the vegetation and a complete flora. Nomenclature follows USDA (1995).

Use of the area occupied by the INEEL before 1950 is not well documented. Much of the upper Snake River Plain has been grazed by livestock since the late 1800s (Harniss 1968). The area was crossed by a trail used for moving cattle to eastern markets during the late 1870s, and it was used extensively for spring and fall sheep grazing. Harniss and West (1973) concluded that the area was severely overgrazed prior to 1950. The low cover of perennial grasses in 1950 supports that conclusion (Anderson and Holte 1981), but, as shown below (see *Results: Long-term trends in precipitation*), prolonged drought during the 1930s and 1940s probably exacerbated grazing impacts.

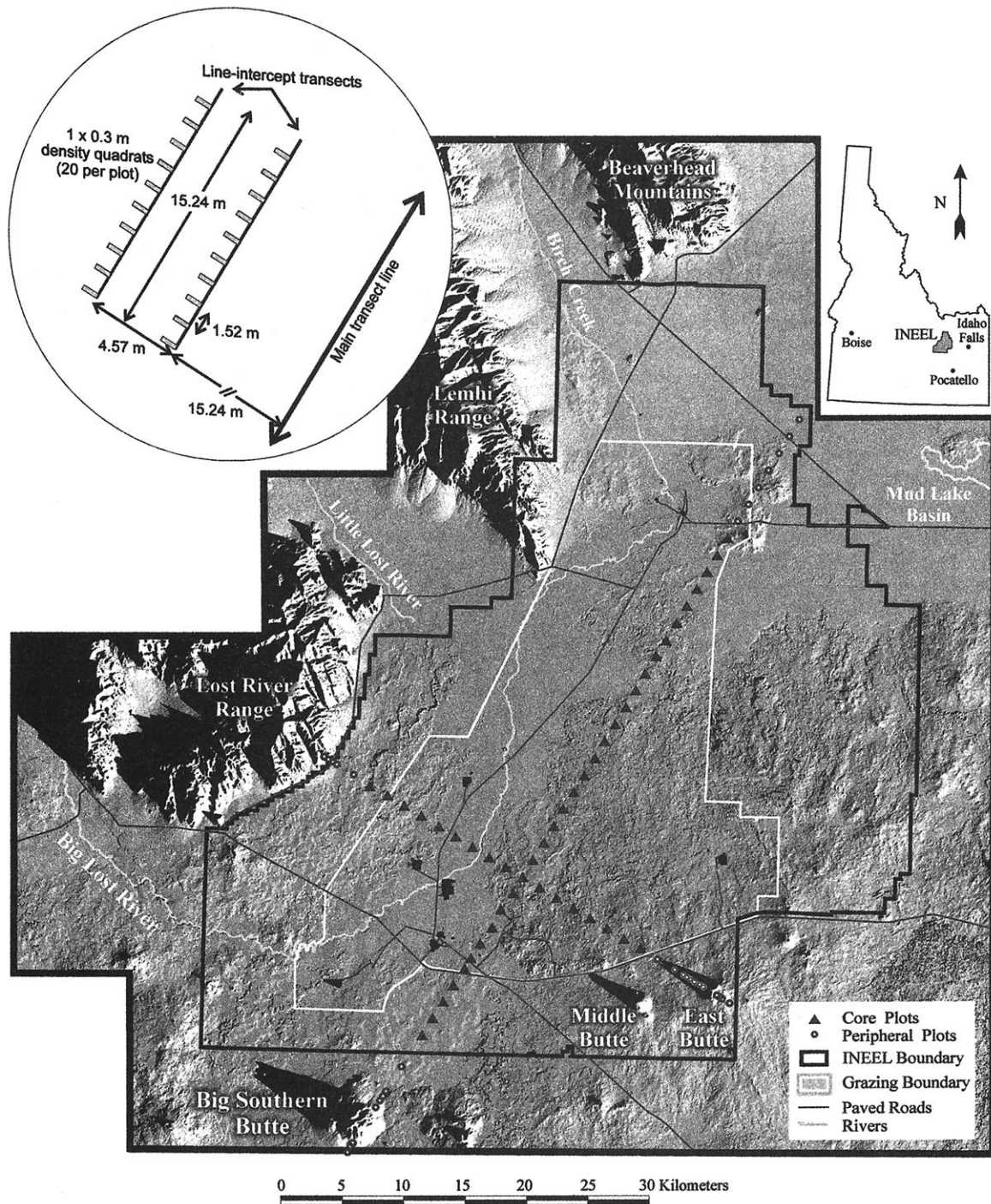


FIG. 1. Shaded relief map of the Idaho National Engineering and Environmental Laboratory (INEEL) showing the locations of the permanent vegetation plots along two perpendicular transects. The area within the white boundary is closed to livestock grazing. The left inset shows the layout of the two 15.24-m line-intercept transects and 20 density quadrats (0.3×1 m) at each of the plots; the right inset shows the location of INEEL in Idaho (USA). Elevations of core plots range from 1458 m to 1520 m on the southwest–northeast transect and from 1488 m to 1581 m on the southeast–northwest transect.

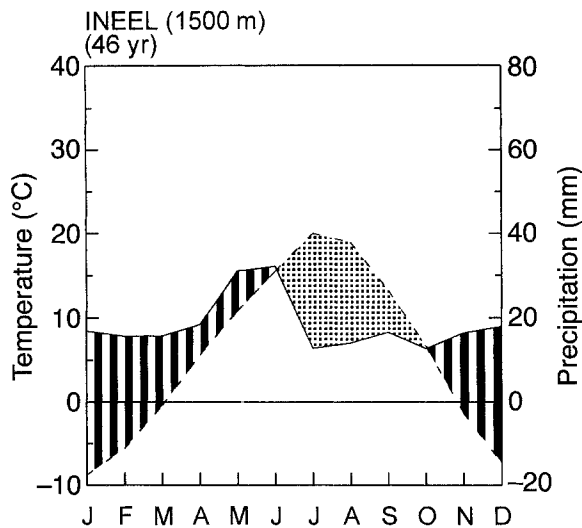


FIG. 2. Climate diagram (sensu Walter et al. 1975) for the Idaho National Engineering and Environmental Laboratory (INEEL), based on data for 46 yr from the Central Facilities Area (U.S. National Oceanic and Atmospheric Administration [NOAA], Idaho Falls, Idaho, USA, unpublished data). The solid curve depicts mean monthly precipitation; the dashed curve shows mean monthly temperatures. Vertical hatching indicates periods when precipitation generally exceeds potential evapotranspiration. The stippled area indicates periods when potential evapotranspiration generally exceeds precipitation.

Although domestic livestock have been excluded from a portion of the area since 1950, native herbivores are common and sometimes very abundant. The area provides winter range for large numbers of pronghorn (*Antilocapra americana*), and some pronghorn and a few mule deer (*Odocoileus hemionus*) are year-long residents. Elk (*Cervus elaphus*) colonized the INEEL during the mid-1980s (Moritz 1988), and two herds of about 80 animals each were present by 1989 (Strohmeier 1992). Since then, numbers have varied in annual censuses from 53 in summer to >350 individuals in winter (R. Warren, unpublished data). Populations of black-tailed jackrabbits (*Lepus californicus*) are cyclic, reaching high densities at ~10-yr intervals (Anderson and Shumar 1986). The most recent noteworthy peak in the jackrabbit population occurred in 1981 when densities reached ~2 jackrabbits/ha. Except for a minor increase in the early 1990s (Porth 1995), jackrabbit populations have been very low since 1983 (J. Anderson and R. Warren, unpublished data). Scattered populations of cottontail rabbits (*Sylvilagus nuttallii*) and pygmy rabbits (*Sylvilagus idahoensis*) also exist (Wilde 1978), and small mammals can be locally abundant (Groves and Keller 1983).

Precipitation data and estimates

Precipitation data from the station at the INEEL Central Facilities Area (CFA) are available from 1950 to present. To estimate INEEL precipitation prior to 1950,

TABLE 1. Average percent cover of vascular plants (by growth form and species) for 47 core vegetation plots at the Idaho National Engineering and Environmental Laboratory (southeastern Idaho, USA), measured by point interception in 1995.

| Plant species | Cover (%) | Relative cover (%) |
|--|-----------|--------------------|
| Shrubs | | |
| <i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> | 9.448 | 25.152 |
| <i>Chrysothamnus viscidiflorus</i> | 7.655 | 20.132 |
| <i>Artemisia tridentata</i> ssp. <i>tridentata</i> | 1.699 | 4.465 |
| <i>Leptodactylon pungens</i> | 0.539 | 1.417 |
| <i>Grayia spinosa</i> | 0.417 | 1.100 |
| <i>Atriplex confertifolia</i> | 0.352 | 0.926 |
| <i>Tetradymia canescens</i> | 0.347 | 0.914 |
| <i>Krascheninnikovia lanata</i> | 0.273 | 0.718 |
| Others (n = 4) | 0.148 | 0.423 |
| Total shrub cover | 19.74 | 51.88 |
| Perennial graminoids | | |
| <i>Elymus elymoides</i> | 1.460 | 3.838 |
| <i>Stipa comata</i> | 1.376 | 3.617 |
| <i>Elymus lanceolatus</i> | 0.985 | 2.588 |
| <i>Agropyron desertorum</i> | 0.567 | 1.492 |
| <i>Oryzopsis hymenoides</i> | 0.405 | 1.066 |
| <i>Pascopyrum smithii</i> | 0.253 | 0.665 |
| <i>Poa nevadensis</i> | 0.181 | 0.475 |
| <i>Pseudoroegneria spicata</i> | 0.149 | 0.392 |
| <i>Poa secunda</i> | 0.139 | 0.367 |
| Others (n = 6) | 0.118 | 0.311 |
| Total graminoid cover | 5.63 | 14.81 |
| Perennial forbs | | |
| <i>Phlox hoodii</i> | 1.136 | 2.986 |
| <i>Astragalus lentiginosus</i> | 0.306 | 0.805 |
| <i>Astragalus filipes</i> | 0.236 | 0.621 |
| <i>Erigeron pumilus</i> | 0.154 | 0.404 |
| <i>Astragalus ceramicus</i> | 0.148 | 0.388 |
| <i>Psoralea lanceolata</i> | 0.130 | 0.342 |
| <i>Phacelia hastata</i> | 0.128 | 0.336 |
| Others (n = 36) | 0.617 | 1.622 |
| Total perennial forb cover | 2.85 | 7.50 |
| Succulents | | |
| <i>Opuntia polyacantha</i> | 0.50 | 1.31 |
| Native annuals and biennials | | |
| <i>Descurainia pinnata</i> | 0.748 | 1.967 |
| <i>Gayophytum diffusum</i> | 0.707 | 1.858 |
| <i>Lappula redowski</i> | 0.573 | 1.507 |
| <i>Gilia sinuata</i> | 0.522 | 1.373 |
| <i>Cordylanthus ramosus</i> | 0.517 | 1.358 |
| <i>Collomia tenella</i> | 0.369 | 0.969 |
| <i>Eriastrum sparsiflorum</i> | 0.293 | 0.771 |
| <i>Machaeranthera canescens</i> | 0.273 | 0.718 |
| <i>Eriogonum cernuum</i> | 0.232 | 0.609 |
| <i>Chenopodium leptophyllum</i> | 0.204 | 0.537 |
| <i>Cryptantha scoparia</i> | 0.182 | 0.479 |
| <i>Chaenactis fremontii</i> | 0.167 | 0.438 |
| Others (n = 16) | 0.264 | 0.693 |
| Total native annual/biennial cover | 5.05 | 13.28 |
| Introduced annuals and biennials | | |
| <i>Bromus tectorum</i> | 2.280 | 5.994 |
| <i>Sisymbrium altissimum</i> | 0.710 | 1.868 |
| <i>Descurainia sophia</i> | 0.656 | 1.724 |
| <i>Alyssum desertorum</i> | 0.563 | 1.479 |
| Others (n = 5) | 0.053 | 0.140 |
| Total introduced annual/biennial cover | 4.26 | 11.21 |
| Unknowns | | |
| | 0.008 | 0.021 |
| Total vascular plant cover | 38.04 | 100.00 |

Notes: Within plant growth forms, species are listed in order of descending cover values. Cover is shown for each species having absolute cover >0.1% and for various growth forms. Relative values are based on total vascular plant cover.

data from 1950 through 1990 for three surrounding locations (Arco, Blackfoot, and Idaho Falls) were used as independent variables in a stepwise multiple regression with actual INEEL precipitation as a dependent variable. The independent variables that explained the greatest amount of variance in the actual INEEL precipitation were used to estimate precipitation from 1905 to 1949. This analysis was done separately for water-year (October through September) and for growing-season (April through July) precipitation. Data from Arco and Blackfoot together explained the greatest amount of variance in INEEL precipitation. For years in which data from one or both of these sites were missing, data from the available sites were used to estimate INEEL precipitation. None of those stations had data for 1944, so the monthly 1950–1995 data from CFA were regressed against those from Pocatello (the nearest Snake River Plain station from which 1944 data were available) to predict 1944 precipitation at INEEL. Average water-year and growing-season precipitation were calculated using estimated and actual INEEL data from 1905 through 1995. Five-year sliding averages were calculated by averaging precipitation in the current year with that in the four preceding years.

Permanent vegetation plots

Vegetation studies were initiated at the INEEL in 1950 with the establishment of 94 permanent sample plots along two perpendicular lines (Fig. 1). Most of these were at 1.6-km intervals, but intervals were shorter near the buttes on the southern and eastern sides of the INEEL. Plowing destroyed two plots before 1957. The remaining 92 plots were sampled in 1950, 1957, 1965, 1975, 1985, and 1995. A subset of 35 plots, analyzed by Anderson and Holte (1981) and Anderson (1986), was sampled in 1978, 1983, and 1990.

Forty-four plots are within the area officially closed to livestock grazing (Fig. 1). This area comprises the central portion of the INEEL, which lies at the lowest elevation. Two plots just within the northern boundary of the closed area have been grazed recently and were not included. However, we included five plots that lie outside the grazing boundary as “closed” because they have been inaccessible to livestock since the INEEL was established. For convenience, we refer to these 47 plots as “core plots” and to those in areas subject to grazing as “peripheral plots”. For the current study, we performed numerous cluster analyses and ordinations of the data from all 47 plots within the closed area and from all years. These analyses failed to identify a consistent homogenous subset of plots (results not shown). Therefore, we used data from all 47 plots for the current analyses whenever possible. For some analyses, we used data from the 35 plots that were sampled in every census year. For analyses concerning relationships between species richness and cover or change in cover, we combined data from core and peripheral plots to make the sample as large as possible.

Vegetation sampling

Cover, density, and frequency were assessed during June, July, or August, according to the original sampling design (see Anderson et al. [1978] for details). Two parallel 15.24-m transect lines were established in 1950 at each plot (Fig. 1). Crown cover of shrubs and basal cover of perennial grasses were measured by line interception (Canfield 1941) along the two transect lines (in the original sampling design, cover estimates were limited to shrubs and perennial grasses). Ten density quadrats (each 0.3×1 m) were placed at 1.52-m intervals along each transect line. The density of each perennial species in each of the 20 quadrats was recorded. Tillers of perennial rhizomatous grasses were counted as individuals. Annuals were inventoried in a 0.1×0.1 m subsection of each quadrat.

Because the original sampling design did not estimate abundance for all growth forms on a common scale, we estimated cover of all vascular plants in 1995 by point interception (Floyd and Anderson 1982) to provide a more comprehensive description of the vegetation (Table 1) and to test the hypotheses concerning invasibility. A 0.5×1 m point sighting frame, with 36 points at 0.1-m intervals, was centered at 1-m intervals over a taut tape. The plant species or other entity (e.g., bare ground) under each point was recorded to estimate canopy cover of shrubs and forbs and basal cover of graminoids. Fifteen frames were examined on each of the original transect lines; 20 additional frames were examined on a third line 20 m in length, providing a total sample of 50 frames per plot.

Data analyses

Because of discrepancies in the identification of grass species in the genus *Poa* by different investigators over the 45-yr period, the species in this group were pooled for the current analyses. Sample sizes for analyses of density data were 46 for 1950 and 40 for 1957 because some of the original data sheets are missing.

We examined relationships between cover and precipitation using both water-year and growing-season precipitation. For total shrub or total grass cover and for four common species in each of those groups (including *Poa* spp.), we tested for significant correlations between cover and precipitation in the census year, precipitation in each of the four years preceding the census year, and precipitation of the census year averaged with 1–4 preceding years. Sample size for these analyses was nine, with each point representing average cover on the core plots and either annual or average precipitation. The resulting relationships were compared to see which precipitation value was the best predictor of average cover. Because we were interested in identifying potential relationships in these analyses, we used $\alpha = 0.05$ to indicate statistical significance despite doing repeated correlation analyses. Applying a Bonferroni-

type correction to maintain a constant alpha level would have increased the probability of a Type II error. *P* values between 0.03 and 0.05 were taken as suggestive of relationships, recognizing that additional research would be required to confirm them.

To assess changes in similarity among plots through time, we calculated percentage similarity (PS) as the sum of minimum proportional abundance of each species in a pair of plots (Whittaker 1975), using data for plots that were sampled in each census year. PS was calculated for each pair of plots and the average of all pairwise similarities was calculated for each year. These annual averages were then plotted against time.

We addressed relationships between cover and species richness in two ways, and separately for shrubs and perennial grasses. First, for each sample year we tested for correlations between total cover of shrubs or perennial grasses and species richness of the same group on individual plots. Sample sizes for these analyses ranged from 35 to 94 plots, depending on the number of plots that were sampled in a given year. Second, we tested for correlations between average cover of shrubs or perennial grasses over the nine census years and average species richness of each group over the same years. For these analyses we used the subset of 35 plots that was sampled in each of nine sample years.

We tested for relationships between species richness and the stability of cover in two ways. First, we calculated the absolute change in cover of all shrubs or all perennial grasses between each consecutive pair of censuses and averaged those eight values for each plot. We then tested for correlation between mean change in cover with mean species richness for the nine census dates. We performed this analysis for the subset of 35 plots that were sampled at every census and for a subset of 78 plots that were sampled in 1950, 1957, 1965, 1975, 1985, and 1995. Second, we calculated the standard deviation and coefficient of variation of cover separately for shrubs and for perennial grasses and tested for correlations between those values and mean species richness for the same nine sample years. This analysis was performed for the subset of 35 plots that were sampled at every census. In addition to these separate analyses for shrubs and for perennial grasses, we performed similar analyses for combined cover and species richness of shrubs and perennial grasses.

RESULTS

Long-term trends in precipitation

In 1950 when the first vegetation samples were taken at the Idaho National Engineering and Environmental Laboratory (INEEL; Idaho, USA), the region was in the depths of an intense, sustained drought. From 1933 through 1956, water-year precipitation exceeded the long-term mean only four times (Fig. 3). Estimated precipitation was above the long-term mean in 1944

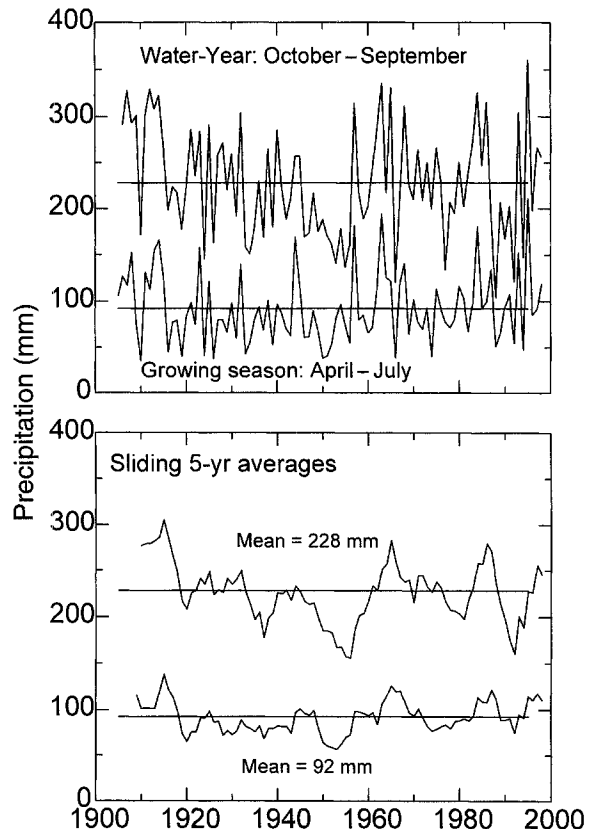


FIG. 3. Precipitation data for the Idaho National Engineering and Environmental Laboratory (INEEL). The upper curve in each panel shows water-year (October–September) precipitation; the lower curve shows growing-season (April–July) precipitation. Horizontal lines show water-year or growing-season means. Sliding averages represent the average of precipitation in the current year and four preceding years. Data for years prior to 1950 were estimated using correlations between INEEL data and precipitation at 2–3 nearby locations (see *Methods: Precipitation data and estimates*). Means shown include estimates for years prior to 1950.

and 1945, but water years from 1949 through 1956 were very dry. Five-year sliding averages show a generally decreasing trend in water-year as well as growing-season precipitation from the early 1900s through the mid-1950s, and they clearly indicate the duration and severity of the drought in the 1930s, 1940s, and early 1950s (Fig. 3). After 1956, precipitation increased markedly, and the sliding averages generally were above the long-term averages from the late 1950s through the mid-1970s. Drought in the late 1970s was followed again by above-average precipitation in the early 1980s. The late 1980s and early 1990s water years were again very dry, but 1993 and 1995 were exceptionally wet years. June 1995 was the wettest month of record at the Central Facilities Area, and precipitation during the 1995 water year was the highest in 90 yr (Fig. 3). The five-year averages suggest precipitation cycles of about 20 yr duration (Fig. 3).

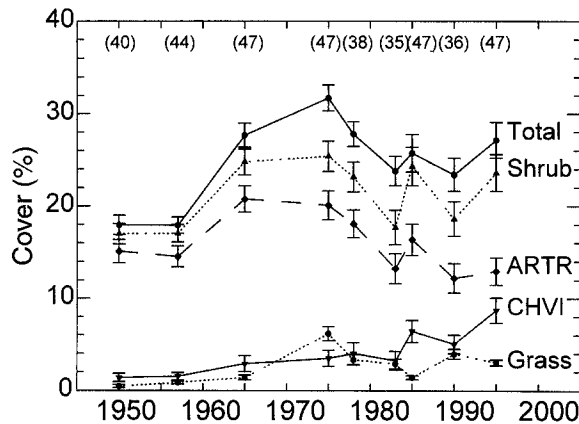


FIG. 4. Trends in total cover, shrub and perennial grass cover, and the cover of the two dominant shrubs, *Artemisia tridentata* (ARTR) and *Chrysothamnus viscidiflorus* (CHVI), from 1950 to 1995 for permanent plots at the Idaho National Engineering and Environmental Laboratory. Data are means \pm 1 SE. Numbers in parentheses at the top of the frame show the number of plots for which data are available in each census year.

Long-term trends in plant cover

Shrubs dominated vegetative cover in all sample years (Fig. 4), with cover ranging from 17% in 1950 and 1957 to a high of 25% in 1975. The dominant shrub was *Artemisia tridentata*, which contributed 84% of the shrub cover in 1950. The decrease in shrub cover after 1975 (Fig. 4) was largely due to widespread mortality of *A. tridentata* (Fig. 5). The second most abundant shrub was *Chrysothamnus viscidiflorus* (Figs. 4 and 5, Table 1). Although *A. tridentata* cover decreased markedly after 1975, that of *C. viscidiflorus* generally increased over the 45 yr. Cover of *C. viscidiflorus* in 1995 was 6.3 times that in 1950 (Fig. 5).

Populations of the small shrub *Leptodactylon pungens* were apparently very small in the early census years but had increased substantially by 1983 (Fig. 5). Its cover has remained relatively high in the most recent censuses. Cover data for the only common succulent at the study area, *Opuntia polyacantha*, were not collected in all of the censuses, but the available data show an increase between 1950 and 1965 and a decline in the most recent samples (Fig. 5).

Cover of perennial grasses was much less than that of shrubs (Table 1, Fig. 4), but their cover increased quasi-exponentially from 0.5% in 1950 to 6.2% in 1975. Following this 13-fold increase, perennial grass cover decreased and has fluctuated between 1.4 and 4.0% in recent sample years. The peak in perennial grass cover apparently lagged behind that of shrubs by a decade, but this may reflect the lack of data for intervening years.

Cover of the most common grasses increased many-fold between 1950 and 1975 (Fig. 5). Cover of *Elymus elymoides*, *Oryzopsis hymenoides*, and *Stipa comata* declined sharply after 1975, while that of *E. lanceolatus*

and *Poa* (data not shown) remained high between 1975 and 1983, but then dropped sharply by 1985. Cover of *E. lanceolatus*, *E. elymoides*, and *S. comata* increased between 1985 and 1990, and all but *E. lanceolatus* remained high in 1995 (Fig. 5). In contrast, cover of *O. hymenoides* has remained low over the past decade, at about the same level that it was in 1957.

Although there were cases where high cover coincided with wet periods (e.g., cover of *A. tridentata* in 1965), there was no case where the cover of a common species appeared to closely track precipitation (Fig. 5). Furthermore, neither total cover of shrubs nor of perennial grasses was correlated with either water-year or growing-season precipitation received in the years the samples were taken ($P > 0.25$ in all cases). In only one case was cover of an individual species or species group correlated with water-year precipitation of the years the samples were taken; combined cover of *Poa* spp. was positively but weakly correlated with water-year precipitation ($P = 0.050$; all others $P > 0.25$). Similarly, cover of only one species or species group was correlated with growing-season precipitation of the sample years, namely a positive correlation for *Atriplex confertifolia* ($P = 0.032$; all others $P > 0.14$).

In no case was total cover or cover of a member of either shrubs or perennial grasses correlated with precipitation received in the year preceding the sample year. However, a number of significant relationships between cover and precipitation received from three to five years earlier were found. Total cover of perennial grasses and that of *Stipa comata* were positively correlated with water-year precipitation four years earlier (Fig. 6). Total shrub cover was positively correlated with water year precipitation 2 yr earlier (Fig. 6) and with mean water-year precipitation of the sample year plus three ($P = 0.054$) or four ($P = 0.022$) previous years. Similar trends are suggested for *Artemisia tridentata* (3-yr lag) and *Chrysothamnus viscidiflorus* (4-yr lag) (Fig. 6). Surprisingly, there was a strong negative correlation between cover of *Tetradymia canescens* and growing-season precipitation received 3 yr earlier (Fig. 6). Cover of *T. canescens* was also negatively correlated with mean water-year precipitation for the sample year plus three previous years ($P = 0.018$).

Long-term trends in density of plants

There were no obvious correlations between long-term changes in plant density and precipitation patterns (Figs. 7 and 8). Mean density of shrubs has changed little over 45 yr, but the standard errors for mean shrub densities for 1950 and 1957 were much higher than those for subsequent years (Fig. 7). Density of the dominant shrub, *Artemisia tridentata*, has decreased considerably in recent decades (Fig. 8), corresponding with its decrease in cover (Fig. 5). Concomitantly, density (Fig. 8) and cover (Fig. 5) of *Chrysothamnus viscidiflorus* were higher after 1978 than at any previous cen-

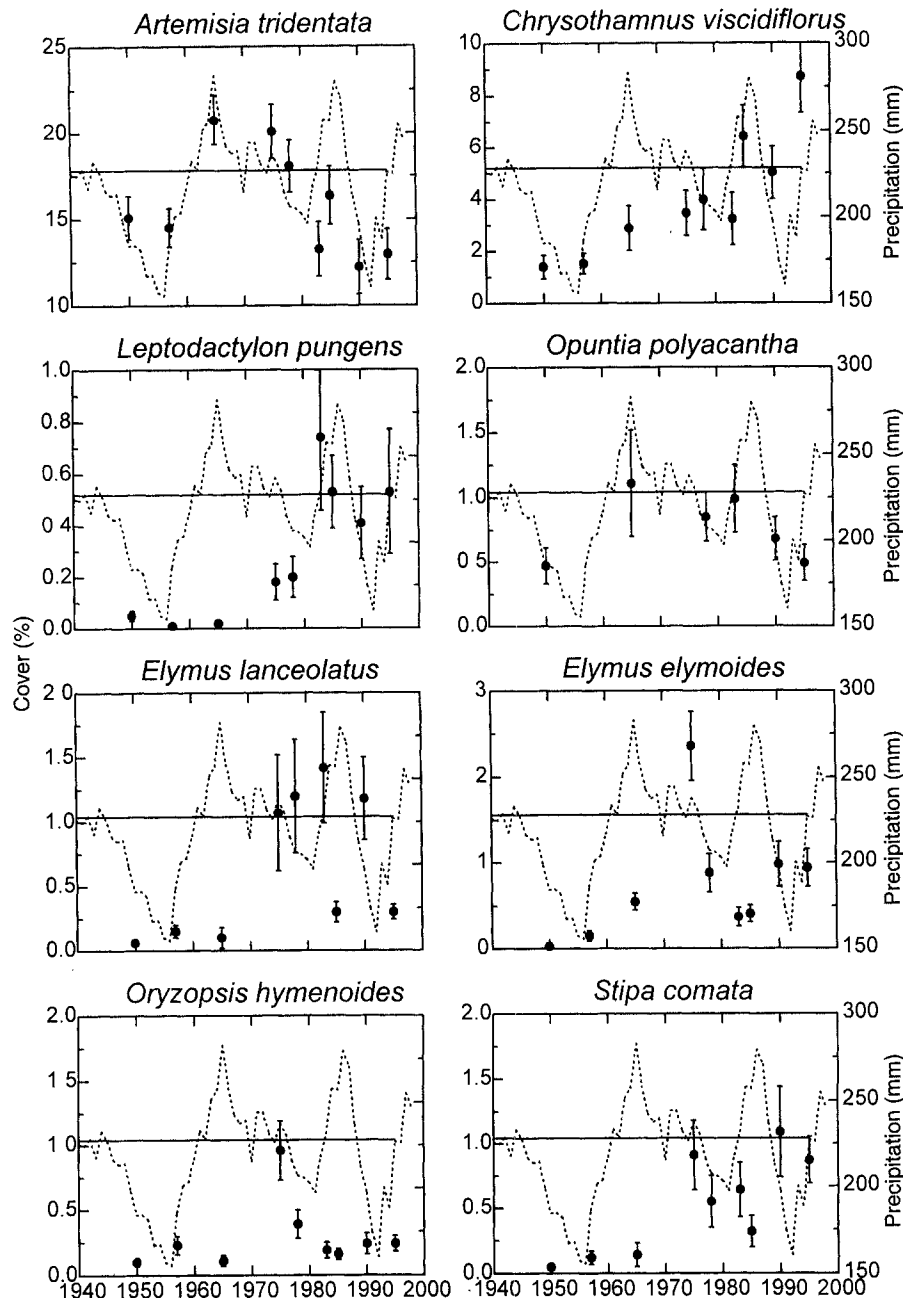


FIG. 5. Percent cover of some common perennial species at the Idaho National Engineering and Environmental Laboratory. Data are means ± 1 SE. In each panel, the dotted curve represents the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal line shows the long-term mean water-year precipitation. Cover data were not collected for *Opuntia polyacantha* in 1957, 1975, and 1985.

sus. There was no consistent trend in the density of the only common succulent on the study area, *Opuntia polyacantha* (Fig. 8).

The mean density of perennial grasses changed little between 1950 and 1978 but then increased sharply and was over two-fold higher in 1985 than in previous sample years (Fig. 7). Although the density of the most common grasses increased over the last two decades, the years of highest density did not coincide. Density

of *Elymus lanceolatus* and *E. elymoides* peaked in 1985 during a wet period, while that of *Stipa comata* was highest in 1990, during a drought (Fig. 8). Density of those three groups fluctuated widely in the most recent samples, whereas that of *Oryzopsis hymenoides* has fluctuated little over the entire 45 yr (Fig. 8). Obtaining accurate density data for rhizomatous grasses is difficult, but the density data for *Elymus lanceolatus* is closely correlated with frequency data for that species

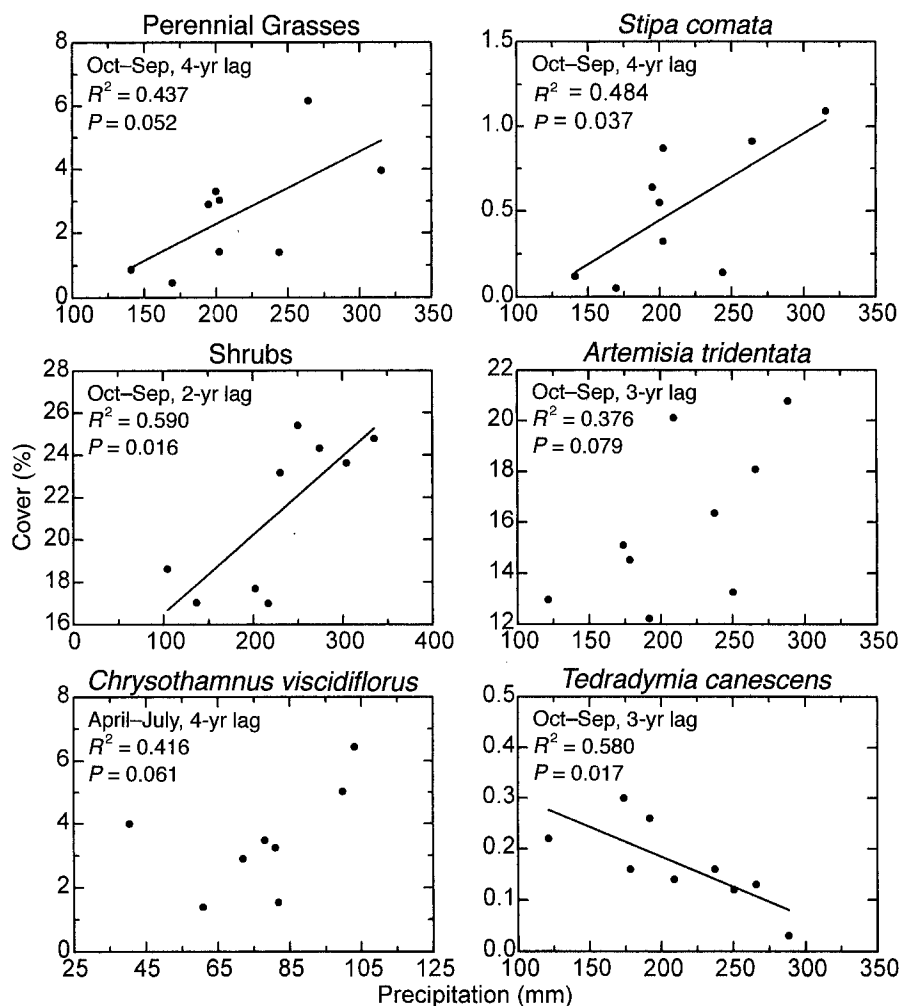


FIG. 6. Relationships between mean cover and precipitation. For each species or group of species, the figure presents the most significant relationship between mean cover and annual or growing-season (April–July) precipitation in the current year or any of the preceding five years.

across the core plots (mean R^2 for sample years = 0.60; $P < 0.001$ in each year). Thus, we are confident that the density data are indicative of the number of individual plants.

The mean density of perennial forbs remained quite low between 1950 and 1965, but increased significantly over the past two decades (Fig. 7). Forb density in 1995 was about three times that recorded in the earliest samples. Density of annuals has varied considerably, but no trend is apparent (Fig. 7). Density of annuals was much higher in 1975 than in any other sample year, apparently a consequence of abundant precipitation and a cool spring and early summer (R. Jeppson, *personal communication*). That was also the year of the highest recorded shrub and perennial grass cover (Fig. 4).

In most cases, trends for density have not paralleled those for cover. For perennial grasses, shrubs, and for all but one of the common species in those groups, mean cover was not correlated with mean density

across the eight years for which both cover and density were sampled. The only species for which this relationship was significant was *Stipa comata* (core plots, $R^2 = 0.53$, $n = 8$, $P = 0.042$; all plots, $R^2 = 0.49$, $n = 8$, $P = 0.056$).

Relationships between shrub and grass cover, and changes in plot similarity through time

There were significant negative correlations between cover of perennial grasses and cover of shrubs in seven of the nine sample years (Fig. 9). This analysis also shows that the plots have become more heterogeneous in terms of vegetal cover since 1950. In 1950 shrub cover ranged from 1.2 to 30% across the plots sampled, whereas values ranged from 3 to 48% in 1975 and from 1.2 to 62% in 1995. This increase in heterogeneity is apparent in the amount of scatter on the abscissa of Fig. 9. Similarly, scatter on the ordinate of Fig. 9 indicates variation in grass cover. Cover of perennial

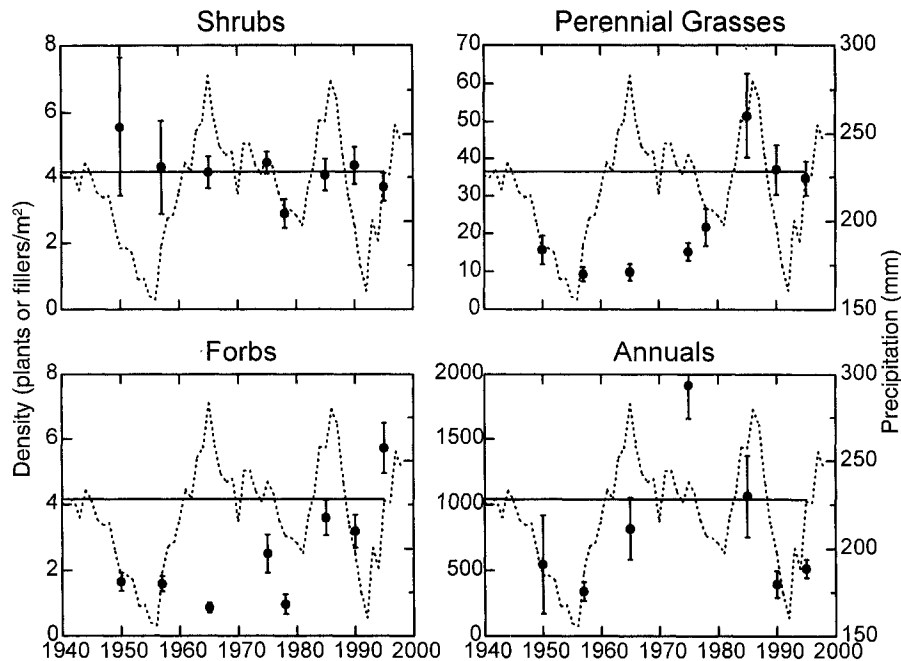


FIG. 7. Density of four plant groups at INEEL. Data are means \pm 1 SE. The dotted lines represent the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal lines show the long-term mean water-year precipitation.

grasses across plots ranged from 0 to 6.5% in 1950, from 0.6 to 27% in 1975, and from 0.6 to 8% in 1995.

This increase in heterogeneity is also reflected in a large decrease in percentage similarity among the core plots over the 45 yr of record (Fig. 10). Mean percentage similarity decreased monotonically with time, from 72% in 1950 to 40% in 1995.

Trends in species richness and relationships between richness and cover

Aggregate species richness for shrubs and perennial grasses on the core plots changed little during the 45 yr (Table 2). Only three species of perennial grasses, *Sporobolus cryptandrus*, *Stipa thurberiana*, and *Elymus triticoides*, occurred in recent censuses but not in early ones. It is unlikely that any of these are new immigrants to the general area sampled by these plots. In contrast to aggregate species richness, mean species richness per plot of shrubs, perennial grasses, and perennial forbs recorded on the line²-intercept transects and in the density quadrats generally increased from 1950 to 1995 (Fig. 11). The rate of increase in richness was higher for perennial grasses than for shrubs. The mean number of species of annuals was more variable, with richness highest in 1975 and 1995, census years that had high spring/early summer precipitation (Figs. 3 and 11).

Shrub cover was positively correlated with shrub species richness in the last six of nine census years (Fig. 12). Similarly, perennial grass cover was positively correlated with perennial grass species richness in five of nine sample years (Fig. 13), but the years in

which those relationships were significant for shrubs and grasses did not always coincide. Cover of shrubs and perennial grasses combined was significantly correlated with combined species richness in four of nine years ($P < 0.05$), and in each case the relationship was positive.

Consistent with the results for individual years, average cover of shrubs was positively correlated with average shrub species richness, and average perennial grass cover was positively correlated with average perennial grass species richness (Fig. 14). Likewise, average cover of shrubs and perennial grasses combined, on 35 plots over nine census years, was positively correlated with average species richness of shrubs and perennial grasses ($R^2 = 0.16$, $P = 0.016$).

The average change in shrub cover and the standard deviation of shrub cover were positively correlated with average shrub species richness (Fig. 14), indicating that absolute shrub cover changed more from year to year on plots having more species of shrubs. Neither average change nor variability in perennial grass cover was related to average perennial grass species richness (Fig. 14), but for the core and peripheral plots combined, which were sampled in fewer years, the relationship between average change in cover and average species richness was significant and positive for both shrubs and perennial grasses ($P = 0.029$ and $P < 0.001$, respectively). Furthermore, for the 35-plot subset, change in cover of shrubs and perennial grasses combined was positively correlated with combined average species richness ($P = 0.037$), and the standard deviation of cover of shrubs and perennial grasses combined

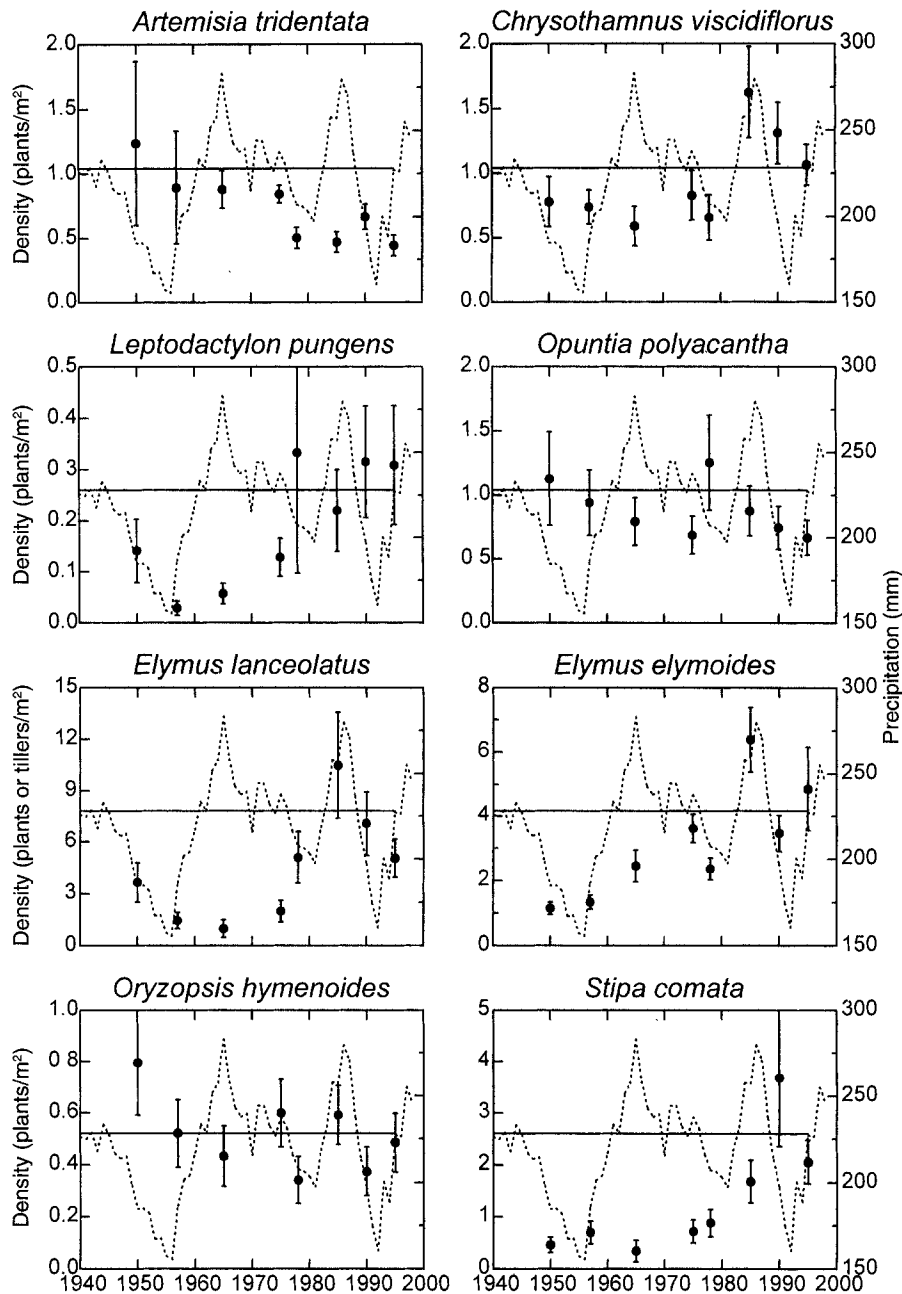


FIG. 8. Density of common perennial species. Data are means \pm 1 SE. The dotted lines represent the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal lines show the long-term mean water-year precipitation.

was positively correlated with average combined species richness ($P = 0.030$).

The coefficient of variation (CV) of cover was negatively correlated with average species richness of both shrubs and perennial grasses (Fig. 14). For shrubs, CV of cover was negatively correlated with mean cover ($R^2 = 0.37$, $P < 0.001$), indicating that plots having more shrub cover tended to vary less relative to the mean cover than plots with less shrub cover. Thus, the stability of cover may be a function of some aspect of shrub cover (e.g., shrub size) rather than shrub species

richness (Huston 1997). However, for perennial grasses the CV of cover was not correlated with mean perennial grass cover ($R^2 = 0.035$, $P = 0.28$). Therefore, for this functional group, stability of cover appears to be directly related to species richness. The CV of cover of shrubs and perennial grasses combined was not significantly correlated with average combined species richness ($P = 0.25$).

We found no significant correlation between species richness and the magnitude of the change in percentage similarity as measured by the minimum, the maximum,

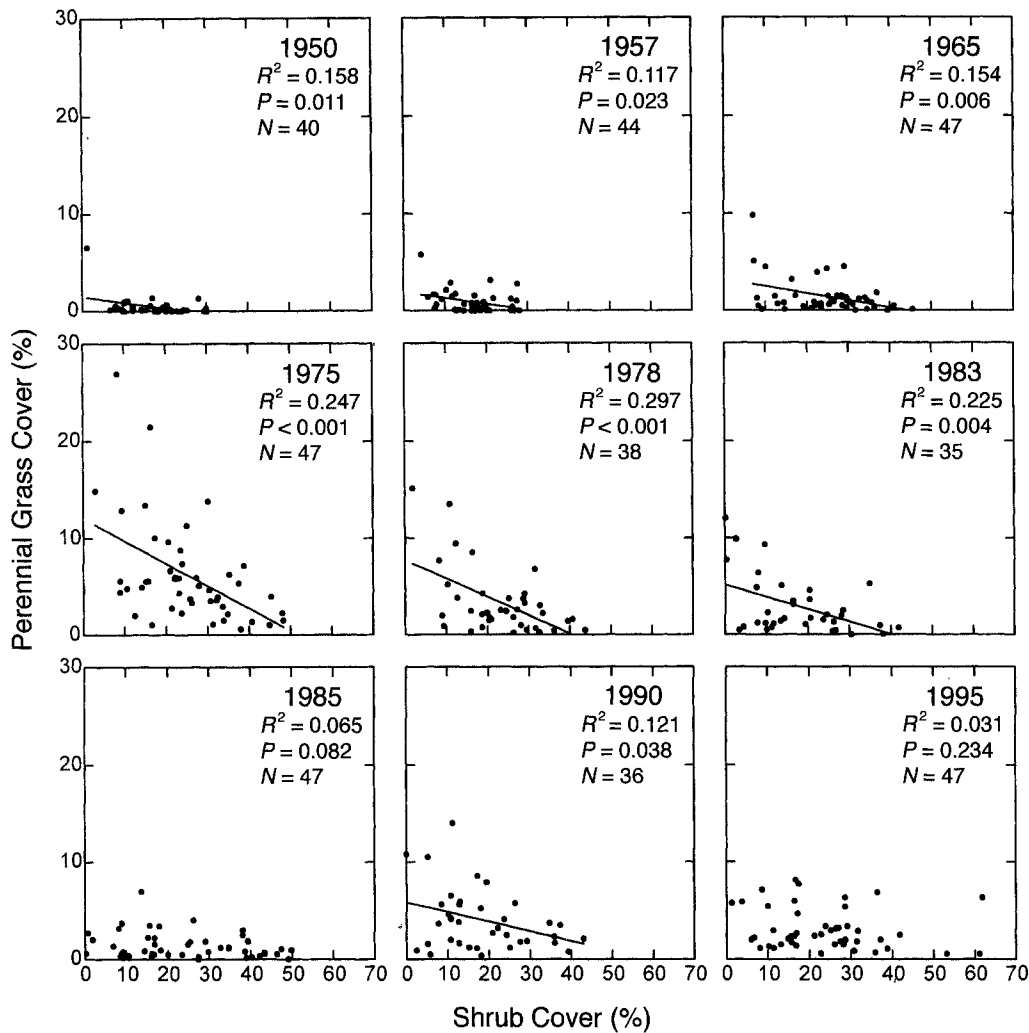


FIG. 9. Mean percent cover of perennial grasses plotted against mean percent cover of shrubs. Each graph represents one year, and each point represents one plot. Regression lines are shown for those years in which there was a significant correlation between perennial grass and shrub cover. N is the number of plots sampled in that year.

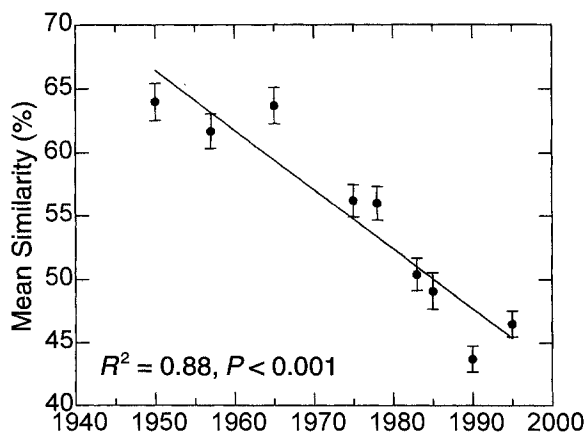


FIG. 10. Mean percentage similarity for a subset of 25 plots (see *Methods: Data analyses*), based on perennial grass and shrub cover, for each of the nine census years.

or the mean of the plotwise year-to-year comparisons ($P > 0.1$ in all cases). Thus, stability in species composition did not appear to be related to species diversity.

Relationships between cover or species richness and abundance of nonnative species

The number of plots on which nonnative species were recorded generally increased from 1950 to 1995, but the average density of nonnative species did not show any consistent trend with time (Table 3). The density of nonnative species was negatively correlated with total cover of native shrubs and perennial grasses in three of seven sample years (Table 3). Based on the 1995 point-frame data, which estimated cover for all species, cover of nonnative species was negatively correlated with cover of native species (Fig. 15A). Those

TABLE 2. Number of 35 plots on which species, or species groups, were recorded in either cover or density samples in each of eight census years, together with species richness of shrubs and perennial grasses on the aggregate 35-plot sample.

| | 1950 | 1957 | 1965 | 1975 | 1978 | 1985 | 1990 | 1995 |
|------------------------------------|------|------|------|------|------|------|------|------|
| Plant species | | | | | | | | |
| <i>Artemisia tridentata</i> † | 35 | 35 | 35 | 35 | 35 | 34 | 34 | 35 |
| <i>Chrysothamnus viscidiflorus</i> | 22 | 19 | 21 | 21 | 21 | 25 | 27 | 29 |
| <i>Leptodactylon pungens</i> | 10 | 6 | 9 | 11 | 11 | 11 | 13 | 11 |
| <i>Grayia spinosa</i> | 1 | 9 | 8 | 6 | 7 | 4 | 5 | 6 |
| <i>Tetradymia canescens</i> | 6 | 5 | 3 | 7 | 4 | 5 | 7 | 6 |
| <i>Gutierrezia sarothrae</i> | 0 | 1 | 0 | 7 | 5 | 6 | 6 | 5 |
| <i>Krascheninnikovia lanata</i> | 4 | 2 | 3 | 3 | 3 | 2 | 2 | 3 |
| <i>Eriogonum microthecum</i> | 0 | 0 | 3 | 4 | 3 | 4 | 4 | 1 |
| <i>Atriplex confertifolia</i> | 5 | 1 | 2 | 1 | 0 | 1 | 1 | 1 |
| <i>Haplopappus nanus</i> | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Artemisia arbuscula</i> | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Atriplex canescens</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Artemisia tripartita</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Elymus elymoides</i> | 28 | 27 | 33 | 34 | 31 | 30 | 30 | 30 |
| <i>Elymus lanceolatus</i> | 24 | 22 | 24 | 26 | 30 | 29 | 29 | 33 |
| <i>Oryzopsis hymenoides</i> | 23 | 22 | 18 | 29 | 25 | 25 | 21 | 28 |
| <i>Stipa comata</i> | 15 | 17 | 12 | 22 | 22 | 26 | 24 | 26 |
| <i>Poa</i> sp. | 10 | 12 | 16 | 14 | 17 | 20 | 22 | 25 |
| <i>Leymus cinereus</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| <i>Carex douglasii</i> | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 |
| <i>Stipa occidentalis</i> | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Sporobolus cryptandrus</i> | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 |
| <i>Stipa thurberiana</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Elymus triticoides</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Species richness | | | | | | | | |
| Shrubs | 9 | 10 | 9 | 9 | 9 | 9 | 9 | 10 |
| Perennial grasses | 7 | 7 | 6 | 7 | 6 | 10 | 8 | 9 |

Notes: Thirty-five plots were used in this analysis because data are available for them for the eight census years. This table includes all species that were recorded in any of the census years in which both cover and density were sampled.

† Includes *A. tridentata* ssp. *tridentata* and *A. tridentata* ssp. *wyomingensis*.

data also showed that richness of nonnative species was negatively correlated with cover of native species ($R^2 = 0.16$, $P = 0.008$) but strongly positively correlated with cover of nonnative species ($R^2 = 0.30$, $P < 0.001$).

We found no significant relationship between native species richness based on density data and the density of nonnative species. Richness of native shrubs plus perennial grasses and of native shrubs only, based on cover data, was positively correlated with nonnative species density in only one of seven years ($P = 0.043$ and $P = 0.019$, respectively). Similarly, based on the 1995 point-frame data for nonnative species, neither cover nor richness was correlated with native-species richness.

The invasive annual grass, *Bromus tectorum*, was recorded in the first vegetation samples at the INEEL in 1950, but occurred on only nine peripheral plots on the south and east ends of the permanent transects (Table 4); it was not recorded on any core plot prior to 1975 when it occurred on 17 core plots. In 1995, it was recorded on 26 of 47 core plots (Table 4) and accounted for 6% of their vascular plant cover (Table 1). Density of *B. tectorum* on the core plots was negatively correlated with total cover of native perennials in 1990 ($P = 0.011$), and a similar negative relationship was marginally significant for 1975 ($P = 0.074$). The 1995

point-frame data showed a strong negative relationship between cover of *B. tectorum* and cover of native species (Fig. 15B).

DISCUSSION

Long-term dynamics

The 1950 data support the suggestion that the area was heavily grazed by domestic livestock before establishment of the Idaho National Engineering and Environmental Laboratory (INEEL, Southeastern Idaho, USA; Harniss and West 1973). Very low cover of perennial grasses, low density and richness of perennial forbs, dominance of plots by *Artemisia tridentata* and other shrubs, and relative homogeneity of plots are all consistent with differential responses of species to heavy grazing. Composition and structure of the vegetation in 1950 were undoubtedly also influenced by the severe and prolonged drought conditions through the 1930s and 1940s (Fig. 3), as documented for other steppe ecosystems in the region (Pechanec et al. 1937, Mehringer and Wigand 1990). Under drought conditions, stress-tolerant shrubs such as *A. tridentata* are promoted (West 1983b), while faster growing but less tolerant perennial grasses and forbs suffer considerable mortality. The most palatable species—perennial grass—

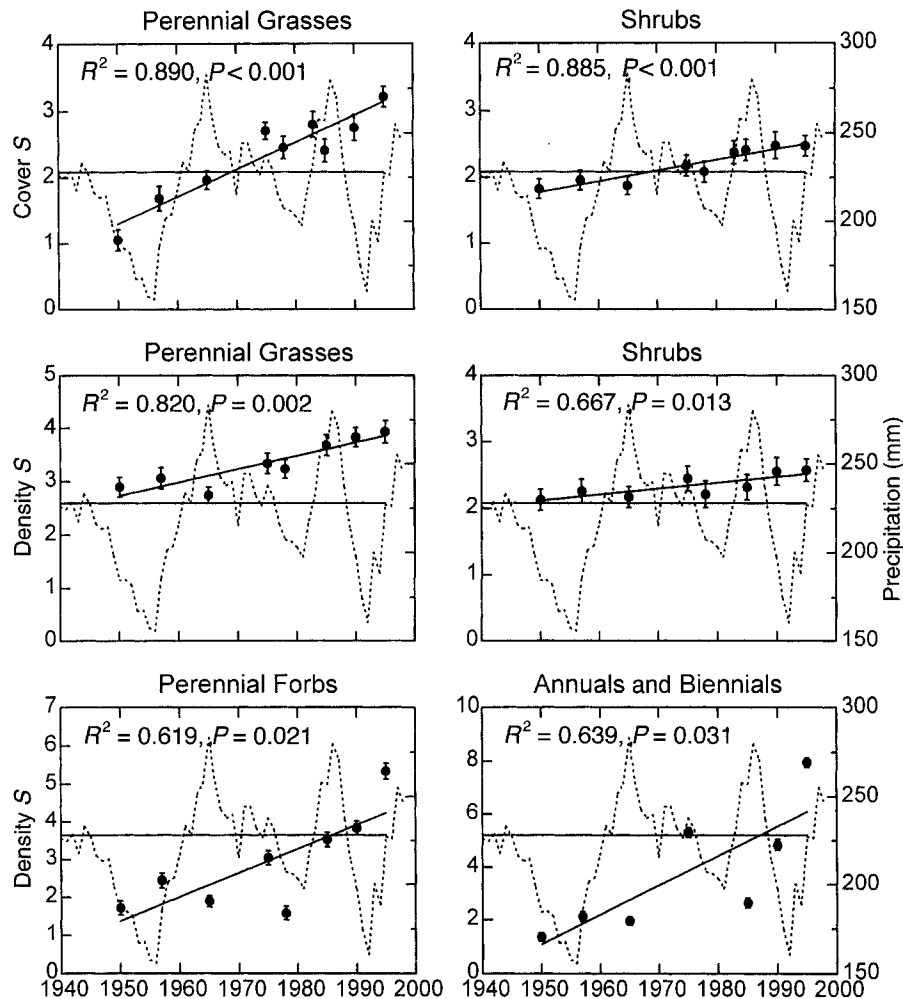


FIG. 11. Species richness (S) of perennial grasses and shrubs from line-interception cover samples (Cover S ; top two graphs) and of perennial grasses, shrubs, perennial forbs, and annuals + biennials from density samples (Density S ; bottom four graphs). Data are means \pm 1 SE. The dotted lines represent the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal lines show the long-term mean water-year precipitation.

es and forbs—are likely to be the least drought tolerant. Thus, drought and grazing have similar, synergistic effects (Pechanec et al. 1937). Widespread local extinction of populations due to either cause would tend to homogenize vegetation across the landscape.

Despite the depauperate and homogeneous conditions in 1950, vegetation on the permanent plots at the INEEL has been anything but static over the past 45 yr, clearly refuting the prediction of long-term stability under shrub dominance. Mean richness per plot of all growth forms increased steadily (Fig. 11). After the first 25 yr, cover of perennial grasses was 13 times that recorded initially. Subsequently it fluctuated more than fourfold, from 6.2% in 1975 to 1.4% in 1985, but remained high relative to 1950 (Fig. 4). In this context, it is important to note that basal cover undoubtedly underestimates the importance of perennial grasses relative to that of shrubs and forbs in these communities.

Furthermore, the substantial increase in cover of perennial grasses through 1975 was not at the expense of the shrub overstory. Shrub cover increased markedly in the first 15 yr and remained high through 1975.

Widespread mortality of *Artemisia tridentata* reduced cover of that species substantially after 1975. Extensive shrub die-off was observed throughout much of the Intermountain West during the late 1970s and 1980s, but there is little consensus about its causes (McArthur et al. 1990). Previous episodes of high sagebrush mortality in the region have been attributed to infestations of sagebrush webworm (*Aroga websterii*; Sneva et al. 1984) and high vole populations (Mueggler 1967). Other putative causes include anoxic soils and increased susceptibility to fungal parasites due to increased precipitation in the early 1980s. Vole populations were high at the INEEL in the mid-1980s, which may have caused some mortality, but it seems likely

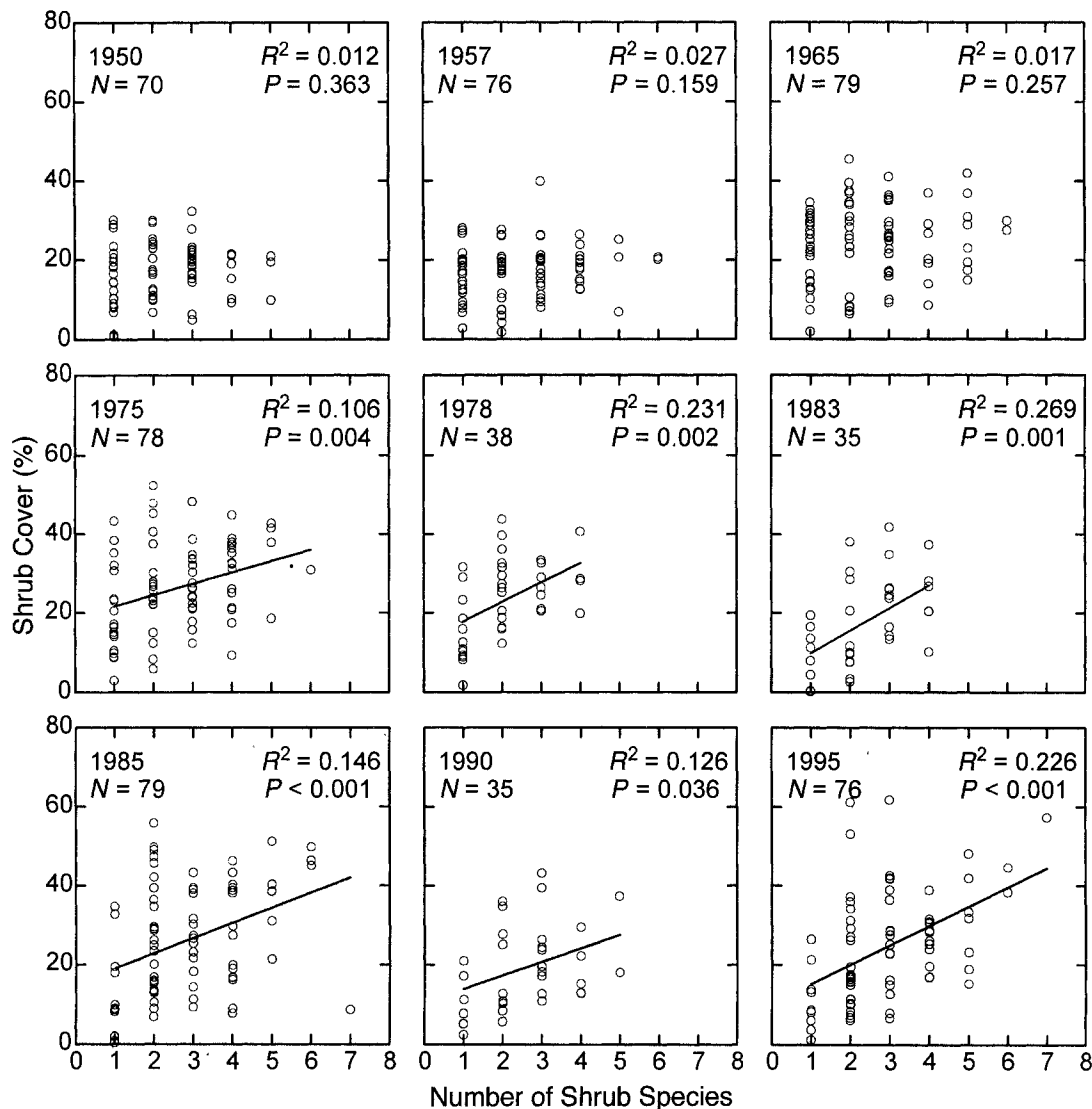


FIG. 12. Relationships between shrub cover and species richness for all plots sampled in each of nine census years. Each point represents one plot. N is the number of plots sampled in each census year.

that multiple stressors were involved because mortality continued well after vole populations declined (J. Anderson, *personal observation*).

Species richness for the aggregate 35-plot sample has not changed appreciably since 1950 (Table 2); however, the data show a general, consistent increase in species richness per plot (Fig. 9). These results suggest that the increase in richness of individual plots was not a consequence of immigration of new species or species that had become extinct at the INEEL. Instead, populations that were small and isolated in 1950 likely have increased in size and distribution, thereby increasing the number of species found on a given plot. Anderson (1986) documented an increase in the distribution of perennial grasses on 35 plots and attributed that trend to greater availability of propagules as previously depleted grass populations increased between 1965 and

1975. This trend is apparent in Table 2 for perennial grasses but not for shrubs.

Other than the increase in cover of perennial grasses during the first 2.5 decades and the general increase in average species richness, we found little evidence of directional changes in plant species composition. The only obvious directional change among the common shrub or perennial-grass species was a consistent increase in the cover of *Chrysothamnus viscidiflorus*. There was no evidence of seral replacement among the perennial grasses. Ordinations of the data from the core plots as well as from smaller subsets of plots having high similarity, using detrended correspondence analysis and nonmetric multidimensional scaling (McCune and Mefford 1995), failed to identify any common trajectories of plots through time (results not shown). Species abundance data, then, do not suggest directional

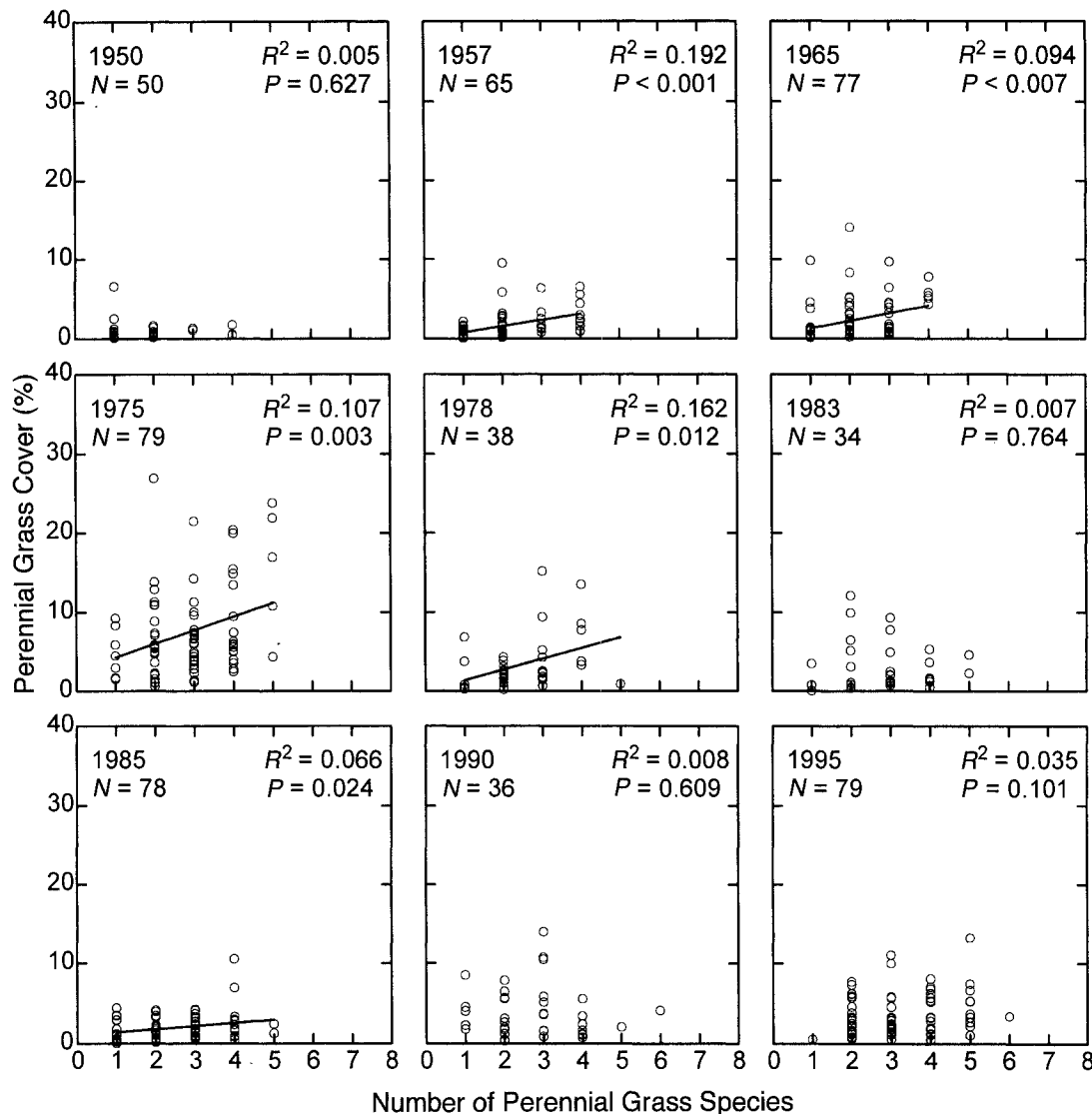


FIG. 13. Relationships between cover and species richness of perennial grasses for all core + peripheral plots sampled in each of nine census years. Each point represents one plot. N is the number of plots sampled in each census year.

succession as might have been predicted by classic models of rangeland succession (e.g., Dyksterhuis 1949, Huschle and Hironaka 1980). The substantial fluctuations in cover of shrubs and perennial grasses from 1975 to 1995 (Fig. 4) may represent the “normal” range of variation characteristic of sagebrush steppe at decadal time scales.

Contemporary state-and-transition models for sagebrush steppe (Laycock 1991, West 1999) would not have predicted the observed changes in this ecosystem either, given the state of the vegetation in 1950. State II in Laycock’s (1991:431) model, “Dense sagebrush cover; depleted perennial herbaceous understory with sagebrush seedlings present,” is predicted to “remain stable for long periods of time” (Laycock 1994:269). Laycock (1991:431) argued that the threshold from that

stage to an “open stand of sagebrush with productive herbaceous perennial understory” (Stage I in the model) is difficult to cross in the absence of fire or other force that kills adult sagebrush. Our data show that such a transition occurred in 25 yr, before sagebrush cover was reduced. Abundance of the constituent species has fluctuated since then, but composition has not differed markedly from that in nearby areas considered to be pristine (Tisdale et al. 1965, Passey et al. 1982).

Why did vegetation at the INEEL not respond as contemporary models might have predicted? We think there are two primary reasons. First, some studies that have shown long-term stability of dense shrub cover were based on data from one or relatively few exclosures (e.g., Rice and Westoby 1978, Holechek and Stephenson 1983, Sneva et al. 1984), while our data are

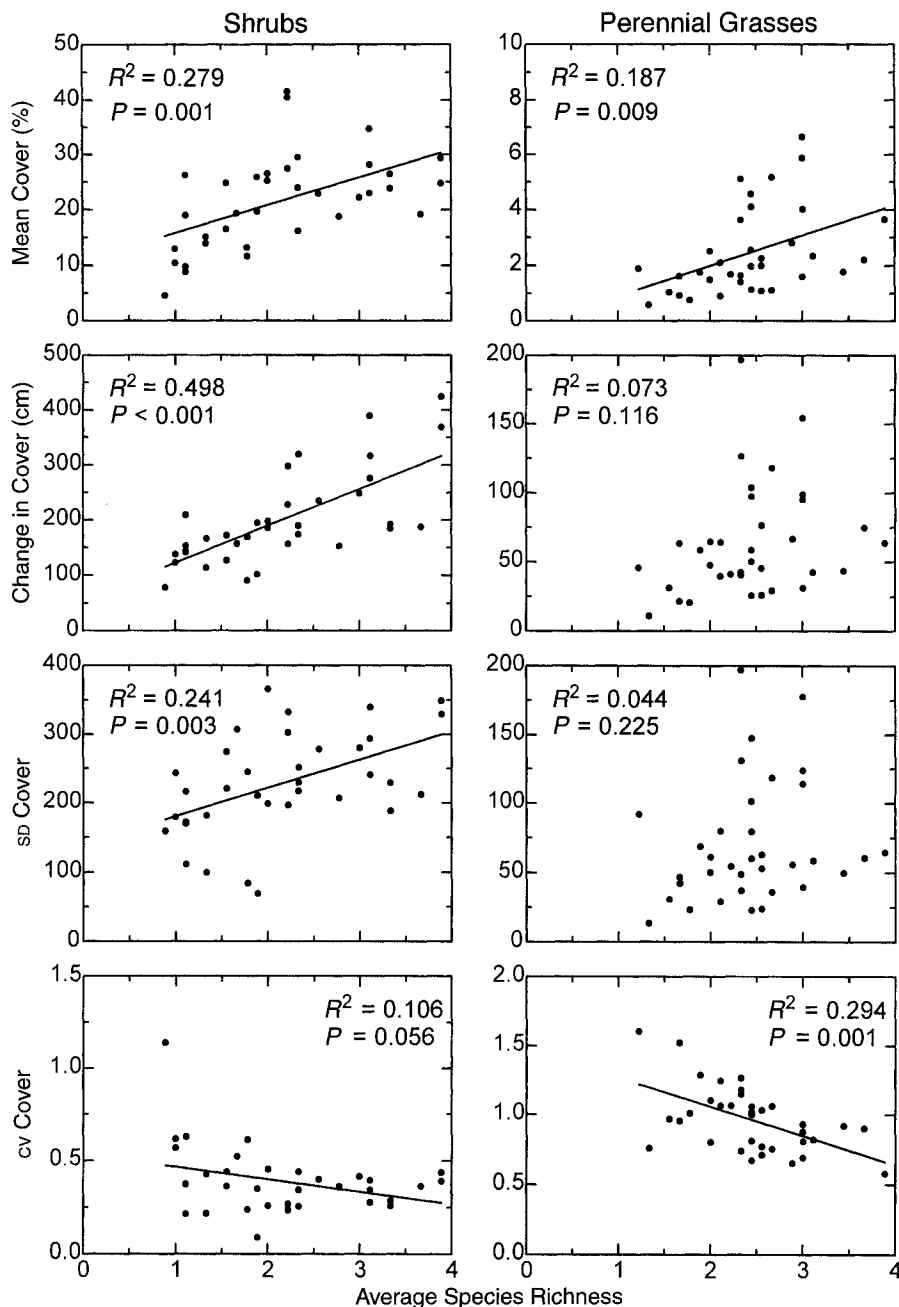


FIG. 14. Relationships between mean cover and mean species richness, for shrubs and perennial grasses, on 35 plots that were sampled in all nine census years. Mean cover is the mean from all nine census years. Change in cover is the mean of the absolute values of change in cover between subsequent censuses. Standard deviation (SD) and coefficient of variation (cv) of cover were calculated based on all nine census years.

from a large number of plots that better represent landscape-scale dynamics. Vegetation on some plots in our study has changed very little over 45 yr, while other plots have changed substantially. The second and probably more important reason for the observed changes at the INEEL is that viable remnant populations of native grasses and forbs were present in 1950 and were able to take advantage of improved growing conditions.

Indeed, a few other studies have shown that arid and semiarid communities can respond to reduced stocking rates and favorable precipitation with increased production of native perennial grasses and forbs if residual populations of such natives are present (Robertson 1971, Turner 1990, Holechek et al. 1994).

Another factor that may have facilitated the transition was the rarity of *Bromus tectorum* and other in-

TABLE 3. Results of correlations between density of non-native species and cover of native perennial species in seven census years.

| Year | N^\dagger | Mean density (plants/m ²) | Frequency ‡ | r | P |
|------|-------------|---------------------------------------|-----------------------|--------|-------|
| 1950 | 39 | 13.33 | 8 | -0.182 | 0.269 |
| 1957 | 44 | 2.7 | 21 | 0.055 | 0.725 |
| 1965 | 47 | 12.1 | 9 | -0.371 | 0.010 |
| 1975 | 47 | 14.08 | 23 | -0.333 | 0.022 |
| 1985 | 47 | 13.76 | 24 | -0.176 | 0.237 |
| 1990 | 36 | 11.81 | 27 | -0.381 | 0.022 |
| 1995 | 47 | 9.59 | 36 | -0.247 | 0.094 |

$^\dagger N$ = the number of core plots that were sampled in a given year.

‡ The number of plots upon which nonnative species were recorded.

vasive annuals on most of the core plots until 1975 (Table 4). We can only speculate about how vegetation dynamics might have differed had *B. tectorum* been abundant in 1950, but because it is so competitive with seedlings of native species (Harris and Wilson 1970, Reichenberger and Pyke 1990) it is possible that it would have slowed or precluded the growth of some native perennial populations.

Changes in plot similarity through time

The 45-yr period has witnessed a substantial increase in heterogeneity in vegetative structure among plots (Figs. 9 and 10). As the number of species per plot increased, the plots diverged in species composition and relative abundances. This is precisely the outcome that one might expect as a sagebrush rangeland recovers from the combined effects of prolonged drought and livestock grazing. Increased precipitation coupled with reduced grazing pressures allowed species to respond to the small-scale (0.1 to 100 m) differences in soil nutrients, infiltration, and runoff that create a mosaic of patches (Walker 1993) in which different species are superior competitors. Although the core plots cover an area that is fairly uniform with respect to soils, topography, and slope, these factors do vary among plots. Furthermore, samples taken at each plot cover an area large enough to include considerable variation in microtopography, soil depth, and soil resources. Substantial spatial variability in the concentrations of essential plant nutrients exists at the scale of individual plants in sagebrush steppe (Charley and West 1975, Jackson and Caldwell 1993a, b, Ryel et al. 1996). Ryel et al. (1996:299) found that "patches of high internal uniformity" of soil nutrients were generally smaller than 2 m in diameter in a sagebrush community of southeastern Idaho.

In addition to deterministic competitive outcomes, it is likely that stochastic factors also contributed significantly to the observed increase in heterogeneity. Plant establishment depends on availability of propa-

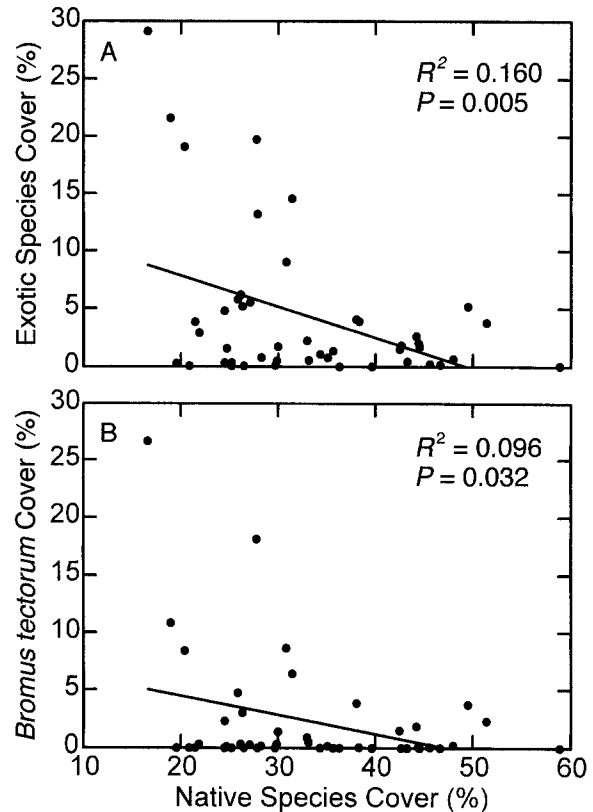


FIG. 15. Relationships between (A) exotic-species cover and native species cover and (B) between cover of *Bromus tectorum* and native-species cover based on point interception cover estimates in 1995 for the 47 core plots.

gules and arrival of those propagules at "safe sites" for germination (Harper 1977). As depleted populations recover, arrival of propagules at suitable sites depends on a multitude of factors including proximity of source plants, dispersal characteristics of the propagules, barriers to dispersal (e.g., other plants, microtopography), and the vagaries of weather (wind speed

TABLE 4. Occurrence of the invasive annual grass *Bromus tectorum* based on density data.

| Year | N^\dagger | Frequency ‡ | Mean density (plants/m ²) | Density range § |
|------|-------------|-----------------------|---------------------------------------|---------------------|
| 1950 | 39 | 0 | 0 | ... |
| 1957 | 44 | 0 | 0 | ... |
| 1965 | 47 | 0 | 0 | ... |
| 1975 | 47 | 17 | 11 | 0.5–135 |
| 1985 | 47 | 13 | 11 | 1.7–145 |
| 1990 | 36 | 21 | 11 | 0.2–67 |
| 1995 | 47 | 26 | 6 | 0.2–64 |

$^\dagger N$ is the number of core plots that were sampled in a given year.

‡ The number of plots upon which *B. tectorum* was recorded.

§ The range of densities on the plots where *B. tectorum* was recorded in that year.

and direction, rainfall amount and intensity). Priority effects may also be important as propagules arriving first may gain a competitive advantage over those arriving later.

Our data do not support Laycock's (1994:272) opinion that "if grazing were completely removed, diversity of both plants and animals on the landscape level probably would decrease on most areas of public lands" in the United States. His prediction stems from studies in grasslands showing that grazing increases patchiness of plants and reduces "a relatively few dominants in a system and they are replaced by more numerous secondary species" (Laycock 1994:264). Laycock's conclusion is probably correct for grassland ecosystems having a long evolutionary history of intense grazing pressure, but it may not be applicable to semiarid ecosystems where unpalatable shrubs are dominants (e.g., sagebrush steppe) or may quickly become dominants with heavy livestock grazing or drought (e.g., desert grasslands of southwestern United States; Buffington and Herbel 1965, Gibbons and Beck 1988). As we have argued above, livestock grazing in such shrub-dominated systems intensifies shrub dominance, reduces or eliminates populations of palatable species, and tends to homogenize vegetation at the landscape scale.

Is precipitation a major driver of vegetation dynamics in this shrub steppe?

Because availability of water is the major limiting factor in semiarid ecosystems, one might expect a close correlation between cover and precipitation (Noy-Meir 1973). Several early investigations reported strong correlations between productivity and various measures of current-year precipitation in sagebrush steppe (reviewed by Sneva and Hyder [1962]). However, these studies typically only measured forage production, and some were conducted on areas seeded with exotic perennial grasses. Other investigators failed to find significant relationships between density, cover, or biomass and precipitation (West et al. 1979, Passey et al. 1982). Passey et al. (1982) measured production for 10 yr at 17 relict sites, assumed to represent "climax vegetation;" 10 sites were within kipukas (islands of vegetation surrounded by recent lava flows) on the upper Snake River Plain that had never been grazed by domestic livestock. They found no significant correlation between water-year (October–September) precipitation and aboveground production for any of the 17 sites. Negative correlations between production and subsets of current-year precipitation in two cases appear to be spurious (Passey et al. 1982: Table 6). They concluded that both total production and production of individual species "are inherently erratic enough to preclude the development of precise production indices from precipitation data alone" (Passey et al. 1982:30).

We did not find significant correlations between cover and precipitation received during the census year. However, it is likely that the 50% increase in shrub

cover between 1957 and 1965 was in response to relatively high precipitation. Density of the most common shrubs did not increase during that period (Fig. 8), so the increase in cover apparently resulted largely from increases in the size of existing shrubs rather than from recruitment of new individuals. It also is likely that the exponential-like increase in cover of perennial grasses over the first 25 yr resulted from favorable moisture conditions in the 1960s and 1970s (Fig. 3). The sampling frequency is not sufficient to determine how closely changes in cover may track precipitation, but correlation analyses indicate there may be 2- to 4-yr lags in the responses of species or functional groups to precipitation patterns (Fig. 6). Similar lags were reported for arid chenopod shrublands in South Australia by Noble (1977), who attributed the long carry-over effects seen in some species to shoot longevity.

Lags might also result from pulses in recruitment or high mortality. The effect of mortality on cover would be apparent at the next census, but the relatively low sampling frequency may introduce what appear to be lags in response to precipitation. On the other hand, lags resulting from recruitment pulses are a consequence of the time required for recruits to reach sufficient size to contribute significantly to cover. Since the 1983 census, trends in cover of shrubs and of perennial grasses have been largely out of phase (Fig. 4). Similarly, density and cover of perennial grasses have been out of phase (Figs. 4 and 7). Following a generally wet period in the early 1980s, cover of both *Artemisia tridentata* and *Chrysothamnus viscidiflorus* had increased by 1985. Cover of perennial grasses in 1985, however, was anomalously low (Fig. 4), whereas their density was much higher than that recorded in any other year (Fig. 7). These data indicate substantial recruitment of perennial grasses in the early 1980s, but these recruits were apparently still very small in 1985. Density data (Fig. 7) suggest some mortality of perennial grasses during the drought of the late 1980s, but the survivors had increased sufficiently in stature to result in a 2.8-fold increase in perennial grass cover from that in 1985 by 1990 (Fig. 4). West et al. (1979) reported similar results from a demographic analysis of sagebrush-steppe plants in permanent plots at the U.S. Sheep Experimental Station in eastern Idaho. Although they did not find evidence for recruitment pulses according to their strict criteria, they did find years with exceptionally high numbers of seedlings. They reported that years having the highest plant densities coincided with or closely followed those having the lowest basal cover and argued that more space would be available for seedling establishment in years with low cover.

Our data indicate that individual species within the guild of perennial grasses responded individually to temporal environmental variation. Aside from a general increase in cover of grasses early on, members of this putative functional group responded differentially to environmental conditions. Cover of some species

increased between consecutive censuses, while that of others decreased, and the direction and magnitude of those differential responses varied from one census interval to the next (Fig. 8). Similar findings were reported by Passey et al. (1982:25), who observed that production of individual species “fluctuated widely from year to year, but all species in a plant community did not fluctuate to the same degree and often not in the same direction. Growing conditions favorable for one species were often unfavorable for another.”

There is no obvious explanation for the negative relationship between the cover of *Tetradymia canescens* and precipitation received three years earlier (Fig. 6), but the strength of the relationship suggests that it is not a spurious result. It provides yet another example of the differential responses of species within a putative functional group (shrubs) to an environmental variable. Given such differential responses of species, lags between recruitment events and maturation, plasticity in the size of individuals independent of their age (West et al. 1979), and stochastic variation in timing and amounts of precipitation, we should not expect to see close correlations between precipitation and cover of individual species or functional groups, even if precipitation is a major driver of vegetation dynamics in this system.

Cover data for perennial grasses and shrubs indicate that, at least in certain years, competition may affect the abundance of some species. There were significant negative correlations between grass cover and shrub cover in years when the abundances of these groups were highest. The pattern of change in cover of these two groups suggests that grass cover is constrained on plots with greater shrub cover (Fig. 9). These data are consistent with the hypothesis that biotic interactions, such as competition or predation, can play important roles in determining the distribution and abundance of plant species at the site, but that their effect is controlled by the availability of water. Because the availability of water is highly variable in time, the responses of vegetation to changes in the type and intensity of disturbance probably take longer here than in many other systems that are limited by resources that are less variable in time. Furthermore, the large variation in precipitation on both year-to-year and longer-term time scales may be important in ensuring the coexistence of shrubs and perennial grasses in this ecosystem. This variation contributes to the dynamics that preclude convergence on a stable species composition at the scale of an individual sample plot.

Relationships between species richness and cover

Grime (1997:1261) speculated that high biodiversity might be “vitally important” in semiarid and other ecosystems that “experience drastic fluctuations on a seasonal or longer time scale.” Our results support this view by providing evidence for links between plant species diversity and function in sagebrush steppe. Our

positive correlations between cover or stability of cover and species richness are consistent with those of recent studies from experimental plots in which species composition was manipulated (e.g., Tilman and El Haddi 1992, Tilman and Downing 1994, Tilman et al. 1996, 1997a, Hector et al. 1999). We found similar relationships in an ecosystem where water is the major limiting factor—an ecosystem having different dominant species, a different dominant growth form, and lower overall vegetative cover than the more mesic sites in Minnesota (USA) studied by Tilman and colleagues and in Europe (Hector et al. 1999).

The data clearly support the prediction that cover in sagebrush steppe is generally higher in areas having greater richness of vascular plants (Figs. 12, 13, and 14). These results imply that productivity would also be positively related to species richness. The relationship held for shrubs and perennial grasses separately, but not always in the same year (Figs. 12 and 13). These results indicate that species diversity within functional groups may be at least as important as functional-group diversity in this ecosystem type, in contrast to the results from grasslands (e.g., Hooper and Vitousek 1997, Tilman et al. 1997a).

We see three hypotheses to account for a positive relationship between cover and species richness. The first is that in plots having more species there is better use of limiting resources because of niche diversification in resource-acquisition patterns; consequently, those plots produce higher total vegetative cover (McNaughton 1993, Tilman et al. 1996). Tilman et al. (1996) reported positive correlations between vascular-plant cover and species diversity in experimental plots as well as in native savanna in east central Minnesota and offered evidence of more complete utilization of available soil nitrogen on plots having more plant species. It is not clear what differences in resource acquisition might have contributed to this pattern in this sagebrush steppe, but N is a limiting resource here as well (Toft et al. 1989). Bilbrough and Caldwell (1997) found differential responses to pulses of N among sagebrush-steppe species; they speculated that competition is likely intense for early spring N pulses. Thus, niche differentiation with regard to nutrient acquisition might contribute to the observed cover–richness relationship.

Unlike the grasslands of Minnesota, this shrub-steppe vegetation is clearly water limited, and plants extract virtually all of the available soil moisture each year (Anderson et al. 1987). Seasonal patterns of water use are similar among dominant perennial species because of the strongly seasonal availability of soil moisture (Anderson et al. 1987), which would limit temporal partitioning of water use within the growing season. However, there is some differentiation of rooting depths, particularly between shrubs and perennial grasses, which might increase productivity on plots where both growth forms are present. Experimental plots from which dominant *Artemisia tridentata* shrubs

have been removed show higher levels of moisture remaining deep in the soil profile at the end of the growing season (R. Inouye, *unpublished data*). Hydraulic lift of deep soil moisture allows *A. tridentata* to remain active after shallow soil moisture is depleted (Richards and Caldwell 1987) and potentially could enhance productivity of neighbors as well (Caldwell and Richards 1989). Similarly, the deep-rooted shrub *Chrysothamnus nauseosus* depends heavily on deep soil moisture reserves (Evans and Ehleringer 1994); removal of *C. nauseosus* in a natural stand indicated that it has little competitive influence on the water relations of a co-existing bunchgrass (Sirotiak 1990).

The second hypothesis to account for a positive relationship between cover and species richness is the so-called "sampling effect," the idea that when more species are present it is more likely some species will be better able to take advantage of the prevailing environmental conditions in a given year (Huston 1997). While the sampling effect is viewed by some as a statistical artifact in experiments in which species composition is randomly determined (Huston 1997, Huston et al. 2000), in a natural community the sampling effect is a mechanism by which species richness could affect productivity. This sort of temporal niche partitioning with respect to year-to-year variability in climate is thought to promote co-existence among species (Chesson and Huntly 1989, 1993, 1997), and it may in turn contribute to maintenance of higher mean levels of productivity and to reduced relative variability in productivity among years.

The third hypothesis is that the observed relationships between species richness and cover reflect a productivity gradient among the plots. Along a gradient from very low to high productivity, diversity typically is highest at intermediate levels (Grime 1973). In our situation, where productivity may be severely constrained by water availability and edaphic factors including shallow soils, we would expect plots to vary in their capacity to produce biomass. A higher capacity for biomass production on some plots may allow more species to coexist (Huston 1997).

The data from the permanent plots do not provide a basis for choosing among the three hypotheses. Furthermore, these explanations are not mutually exclusive; it seems likely that the observed relationships may reflect a combination of the suggested mechanisms. For example, legumes, especially species of *Astragalus*, are quite common across the sampled landscape (Table 1). Plots having higher species richness would have a higher probability of including N-fixing species. Thus, inclusion of legumes in the species assemblage may contribute to higher productivity accompanying higher species richness, as has been observed in various experimental grassland plots (Tilman et al. 1997a, Hooper and Vitousek 1997, Hector et al. 1999).

Relationships between species richness and stability of cover

Species diversity has been linked to various indices of functional stability in natural communities (McNaughton 1993), including resistance to drought (Frank and McNaughton 1991, Tilman 1996) and grazing (McNaughton 1985). Data from the INEEL permanent vegetation plots provide additional evidence that cover tends to be more stable on plots having higher species richness. Whereas the magnitude of year-to-year change in absolute cover was higher on plots having more species of either shrubs or perennial grasses, the change in cover relative to the mean value per plot was lower (Fig. 14). At least for perennial grasses, greater stability appears to be directly associated with species richness (see Fig. 14). These findings have important implications for the sustainable management of semi-arid rangelands. The observation that the absolute magnitude of change in cover from year to year is higher on more diverse plots implies that such plots will respond with higher increases in productivity during periods of favorable moisture. Furthermore, greater stability of relative cover on more diverse plots implies that more productive plots will tend to maintain higher levels of productivity during unfavorable times.

Relationships between species diversity or cover and invasibility

Lonsdale (1999:1533) described the idea that communities richer in native species are less invasible as "a commonly accepted ecological truism." His analysis of global patterns of plant invasions failed to support that generalization; instead, he found that exotic-species richness often is positively correlated with native-species richness because "exotic species richness responds to greater habitat diversity in the same positive way" as does that of native species (Lonsdale 1999:1533). Similarly, we found no evidence that the number or abundance of exotic species was negatively related to native-species richness. For some census years, however, as cover of native species increased, the density, richness, or cover of exotic species decreased. Thus, good cover of perennial species in sagebrush steppe appears to increase resistance to invasion.

Bromus tectorum is among the most invasive of introduced species in the Intermountain West. By increasing fire frequency (Whisenant 1990) and out-competing native perennial grasses (Reichenberger and Pyke 1990), *B. tectorum* has effected the conversion of millions of hectares of sagebrush-steppe to annual communities. Data from the long-term vegetation plots indicate a very rapid expansion of the distribution of *B. tectorum* at the INEEL in the decade between 1965 and 1975, and the number of plots upon which it was recorded has generally increased in more recent samples (Table 4). The distribution of *B. tectorum* at the INEEL is somewhat limited by edaphic factors; it oc-

curs rarely on sites having fine-textured, clayey soils (Rasmuson 1996). Although *B. tectorum* has spread to most areas having coarser soils, it has displaced the native vegetation on those areas only infrequently. The 1995 point-frame data indicate that cover of *B. tectorum* is strongly inhibited by cover of native species (Fig. 15B). Studies of postfire vegetation on areas burned recently by wildfire show that invasion by exotic species is severely limited on areas where perennial grasses and forbs resprout in abundance (S. Buckwalter and J. Anderson, *unpublished data*). Thus, the bulk of the evidence available suggests that where native plant populations in sagebrush steppe are thriving, *B. tectorum* does not pose the threat that it does where populations of native perennials have been depleted.

Conclusions

We conclude that the increases in plant-species diversity and heterogeneity from 1950 to 1975 are largely the result of a recovery of vegetation from drought and grazing, reflecting an increase in the extent to which local variation in resource availability and stochastic variables determined the distribution and abundance of species. The increase in average species richness per plot, the increase in average frequency of perennial grasses, and the increase in among-plot heterogeneity with time all are consistent with this conclusion. Vegetation dynamics of this sagebrush steppe can be understood as the result of ongoing interactions between a spatially and temporally heterogeneous environment and a suite of species that differ in dispersal capacities and in their potential for establishing and/or persisting under varying environmental conditions (Brand and Parker 1995). These observations make it clear that a large-scale perspective is needed to understand the vegetation dynamics of even this relatively homogeneous sagebrush-steppe. It is simply not possible to infer trends accurately from one or a few plots.

We also conclude that species richness is an important factor driving the functioning of semiarid sagebrush-steppe ecosystems. The correlations among richness, cover, and variation in cover are highly significant and show that, regardless of the cause, plots having greater species richness tend to vary less in cover, and presumably in productivity, in relation to their mean level. Plots having greater species richness also tend to maintain higher levels of cover. In addition, adequate cover of native species appears to render these semiarid communities more resistant to invasion. Therefore, maintaining or recovering richness of native species should be a high priority.

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