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The effects of precipitation timing on sagebrush steppe vegetation

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Abstract

Changes in precipitation patterns and inputs have the potential to cause major changes in productivity, composition, and diversity of terrestrial plant communities. Vegetation response to altered timing of precipitation was assessed during a 7-year experiment in an *Artemisia tridentata* spp. *wyomingensis* community in the northern Great Basin, USA. Four permanent rainout shelters excluded natural rainfall, with seasonal distribution of precipitation controlled with the use of an overhead sprinkler system. Precipitation treatments under each shelter were WINTER, SPRING, and CURRENT. The WINTER treatment received 80% of its water between October and March; in the SPRING treatment 80% of total water was applied between April and July; and the CURRENT treatment received precipitation matching the site's long-term (50 years) distribution pattern. A CONTROL treatment, placed outside each shelter replicate, received natural precipitation inputs. CURRENT, WINTER, and CONTROL treatments had similar in soil water-content patterns and thus, there were few consistent differences in vegetation response. The SPRING treatment resulted in more bare-ground and lower plant productivity compared to other shelter treatments. This result contrasted with our initial hypothesis that shallower-rooted grasses would gain a competitive advantage over shrubs if precipitation was shifted from winter to spring. Our results also demonstrated the resilience of these communities to climate perturbation as many of the vegetation shifts did not begin until the fourth year after treatments were applied.

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1. Introduction

Precipitation exerts primary control of plant productivity and composition in semi-arid and arid land plant communities (Pechanec et al., 1937; Noy-Meier, 1973; Passey et al., 1982; Graetz et al., 1988). The frequency and seasonal distribution of precipitation play a major role in the availability of water within soil profiles, thus, strongly influencing arid land plant composition and dynamics (Graetz et al., 1988; Comstock and Ehleringer, 1992; Ojima et al., 1993; Ehleringer et al., 1999). Winter precipitation is more likely to percolate deeper into the soil profile, whereas, summer precipitation may evaporate before infiltrating (Schwinning et al., 2003). In the northern Great Basin of the United States, the majority of annual precipitation is received during the winter and early spring. This climatic regime favors growth and development of deep-rooted shrubs and cool season plants using the C₃ photosynthetic pathway (Comstock and Ehleringer, 1992). The prevalence of summer precipitation on the Colorado Plateau and Great Plains results in a higher proportion of shallower-rooted summer active species using the C₄ photosynthetic pathway (Comstock and Ehleringer, 1992; Cook and Irwin, 1992).

Climate change brought on by anthropogenic activities forecasts not only global warming but alteration of precipitation regimes by affecting timing, frequency, and intensity of precipitation events (Easterling et al., 2000; NAST, 2000; IPCC, 2001). Alteration of precipitation patterns has the potential to cause major changes in vegetation, soils, biodiversity, and ecological processes in terrestrial ecosystems (Neilson et al., 1989; Brown et al., 1997; Ehleringer et al., 2001). Experimental evidence indicates that reducing storm frequency and increasing rainfall quantity per storm increases temporal variability of soil moisture and decreases above-ground production in tall grass prairie of the central United States (Fay et al., 2002; Knapp et al., 2002). Shifting from a winter to spring precipitation pattern reduced productivity in the sagebrush steppe of the northern Great Basin (Svejcar et al., 2003, pp. 90–106). Atmospheric increases in CO₂ and climate change also have the potential to increase the competitiveness of invasive weeds in arid lands as documented by increased *Bromus tectorum* productivity in response to elevated CO₂ in southern Nevada (Smith et al., 2000).

We investigated the effects of altered timing of precipitation to vegetation dynamics in an *Artemisia tridentata* spp. *wyomingensis* community in the northern Great Basin over 7 years. We hypothesized that herbaceous plants, particularly perennial grasses, would better adapt to a shift toward a spring precipitation distribution and productivity and composition would either remain stable or increase. Perennial grasses in this system have more shallow-fibrous roots compared to *A. tridentata* (Branson et al., 1976; Reynolds and Fraley, 1989; Dobrowski et al., 1990). Evidence from ecological studies conducted in our area indicated that cool season species would respond to late spring and summer moisture with increased growth (Bates et al., 2000). We also hypothesized that a shift to a greater percentage of winter precipitation would increase cover and recruitment of *A. tridentata* compared to herbaceous perennials. Increased winter precipitation was expected to enhance water recharge in the lower part of the soil profile and thus favor

deeper-rooted species such as *A. tridentata*. Higher than average winter precipitation in the 1990s in the south-western United States may have been responsible for the three-fold increase in shrub densities observed by Brown et al. (1997). Because the precipitation pattern applied to the CURRENT treatment conformed to long-term trends, we did not expect vegetation in this treatment to change relative to ambient conditions. Further, we expected that total vegetation cover and bare ground would not be influenced by rainfall distribution.

2. Methods

2.1. Study area and experimental design

The study was conducted on the Northern Great Basin Experimental Range (119°43'W, 43°29'N), 67 km west of Burns, Oregon, USA. The study site is co-dominated by *A. tridentata* spp. *wyomingensis*¹ and perennial bunch grasses: *Stipa thurberiana*, *A. spicatum*, and *Poa sandbergii*. All herbaceous species present were cool season plants that utilize the C₃ photosynthetic pathway. Elevation is 1380 m and slope is 0–1%. Soils were classed as a Vil-Decantl, Variant-Ratto complex and are well drained with a duripan beginning at 30–50 cm (Lentz and Simonson, 1986). Gravimetric field capacity of soils was 23% (0–15 cm) and 25% (15–30 cm). Annual precipitation has averaged 300 mm since measurements began in the 1930s. Historical distribution of precipitation was 60% from October to March, 30% from April to July, and 10% in September. Annual precipitation is highly variable year to year. The wettest year on record in 1993 (530 mm precipitation) was followed by the driest year on record in 1994 (140 mm precipitation). Winter precipitation tends to be in the form of snow, although during the study period there was little snow accumulation during the winter months.

Four, fixed location rainout shelters were built in late summer 1994. The design of the shelters and sprinkler application system was described by Svejcar et al. (1999). Rainout shelters were 30 m × 12 m in size and were open on all sides. The original transparent fiberglass roof was replaced in summer 1998 with Dynaglass[®], a clear polycarbonate material.² Precipitation treatments began in fall 1994. Treatment plots were 8.0 × 8.0 m² in size with a 2 m buffer strip bordering each plot. Shelter effects to environmental conditions (soil and air temperature, PAR, wind speed, and RH) are reported in Svejcar et al. (1999). Average soil temperatures were about 1–2 °C warmer and wind speeds were 25% less under the shelters than in CONTROL plots (Svejcar et al., 1999, 2003).

Treatments were randomly assigned as WINTER, SPRING, and CURRENT under each shelter. The WINTER treatment received 80% of its water between October and March; the SPRING treatment received 80% of its water between April and July; and the CURRENT treatment received precipitation corresponding to

¹Nomenclature used is from Hitchcock and Cronquist (1987).

²Mention of trade names does not indicate an endorsement by USDA-ARS or Oregon State University.

Table 1
Precipitation distribution for the shelter treatments (WINTER, SPRING, CURRENT) and CONTROL

Year and treatment	Winter (Oct.–April) Application target (mm)	Spring–Summer (May–July)	Fall (August–Sept.)	Precipitation total
Control ^a	180	90	30	300
Current	153	40	10	203
Winter	183	20	0	203
Spring	45	158	0	203

^a50-year precipitation distribution average.

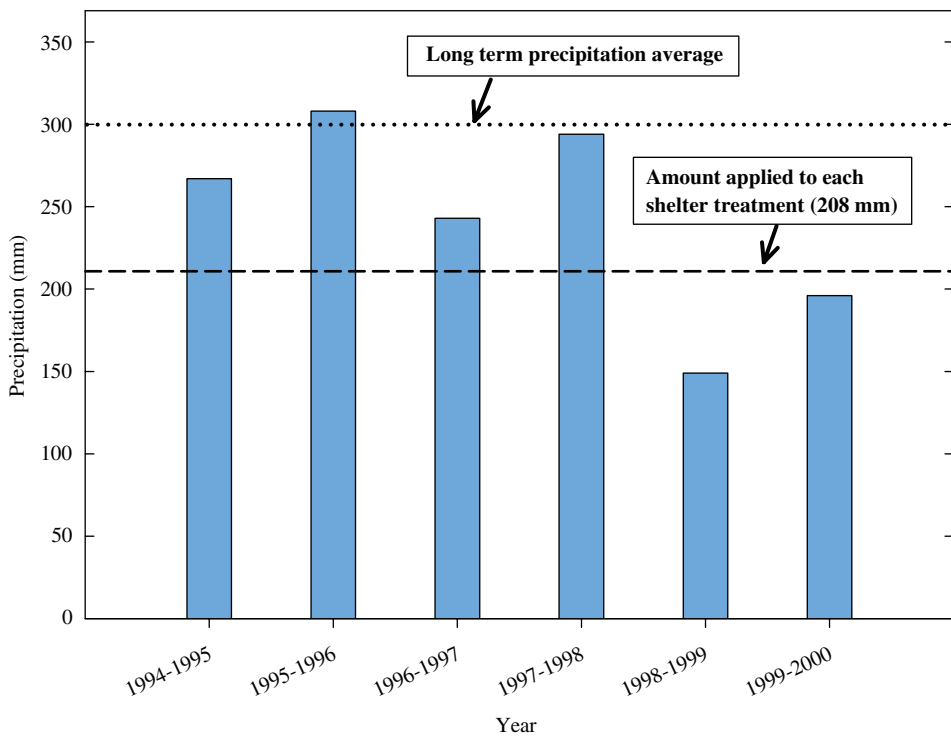


Fig. 1. Annual precipitation (mm) from 1994 to 2000 in the CONTROL and showing the long-term average for the site (300 mm) and the level applied to each shelter treatment (203 mm).

long-term (50 years) distribution patterns. The watering distribution schedule is shown in [Table 1](#). CONTROL plots of identical size were located 10 m south of each shelter and received natural precipitation ([Fig. 1](#)). All shelter treatments received a total of 203 mm of water annually, which is 68% of the site’s long-term annual average. In a natural setting this would be considered a drought. However, it was

determined in the first year of the study that applying 300 mm of water was excessive, as soils became super-saturated. Thus, the amount of water input was reduced, alleviating the saturated conditions. Because all shelter treatments received the same amount of water, the study provides an indication of effects to vegetation with shifts in seasonality of precipitation. Though less water was applied in total, more was applied in fewer events and was effective at wetting the soil profile for the WINTER and CURRENT treatments when compared to CONTROLS (Svejcar et al., 2003).

Typically, shelter treatments received annual precipitation totals in 13–20 events each year (averaging between 10 and 15 mm per event but occasionally up to 25 mm). In a natural setting, there are many smaller storm events during a given year. These small events are not that effective at wetting the soil, especially by late spring when evaporative demand increases. For example, in 1999 the control treatment experienced 90 storm events, but 67% of the events were recorded as being less than 2.5 mm of water. In the study it was not feasible, logistically and because of environmental conditions, to duplicate this number of events under the shelters.

2.2. Precipitation application and soil water-content

Water applied to shelter treatments was collected using five rain gauges placed in each experimental unit. Gauges were constructed of 2-liter plastic soft drink containers and anchored to the ground with steel rods (Wrage et al., 1994). Collected water was measured immediately after application. Precipitation in the CONTROL was determined from a tipping bucket rain gauge. Under the shelters, water application was not feasible between mid-November and mid-February because of cold air temperatures which froze sprinkler heads or caused heavy accumulations of ice on plants, with the potential to cause significant mechanical damage.

Gravimetric soil water-content was measured biweekly in the 1998 and 1999 growing season (April–September) at 0–15 and 15–30 cm. Two subsamples, randomly placed in bare interspaces were collected for each depth in each treatment replicate. Soils were weighed, dried at 106 °C for 48 h, and re-weighed to determine gravimetric water-content.

2.3. Vegetation measurements

Plant response parameters measured were shrub cover and density, herbaceous biomass, herbaceous cover and density, reproductive success, and reproductive shoot density and weight. Shrub cover was estimated by the line intercept method (Canfield, 1941). Three, 8-m transects, spaced 2-m apart were permanently established in each experimental unit. Density of mature shrubs was determined by counting all rooted plants in $8 \times 2 \text{ m}^2$ belt transects. Herbaceous cover and density were determined inside 0.2 m^2 ($40 \times 50 \text{ cm}^2$) frames. Frames were placed every meter along the 8-m transect lines (starting at 0.5 m). Cover of herbaceous plants, litter, rock, and bare ground were estimated visually. Densities of herbaceous species and shrub seedlings were determined by counting all individuals rooted

within frames. Vegetation was sampled in mid-June in 1994–2000 and early August 1995–1999.

The June sampling captured cover and density at peak production for the understory component. The August sampling was designed to capture continued growth and any changes in cover through the summer in all treatments. The two sampling dates proved unnecessary for comparing among treatments. Plants in the SPRING treatment stayed active longer but treatment relationships for cover, density, and biomass were consistent across sampling dates. Thus, presented data will focus on the June sampling.

Herbaceous biomass was determined in September 1998, June 1999, and June 2000. Plants were clipped to a 2 cm stubble height inside five, 1 m² frames in each treatment replicate. Biomass was separated into five functional groups; perennial grasses, *P. sandbergii*, perennial forbs, *B. tectorum* (annual grass), and annual forbs. *P. sandbergii* is a common perennial grass but is shallow rooted, and grows and develops earlier in the spring than other bunchgrass species (Rickard and Vaughn, 1988; Link et al., 1990).

Reproductive success was determined by tracking plant phenology from growth initiation to seed dispersal over six growing seasons (1995–2000). Phenology was collected on a weekly to biweekly schedule in 1995 and 1996 and on a weekly basis from 1997 through 2000. Reproduction was rated successful if plants completed all growth phases from initiation or germination through seed dispersal. Plants monitored were *A. tridentata* spp. *wyomingensis*, *S. thurberiana*, *Sitanion hystrix*, *Collinsia parviflora*, and, as a group, we monitored the perennial forbs *Agoseris glauca* and *Crepis acuminata*. Three individuals (*A. tridentata*, *S. thurberiana*, *S. hystrix*) or groups of individuals (e.g. *A. glauca* and *C. parviflora*) of each species were monitored in each treatment replicate. Reproductive density and shoot weights were estimated for *A. tridentata* spp. *wyomingensis*, *S. thurberiana*, and *S. hystrix* in 1998, 1999, and 2000. *Artemisia tridentata* reproductive shoots were counted within two 20 cm² frames on three plants per replicate. All reproductive shoots were then harvested, dried (at 48 °C) and weighed to obtain an average shoot weight. *Stipa thurberiana* and *S. hystrix* reproductive tillers were counted on four plants per replicate in July 1998, 1999, and 2000. Plants were clipped to a 2-cm stubble height and dried; then separated into dead, live, and reproductive components and weighed.

2.4. Statistical analysis and data presentation

A randomized block design was used with four replicates of each treatment. A repeated measures analysis of variance (ANOVA) was used to assess year (df = 6), treatment (df = 3), interaction effects on herbaceous and shrub cover, density, and reproductive success (df = 18, error df = 81). Pre-treatment data (plant cover and density) were analysed to test for pre-existing differences among treatments. Vegetation cover and density were also analysed by year using ANOVA to assist in explaining interactions. Biomass (herbaceous and reproductive) and reproductive densities were compared among treatments using a repeated measure ANOVA for randomized block design. Main effects were year (df = 2) and treatment (df = 3) and

the year by treatment interaction ($df = 6$, error $df = 21$). Soil water-content was analysed within years using repeated measures ANOVA. Main effects for soil water-content were treatment ($df = 3$), soil depth ($df = 1$), and time ($df = 19$). All statistical analyses were performed using the Statistical Analysis System (SAS Institute, 2001). Arcsine square root transformations of cover and density data were used to meet ANOVA assumptions of normality and homogeneity of variance. Non-transformed means are reported from statistical comparisons of the transformed means. Statistical significance of all tests were set at $p < 0.05$. Treatment means and their interactions were separated using Fisher's protected LSD procedure.

3. Results

3.1. Precipitation application and soil water-content

The CONTROL treatment illustrates the variability of precipitation among (Fig. 1) and within years (Fig. 2) that are characteristic of the sagebrush ecosystem. Annual precipitation amounts for the CONTROL in 1998–1999 and 1999–2000 were significantly less than the long-term average (Fig. 1, $p < 0.01$). Precipitation in the CONTROL was also less than the shelters in the last 2 years of the study. The CONTROL received five times as much water in the spring–summer (March–July) period in 1997–1998 compared to the same period in 1998–1999. Except for winter 1997–98, there was little snow accumulation during the winter months of the study. Winter precipitation during most of the study arrived as rain or wet snow that melted quickly.

CURRENT and WINTER treatments tended to have equivalent soil water-content at the start of each growing season when compared to the CONTROL in both 1998 and 1999 (Fig. 3A and B). CURRENT and WINTER treatments resulted in higher soil profile water-contents than the SPRING treatment between the months of March and May in both 1998 and 1999. Soil water-content in the SPRING treatment was greater than the other treatments from late June until mid-August in 1998 and 1999. However, soils at both depths in the SPRING treatment never reached field capacity.

3.2. Herbaceous biomass

Herbaceous biomass production was influenced by the different precipitation treatments. There was a year by treatment interaction for *P. sandbergii* biomass (Table 2). The interaction resulted from the CONTROL treatment having greater *P. sandbergii* biomass than the WINTER and CURRENT treatments in 1999, but in 2000 the WINTER was greater than CURRENT and CONTROL treatments (Fig. 4A). In both years, the SPRING treatment was significantly less than other treatments for *P. sandbergii* biomass.

Means separation indicated that the SPRING treatment was less than one or more of the other treatments for biomass of perennial grasses, perennial forbs,

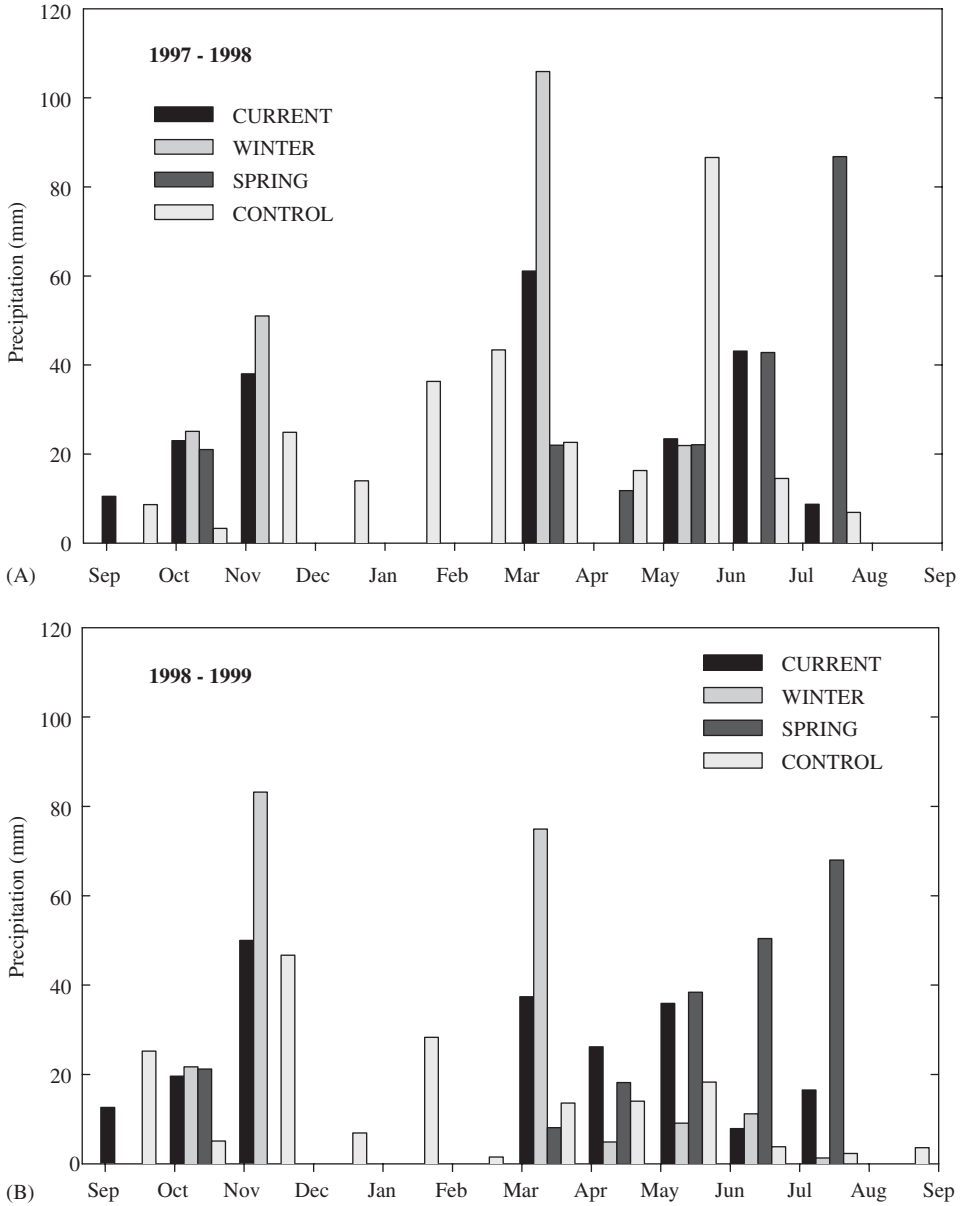


Fig. 2. Monthly water applications (mm) for the shelter treatments and precipitation (mm) in CONTROL in (A) 1997–1998 and (B) 1998–1999.

B. tectorum, and total herbaceous when compared across the three sample years (Table 2). However, when analysed by year, a consistent trend for these response variables was not obvious, except for total biomass (Fig. 4B–E). Among the three

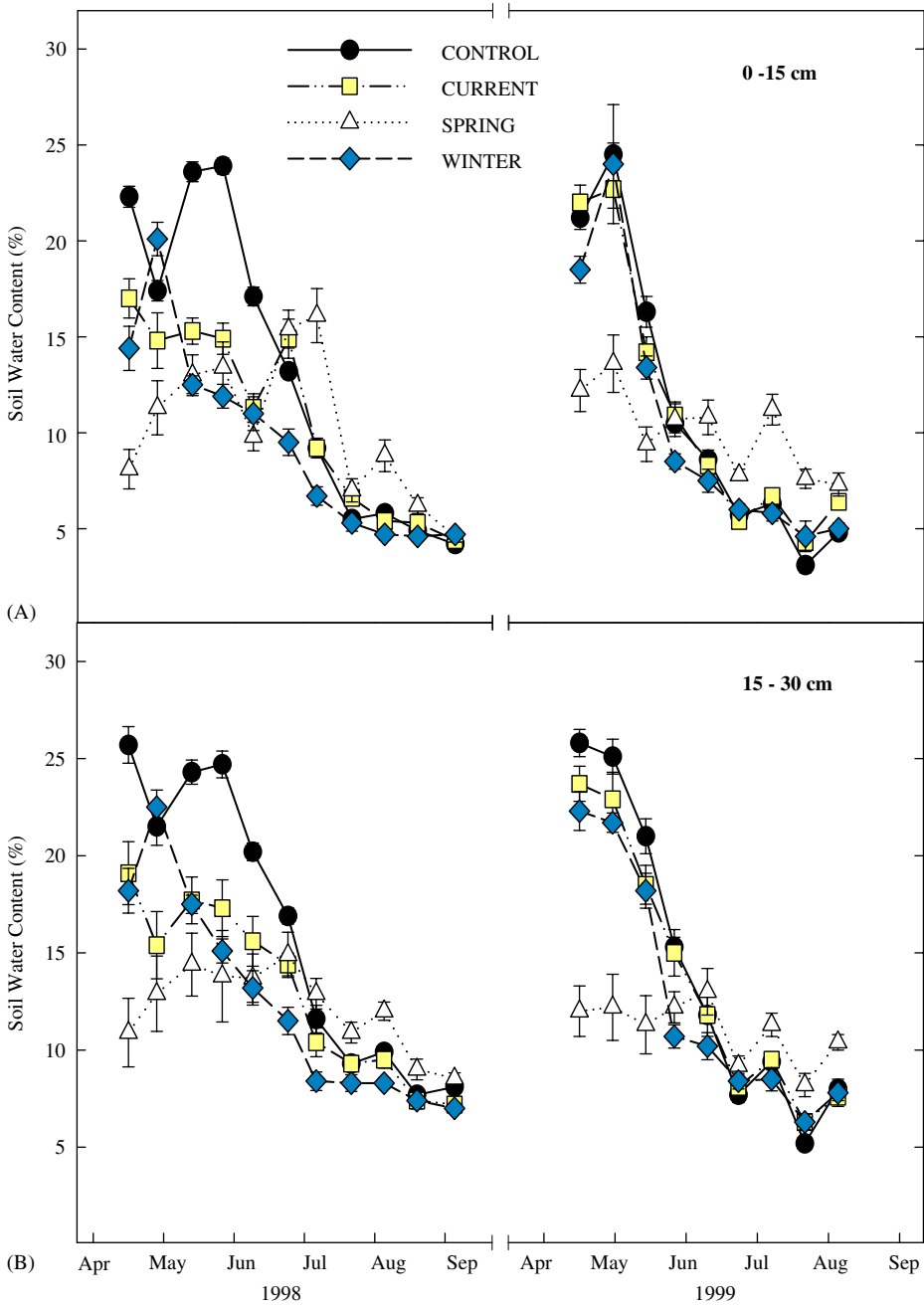


Fig. 3. Soil water-content (% gravimetric) for the shelter treatments and CONTROL at (A) 0–15 cm and (B) 15–30 cm for the 1998 and 1999 growing seasons. Values are in means \pm one standard error ($N = 4$).

Table 2
Analysis of variance *P* values for biomass, cover, and density by species and functional group for interaction and main effects

Functional group/species	Biomass (kg ha ⁻¹) ^a			Cover (%)			Density (# plants m ⁻²)		
	Year by treatment	Year	Treat.	Year by Treat.	Year	Treat.	Year by treatment	Year	Treat.
	Year by treatment	Year	Treat.	Year by Treat.	Year	Treat.	Year by treatment	Year	Treat.
<i>A. tridentata</i> spp. <i>wyomingensis</i>	—	—	—	0.9961	0.0942	0.0961	0.9474	0.4208	0.0910
<i>Poa sandbergii</i>	0.0251*	0.0230*	0.0002*	0.0041*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	0.0142*
<i>Agropyron spicatum</i>	—	—	—	0.9895	0.0583	0.2122	0.3820	0.4164	0.9876
<i>Sitacion hystrix</i>	—	—	—	0.0678	<0.0001*	0.0009*	0.0080*	0.0005*	0.0375*
<i>Stipa thurberiana</i>	—	—	—	<0.0001*	<0.0001*	<0.0001*	0.6022	<0.0001*	0.0724
Total perennial grasses	0.8657	0.4494	0.0455*	0.0069*	<0.0001*	<0.0001*	0.0258*	0.4778	0.0057*
<i>Bromus tectorum</i> (Annual grass)	0.7552	0.3164	0.0120*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	0.0261*
<i>Agoseris glauca</i>	—	—	—	0.6846	0.0010*	0.0052*	0.7403	<0.0001*	0.5296
<i>Astragalus lentiginosus</i>	—	—	—	0.4941	0.0867	0.0223*	0.5306	0.0326*	0.7124
<i>Astragalus obscurum</i>	—	—	—	0.9678	0.0014*	0.0103*	0.3866	<0.0001*	0.4370
<i>Crepis acuminata</i>	—	—	—	0.7504	0.2622	<0.0001*	0.0005	<0.0001*	0.0904
<i>Delphinium andersonii</i>	—	—	—	0.9054	0.1670	0.0100*	0.2818	0.0838	0.3312
<i>Lomatium macrocarpum</i>	—	—	—	0.0824	<0.0001*	0.0002*	0.0185	<0.0001*	0.0058*
<i>Lupinus leucophyllus</i>	—	—	—	0.2286	0.1010	0.0056*	0.4240	0.0265*	0.0444*
<i>Phlox longifolia</i>	—	—	—	0.7154	<0.0001*	0.0089*	<0.0001*	<0.0001*	0.1632
Other perennial forbs	—	—	—	0.8125	0.1791	0.0068*	0.8137	0.3438	0.0152*
Perennial forb total	0.4706	0.0008*	0.0004*	0.3219	<0.0001*	0.0002*	<0.0001*	<0.0001*	0.0292*
<i>Alyssum desertorum</i>	—	—	—	0.2413	<0.0001*	0.0031*	<0.0001*	<0.0001*	0.3216
<i>Collinsia parviflora</i>	—	—	—	<0.0001*	<0.0001*	0.0104*	<0.0001*	<0.0001*	0.0002*
<i>Descurainia pinnata</i>	—	—	—	0.2572	0.3094	0.0553	0.0982	0.0294*	0.3216
<i>Microseris gracilis</i>	—	—	—	0.0063*	<0.0001*	0.0073*	<0.0001*	<0.0001*	0.0028*
Other annual forbs	—	—	—	0.4332	0.0315*	0.7732*	<0.0001*	<0.0001*	0.0236*
Annual forb total	0.3502	0.3079	0.4281	0.0795	<0.0001*	0.0023*	<0.0001*	<0.0001*	0.0220*
Total herbaceous	0.3965	0.2597	<0.0001*	0.0004*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	0.0106*
Crust	—	—	—	0.6622	0.2266	0.6836	0.0016*	<0.0001*	0.4078
Moss	—	—	—	0.7831	0.0071	<0.0001*	0.0042*	<0.0001*	0.0074*
Litter	—	—	—	<0.0001*	0.0002*	0.0002*	—	—	—
Bare-ground	—	—	—	<0.0001*	<0.0001*	<0.0001*	—	—	—

All are cool-season (*C*₃) species. Asterisks indicate significance at the 0.05 level.
^aBiomass was grouped by functional group (species or groups are underlined), so individual species analyses are not available.

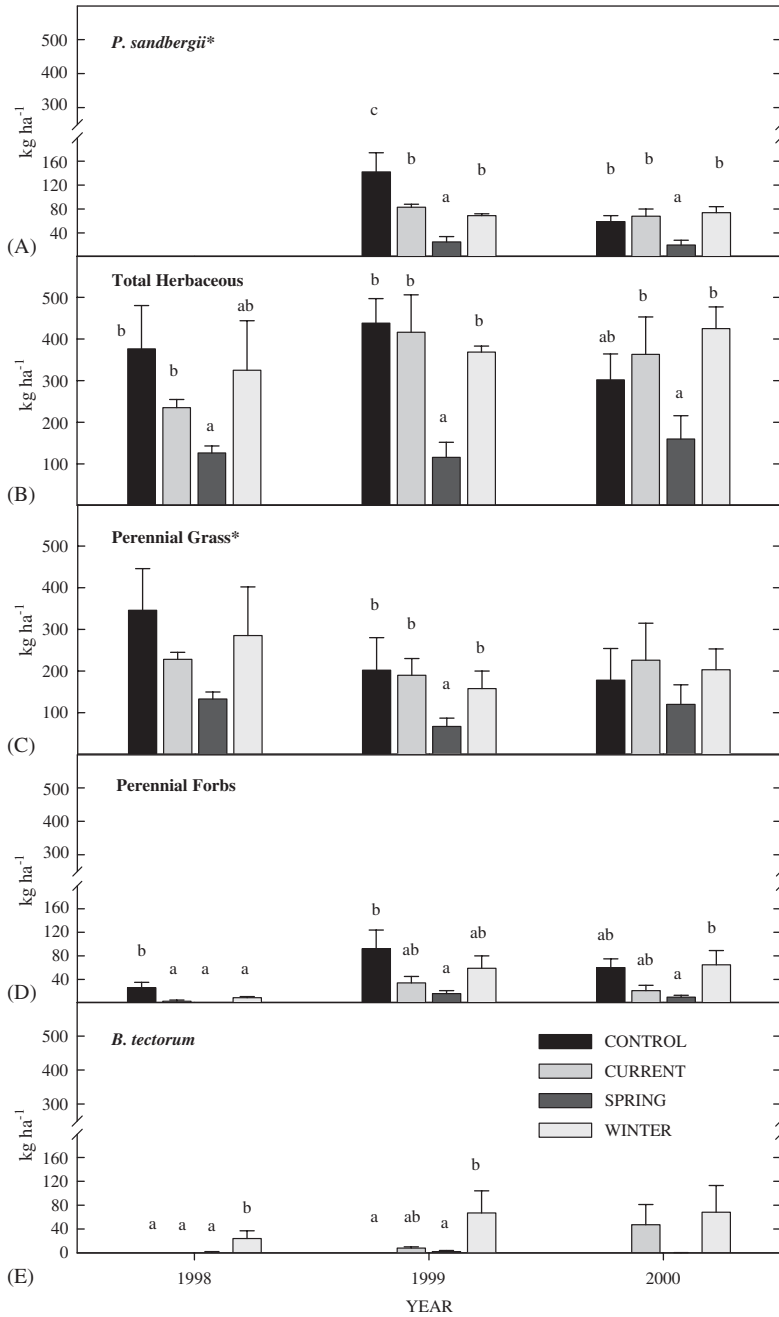


Fig. 4. Biomass (kg ha⁻¹) by functional groups and total herbaceous 1998–2000 for the shelter and CONTROL treatments: (A) *P. sandbergii*; (B) total herbaceous; (C) perennial grasses; (D) perennial forbs; and (E) *B. tectorum*. Data are in means ± one standard error. Significant differences ($P > 0.05$) among the treatments, by year, are indicated by different lower case letters.

shelter treatments, total biomass was greater in the WINTER and CURRENT treatments compared to the SPRING of the last 2 years of the study.

3.3. Plant cover—functional group response

Cover of herbaceous functional groups was also influenced by the different precipitation treatments. There were year by treatment interactions for cover of *P. sandbergii*, total perennial grasses, *B. tectorum*, total herbaceous, litter, and bare ground (Table 2). The treatment differences for these response variables did not materialize until the third (1997) or fourth growing season (1998) after treatment application (Figs. 5 and 6). Perennial grass cover only had 1 year (1997) that showed a strong treatment difference (Fig. 5A). Cover of *P. sandbergii* and perennial forbs were less in the SPRING compared to the other treatments in 1998 and 1999 (Fig. 5B–C). Cover of *B. tectorum* appeared to be establishing a trend of greater cover in the WINTER compared to the other treatments by study's end (Fig. 5D).

At a coarser scale, treatments became more distinct at the conclusion of the study, particularly total herbaceous cover. Herbaceous cover in 2000 was greatest in the WINTER followed in descending order by CURRENT, CONTROL, and SPRING treatments (Fig. 6A). The lower cover in the SPRING treatment was mainly a result of reduced cover of *P. sandbergii* and perennial forbs than the other treatments. Cover provided by litter was lowest in the CONTROL compared to the shelter treatments (Fig. 6B). Bare ground in CURRENT and WINTER treatments declined over time while not changing in SPRING and CONTROL treatments (Fig. 6C). As a result, bare ground was greater in the SPRING and CONTROL treatments compared to the CURRENT and WINTER treatments. *Artemisia tridentata* cover and density did not change nor were any treatment differences detected (Table 2).

3.4. Plant cover and density, species response

Cover and density of individual species were influenced by the different precipitation treatments. There were year by treatment interactions for cover and/or densities of *S. hystrix*, *S. thurberiana*, *P. sandbergii*, *B. tectorum*, *C. acuminata*, *Lomatium nevadensis*, *A. desertorum*, *C. parviflora*, and *Microseris gracilis* (Table 2). For several species some clear trends became obvious and are illustrated by changes in plant densities (Fig. 7A–F). *P. sandbergii* densities increased in the WINTER and CURRENT treatments between 1997 and 1999 and were greater than the SPRING and CONTROL treatments (Fig. 7A). *B. tectorum* and *Crepis acuminata* densities increased in the WINTER treatments and by 1998 were greater than the other treatments (Fig. 7B and C). However, for *S. hystrix*, *S. thurberiana*, *A. desertorum*, *C. parviflora*, and *M. gracilis* the response to precipitation applications was highly variable across years and no clear trends emerged. This is illustrated by the density dynamics of *A. desertorum* and *C. parviflora* (Fig. 7D and E).

Main effects (year and/or treatment) for cover and density were significant for most of the remaining plant species (Table 2, e.g. cover of *C. acuminata* and *L. nevadensis*, and densities of *S. thurberiana* and *A. glauca*). Cover and/or density

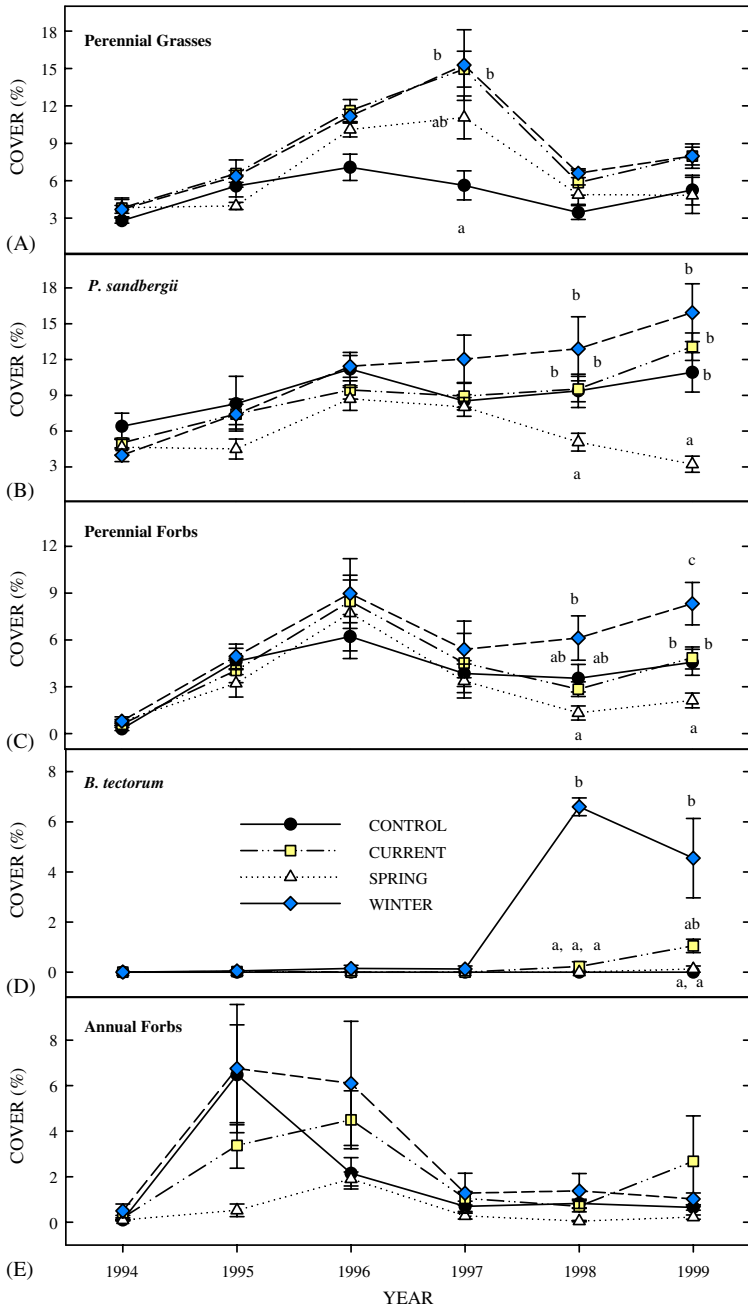


Fig. 5. Functional group cover (%) for the shelter and CONTROL treatments, 1994–1999: (A) perennial grasses; (B) *P. sandbergii*; (C) *B. tectorum*; (D) perennial forbs; and (E) annual forbs. Data are in means \pm one standard error. Significant differences ($P > 0.05$) between treatments, by year, are indicated by different lower case letters.

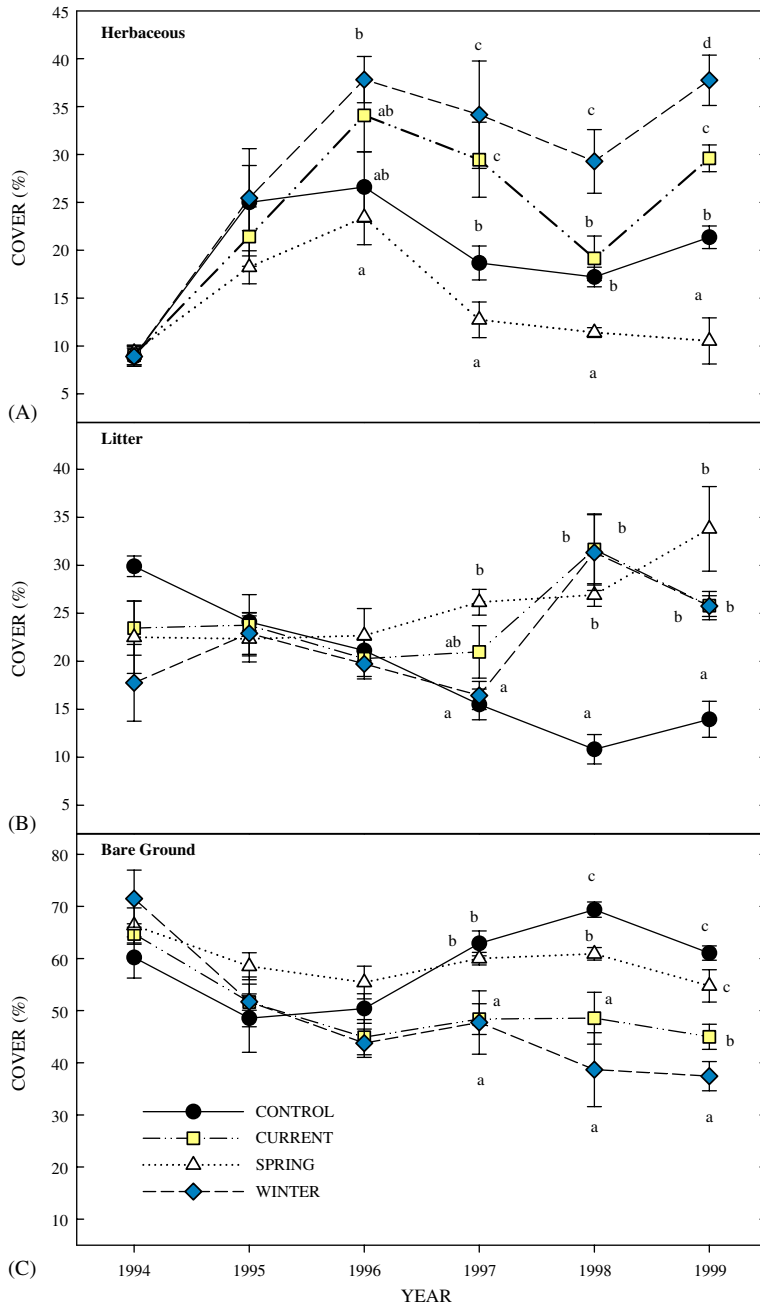


Fig. 6. Cover (%) of; (A) total herbaceous; (B) litter; and (C) bare ground, for the shelter and CONTROL treatments, 1994–1999. Data are in means \pm one standard error. Significant differences ($P > 0.05$) among treatments, by year, are indicated by different lower case letters.

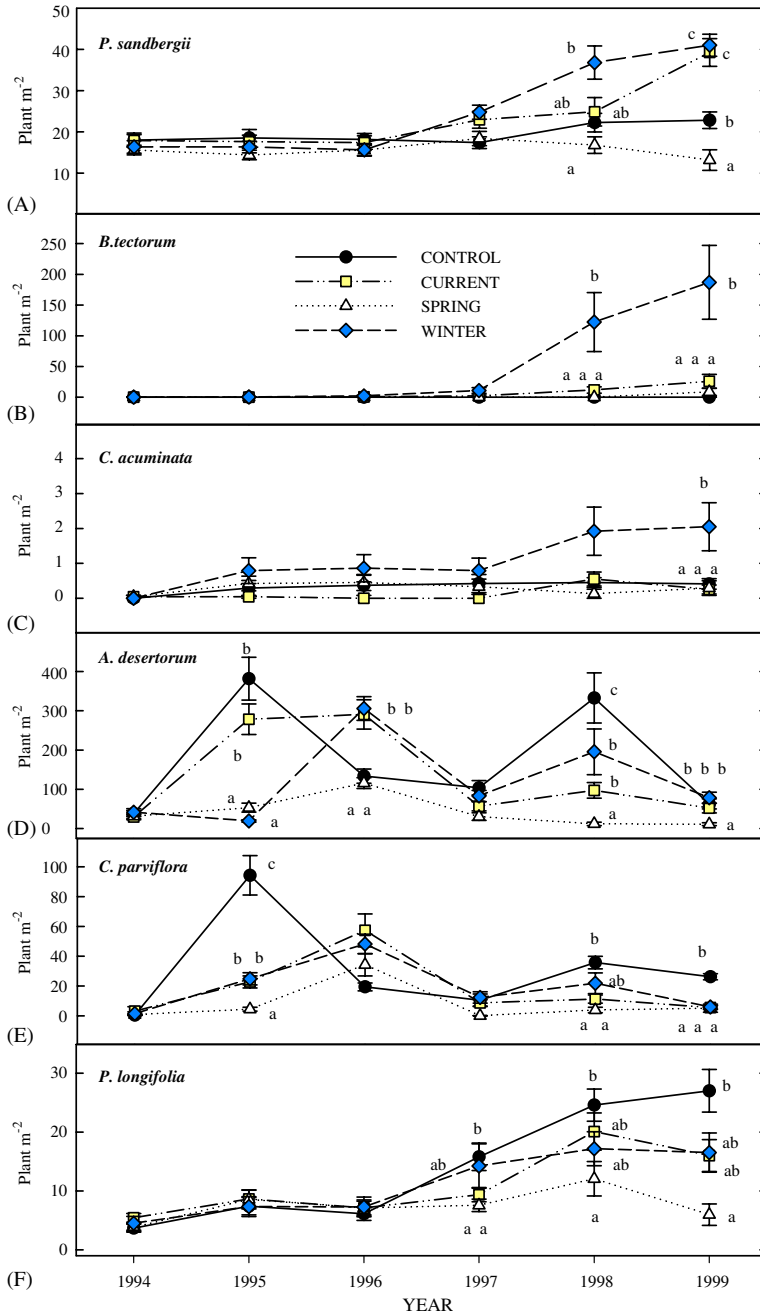


Fig. 7. Densities (plants m⁻²) of: (A) *P. sandbergii*; (B) *B. tectorum*; (C) *C. acuminata*; (D) *A. desertorum*; (E) *C. parviflora*; and (F) *P. longifolia*, for the shelter and CONTROL treatments, 1994–1999. Values are in means ± one standard error. Significant differences ($P > 0.05$) among treatments, by year, are indicated by different lower case letters.

values for these species increased for all or some of the treatments but the SPRING between 1996 and 1999. In the SPRING treatment there was no measurable change in cover or densities of remaining plant species. Several perennial forb species were particularly sensitive to the precipitation applications. Densities of *P. longifolia* increased in CONTROL, WINTER and CURRENT treatments and were greater than the SPRING by the end of the study (Fig. 7F).

3.5. Reproductive development

Reproductive development was affected by the precipitation treatments (Table 3, Figs. 8 and 9). There was a tendency for *A. tridentata* to reach more advanced stages of phenology in the shelter treatments compared to the CONTROL plots (Table 3), though this was not consistent across years (Fig. 8A). Reproductive success of *S. thurberiana* and *S. hystrix* was significantly lower in the SPRING treatment versus the other treatments when analysed over the course of the study (Table 3). However, there was variation in reproductive success for both species across years (Figs. 8B and C), particularly for *S. thurberiana*. Reproductive success of the *A. glauca/C. acuminata* was also highly variable for CONTROL, WINTER, and CURRENT treatments, resulting in a year by treatment interaction (Table 3, Fig. 8D). Nonetheless, *A. glauca/C. acuminata* reproductive success was lowest in the SPRING when compared to the other treatments over the course of the study (Table 3). Reproductive success for *C. parviflora* was lower in the SPRING versus the other treatments (Fig. 8E). In the SPRING treatment, *C. parviflora* did not advance beyond early leaf stage.

Reproductive effort by both *S. thurberiana* and *S. hystrix* exhibited no consistent treatment differences in tiller densities or weights (Figs. 9A–B and 10A–B). Tiller densities and weights of both species were greater in 1999 compared to other years for WINTER, CURRENT, and CONTROL treatments. Reproductive shoot densities for *A. tridentata* were greatest in the SPRING compared to all other treatments during the study (Table 6). This relationship was particularly in evidence the last 2 years of the study (Fig. 9C). Reproductive shoot weight densities of *A. tridentata* were greatest in the SPRING compared to the other treatments, although there was a strong year by treatment interaction (Table 3, Fig. 10C).

4. Discussion

Precipitation timing influenced herbaceous composition and dynamics of the *A. tridentata* steppe community, but not as hypothesized. We had anticipated that the SPRING water application would result in stable or increased cover and biomass of grasses and other herbaceous species because their rooting structures would allow them to utilize soil water in the upper profile more effectively than *A. tridentata*. We expected the WINTER treatment to favor *A. tridentata* because of its ability to access soil water deeper in the profile. Neither of these hypotheses proved to be correct.

Table 3
 Analysis of variance *P* values for reproductive success, reproductive tiller (shoot) density, and reproductive tiller (shoot) weight density for the interaction and main effects for selected herbaceous species and *A. tridentata* spp. *wyomingensis*

Functional group/species	Reproductive success (%)			Reproductive tiller (shoot) density (# cm ⁻²)			Reproductive tiller (shoot) weight density (mg cm ⁻²)		
	Year by treatment	Year	Treat.	Year by treatment	Year	Treat.	Year by treatment	Year	Treat.
<i>A. tridentata</i> spp. <i>wyomingensis</i>	0.0676	<0.0001*	0.0124*	0.4168	0.1178	<0.0001*	0.0075*	0.0118*	<0.0001*
<i>Sitanion hystrix</i>	0.6762	0.4317	<0.0001*	0.6419	<0.0001*	0.3637	0.6882	<0.0113*	0.7609
<i>Stipa thurberiana</i>	<0.0001*	0.3167	<0.0001*	0.0001*	<0.0001*	0.0002*	0.0133*	<0.0379*	<0.0064*
<i>Agoseris glauca/Crepis acuminata</i>	<0.0001*	<0.0001*	<0.0001*	—	—	—	—	—	—
<i>Collinsia parviflora</i>	<0.0001*	<0.0082*	<0.0007*	—	—	—	—	—	—

Asterisks indicate significance at the 0.05 level.

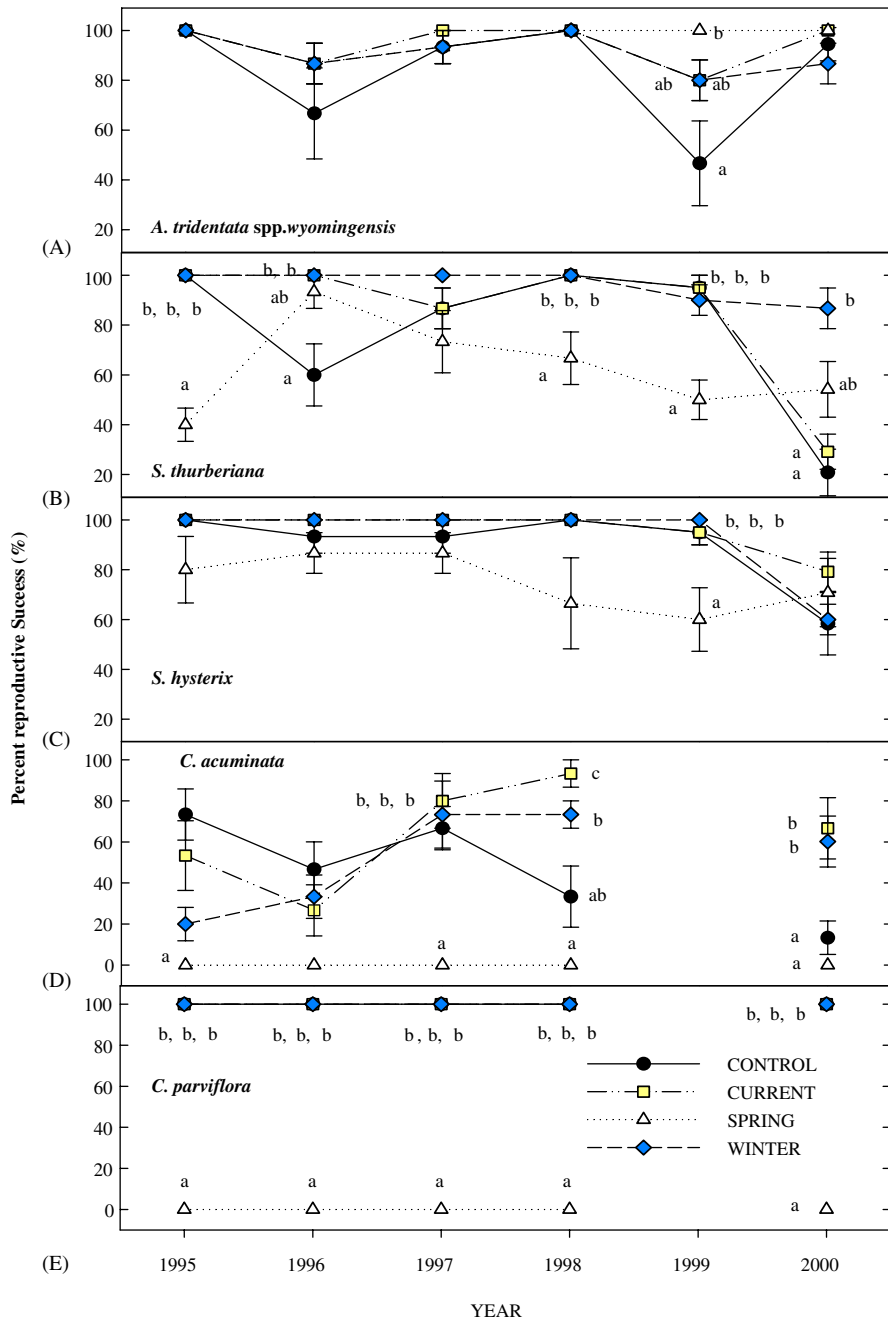


Fig. 8. Percent reproductive success (%) of: (A) *A. tridentata spp. wyomingensis*; (B) *S. thurberiana*; (C) *S. hystrix*; (D) *C. acuminata*; and (E) *C. parviflora*, for the shelter and CONTROL treatments, 1994–1999. Values are in means \pm one standard error. Significant differences ($P > 0.05$) among treatments, by year, are indicated by different lower case letters.

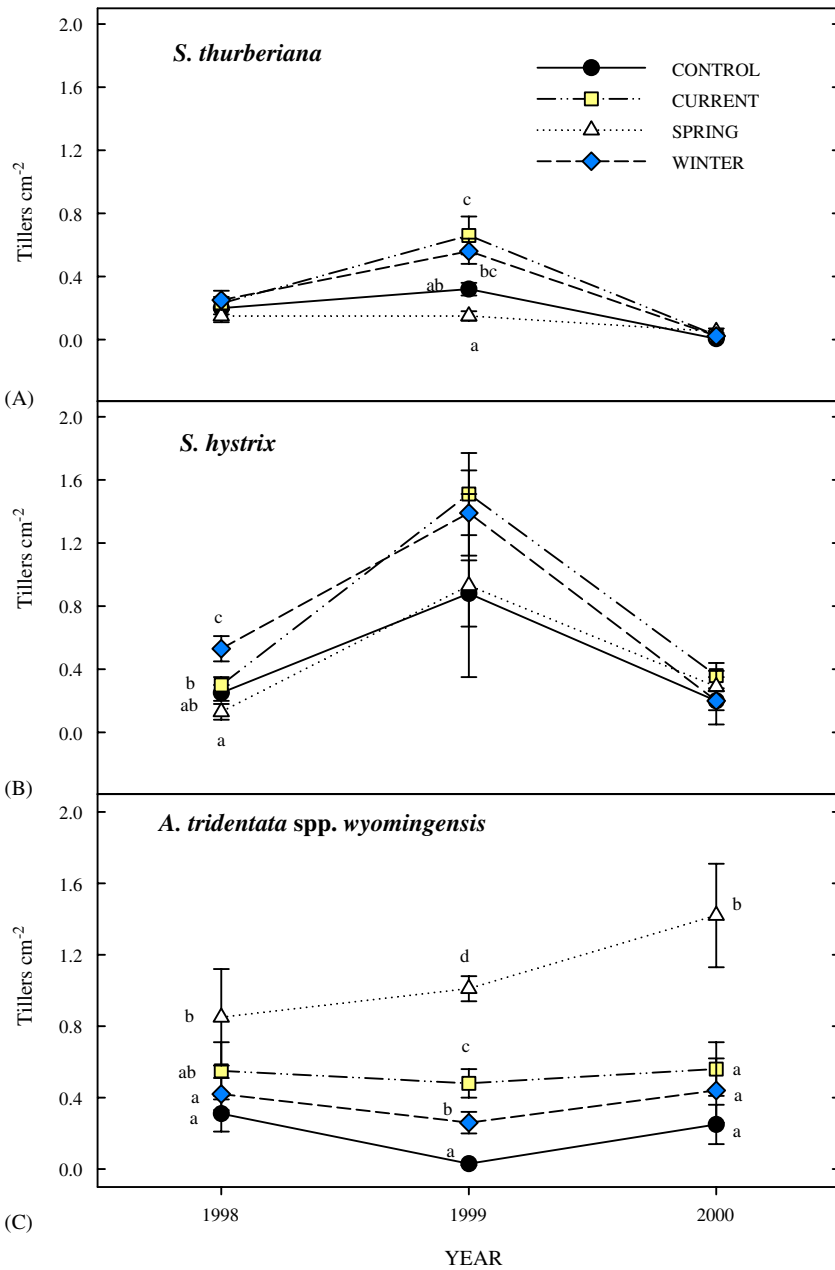


Fig. 9. Reproductive tiller density (tillers cm⁻²) of: (A) *S. thurberiana*; (B) *S. hystrix*; and (C) *A. tridentata* spp. wyomingensis, for the shelter and CONTROL treatments, 1998–2000. Values are in means ± one standard error. Significant differences ($P > 0.05$) among treatments, by year, are indicated by different lower case letters.

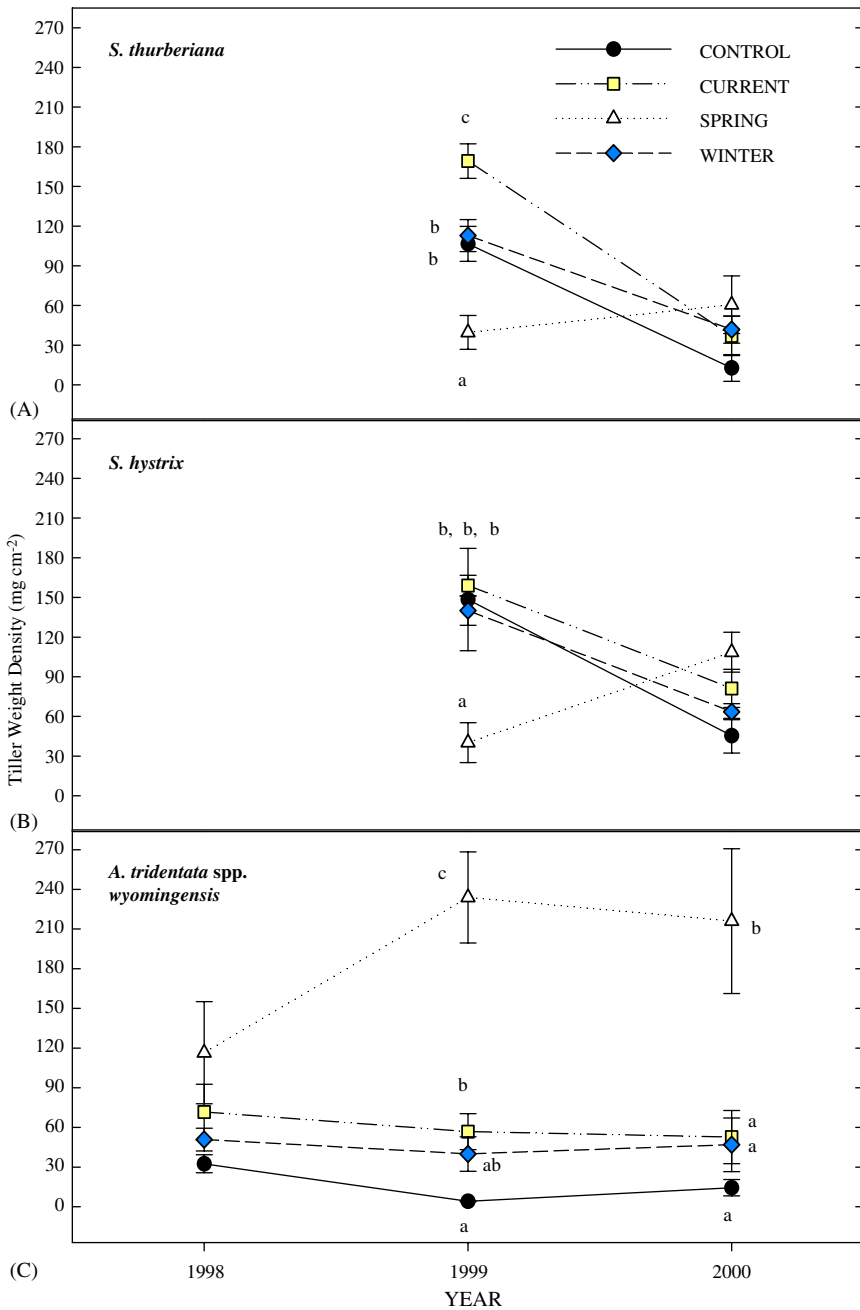


Fig. 10. Reproductive tiller weight density (mg cm^{-2}) of: (A) *S. thurberiana*; (B) *S. hystrix*; and (C) *A. tridentata spp. wyomingensis*, for the shelter and CONTROL treatments, 1998–2000. Values are in means \pm one standard error. Significant differences ($P > 0.05$) among treatments, by year, are indicated by different lower case letters.

4.1. Sagebrush

Artemisia tridentata was unresponsive to the precipitation shifts in terms of cover and density, and thus appeared less likely to be influenced in the short term by climatic shifts than associated herbaceous species. However, visually, sagebrush in the SPRING treatment did not appear to produce as much vegetative biomass as in the other treatments. We did not measure *A. tridentata* biomass because we wanted to minimize destructive sampling. We attempted to use allometric equations developed for this location by Rittenhouse and Sneva (1977) to estimate sagebrush biomass but these models were not sensitive enough to detect differences among treatments.

The SPRING treatment did confer some advantages to reproductive success, stem density, and stem weight density of *A. tridentata* (Figs. 8A, 9C and 10C). The summer water application in the SPRING treatment may provide an explanation. At the Hanford facility in eastern Washington, *A. tridentata* spp. *wyomingensis* has been shown to respond to summer precipitation with increased reproductive shoot development (Evans et al., 1991). *A. tridentata* reproductive shoots initiate growth in mid-June and this is the period the SPRING treatment received frequent water applications. This would explain the high reproductive success of *A. tridentata* and heavier shoot weights in the SPRING compared to the other precipitation treatments. The greater reproductive effort did not result in the recruitment of new individuals.

4.2. Effects of spring precipitation pattern: herbaceous response and soil moisture

Herbaceous plants were detrimentally affected by the SPRING precipitation treatment as indicated by a pattern of lower herbaceous biomass, cover, and densities compared to the other treatments. The herbaceous response in the SPRING treatment likely resulted from reduced availability of soil water during the most active growth period (April–May) (Fig. 2A and B). Even when water was made available in June and July, soils never became thoroughly wetted; thus effective precipitation was less in the SPRING when compared to the other treatments. Soil water-content never rose above 15% gravimetric, even with applications as high as 25 mm. This level of soil water-content was inadequate for stimulating herbaceous growth and development in the spring and summer. Observing the development of plants in the other treatments at this level of soil water-content may explain the lack of response in the SPRING. In WINTER, CURRENT, and CONTROL treatments, by the time soil water content had been drawn down to 15% gravimetric, most herbaceous plants had either entered dormancy (e.g. *P. sandbergii*, annual forbs) or are in later growth stages (seed development) and are not adding additional above-ground biomass.

4.3. Ecological implications of a spring precipitation pattern

Shifting precipitation distribution to a spring/summer pattern (SPRING treatment) has the greatest potential for altering productivity, composition, and structure

of *A. tridentata* steppe vegetation. Annual and perennial forbs native to the system were the least resistant to a timing change, declining in density, cover, and biomass. A long-term shift to a spring/summer dominated precipitation pattern would lead to the forb component being lost or severely reduced, with the potential to reduce ecosystem biodiversity.

Reproductive measurements demonstrated the utility of using certain species as indicators of environmental change in controlled or field experiments. *Collinsia parviflora* and perennial forbs were particularly sensitive to soil water conditions in late winter/early spring. In the SPRING treatment, *C. parviflora* rarely emerged or completed its life cycle and reproductive efforts of perennial forbs were also reduced. Though individuals emerged, the lack of seed development suggests that the seed banks for *C. parviflora* and other forbs are being depleted.

When compared to the other shelter treatments the results also suggest an increase in bare ground with a spring/summer precipitation pattern. Greater levels of bare ground could potentially increase soil erosion in this environment and increase heterogeneity of soil resources. According to Schlesinger et al. (1990), this results in a positive feedback linkage exacerbating desertification processes and further reducing ecosystem productivity.

In retrospect, we probably should not have been surprised by the community dynamics in the SPRING treatment. There is ample documentation in the literature, from experimental evidence (e.g. Caldwell et al., 1977; Sneva, 1982) and from reviews (Comstock and Ehleringer, 1992) that productivity of cold desert C₃ species of the Great Basin are keyed to the recharging of soil moisture during winter. Recent physiological studies indicate that cool season-C₃ species may utilize summer moisture but do not increase carbon assimilation, particularly following winter drought (Schwinning et al., 2002; Schwinning et al., 2005a). Our study tends to confirm these results at the plant community level. Though plant species stayed green longer into the summer in the SPRING treatment, they did not add additional above-ground structures and there was no recruitment of new individuals. When plants do not respond to summer precipitation events it is because there is no incentive to invest in additional structures to exploit available water, as the costs are outweighed by any potential returns in carbon gain (Schwinning et al., 2003; Schwinning and Sala, 2004).

There is evidence that suggests plants in this system will respond to pulses of precipitation in the summer. Bates et al. (2000) observed extensive tillering of C₃ perennial grasses and a second set of reproductive tillers were produced by *P. sandbergii* and *S. hystrix* following 70 mm (3-day event) and 20 mm storm events occurring over a 3-week period in June and mid-July. There are two factors that we believe contributed to this response; (1) there was adequate winter recharge in soils, thus, the root net was probably well developed and able to rapidly exploit available water, and/or (2) the precipitation pulses were large enough to recharge the soil profile sufficiently for plants to make additional investments in new growth. In the SPRING treatment, we suspect that root development was curtailed because of winter drought, thus when water arrived in the late spring and summer, plants did not have the capacity to fully exploit available water. In addition, watering

treatments were never sufficient to recharge the soil profile so there was likely little incentive to increase rooting activity to capture available water. The most water applied in a 1-month period was about 60 mm with a maximum of 25 mm for a single event. There is likely a threshold whereby cool season species will respond to summer moisture but we did not arrive at that level in the study.

4.4. WINTER, CURRENT, and CONTROL treatments: soil water and vegetation response

Generally, we measured few consistent differences among the WINTER, CURRENT, and CONTROL treatments. We had predicted that a shift to greater winter precipitation coupled with reduced spring and summer precipitation would result in deep percolation of water and increase growth of deep-rooted *A. tridentata* compared to more shallow rooted herbaceous plants. The similarity among treatments in soil water-content (Fig. 3) probably explains the resemblance in plant community response. In addition, soils on our site are relatively shallow for the *A. tridentata* spp. *wyomingensis* alliance; 30–50 cm in depth before striking a hard pan. Davies et al. (2004, pp. 28–42) quantified soil characteristics on 150 sites in the alliance scattered across eastern Oregon and northern Nevada. Soils in their study averaged 85 cm in depth with a range from 28 to 215 cm. Because soils on our site are shallow and fine-textured, water cannot easily penetrate below rooting depths of perennial grasses and forbs. For *A. tridentata* to take advantage of additional winter moisture probably requires deeper and/or coarser textured soils. Nonetheless, our results contrast with recent studies that documented increased shrub density and cover with greater long-term winter precipitation in south-eastern Arizona (Brown et al., 1997), and conclusions developed by Schwinning et al. (2005b) found that increased summer drought would favor survivorship of deep-rooted shrubs over shallow rooted plants.

4.5. Shelter effects and vegetation response

Differences in vegetation, litter, and bare ground among WINTER, CURRENT and CONTROL treatments we attributed to the effects of the shelters rather than the watering treatments. The warmer temperatures and reduced diurnal variation under the shelters (Svejcar et al., 1999) may explain the higher densities of *P. sandbergii* and *B. tectorum* in CURRENT and WINTER treatments. Frost heaving and pedestaling at the soil surface was commonly observed in late winter and early spring (February–April) in the CONTROL treatment. Under the shelters, frost heaving was not a factor, which may partially explain the increased establishment by reducing stress of *P. sandbergii* and *B. tectorum* seedlings during the late winter–early spring period. Frost heaving in soils has been reported to reduce *B. tectorum* establishment (Sheley and Larsen, 1994). The warmer temperatures combined with winter moisture application were probable factors for the larger *B. tectorum* biomass values measured in the WINTER treatment. With warmer soil temperatures, *B. tectorum* produces greater shoot biomass (Nasri and Doescher, 1995).

The increase in *B. tectorum* is of concern as its presence has altered historic fire regimes and permanently modified Great Basin plant communities (Young et al., 1987). If temperatures increase as predicted by general circulation models (NAST, 2000; IPCC, 2001), the potential exists for increased annual grass establishment into areas where it is still a minor component of the *A. tridentata* ecosystem. Research has indicated *B. tectorum* can spread, establish, and increase in undisturbed and intact sagebrush communities (Passey et al., 1982; Svejcar and Tausch, 1991). *B. tectorum* dominates extensive areas in the Intermountain region, particularly in areas only slightly warmer than our study site (Young et al., 1987; Pellant, 1990). These areas have converted to systems dominated by annual grass and are now maintained by more frequent fire disturbances. The altered disturbance regime has largely removed or prevented reestablishment of native flora. There are also indications that *B. tectorum* is more competitive with native species with elevated CO₂ levels (Smith et al., 2000). A warmer environment coupled with a winter precipitation regime and greater CO₂ levels would likely permit invasion and dominance by *B. tectorum*, particularly if fire disturbances increase.

Litter breakdown and decomposition appeared to be reduced under the shelters which may explain the higher litter covers in the shelter treatments. Litter material in the CONTROL was more exposed and appeared more readily degraded. Litter in the CONTROL rapidly assumed a bleached appearance after the growing season, while litter under the shelters retained a freshly cured appearance. This may be related to ultraviolet radiation inputs which are an important factor in degradation of plant materials in arid land systems (McKay et al., 1994; Moorehead and Callaghan, 1994; Rozema et al., 1997). Ultraviolet radiation inputs were not measured but would be reduced under the shelters due to the filtering of UV radiation by the roofing material.

5. Conclusions

In other studies, experimentally shifting precipitation patterns, altering storm frequency, or adjusting annual water inputs have had variable effects to plant community productivity and composition. Productivity and composition in plant communities has increased, decreased, or not changed substantially in response to experimental manipulation of precipitation (Grime et al., 2000; Knapp et al., 2002; Svejcar et al., 2003). A shift in precipitation that does not stray far from historical patterns does not appear to cause major disruptions to ecosystem composition or productivity, and in some cases may enhance productivity (Grime et al., 2000). As indicated by our study, increased winter precipitation combined with summer drought appears unlikely to cause major changes to vegetation composition or productivity of *A. tridentata* communities in the northern Great Basin. Schwinning et al. (2005a) suggested that increasing summer drought in cold desert plant communities will potentially reduce fitness of native perennial plants and open sites up to invasion by exotic annuals. We measured increases in annual grass *B. tectorum* but there was no indication that the fitness of native perennials decreased under the

WINTER regime. However, as discussed, the trend of increasing *B. tectorum* is of concern, particularly if regional temperatures increase as predicted.

Major shifts away from historical precipitation patterns have the greatest potential to alter ecosystem function and productivity. Altering the temporal distribution and size of rainfall events in the tall grass prairie of the Great Plains reduced above-ground productivity by 11% (Knapp et al., 2002). In our study, the shift to a spring–summer precipitation pattern approximately halved herbaceous production compared to the other treatments, and bare ground was 20% and 40% greater in the SPRING than CURRENT and WINTER treatments, respectively.

In the past, a great deal of emphasis has been placed on total annual precipitation relative to changes in productivity and composition of semi-arid plant communities. Our results demonstrated that species composition and productivity in the sagebrush steppe can be altered by the timing of precipitation. Others have also established that community response to altered precipitation patterns is a direct result of the timing of water availability within the soil profile (Brown et al., 1997; Schwinning et al., 2005b). This becomes particularly important in making ecological assessments and detecting trends in rangeland condition. Land managers are often presented with the challenge of separating weather effects from those related to management actions. Experimental results from this and other studies should begin to provide managers with knowledge they require to evaluate weather-related changes in semi-arid and arid ecosystems.

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