

The Influence of Precipitation Timing on the Sagebrush Steppe Ecosystem

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Climate influences virtually all aspects of ecosystem development and global distribution (Emmanuel et al. 1985). Some regions have experienced large climatic shifts in the recent past. The northern Great Basin of the western United States has undergone large shifts in temperature and precipitation patterns over the past 10,000 years (Morrison 1964; Mehringer and Wigand 1990; Thompson 1990). Alternating periods of cool/wet, cool/dry, warm/wet, and warm/dry conditions have caused fluctuations in composition, cover, productivity, and distribution of northern Great Basin vegetation (Wigand and Nowak 1992). Tausch et al. (1993) suggest that Great Basin climate was relatively stable during the late Tertiary period (2 to 20 million years before present), but that the Quaternary (the past 2 million years) was a period of high climatic variability. They conclude that climatic variability has resulted in plant communities that are far less stable than we previously assumed. From their assessment of paleobiological research, Graham and Grimm (1990) suggest that past climate change has resulted in individualistic changes in species distributions, rather than shifts in community boundaries. Their conclusions tend to support those of Tausch et al. (1993), that communities may not be stable in the face of climatic shifts.

Changes in seasonal climatic patterns can have a major impact on the dynamics of plant communities. In arid ecosystems there is a strong interaction between rainfall and temperature in determining plant abundance and composition. Rainfall during the hot season results in lower plant available

moisture than an identical rainfall event during the cool season of the year. In arid ecosystems, even small changes in a plant's available moisture can produce major effects on plant composition. In ecosystems dominated by annuals, interannual variation in floristic composition is influenced by rainfall timing, as shown by Peco and Espigares (1994), who concluded that the timing of autumn rainfall determined the floristic composition of annual Mediterranean pastures. The yearly compositional changes were a result of germination characteristics of individual species. In an Australian pasture study, Austin et al. (1981) determined that seasonality of rainfall had more impact on pasture plant dynamics than did grazing intensity. The Intergovernmental Panel on Climate Change (IPCC) has predicted that changes in seasonal patterns of rainfall and temperature will have more impact on plant production than will changes in annual rainfall totals for large areas of Africa and North America (Ojima et al. 1993).

The impacts of climate change are of interest from a scientific standpoint, but also pose questions for management of agricultural and natural ecosystems. Hanson et al. (1993) used three general circulation models (GCMs) and a rangeland model (SPUR) to simulate outputs of a range/livestock system under different climate scenarios. They discovered that changes in production were more closely related to changes in temperature and precipitation than to changes in atmospheric carbon dioxide (CO₂). Their results were dependent on the particular GCM used in the simulation, but one pattern that emerged was an increase in rangeland production, a decrease in forage quality, and a higher year-to-year variability in production relative to current conditions. As both Hanson et al. (1993) and Helms et al. (1996) point out, farmers and ranchers have many management options and will likely adapt to changes, especially if changes occur over relatively long time frames.

The experimental approaches for investigating climate change effects on vegetation consist of indirect and direct methodologies. Indirect methods include paleobotanical studies to assess vegetation changes associated with past climatic shifts (Graham and Grimm 1990; Tausch et al. 1993; Miller and Wigand 1994; Nowak et al. 1994), comparison of vegetation patterns among regions with different climates (Cook and Irwin 1992), and correlating long-term vegetation measurements to yearly weather patterns (Passey 1982).

Although indirect methods of research are useful for predicting climate change responses and interpreting vegetation shifts, they possess a number of limitations. Paleobotanical studies are rather coarse in nature, able to describe changes in abundance of major species or functional groups but unable to

detect changes for most individual species. In addition, the variation in climate over several million years can be dramatic and may not be relevant to predicting changes over the next 50 to 100 years. As with the paleobotany research, it is difficult to know whether regional climate comparisons are relevant to predicting vegetation responses. Vegetation patterns in various regions developed over evolutionary time and may or may not be indicative of what will occur at a decadal time scale. Correlation between vegetation and yearly weather patterns may not be a good indicator of what we would find with a sustained shift in climate because year-to-year fluctuations often fall within the normal variation of the ecosystem.

Direct experimental approaches have been used extensively to evaluate the impacts of elevated atmospheric CO₂ on plant growth (Amthor 1995). Most elevated CO₂ studies have been single-species experiments and thus have not addressed effects to intact multispecies ecosystems (Díaz 1995). It may not be realistic to scale up from results obtained from isolated plants growing under controlled conditions (Körner 1995). More work is needed on intact ecosystems, because interactions among plants are so important and can cause unpredicted results. In a recent study, Harte et al. (1995) used infrared radiators to warm montane meadow plots in the field. The authors concluded that vegetation will play a prominent role in determining soil microclimate response to increased temperature, a fact often obscured by climatic models. The results of Harte et al. (1995) tend to support the assertions of Körner (1995), that research from intact ecosystems may give results that would not have been predicted from controlled studies or models.

An aspect of climate change that is difficult to predict is precipitation, both amount and seasonal distribution. Research on precipitation effects (especially timing) can be difficult to conduct, which partially explains the dearth of data on this subject. As mentioned previously, precipitation distribution in the Great Basin has changed in the past, and there is reason to believe there will be shifts in the future that will affect vegetation composition, distribution, and productivity. Climate models suggest that the Great Basin may experience more summer and less winter precipitation in the future (Neilson et al. 1989). We established a study to investigate the effects of altered timing of precipitation on vegetation (annual amount held constant) in the northern Great Basin. Treatments consisted of higher summer/lower winter precipitation (spring), higher winter/lower spring precipitation (winter), and a treatment conforming to long-term precipitation distribution averages (current

Based on regional comparisons made by Cook and Irwin (1992), we hypothesized: (1) a shift to more summer precipitation (spring treatment) would favor graminoid species over shrubs, (2) a shift to a higher percentage of winter precipitation would favor shrubs and winter annual species, and (3) the treatment receiving the average distribution would show no change relative to ambient plots.

Methods

Study Area and Experimental Design

The study was conducted on the Northern Great Basin Experimental Range (119° 43' W, 43° 29' N) in southeastern Oregon, 67 km west of Burns, Oregon. The Experimental Range is characterized by shrub steppe vegetation represented by sagebrush/bunchgrass and western juniper plant communities.

The study site is codominated by Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*) and the cold-season perennial bunchgrass species Thurber's needlegrass (*Stipa thurberiana*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Sandberg's bluegrass (*Poa sandbergii*). Elevation at the site is 1380 m and the ground is level (0 to 1 percent slope). Soils are well drained and underlain by a duripan between 40–50 cm. Soils on the site were classed as a Vil-Decantl Variant-Ratto complex (Lentz and Simonson 1986). Field capacity of soils is 23 percent (0–15 cm) and 25 percent (15–30 cm) for gravimetric soil water content. Climate is continental with cold-wet winters and dry-warm summers. Annual precipitation at the Experimental Range has averaged 300 mm since measurements began in the 1930s. Distribution of precipitation during this period was 60 percent from October to March, 30 percent from April to June, and 10 percent from July to September. It is important to note that annual precipitation in the Great Basin is extremely variable from year to year. For example, at the Experimental Range the wettest years on record were 1938 and 1993, each with about 530 mm of precipitation. The driest year on record was 1994 with only 140 mm of precipitation.

To assess the effects of timing on soil water and plant community dynamics, five rainout shelters were constructed in 1994. The design of the fixed location rainout shelters and associated irrigation system is described in Svejcar et al. (1999). Rainout shelters were 30 by 12 m in size. Shelters are open on the sides and until 1998 were covered with transparent fiberglass. The fiberglass was replaced in the summer of 1998 with Dynaglass®, a clear

polycarbonate material.¹ Precipitation under the shelters was applied by an overhead sprinkler system.

Precipitation treatments under each shelter were designated as "winter," "spring," and "current." Treatment plots were 10 m by 12 m in size and included a 2 m buffer strip on all sides. The winter distribution treatment received the majority of precipitation (80 percent) between October and March; the spring distribution treatment received the majority of its precipitation (80 percent) between April and July; the current distribution treatment received precipitation conforming to long-term (50 years) distribution patterns at the Experimental Range. The target precipitation distribution schedules for each treatment are shown in table 6.1. The target was for all shelter treatments to receive a total of 203 mm of water annually. During the initial year of study, we found that application of 300 mm of water (the long-term average annual precipitation) resulted in surface puddling and saturated soil. Soil moisture was much higher than would have been expected based on historical precipitation and soil moisture data, because our method of application was more effective at increasing soil moisture than a comparable amount of natural precipitation. This region is characterized by low intensity, relatively long duration storms, with infrequent thunderstorms. The discrepancy between natural precipitation and sprinkler application is probably a result of duration and intensity of moisture fall. Therefore, we chose to decrease the total amount of precipitation applied to the shelter treatments to about 200 mm.

Ambient treatment plots of identical size were located south of each shelter. Ambient precipitation was measured using a tipping bucket rain gauge, and amounts were automatically recorded using an electronic data logger. Ambient plots received natural precipitation; thus, amounts and patterns varied by year.

The experimental design was a randomized complete block with four treatments replicated five times. Understory biomass and cover were compared between treatments (among and by year) using General Linear Model (GLM) statistical techniques for a randomized block design. Main effects for understory biomass and cover were year and treatment. Soil water content was analyzed using a repeated measures analysis of variance (ANOVA) for a randomized block design. Main effects for soil water content were treatment, soil depth, and time. Data was tested for normality (SAS Institute 1988); data not normally distributed were log-transformed to stabilize variance. When interactions were significant, means were separated using Fisher's protected

TABLE 6.1.

Precipitation (mm) patterns for the ambient treatment and the shelter treatments (Current, Winter, Spring) in 1997–98 and 1998–99. Values are the proportion of total precipitation received and the total annual precipitation amounts during the course of the water year (October–September).

Year/Treatment	TREATMENT PERIODS			Precipitation Total
	Winter (October–April)	Spring–Summer (May–July)	Fall (August–September)	
<i>Precipitation applied</i>				
Ambient ¹	180	90	30	300
Current	153	40	10	203
Winter	183	20	0	203
Spring	45	158	0	203
<i>Precipitation applied 1997–98</i>				
Ambient ²	161	108	25	294
Current	122	74	13	209
Winter	182	22	0	204
Spring	55	152	0	207
<i>Precipitation applied 1998–99</i>				
Ambient ²	115	24	10	149
Current	133	60	12	205
Winter	185	21	0	205
Spring	48	156	0	204

¹ Long-term average at the Experiment Range.

² Ambient precipitation levels in 1997–98 and 1998–99 underestimate actual amounts, because the rain gauge was not 100 percent efficient at capturing snow.

Least significant difference (LSD) procedure. Statistical significance of all tests was assumed at $P < 0.05$.

Vegetation Measurements

Herbaceous biomass was estimated in September 1998 and June 1999. In each treatment replicate, five 1.0 m² quadrants were clipped for herbaceous biomass. Biomass was separated into perennial and annual components.

Herbaceous and total ground cover were visually estimated in 1994, 1998, and 1999 within 0.2 m² frames. Frames were placed every meter along a 18 m transect line. Herbaceous cover was separated into perennial and annual components.

growth initiation to seed scatter over five growing seasons (1995–1999). Plants monitored were Wyoming big sagebrush, Thurber's needlegrass, squirreltail (*Sitanion hystrix*), blue-eyed Mary (*Collinsia parviflora*), and as a group we monitored the perennial forbs pale agoseris (*Agoseris glauca*), western hawksbeard (*Crepis occidentalis*), and tapertip hawksbeard (*C. acuminata*). Three plants of each species were monitored in each treatment replicate (15 subsamples per treatment).

Precipitation Application, Soil Water Content, and Temperature

Water applied to shelter treatments was measured with five rain gauges permanently placed in each replicate. Rain gauges were constructed using 2 L plastic soft drink containers and were anchored to the ground with steel rods (Wrage et al. 1994). Measurements were done immediately after water was applied.

Soil water content was determined gravimetrically in 1998 and 1999. Soil water measurements were collected at 0–15 cm and 15–30 cm intervals every two weeks during the growing season (April–September). Two randomly placed subsamples were collected for each depth in each treatment replicate. Soils were weighed, dried at 106°C for 48 hours, and reweighed to determine gravimetric water content.

Soil temperature was recorded in 1996, 1997, and 1998 in each treatment plot with thermocouples placed 5 cm below the surface. Concurrent with temperature, soil surface wetness was estimated at two locations in each plot using a granular matrix sensor (Watermark, Irrometer Co., Riverside, CA) buried at 5 cm. Average hourly temperature and moisture data were estimated from measurements taken at 5 min intervals using onsite data loggers. Data stored in the data loggers was downloaded weekly to a computer. Average monthly soil temperatures and annual soil moisture were calculated from the hourly data. Soil moisture (percent) was estimated from the sensor resistances using a regression equation developed from gravimetric soil water measurements. Although the matrix sensors are not quantitatively accurate when soils dry below about -300 kPa, they were appropriate for this study because we were primarily interested in relative differences in surface wetness as affected by different watering treatments.

Mean (± 1 SE) total biomass (kg/ha) and biomass percentages of perennial and annual vegetation for the four treatments (n = 25).

Year	TREATMENT			
	Winter	Spring	Current	Ambient
<i>September 1998</i>				
Biomass (kg/ha)	338 \pm 56 b ¹	201 \pm 40 a	281 \pm 46 a	371 \pm 67 b
% Perennial	85.1 \pm 6.0 c	99.4 \pm 0.3 d	98.7 \pm 0.6 d	96.9 \pm 0.8 d
% Annual	14.9 \pm 6.0 e	0.6 \pm 0.3 f	1.3 \pm 0.6 f	3.1 \pm 0.8 f
<i>June 1999</i>				
Biomass (kg/ha)	472 \pm 87 h	148 \pm 30 g	464 \pm 66 h	426 \pm 47 h
% Perennial	81.9 \pm 5.6 m	95.6 \pm 2.5 o	85.9 \pm 4.3 m	99.4 \pm 0.3 o
% Annual	18.1 \pm 5.6 z	4.4 \pm 2.5 y	14.1 \pm 4.3 z	0.6 \pm 0.3 y

Within a row, means followed by the same lowercase letter were not different ($P > 0.05$).

Results

Plant Community Dynamics

BIOMASS. Total biomass production in September 1998 and June 1999 was significantly less in the spring treatment versus other treatments (table 6.2). As a percentage of total biomass production, the winter treatment had the greatest amount of annual plant production. Annual plant production in the winter treatment was significantly greater than spring and ambient treatments in both years. In 1999, the percentages for annual and perennial production were not significantly different between current and winter treatments.

COVER. Prior to shelter construction and treatment initiation in 1994, there were no differences in herbaceous (perennial, annual) cover among experimental units (table 6.3). Bare ground was somewhat lower in the ambient and spring treatments compared with current and winter treatments in 1994 but did not differ statistically.

In 1998 and 1999, herbaceous cover increased in all treatments from 1994. The increases in cover were not the same among treatments. Total herbaceous cover and annual cover were significantly greater in the winter versus the other treatments. The current treatment also had significant gains

TABLE 6.3.

Mean (± 1 SE) total herbaceous cover and perennial and annual vegetation cover for the four treatments, given as a percentage of total area in treatment plot ($n = 15$).

Year/Response Variable	TREATMENT			
	Winter	Spring	Current	Ambient
<i>1994</i>				
Bare ground	71.8 \pm 2.8	64.2 \pm 3.0	66.8 \pm 2.5	60.2 \pm 4.7
Herbaceous cover	9.1 \pm 0.8	9.9 \pm 0.7	9.8 \pm 0.7	9.7 \pm 0.9
<i>Perennial</i>	8.4 \pm 0.7	9.8 \pm 0.7	9.6 \pm 0.7	9.6 \pm 1.0
<i>Annual</i>	0.7 \pm 0.3	0.1 \pm 0.0	0.2 \pm 0.0	0.1 \pm 0.0
<i>1998</i>				
Bare ground	38.2 \pm 3.2 a ¹	58.8 \pm 3.0 c	45.0 \pm 3.9 b	68.3 \pm 3.7 d
Herbaceous cover	28.1 \pm 2.0 o	15.4 \pm 2.5 m	19.8 \pm 1.6 t	17.4 \pm 1.0 mt
<i>Perennial</i>	23.4 \pm 1.9 s	15.2 \pm 2.4 q	19.0 \pm 1.5 r	16.4 \pm 1.0 rq
<i>Annual</i>	4.7 \pm 1.4 y	0.3 \pm 0.2 x	0.8 \pm 0.3 x	1.0 \pm 0.2 x
<i>1999</i>				
Bare ground	35.0 \pm 2.3 a	55.6 \pm 2.5 c	43.2 \pm 2.4 b	59.9 \pm 3.8 c
Herbaceous cover	38.0 \pm 1.8 p	12.8 \pm 2.4 m	30.5 \pm 2.3 o	22.0 \pm 0.6 t
<i>Perennial</i>	29.6 \pm 2.2 s	12.5 \pm 2.3 q	27.3 \pm 2.1 s	21.3 \pm 1.0 r
<i>Annual</i>	8.4 \pm 2.3 y	0.3 \pm 0.1 x	3.2 \pm 1.1 x	0.6 \pm 0.1 x

¹ Within a row, means followed by the same lowercase letter were not different ($P > 0.05$).

in cover, though not as great as those in the winter treatment. Perennial plant cover was significantly lower in the spring treatment versus all other treatments in 1999. Bare ground was highest in the ambient treatment versus the shelter treatments in 1998.

REPRODUCTIVE DEVELOPMENT. Phenological development of all the species monitored was affected by the precipitation treatments (table 6.4). Sagebrush reproductive success (1995–1999) was highly variable in the ambient treatment (47–100 percent) in contrast to all shelter treatments, which had more consistent reproductive development (80–100 percent). Thurber's needlegrass and squirreltail reproductive success was significantly lower in the spring treatment versus the other treatments in 1995, 1998, and 1999. Perennial forb reproductive success was highly variable for all treatments during the study but was consistently the lowest in the spring treatment. Reproductive success for the annual forb *Collinsia* was significantly lower in the spring versus other treatments in all years.

TABLE 6.4.

Mean (± 1 SE) growth development success percent by treatment and year for *Artemisia tridentata* subsp. *wyomingensis*, *Stipa thurberiana*, *Sitanion hystrix*, all perennial forbs, and *Collinsia parviflora* (n = 15). Growth development success was defined as the percentage of observed plants that completed all growth stages between growth initiation and reproduction.

Species/Year	TREATMENT			
	Winter	Spring	Current	Ambient
<i>A. tridentata</i>				
1995	100.0 \pm 0.0	100.0 \pm 0.0	100.0 \pm 0.0	100.0 \pm 0.0
1996	86.7 \pm 8.2	86.7 \pm 8.2	86.7 \pm 8.2	66.7 \pm 18.3
1997	93.3 \pm 6.7	93.3 \pm 6.7	100.0 \pm 0.0	93.3 \pm 6.7
1998	100.0 \pm 0.0	100.0 \pm 0.0	100.0 \pm 0.0	100.0 \pm 0.0
1999	80.0 \pm 8.2	100.0 \pm 0.0	80.0 \pm 8.2	46.7 \pm 17.0
Average	92.0 \pm 2.9b ¹	96.0 \pm 2.2 b	93.3 \pm 2.7 b	81.3 \pm 6.4 a
<i>S. thurberiana</i>				
1995	100.0 \pm 0.0	40.0 \pm 6.7	100.0 \pm 0.0	100.0 \pm 0.0
1996	100.0 \pm 0.0	93.3 \pm 6.7	100.0 \pm 0.0	60.0 \pm 12.5
1997	100.0 \pm 0.0	73.3 \pm 12.5	86.7 \pm 8.2	86.7 \pm 8.2
1998	100.0 \pm 0.0	66.7 \pm 10.5	100.0 \pm 0.0	100.0 \pm 0.0
1999	90.0 \pm 6.1	50.0 \pm 7.9	95.0 \pm 5.0	95.0 \pm 5.0
Average	98.0 \pm 1.4 e	64.7 \pm 5.3 d	96.3 \pm 2.0 e	88.3 \pm 6.4 e
<i>S. hystrix</i>				
1995	100.0 \pm 0.0	80.0 \pm 13.3	100.0 \pm 0.0	100.0 \pm 0.0
1996	100.0 \pm 0.0	86.7 \pm 8.2	100.0 \pm 0.0	93.3 \pm 6.7
1997	100.0 \pm 0.0	86.7 \pm 8.2	100.0 \pm 0.0	93.3 \pm 6.7
1998	100.0 \pm 0.0	66.7 \pm 18.3	100.0 \pm 0.0	100.0 \pm 0.0
1999	100.0 \pm 0.0	60.0 \pm 12.7	95.0 \pm 5.0	95.0 \pm 5.0
Average	100.0 \pm 0.0 h	73.3 \pm 5.8 g	99.0 \pm 1.0 h	96.7 \pm 2.0 h
Perennial forb				
1995	20.0 \pm 8.2	6.7 \pm 6.7	53.3 \pm 17.0	73.3 \pm 12.5
1996	33.3 \pm 10.5	20.0 \pm 8.2	26.7 \pm 12.5	46.7 \pm 13.3
1997	73.3 \pm 16.3	0.0 \pm 0.0	80.0 \pm 13.3	66.7 \pm 10.5
1998	73.3 \pm 6.7	20.0 \pm 13.3	93.3 \pm 6.7	33.3 \pm 14.9
Average	50.0 \pm 7.5 n	11.7 \pm 4.4 m	63.3 \pm 8.2 n	55.0 \pm 7.0 n
<i>C. parviflora</i>				
1995	100.0 \pm 0.0	26.7 \pm 12.5	100.0 \pm 0.0	100.0 \pm 0.0
1996	100.0 \pm 0.0	73.3 \pm 12.5	100.0 \pm 0.0	100.0 \pm 0.0
1997	100.0 \pm 0.0	0.0 \pm 0.0	100.0 \pm 0.0	100.0 \pm 0.0
1998	100.0 \pm 0.0	6.7 \pm 6.7	100.0 \pm 0.0	100.0 \pm 0.0
Average	100.0 \pm 0.0 y	26.7 \pm 7.9 x	100.0 \pm 0.0 y	100.0 \pm 0.0 y

¹ Within a row, means followed by the same lowercase letter were not different ($P > 0.05$).

Precipitation Application and Soil Water Content

Water applied to the shelter treatments and recorded for the ambient plots in 1997-98 and 1998-99 is shown in table 6.1. Water applied to the shelter treatments does not conform exactly to the target schedule. This is especially true for February, when air temperatures were too cold to apply water. Watering during cold winter months was limited because of frequent water line and sprinkler system breakage and because water had a tendency to freeze on plants unless air temperatures were well above freezing. Ambient precipitation recorded at the shelters probably underestimated actual precipitation because the tipping bucket rain gauge used did not capture all moisture received as snow.

Precipitation patterns in the ambient treatment illustrate that variability among years is high in this system. The ambient treatment received almost three times as much moisture in the spring-summer period in 1997-98 compared with the same period in 1998-99. Ambient annual precipitation in 1998-99 was also about 40 percent less than in 1997-98.

Soil water content differed among treatments in the 1998 and 1999 growing seasons (fig. 6.1). In 1998, ambient soil water content was greater than the other treatments between mid-April and early June. Spring soil water content was greater than the other treatments between late June and mid-August. In 1999 soil water in the spring treatment was less than all other treatments until late May. Soil water content was greater in the spring treatment versus the other treatments between late June and mid-August.

Soils at both depths in the spring treatment never approached field capacity (24 percent gravimetric soil water) nor became thoroughly wetted through the profile, despite receiving the same amount of water as the current and winter treatments (table 6.1). Soils in all other treatments started the growing seasons above or just below field capacity in 1998 and 1999.

Surface soil moisture clearly reflected the shifts in precipitation distribution for each treatment, with the spring treatment being significantly drier during the winter period, and wetter than current and winter during the April-June period (fig. 6.2). During the three-year period, current and winter plots tended to dry more quickly than the ambient plots, perhaps because actual precipitation was at or above average during this time.

Soil temperature tended to be lowest in the ambient treatment (fig. 6.3). These differences were probably caused by the insulating effect of the shelters, even though they were open on all sides and well ventilated. The effect seemed to be most pronounced in summer, when soils were dry and plant

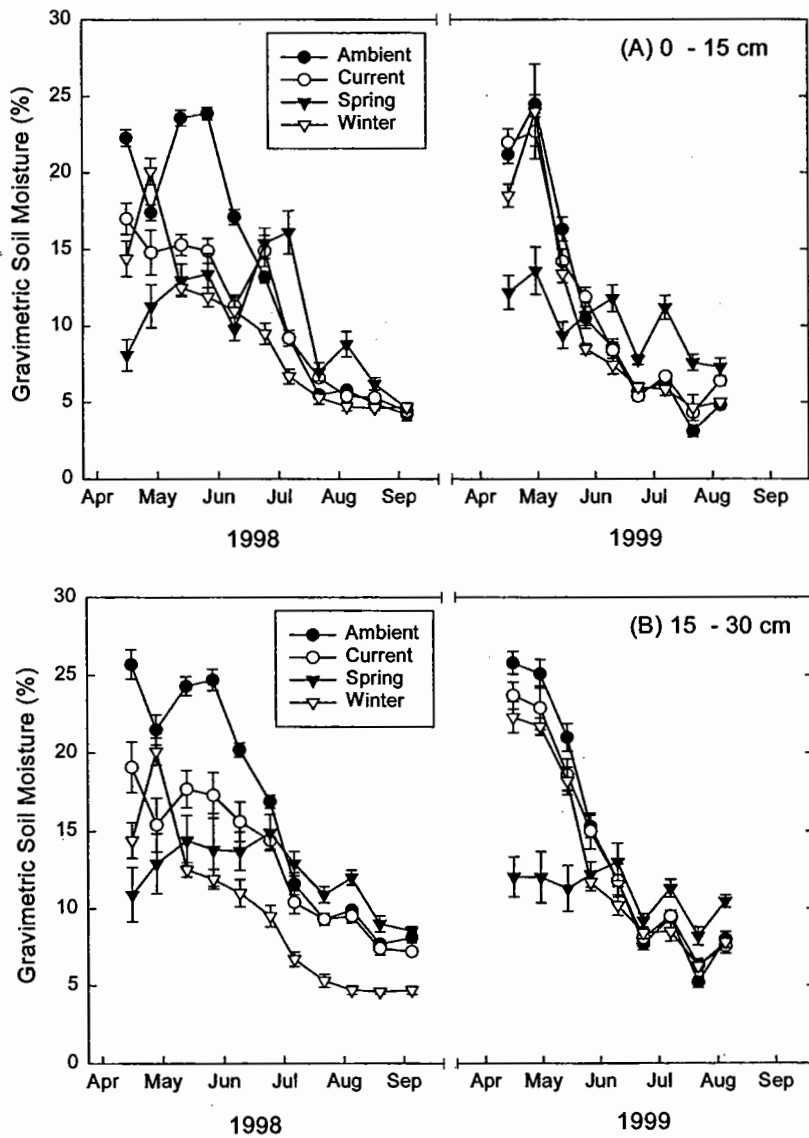


Figure 6.1. Soil moisture (percent) at 0-15 cm (A) and 15-30 cm (B) for the shelter treatments and ambient plots during the growing seasons of 1998 and 1999. Vertical bars are one standard error of the means.

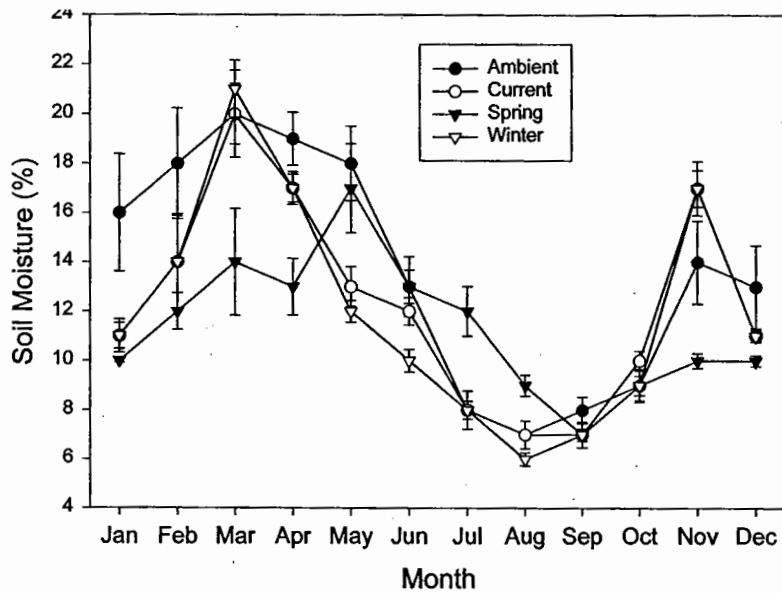


Figure 6.2. Monthly average soil moisture at 5 cm for shelter treatments and ambient plots. Values were calculated from hourly data measured with Watermark® soil sensors. Vertical bars are one standard error of the mean.

growth was decreasing. During the April to June period, soil temperatures on all treatments were similar.

Discussion

Vegetation Response

Precipitation timing affected the growth and structure of the sagebrush steppe community we studied. The effects differed from our initial expectations. Based on ecosystem comparisons such as that of Cook and Irvin (1992) and other studies of grasslands and shrublands (e.g., Coupland 1979; Sala et al. 1989), we predicted that the winter treatment would favor shrubs and the spring treatment would favor grasses. Precipitation during the dormant season (winter) should recharge the lower part of the soil profile, and thus favor tap-rooted species, whereas growing season (spring) precipitation should favor the fibrous-rooted grasses that are effective at using moisture from the upper levels of the soil profile (Coupland 1979; Yoder et al. 1998). Our results contradict those initial predictions. Standing herbaceous biomass was

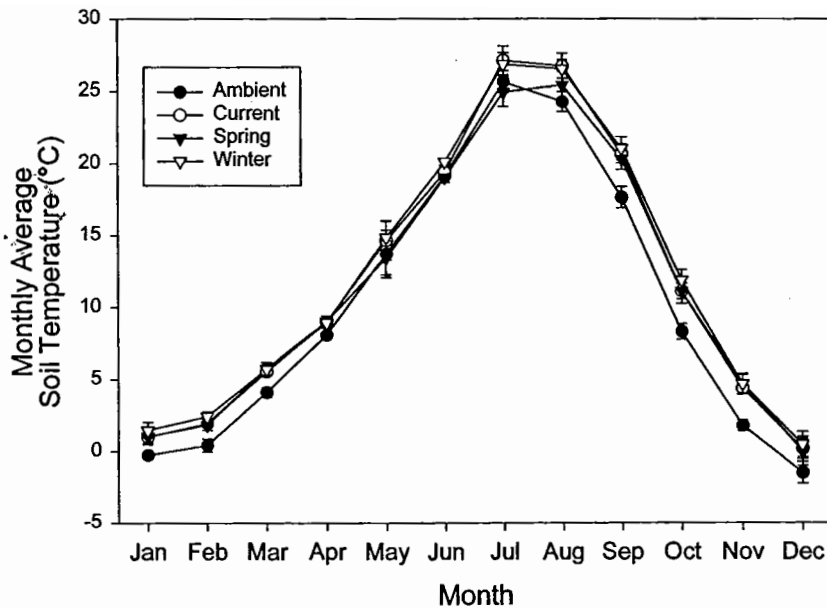


Figure 6.3. Monthly average soil temperature (°C) at 5 cm soil depth during 1996 to 1998. Vertical bars are one standard error of the mean.

consistently lowest in spring compared with other treatments (table 6.2). The spring treatment also had the largest percentage of bare ground and the lowest percentage of herbaceous cover when compared with other shelter treatments (table 6.3). Thus plant productivity and cover may have been limited by the inability of many species to fully complete their life cycle in the spring treatment (table 6.4).

There are two potential explanations for the low productivity of the spring treatment: (1) soil moisture was inadequate during a critical growth period, or (2) the later application of precipitation in the spring treatment resulted in lower plant available moisture, as soil moisture never approached levels developed in the other treatments (fig. 6.1). The fact that the annual forb *Collinsia* did not complete its life cycle (and rarely emerged) during any year of the study in the spring treatment suggests that moisture was lacking during a critical period. In all the other treatments in all years, *Collinsia* completed its life cycle 100 percent of the time (table 6.4). These results demonstrate the utility a species can have as an indicator of a climatic scenario.

The winter treatment was more conducive to growth of annual plants than was the spring treatment (tables 6.2 and 6.3). Production and cover of

annuals was somewhat variable in the current and ambient treatments. The production of annuals in the ambient treatment can probably be explained by the distribution of natural rainfall. During the 1998–99 season, there was very little natural rainfall from March through May, and annual plant production was low in the ambient plots. Most of the annuals in the community we studied were winter annuals (Cronquist et al. 1977), and late winter/early spring moisture appears critical for their development. The higher cover of annuals in the winter treatment was consistent with our original hypothesis.

The dominant shrub, Wyoming big sagebrush, was not influenced significantly by any of the shelter treatments (table 6.4). There was a tendency for sagebrush to reach more advanced stages of phenology in all shelter treatments compared with the ambient plots. The slightly higher temperatures under the shelters or the manner in which water was applied might provide an explanation. Sagebrush overwinters a portion of its leaves and can be photosynthetically active during the winter (Caldwell 1979), whereas the other species we studied initiate growth in the spring. Sagebrush would, therefore, be more likely to be influenced by the higher early season temperatures (fig. 6.3) than would the other species. The slightly lower values for sagebrush development in the winter treatment compared with current and spring (table 6.4) may be because this species often responds to summer rains with increased reproductive shoot development (Evans et al. 1991). The difference is not significant at this point, but it bears watching in the future. Canopy cover estimates also do not show any significant differences among treatments for sagebrush (Bates et al. 1999). It appears that sagebrush is less likely to be influenced in the short term by climatic shifts relative to many of the herbaceous species.

Shelter Effects

The effects of the rain shelters on microclimate were discussed in a technical note published previously (Svejcar et al. 1999). We can add a little more detail to this discussion from data presented in this chapter. Average soil temperature is warmer under the shelters than in ambient plots (see fig. 6.3 for a seasonal comparison of soil temperatures). The differences under the shelters and in ambient plots are evident during all seasons except spring. The greatest similarity among treatments occurred in April, May, and June, which is also the period of maximum plant growth. Soil temperatures for different treatments under the shelters were similar most of the year. The only differences

occurred in July and August, when spring plots were slightly cooler than current or winter plots (fig. 6.3). This is because spring plots received precipitation later into the summer than other treatments (table 6.1), had higher July and August soil moisture (fig. 6.1), and would have experienced some degree of evaporative cooling.

The general approach employed in this study was successful; i.e., we were able to keep total precipitation constant while altering distribution (table 6.1). The only problems we encountered were with the February waterings, when on occasion it was necessary to delay water application for a week or two due to low temperatures. However, when temperatures were too low for watering, they were also too low for much plant growth. Another technical consideration was the wind. We avoided watering during windy periods, and during the spring it was sometimes necessary to apply the water at sunrise before convective winds began.

Conclusions

Changes in precipitation distribution have the potential to influence the structure and productivity of sagebrush steppe vegetation. However, our results do not conform to the original hypothesis that winter precipitation will favor shrubs, and spring/summer precipitation will favor grasses. In this study, shifting precipitation to a spring/early summer pattern had a negative effect on the plant community in terms of herbaceous productivity, vegetation cover, and the ability of some key plant species to reproduce. Herbaceous plants in the environment of the Great Basin are physiologically adapted to a winter/early spring precipitation pattern, where reliable soil water recharge occurs prior to the growing season. Development of a spring/summer precipitation pattern would result in declines and, potentially, the eventual loss of some native annual and perennial forbs. Biomass production would also be reduced. Wildlife, domestic livestock, and other organisms that depend on the production of herbaceous annual and perennial vegetation would be adversely affected by a spring moisture regime. The shelter results also suggest there would be an increase in bare ground with a spring moisture pattern. More bare ground could increase soil erosion, and the open sites created by loss of native plant species may permit invasion by noxious weeds.

We propose two possible explanations for the negative effects of shifting precipitation to spring from winter: (1) the spring/early summer distribution

resulted in plant stress during a critical early growth period (probably March), or (2) applying precipitation later in the growing season reduced effective soil moisture for plant growth (because of higher evapotranspiration) compared with winter application. This study demonstrates that experimental research conducted in the field can provide an important test of assumptions drawn from observational studies.

Notes

1. The mention of trade names does not indicate an endorsement by USDA-ARS or Oregon State University.