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ECOSYSTEMS

Altering Rainfall Timing and Quantity in a Mesic Grassland Ecosystem: Design and Performance of Rainfall Manipulation Shelters

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ABSTRACT

Global climate change is predicted to alter growing season rainfall patterns, potentially reducing total amounts of growing season precipitation and redistributing rainfall into fewer but larger individual events. Such changes may affect numerous soil, plant, and ecosystem properties in grasslands and ultimately impact their productivity and biological diversity. Rainout shelters are useful tools for experimental manipulations of rainfall patterns, and permanent fixed-location shelters were established in 1997 to conduct the Rainfall Manipulation Plot study in a mesic tallgrass prairie ecosystem in northeastern Kansas. Twelve 9 x 14–m fixed-location rainfall manipulation shelters were constructed to impose factorial combinations of 30% reduced rainfall quantity and 50% greater interrainfall dry periods on 6 x 6–m plots, to examine how altered rainfall regimes may affect plant species composition, nutrient cycling, and above- and belowground plant growth dynamics. The shelters provided complete control of growing season rainfall patterns, whereas effects on photosynthetic photon flux density, nighttime net radiation, and soil temperature generally were comparable to other similar shelter designs. Soil and plant responses to the first growing season of rainfall manipulations (1998) suggested that the interval between rainfall events may be a primary driver in grassland ecosystem responses to altered rainfall patterns. Aboveground net primary productivity, soil CO_2 flux, and flowering duration were reduced by the increased interrainfall intervals and were mostly unaffected by reduced rainfall quantity. The timing of rainfall events and resulting temporal patterns of soil moisture relative to critical times for microbial activity, biomass accumulation, plant life histories, and other ecological properties may regulate longer-term responses to altered rainfall patterns.

Key words: climate change; precipitation patterns; rainout shelters; grasslands; soil moisture; net primary production; floristic diversity; life histories; Konza Prairie; long-term research.

INTRODUCTION

Global climate change will likely cause profound effects in terrestrial ecosystems. An important, yet largely unexplored element of global climate change scenarios is patterns of rainfall, one of the primary controls on net primary production over large areas of the earth (Churkina and Running 1998). Predictions from climate change models for continental regions of North America include reduced total amounts of growing season precipita-

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tion and a "repackaging" of rainfall into fewer but larger rainfall events (Easterling 1990; Houghton and others 1990, 1996; Karl and others 1991). Such changes in growing season rainfall patterns may have important ecological consequences for grasslands (Knapp and others 1998a).

Changes in the timing and amounts of growing season precipitation are likely to cause long-term changes in grassland plant community composition. Paleobotanical and historical records show how vegetation zones and grassland/forest boundaries have followed shifting precipitation patterns across the present Central Plains grasslands of the United States (Borchert 1950; Axelrod 1985). In this century, grassland communities in the Great Plains underwent dramatic compositional changes during the severe 7-year drought (1934–41) that marked the 1930s dust bowl era (Weaver 1968). During the dust bowl, tallgrass prairie plant communities dominated by *Andropogon gerardii* and *Sorghastrum nutans* were replaced by midgrass communities dominated by species normally found farther west, such as *Agropyron smithii* and *Bouteloua curtipendula*.

Existing patterns of aboveground net primary productivity (ANPP) also correlate strongly with regional gradients in precipitation (Diamond and Smeins 1988; Sala and others 1988). Thus, shorter-term changes in ANPP also may result from altered precipitation regimes. From an agricultural perspective, composition and productivity responses to altered precipitation regimes are important, because they influence the capacity of grasslands to support livestock production. From a conservation standpoint, grassland ecosystem responses to altered precipitation patterns may have important consequences for regional patterns of biological diversity.

Experimental approaches to studying precipitation impacts on ecosystems often involve the use of rainout shelters to exclude natural precipitation. Rainout shelters can provide considerable flexibility in experimental precipitation manipulations. Simple shelters can provide control over the timing of drought. More elaborate shelters can include irrigation systems (Arkin and others 1976; Ries and Zachmeier 1985; Miller and others 1991; Svejcar and others 1999) that allow for control over the daily, weekly, or seasonal timing and extent of wet and dry periods, independent of patterns of ambient rainfall. The use of rainout shelters also provides choice in experimental design and location, and the potential to conduct long-term experimental manipulations.

Numerous designs for fixed and mobile rainout shelters have been described. These range from small, fixed structures intended to exclude rainfall from the root zones of a single plant (Jacoby and others 1988) to moveable, building sized structures covering 700 m^2 (Martin and others 1988). There are some basic design criteria applicable to all rainout shelters, the foremost being effective exclusion of rainfall, but in addition shelters should cause minimal alteration of microclimate conditions other than rainfall, withstand adverse weather conditions, and be accompanied by some method of controlling surface and subsoil water movement (Foale and others 1986; Hatfield and others 1990).

Moveable shelters are usually large prefabricated metal or fiberglass buildings mounted on rails (Arkin and others 1976; Upchurch and others 1983; Dugas and Upchurch 1984; Ries and Zachmeier 1985; Kuja and others 1986; Martin and others 1988; Miller and others 1991). In practice, moveable shelters are positioned over an experimental plot only while rain is falling. The rest of the time they occupy an equal-sized "parking space" adjacent to the plot. This doubles the space required for an experiment and often includes a costly infrastructure of drive mechanisms and automatic control systems. However, an important benefit gained from moveable rainout shelters is minimal microclimate effects on vegetation and soils, because these shelters are over the experimental plots for only a small proportion of the growing season (Dugas and Upchurch 1984).

Large movable shelters are used mostly for crop research. Because native ecosystems are often much more variable than cropping systems in soils, vegetation, and other characteristics, replication is necessary to reliably detect treatment effects (Svejcar and others 1999). The simplicity and lower construction costs of fixed-location shelters can allow for needed replication. However, the major tradeoff is the presence of chronic microclimate impacts. Typical microclimatic impacts of fixed rainout shelters include increased air temperature, decreased solar radiation, wind, and vapor pressure deficit (Dugas and Upchurch 1984; Jacoby and others 1988; Kvien and Branch 1988; Clark and Reddell 1990; Huang and others 1994; Hudak and Patterson 1996). Even though fixed shelters can be designed to minimize these effects, they must be accompanied by unsheltered control plots to evaluate the impacts of the shelters.

We recently initiated a long-term study of rainfall patterns in a native tallgrass prairie ecosystem in northeastern Kansas, USA. Since 1997, rainfall patterns have been manipulated in native prairie by using a series of study plots covered by fixed-location rainout shelters with irrigation systems, which we call rainfall manipulation plots (RaMPs). The

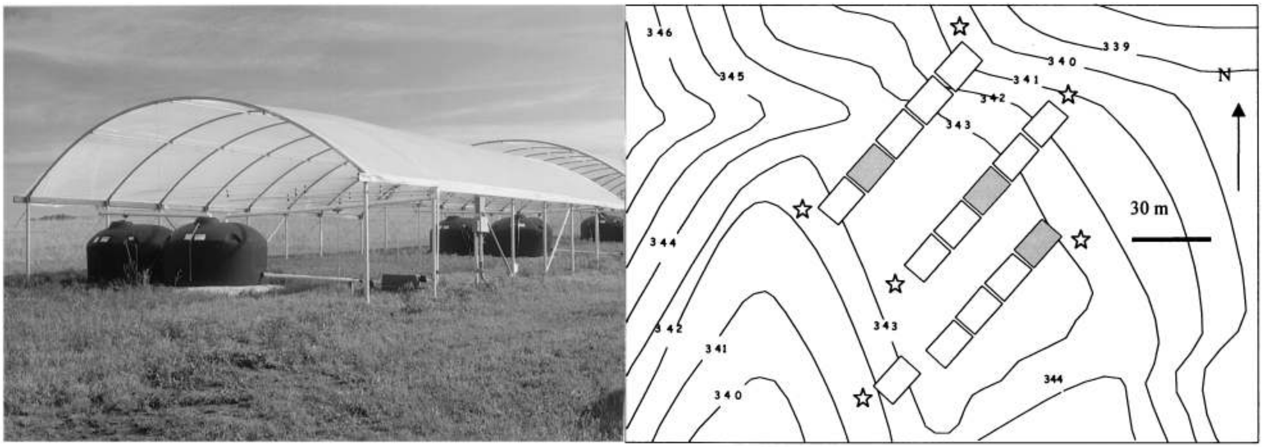

Figure 1. Left: One of 12 rain exclusion shelters, showing rainfall storage tanks and irrigation system erected for the rainfall manipulation plot study at Konza Prairie Biological Station in northeastern Kansas. See text for full description. **Right**: Map showing site topography and study plot layout. Rectangles denote perimeters of rain exclusion shelters. Shaded rectangles are no-shelter control plots. Stars indicate locations of rain gauges used to monitor natural rainfall and determine quantities for experimental application. Elevations in meters above mean sea level.

objectives of the RaMP experiment are to assess changes in plant species composition, nutrient cycling, ANPP, and above- and belowground plant growth dynamics under altered rainfall regimes, specifically reduced growing season rainfall quantity, and fewer but larger rainfall events. This paper describes (a) the design of the shelters and irrigation systems, (b) an evaluation of their impacts on microclimate, and (c) ongoing measurements of ecosystem responses to altered rainfall and first-year patterns of ANPP, soil CO_2 flux, and flowering plant phenology and diversity.

METHODS

Study Site

The RaMP study is located at the Konza Prairie Biological Station, near Manhattan, Kansas (39°05′N, 96°35′W). Konza Prairie is in the Flint Hills, a 1.6-million-ha region spanning eastern Kansas from the Nebraska border south into northeastern Oklahoma. Flint Hills is the largest remaining area of unplowed native tallgrass prairie in North America and supports a significant livestock industry. Konza Prairie is an ecological research preserve and a National Science Foundation Long-Term Ecological Research site with a major focus on how climatic variability, along with periodic fire and ungulate grazing, affects tallgrass prairie ecosystem structure and function. Long-term records of climate and the effects of fire and grazing on plant species composition and productivity are available (Gibson and Hulbert 1987, Knapp and others 1998a).

Total precipitation at Konza Prairie averages 835 mm y^{-1}, with 75% falling during the growing season, May through September. Growing season rainfall is bimodal, with high monthly rainfall totals during May and June, low rainfall and high temperatures in July and August, and a second, lesser rainy period in September. Variation from these general precipitation patterns is common, both in yearly totals and seasonal distribution (Hayden 1998).

The vegetation of Konza Prairie is classified as native tallgrass or bluestem prairie (Küchler 1964; Hulbert 1973) and is a matrix of perennial, warm-season C_4 grasses, accompanied by numerous less abundant C_3 species in the Compositae, Fabaceae, Brassicaceae, and other families (Freeman 1998). Over 500 species representing more than 90 families have been recorded (Freeman and Hulbert 1985).

The RaMP site is dominated by three warm season C_4 tallgrasses, *Andropogon gerardii*, *Sorghastrum nutans*, and *Sporobolus asper*, and the forbs *Solidago canadensis*, *Aster ericoides*, and *S. missouriensis*. Woody species, primarily *Rosa arkansana* and *Amorpha cansescens* occur in a few plots, but in preliminary surveys all woody species had mean cover values less than 2% and accounted for less than 1% of total biomass.

Fifteen rainfall manipulation plots are arranged five plots per block in three blocks aligned on a southwest-northeast axis (Figure 1). The blocks differ primarily in soil depth. The middle block is on deeper, rock-free soils to 1.2 m depth, whereas the north and south blocks are located at a slightly higher elevation where a loose limestone layer occurs at approximately 0.75 m depth. The soils are Irwin silty clay loams with slope less than or equal to 4% (Jantz and others 1975). The study site is relatively uniform in soil total N and C, floristic composition, and ANPP, based on preliminary surveys. Before this experiment, the site was burned during March or April in 11 of the last 14 years, and it will be burned annually during late March for the duration of the RaMP study. Frequent burning early in the growing season is a common management practice in Flint Hills grasslands because it favors plant species suitable for livestock grazing (Owensby and Anderson 1967). Historically, spring is thought to be the most likely time for fires caused by natural sources (Hulbert 1973).

Shelter Design

All 15 plots were initially prepared for the experiment by installing a vertical perimeter barrier of galvanized sheet metal. This barrier enclosed a 7.6 x 7.6–m area to 1.2-m depth and extended 10 cm above the soil surface to minimize surface and subsoil water flow and root/rhizome penetration from outside the plot. Four rainfall manipulation treatments (three replicates) then were assigned to 12 of the plots in a randomized complete block design (Figure 1). The three remaining plots serve as unsheltered controls for effects caused by the shelters and irrigation systems.

The rainout shelters built over the 12 experimental plots consist of a galvanized tubular steel frame supporting a clear plastic roof, rainfall collection and storage equipment, and an irrigation system for rainfall reapplication (Figure 1). The basic shelter is an "off-the-shelf" commercial greenhouse design (Rainbow Plus; Stuppy Greenhouse Manufacturing, Inc., North Kansas City, MO, USA), 9.14 m wide x 14.0 m long (128 m^2), with 1.8-m eaves. These dimensions were planned so that natural rainfall would be excluded from a 6 x 6–m core plot allocated for measurements of plant and soil responses. Disturbance of this core plot was carefully avoided during all phases of shelter construction. The shelters are anchored in 1.2-m-deep concrete footings and braced with external guy wires (Figure 1) to maximize their stability in high winds.

The plastic roofs consist of a single layer of clear, 6 mil, 3-year UV-transparent polyethylene greenhouse film (Duragreen Marketing USA Inc., Mount Dora, FL, USA). The poly film attaches to the shelter with a wire clip system (Polylock, Stuppy Greenhouse Manufacturing, Inc.). Shelter sides and ends remain open to maximize air movement and minimize temperature and relative humidity artifacts. Because our experimental protocol calls for manipulating growing season rainfall, the poly sheets are installed each April and removed in October.

Natural rainfall for experimental application to the plots is collected off a 9.14 x 9.44–m (86.3 m^2) subsection of the roof, through a system of gutters and PVC downspouts connected to two 4164-L black polyethylene storage tanks (model 171; Snyder Industries, Lincoln, NE, USA). Total storage capacity is approximately 10 cm of rainfall. Black tanks were chosen to minimize light penetration and subsequent algae growth.

The irrigation system consists of 13 eave-height irrigation nozzles arranged in a square grid that irrigates an 86.3-m^2 area centered on the core measurement plot. The grid contains one 891.5-L-h^{-1} high volume, low drift nozzle (Senninger Irrigation Inc., Orlando, FL, USA) surrounded by 12 98.0-L-h^{-1} nozzles. This nozzle configuration provides even water distribution across the core measurement plot. Each nozzle is pressure regulated to 41.37 KPa, allowing a maximum application rate of 2068 L h^{-1}, or approximately 2.5 cm h^{-1}. Water is pumped from the tanks to the nozzles by a cast-iron self-priming centrifugal pump powered by a 0.37-kW single-phase electric motor (model 1P852; Dayton Electric Manufacturing Co., Niles, IL, USA) controlled by an electronic timer (Intermatic ET100C; Intermatic Incorporated, Spring Grove, IL, USA), allowing manual or programmable pump operation. Rainfall applications are quantified with a positive displacement meter (FTB 6207; Omega Engineering Inc., Stamford, CT, USA). The irrigation system is plumbed with Schedule 40 PVC pipes and threaded fittings for easy maintenance and winter dismantling.

Natural rainfall quantities at the RaMPs study site are measured with six plastic wedge gauges (6.35 x 5.84–cm opening, Tru Chek; Edwards Manufacturing Co, Albert Lea, MN, USA) placed near the ends of each block of RaMPs (Figure 1). An average value from the six gauges is used to document each rain event and to calculate the quantity of collected rainwater to be applied in each experimental treatment. The accuracy of the wedge gauge rainfall estimates was assessed by regressing them against rainfall readings from a standard Belfort-type recording rain gauge at the Konza Prairie headquarters weather station (0.5 km southeast of the study site). The efficiency of rainfall collection off the roofs was assessed by comparing the calculated amount of rain that fell on the roof collection area, based on measured rainfall amounts, with the quantity of rainfall found in the storage tanks, determined from flowmeter records. An array of 12 rain gauges was placed under each of two shelters to check their effectiveness at excluding natural precipitation. The extent of chemical change to rainwater stored in the increased interrainfall interval treatments was examined by comparing concentrations of NO_3^--N, NH_4^+-N, and PO_4^{3-}-P in fresh rainwater samples with water samples from storage tanks. Water samples were analyzed colorimetrically on an Alpkem RFA 300 autoanalyzer (DI Analytical, College Station, TX, USA.

Shelter Microenvironment

Light, temperature, and vapor pressure deficit under the shelters were characterized in a subset of the RaMPs. Sensors for photosynthetic photon flux density (PFD), net radiation, air, soil, and stored water temperature were placed in each of the four shelters (except two for water temperature) and in the unsheltered control plot in the middle block of RaMPs. Measurements of PFD were made with a quantum sensor (LI-190SB; LiCor Inc., Lincoln, NE, USA), and net radiation with a Fritschen-type net radiometer (model 605; C.W. Thornthwaite Associates, Pittsgrove, NJ, USA). Soil, air, and stored water temperatures were measured with thermisters (model 107; Campbell Scientific, Logan, UT, USA). Radiation and air temperature sensors were mounted in the center of the plot, 1.5 m above ground level. The air temperature thermister was shielded in an aspirated white PVC housing. Soil temperature thermisters were buried at 5 and 15 cm near the center of each plot. Radiation and temperature sensors were cross-calibrated before field deployment. Sensor outputs were recorded with Campbell CR10X data loggers programmed to compile 1-min averages. Data logger and pump controls were housed in watertight metal electrical boxes. Vapor pressure deficits were determined from water vapor flux measurements made with a closed loop infrared gas analysis system (LI-6200; LiCor, Inc.). These readings were taken on eight cloud-free days from June to September 1998.

Spatial and temporal patterns of soil water content in the upper soil horizons of the RaMPs were characterized using time domain reflectometry (Topp and others 1980). Probe pairs at 15- and 30-cm depth were placed at 16 positions within the 6 x 6–m sampling areas of two sheltered plots and one unsheltered control plot. Soil moisture measurements were conducted weekly from June through October 1998. This intensive sampling was conducted to determine if irrigation applications resulted in even soil water content across the core measurement plot.

Rainfall Manipulation Treatments

Experimental applications of rainfall were conducted according to the following protocol, which is a factorial combination of two treatments: (a) altered growing season (May-September) rainfall quantity, and (b) altered timing of growing season rainfall events.

1. Natural quantity and interval. This treatment replicates the naturally occurring rainfall regime. Each time a natural rainfall event occurs, the quantity of rain that fell is immediately applied to the plots.
2. Increased interval. Rather than immediately applying rainfall as it occurs, rainfall is stored and accumulated to lengthen the dry intervals by 50%. The accumulated rainfall is applied as a single large event at the end of the dry interval. Over the season, the naturally occurring quantity of rainfall is applied, but the timing of events is altered, repackaging the rain into fewer, larger events.
3. Reduced quantity. In this treatment, only 70% of the naturally occurring rainfall is immediately applied. This imposes reduced amounts of rainfall without altering the timing of rainfall events.
4. Reduced quantity and increased interval. Rainfall intervals are lengthened by 50%, and only 70% of the accumulated rainfall is applied, imposing both reduced quantity and altered timing of events.

The 30% reduction in rainfall quantity and 50% increase in length of interrainfall dry periods were chosen because they represent rare but documented patterns in the current climate and are in the direction predicted by many climate change models for the Great Plains (Waggoner 1989; Easterling 1990; Houghton and others 1990, 1996). The 30% reduction exceeds natural interannual variability in growing season precipitation at the RaMPs site [standard deviation (SD) = 25% of the mean based a 100-year record] and is typical of rainfall amounts presently occurring in midgrass prairies west of our study site. We opted to base our rainfall manipulations on the actual rainfall regime occurring during the study, rather than long-term average rainfall, because using long-term averages would render the unsheltered plots invalid as controls for effects of the shelter.

Table 1. Rainfall Manipulation Plot Study Response Variables and Measurement Frequencies

Response	Frequency
Microclimate	Continuous
Flowering phenology	Biweekly
Rainwater chemistry	Weekly[a]
Grass/forb photosynthesis, water status, tissue N	Weekly[a]
Soil CO_2 flux	Weekly[a]
Soil water content	Weekly[a]
Root distribution and turnover	Monthly
Litter decomposition/ mineralization	Seasonal
Soil organic matter and N	Seasonal
Root biomass and nutrients	Seasonal
N availability	Seasonal
Microbial biomass C and N	Seasonal
Plant species composition	Seasonal (spring, fall)
Aboveground NPP	Fall (peak biomass)

[a] *These variables measured more frequently around selected rainfall events.*

Several rules govern the implementation of these treatments. Immediate rainfall applications must take place within 12 h of the corresponding natural rainfall event. For the increased interval treatments, naturally occurring dry periods are defined as those with no rainfall event over 5 mm in 24 h, because events smaller than this threshold are almost entirely intercepted by the plant canopy (Seastedt 1985) and thus have little effect on soil or plant water status. The length of the increased dry period is determined as 1.5 times the length of the most recent natural dry period. All treatment applications are made with wind speeds below 4.5 m s^{-1}, to avoid uneven soil moisture distributions. This condition is easily met by early morning applications during windy periods.

Measurements of Ecosystem Responses to Altered Rainfall

Numerous plant and soil parameters are being measured in the RaMPs project (Table 1). Methods are standardized as much as possible with those of the Konza Long-Term Ecological Research (LTER) program (Knapp and others 1998a), enabling direct comparisons with long-term records of productivity, species composition, plant growth and physiology, and belowground processes. Microclimate characteristics will be monitored continuously for the entire experiment. Soil water content is monitored at least weekly, more often around selected events such as large experimental rainfalls after prolonged dry periods. Soil water content is our primary indicator of the comparability of our experimental rainfall applications to natural rains. Plant gas exchange and water status and soil CO_2 flux serve as primary indicators of plant and soil responses to rainfall patterns. These variables will be monitored intensively for the first 5 years of the study, less intensively in later years. Soil nutrients, species composition, and ANPP are integrators of the effects of altered rainfall patterns over the longer term.

Patterns of soil CO_2 flux, ANPP, flowering duration for dominant warm season grasses, and overall floristic diversity are presented for 1998, the first year of rainfall manipulations. These parameters were chosen because they are indicators of possible short- and long-term soil and plant responses to altered rainfall regimes. Soil CO_2 flux was measured with a closed-flow gas exchange system (LiCor 6200; LiCor Inc.) by using methods of Knapp and others (1998b). ANPP was estimated from dry weights of early November harvests of all aboveground vegetation. The duration of flowering for five grass species was determined from twice-weekly surveys during the peak flowering period for these grasses (late August through September). Plant species composition was quantified by visually estimating percent cover for all plant species in four contiguous 1-m^2 permanent quadrats per plot, in May and August. Species richness and the Shannon diversity and evenness indices were calculated from the cover estimates.

Each RaMP is an experimental unit in this design, so plot averages of each response variable were used to calculate treatment means ± 1 standard error (SE) and for randomized complete block analysis of variance (Proc GLM; SAS Institute 1989). Orthogonal contrasts were constructed to test for shelter effects (unsheltered plots vs the natural quantity/timing treatment) and for quantity and timing main effects and their interaction.

RESULTS

Rainfall Collection, Storage, Application

Wedge gauge rainfall estimates, upon which collection and application calculations were based, compared closely to rainfall measurements from the Konza Prairie headquarters recording rain gauge (gauges = 1.0051*headquarters − 0.4893, r^2 = 0.982). The efficiency of rainfall collection off the shelter roofs was over 97%. When averaged over the 1998 season, the calculated rainfall collection

Table 2. Rainwater Inorganic Nitrogen and Phosphorous Concentrations in Natural Precipitation and in Rainwater Stored in the Increased Rainfall Interval Treatments

	Natural Precipitation	Stored Precipitation	T	*P* value
NO_3-N ppb	402.85 ± 91.09[a]	420.82 ± 87.77	0.562	0.6135
NH_4-N ppb	563.23 ± 11.53	364.10 ± 53.53	3.583	0.0231
PO_4-P ppb	37.48 ± 29.78	9.18 ± 4.79	1.890	0.1320

[a] *Values are means ± SE averaged over June, July, and August 1998 and weighted for precipitation volumes.*

Table 3. Microclimate Characteristics under Rain Exclusion Shelters and for a Nonsheltered Control Plot during the 1998 Growing Season

Microclimate Parameter	No Shelter	Rain Exclusion Shelter	*t*	df	*P*
PFD (μmol m^{-2} s^{-1})	1832.21 ± 11.23	1440.84 ± 37.34	10.04	16.5	<0.0001
Net radiation (W m^{-2})					
Day	597.94 ± 5.43	461.08 ± 22.42	5.93	15.6	<0.0001
Night	−41.74 ± 2.95	−14.84 ± 0.99	8.63	17.1	<0.0001
Air temperature (°C)					
Day	36.34 ± 0.39	36.30 ± 0.39	0.06	28	0.9525
Night	24.46 ± 0.76	24.34 ± 0.74	0.11	28	0.9109
Vapor pressure deficit (KPa)	3.29 ± 0.27	3.26 ± 0.23	0.07	28	0.9484
Soil temperature (°C)					
5 cm					
Day	25.31 ± 0.31	26.86 ± 0.25	3.88	28	0.0006
Night	23.13 ± 0.43	24.35 ± 0.36	2.19	28	0.0368
15 cm					
Day	28.61 ± 0.35	30.38 ± 0.38	3.46	28	0.0017
Night	23.52 ± 0.34	25.06 ± 0.31	3.38	28	0.0021
Soil moisture (%WV)					
15 cm	24.70 ± 0.45	25.05 ± 0.62	0.41	15	0.6892
30 cm	28.60 ± 0.61	29.20 ± 0.55	0.75	15	0.4622

Values for PFD, net radiation, and air and soil temperatures were based on daytime maxima and nighttime minima from 15 cloud-free days during June, July, and August. Vapor pressure deficits were taken on 8 days during the same period. Soil moisture values were averaged from weekly readings taken over the entire growing season. Values are means ± 1 SE, with differences between means assessed by two sample t tests.

amounts did not differ from the actual amounts present in the storage tanks (actual storage: 2058.5 ± 253.0 L; rain gauge estimate: 1998.4 ± 253.1 L; $t = 0.1677$, $P = 0.8670$, degrees of freedom (df) = 127). The rain gauge arrays placed under two shelters showed that no measurable natural rain reached the core measurement plots. Thus, experimental applications provided the only measurable water inputs. Rainfall application rates averaged 1953.7 ± 15.4 L h^{-1}, or approximately 2.34 cm h^{-1}. Storage caused only minor changes in rainwater inorganic nitrogen and phosphorous concentrations (Table 2). Concentrations of NH_4-N were approximately 35% lower in stored precipitation than in ambient rainfall, but no significant changes in NO_3-N or PO_4-P were detected. Stored water temperatures were well buffered from fluctuations in ambient air temperatures, always remaining at least several degrees below maximum daytime air temperatures (data not shown).

Shelter Microclimate

Peak daytime PFD and net radiation influxes were both reduced by approximately 22% under the shelters compared with the unsheltered control plots (Table 3). Reductions in PFD and net radiation were caused partly by the imperfect transparency of the poly greenhouse film, and partly by transient shading from roof structural members and irrigation system components. Nighttime net radiation loss from under the shelters was reduced by 65% compared with unsheltered plots (Table 3).

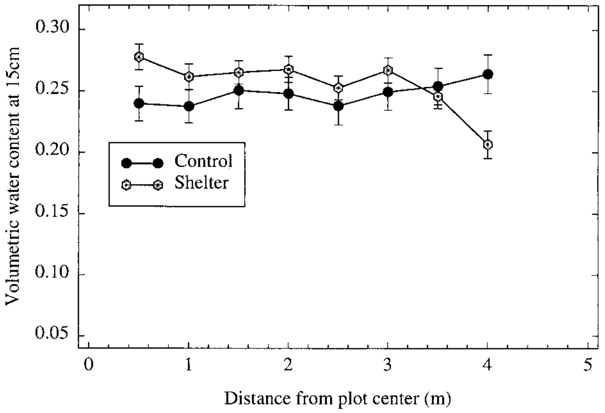

Figure 2. Spatial distribution of soil moisture resulting from irrigation in rain exclusion shelters and in control plots receiving only natural rainfall. Data are means ± 1 SE, averaged over the 1998 growing season.

No effects of the shelters on day or nighttime air temperatures or midday vapor pressure deficits were noted (Table 3). However, daytime maximum and nighttime minimum soil temperatures were 1.2–1.8°C higher under the shelters than in unsheltered plots. Average growing season soil water content under shelters was within 1% of the unsheltered control plot at 15- and 30-cm depths (Table 3). Soil water at 15-cm depth was evenly distributed spatially, differing by less than or equal to 1.5% within 3.5 m of the plot center (Figure 2). Soil water content decreased slightly beyond 3.5 m, in the corners of the 6 x 6–m measurement plot. Soil water content distributions at 30 cm closely followed 15-cm soil water patterns (data not shown).

Preliminary Responses to Altered Rainfall

Total growing season rainfall for 1998 was about average, at 622 mm. From June 1 through October 1 1998, 28 natural rainfall events occurred (Figure 3), averaging 19.08 ± 3.82 mm (mean ± 1 SE) per event. Large natural rainfalls occurred June 22–23 (68 mm), July 23 to August 03 (236 mm), and September 20–21 (65 mm). This natural rainfall regime translated into four rainfall events in the increased interval treatments, on June 22 (88 mm), July 13 (59 mm), August 02 (232 mm), and September 12 (29 mm).

The repackaging of rainfall into fewer, larger rainfall events in the increased interval treatments changed soil wetting and drying cycles (Figure 3). For example, soil water content declined slowly in the natural timing treatments from late June through mid-July, because of six 20-mm or less rainfalls after the large June 22 event. In contrast, soil water content declined rapidly during the same period in the increased interval treatments. A similar pattern also was seen in August, when small late August rains reversed a decline in soil water content, whereas soil drying continued in the increased interval plots.

Reducing the quantity of rainfall by 30% had less pronounced effects on soil moisture (Figure 3). Reduced quantity generally had little effect on soil water content when rainfall was applied at natural intervals. During the July period of relatively small rain events, soil water content was lower when rainfall quantity was reduced, but not significantly. Rainfall quantity did affect soil water content in increased interval treatments during two periods, the second halves of July and September. At other times, extremely large rain events (late June and early August) equalized soil water content regardless of the quantity applied, and up to 1 month elapsed before effects of application quantity reappeared.

Rainfall interval was the primary influence on soil and plant responses (Figure 4, Table 4), with increased intervals reducing soil CO_2 flux, total ANPP, and flowering duration to various extents. Rainfall interval was the only factor affecting soil CO_2 flux. Total ANPP was reduced in all treatments compared with the natural rainfall regime, although interval was the only significant effect. Flowering duration was reduced only when increased interval and reduced quantity were combined. Species richness averaged 16.53 ± 0.84 per plot, with no rainfall manipulation effects ($P = 0.10$ to 0.58). Comparisons of ambient treatments with unsheltered controls indicated that none of the responses was affected by the presence of the shelters and irrigation systems (Table 4) except for soil CO_2 flux, which was approximately 15% higher in the unsheltered control plots than the natural quantity/interval plots.

DISCUSSION

Shelter Effectiveness and Microclimate

During their first growing season of operation, the RaMP shelters proved to be effective tools for altering the timing and amount of rainfall. The shelters excluded all natural rainfall, efficiently collected rainfall for storage, and allowed accurate quantities of stored rainfall to be applied at prescribed times and amounts, independent of natural precipitation events. Microclimate alterations observed under our rainout shelters were generally comparable to those seen in other fixed shelter designs (Kvien and Branch 1988; Clark and Reddell 1990; Huang and

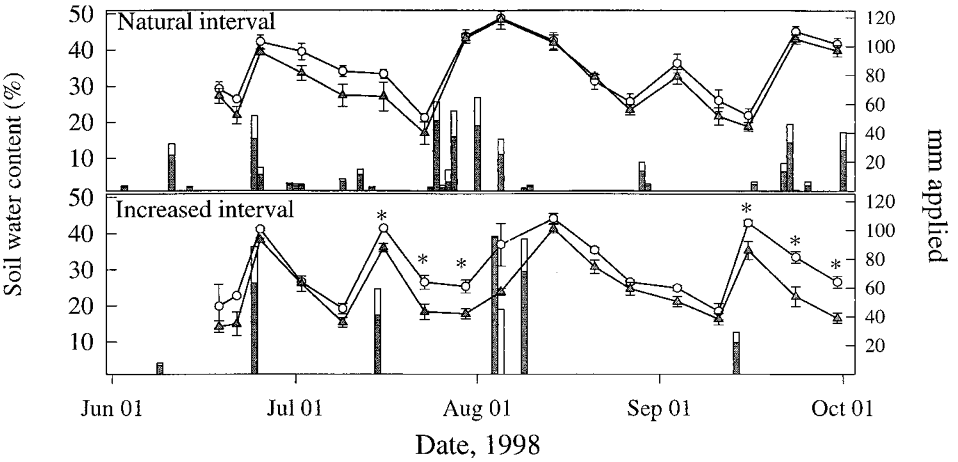

Figure 3. Interval and quantity of experimental rainfall applications (bars) and patterns of soil moisture (lines, means ± 1 SE) during June through September 1998 in the rainfall manipulation plot experiment. Open symbols and bars denote values for natural precipitation quantities, shaded symbols and bars for 30% reductions in precipitation quantity. Asterisks indicate significant ($P \leq 0.05$) differences in soil water content on individual dates between natural and reduced quantity treatments.

others 1994; Bredemeier 1995; Hudak and Patterson 1996). The main shelter effect was to reduce solar inputs and nighttime reradiation. In other similar rainout shelters (Clark and Reddell 1990; Svejcar and others 1999) slightly higher solar input reductions were reported due to differences in roof material and roof structural support design, although no effects on plant growth or yield were noted (Clark and Reddell 1990). PFD under our shelters remained above levels that light-saturate photosynthesis in most prairie plants (Turner and Knapp 1996). A slight soil warming also was found under our shelters, which was expected, and may result from the reduced nighttime radiative cooling (Table 2; Kvien and Branch 1988).

The storage of rainwater in the increased rainfall interval plots caused slight changes in water quality. Water temperatures were well buffered despite the use of black storage tanks to minimize algae growth. Although NH_4-N concentrations were reduced in stored water, rainwater ammonium inputs are a small fraction of plant-available nitrogen in a growing season, which comes mostly from mineralization of soil organic matter (Blair and others 1998). Thus, reduced NH_4-N is unlikely to affect plants in the short run. However, long-term impacts from reduced NH_4-N cannot be discounted, because rainfall is also the primary source of new nitrogen inputs to the system. Water chemistry will be monitored over the course of the study and adjusted as necessary.

Soil moisture, air temperature, and vapor pressure deficits were essentially unaffected by the shelters. Experimental applications at natural intervals and quantities resulted in overall soil water contents similar to the unsheltered plots, and soil water contents were reasonably uniform across the 6 x 6–m core measurement area. Other fixed-shelter designs have reported slightly larger (1–3°C) increases in air temperature under shelters compared with unsheltered control plots (Jacoby and others 1988; Clark and Reddell 1990; Huang and others 1994; Bredemeier 1995). Clark and Reddell (1990) found that wind speeds through their shelters were high enough to equalize shelter air temperatures with the surroundings. There were no observable differences in vapor pressure deficits at the plant canopy level due to the shelters. Higher vapor pressure deficits would be expected under the shelters if outside air were not able to adequately flow through the shelters and could cause significant effects on plant and soil water relations.

Preliminary Soil and Plant Responses

Of the treatments imposed, increasing the interval between rainfall events had the most pronounced effects on soil and plant responses in the first year of the study. Increasing the interval between rainfall events created soil water deficits during periods when natural rainfall patterns maintained higher soil moisture. Soil CO_2 flux was affected only by increased intervals. The primary sources of soil CO_2, root and microbial respiration, are strongly responsive to soil moisture cycles (Hayes and Seastedt 1987; Knapp and others 1998a; Rice and others 1998). There were two substantial decreases in soil moisture during July, which caused a 22% average reduction in soil water content for the month. Lowered soil CO_2 flux indicates the possibility of long-term effects of rainfall timing on nitrogen availability, because microbial activity accounts for most N mineralization (Rice and others 1998). The July dry

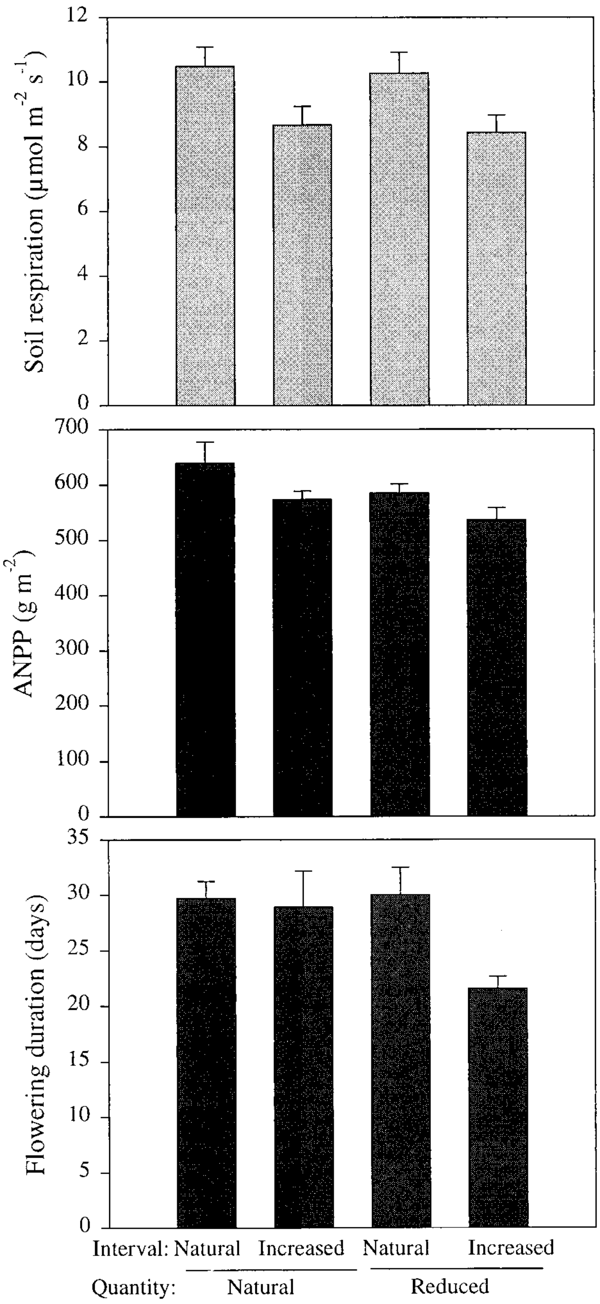

Figure 4. Soil CO_2 flux, ANPP, and flowering duration for dominant warm season grasses in the rainfall manipulatin plots for the 1998 growing season. All values are means ± 1 SE, and soil CO_2 flux is the average of weekly measurements over the season. Analysis of variance statistics are shown in Table 4.

periods also may explain reduced ANPP caused by increased rainfall intervals, because they preceded the normal period of peak biomass accumulation in early to mid-August (Briggs and Knapp 1995).

Reductions in rainfall quantity alone had little or no effect on CO_2 flux or ANPP. Quantity effects on soil moisture were intermittent. Large rains periodically saturated soils in all treatments, and typically several weeks passed before soil water contents decreased enough for the effects of reduced rainfall quantity to appear. These large events may also have caused deep soil recharge, moisture that could contribute to plant productivity but was not reflected in soil water content measurements by using 30-cm probes.

Flowering in the warm season grasses was only affected when reduced rainfall quantity was combined with increased intervals. This was a different pattern than for CO_2 flux and ANPP but consistent with patterns of soil moisture during the flowering observations. Soil moisture averaged 15–23% less in increased interval/reduced quantity plots compared with other treatments for this period. Thus, like CO_2 flux and ANPP, flowering phenology depends primarily on patterns of soil moisture during the relevant part of the growing season.

Floristic diversity did not change after one growing season of rainfall manipulations. Because this assemblage consists almost entirely of perennials, short-term changes in soil moisture dynamics would have little immediate effect on composition, and the cumulative effects of altered soil moisture dynamics make take several growing seasons to appear. The RaMPs experiment is planned to run for at least 10 years, which is probably the minimum necessary to replicate the temporal scale over which rainfall regimes would be expected to change (Schindler 1998), and the slow response times of a perennial vegetation community.

CO_2 flux was the only response variable for which shelter effects were observed. Increased CO_2 flux in sheltered plots receiving the natural rainfall regime compared with unsheltered control plots probably reflects the 1–2°C higher soil temperatures caused by the shelters. This small temperature difference is adequate to explain the larger (15%) difference in CO_2 flux because the temperature CO_2 relationship is nonlinear (Knapp and others 1998b). As with floristic diversity, cumulative effects of this initially small difference may be observed in future years.

In conclusion, these rainout shelters proved well suited for conducting experimental manipulations of rainfall timing and amount in a native tallgrass prairie ecosystem. The primary strength of the shelters is their complete control over the rainfall regime, and their main effect on microclimate was lowered light levels. Preliminary results from the first growing season of rainfall manipulations show that rainfall manipulations can affect plant and soil

Table 4. Analysis of Variance Statistics [F (P Value)] for Soil CO_2 Flux, ANPP, and Flowering Duration in Dominant Grasses for the First Year (1998) of Rainfall Manipulations

	Soil CO_2 Flux	ANPP	Flowering Duration
Block	4.26 (0.0550)	0.96 (0.4221)	5.13 (0.0368)
Shelter effect	11.66 (0.0092)	1.71 (0.2269)	3.03 (0.1201)
Quantity	0.02 (0.9036)	3.40 (0.1024)	4.84 (0.0589)
Timing	22.97 (0.0014)	5.28 (0.0507)	8.27 (0.0206)
Interaction	0.04 (0.8485)	0.11 (0.7468)	5.64 (0.0450)

processes, with the "repackaging" of rainfall into fewer but larger events being potentially at least as important as reductions in rainfall quantity for several plant and soil responses. The interval between experimental rain events and resulting temporal patterns of soil moisture relative to critical phases for microbial activity, biomass accumulation, plant life histories, and other major ecological processes may regulate longer-term responses to altered rainfall patterns.

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