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Rainfall Timing, Soil Moisture Dynamics, and Plant Responses in a Mesic Tallgrass Prairie Ecosystem

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Grasslands occur in well-defined climatic zones based on temperature and rainfall regimes (Hayden 1998). The present distribution of North American grasslands is largely the result of climatic zones that developed during the Miocene-Pliocene transition (Borchert 1950; Axelrod 1985). North American grasslands have persisted because of the relative stability of these climatic patterns, and in some cases because of the additional presence of periodic fires (Wells 1970; Knapp, Briggs, et al. 1998)

Evidence is accumulating that climatic patterns in North American grasslands will change in the coming decades, due to continuing increases in the concentration of atmospheric CO_2 and other greenhouse gases (Schneider 1993; Houghton 1997). Predictions from atmospheric general circulation models (GCMS) suggest that grasslands in the Central Plains region will experience higher growing season temperatures and changes in the patterns of growing season rainfall. Predicted changes in rainfall patterns include reduced total growing season rainfall, increased occurrence of convective rainfall events, longer dry intervals between rainfalls, and lower soil moisture (Manabe et al. 1981; Giorgi et al. 1994; Karl et al. 1996; Gregory et al. 1997; Watson et al. 1997).

Most North American ecosystems, including the Central Plains grasslands, are expected to be moderately to highly sensitive to changes in climate (Watson et al. 1997). The predicted reduction in growing season rainfall would almost certainly affect grassland distribution, diversity, and productivity, but the effect of redistributing rainfall into fewer, larger events might be just as important (Hall and Scurlock 1991). However, the effects of the temporal distribution of rainfall events have rarely been examined (Georgiadis et al. 1989), despite the possible consequences for the conservation and sustainable use of grasslands. For example, changes in the temporal distribution of rainfall may cause the ranges of species or assemblages of conservation concern to expand, contract, or migrate. This would complicate the process of choosing lands for preservation, and managers at existing preserves may find themselves stewarding different assemblages than originally intended. A rainfall redistribution might also render ecosystems more susceptible to invasions by exotic species (Dukes and Mooney 1999). In grasslands used for agriculture, altered rainfall patterns could reduce the aboveground net primary productivity (ANPP) and shift the species composition of grasslands, affecting their carrying capacity for livestock production (Gregory et al. 1999).

In this chapter, we review the range of ecosystem responses that might result from altered rainfall regimes in mesic tallgrass prairie. We also describe preliminary results from an ongoing field experiment on the impacts of alterations in rainfall timing and amount, at the Konza Prairie Biological Station. Konza Prairie is in the Flint Hills (39°05′ N, 96°35′ W), a 1.6 million ha region spanning eastern Kansas, from the Nebraska border south into northeastern Oklahoma. This region is the largest remaining tract of unbroken tallgrass prairie in North America (Samson and Knopf 1994). Konza's climate falls within well-recognized temperature and rainfall parameters for grassland biomes. Total rainfall averages 835 mm y^{-1}, with 75 percent falling during the growing season months of April through October. 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 rainy period in September. High variability is common in yearly rainfall totals and in seasonal distribution (Hayden 1998).

Mesic grassland plant communities such as those at Konza Prairie are typically composed of species from several functional groups (Körner 1994). These include warm-season C_4 grasses, cool-season C_3 graminoids (grasses and sedges), and a diverse array of other C_3 herbaceous dicots (hereafter referred to as "forbs"), including nitrogen-fixing leguminous species, trees, and shrubs. Relatively pristine, frequently burned tallgrass prairies are usually dominated by two groups, C_4 grasses and C_3 forbs, and species abundance patterns in these prairies typically fit a core-satellite model (Collins and Glenn 1991; Hartnett and Fay 1998). The C_4 grasses consist of relatively few species but account for roughly 80 percent of the biomass and canopy cover (Briggs and Knapp 1995; Knapp and Medina 1999). Conversely, forbs constitute a small fraction of the biomass but a large fraction of the species.

Background

Vegetation/Rainfall Relationships

Historic changes in climatic patterns in the Central Plains have always been accompanied by changes in vegetation. Paleobotanical evidence indicates that the Central Plains have become more arid since the middle Miocene, a trend marked by the replacement of semi-open forests by grasslands (Axelrod 1985). More recently, rapid compositional changes in plant communities were witnessed during the 1930s Dustbowl era in the Central Plains (Weaver 1968). During this severe drought, which lasted from 1934 to 1941, tallgrass prairie dominants such as big bluestem *(Andropogon gerardii),* switchgrass *(Panicum virgatum),* and Indian grass *(Sorghastrum nutans)* were replaced by mid- and shortgrass species such as buffalograss *(Buchloe dactyloides),* blue grama *(Bouteloua gracilis),* and sideoats grama *(B. curtipendula).*

Modern regional patterns of grassland plant species composition and productivity also correlate with patterns of rainfall. Diamond and Smeins (1988) found a continual replacement of little bluestem *(Schizachyrium scoparium)* by big bluestem on a south-to-north temperature and rainfall gradient from coastal Texas to North Dakota. The Central Plains is a vast west-to-east gradient in grassland species composition, with the transition from shortgrass to midgrass to tallgrass prairie (Küchler 1964) following the eastward increase in annual rainfall. ANPP also increases along this west-to-east gradient (Sala et al. 1988). Relationships between ANPP and quantity of rainfall are strongest in the drier western portions of the Great Plains (Epstein et al. 1997), and weaker in the more mesic eastern portions of the Great Plains, because of the variable rainfall regime. Because Konza Prairie is located in the transition zone from mesic tallgrass to more xeric midgrass prairie and has inherently variable climatic patterns, it is well suited for studies on the interplay between rainfall quantity and timing.

Mechanisms of Mesic Grassland Responses to Rainfall

Long-term responses of grasslands to variation in the amount and timing of rainfall events should depend on three basic factors: (1) the nature of short-term, rainfall-induced dynamics in soil moisture and plant-available water, (2) long-term trends in nutrient availability, and (3) resultant plant growth and physiological responses. Soils act like capacitors, causing water that comes in relatively brief rainfall events lasting minutes or hours to remain available to plants and soil microorganisms for days to a few weeks. Plant water status responds rapidly to changes in plant-available soil moisture, and plant growth and photosynthetic carbon gain are reduced by water stress. However, differences in morphology and physiology between forb and C_4 functional groups confer different degrees of drought tolerance. For example, compared to forbs, C_4 grasses generally have higher water and nitrogen use efficiencies, photosynthetic rates, and optimal temperatures. C_4 grasses also typically possess several mechanisms of drought tolerance including leaf rolling, translocation of nitrogen to belowground storage, and tolerance of low water potentials (Knapp and Medina 1999). Leaf water potentials as low as -6.0 MPa have been recorded for the C_4 grass *Andropogon gerardii* under midsummer drought (Hake et al. 1984; Knapp 1984). Although C_4 grasses produce deep roots, most of the root mass is relatively shallow and fibrous, making C_4 grasses best suited to exploiting water high in the soil profile. On the other hand, forbs often have a greater proportion of deeper roots compared with grasses and, thus, can access deeper water supplies. Some forb species possess well-developed belowground water storage organs, which enable them to delay or avoid experiencing severe water deficits (Knapp and Fahnestock 1990). Certainly, species within functional groups vary in these traits and will vary in response to altered rainfall regimes, but functional group generalizations provide a framework for predicting general trends in diversity and productivity under altered rainfall regimes (Körner 1994).

Conceptual Model and Hypothesized Responses

Key processes affecting grassland composition and productivity responses to an altered rainfall regime are summarized in figure 9.1. This conceptual model assumes that rainfall patterns drive soil moisture dynamics. These in turn act on plant growth and physiological parameters, and on soil processes affecting nutrient availability, culminating in changes in ANPP and species diversity through time.

Under current rainfall regimes in Flint Hills grasslands, relatively fre-

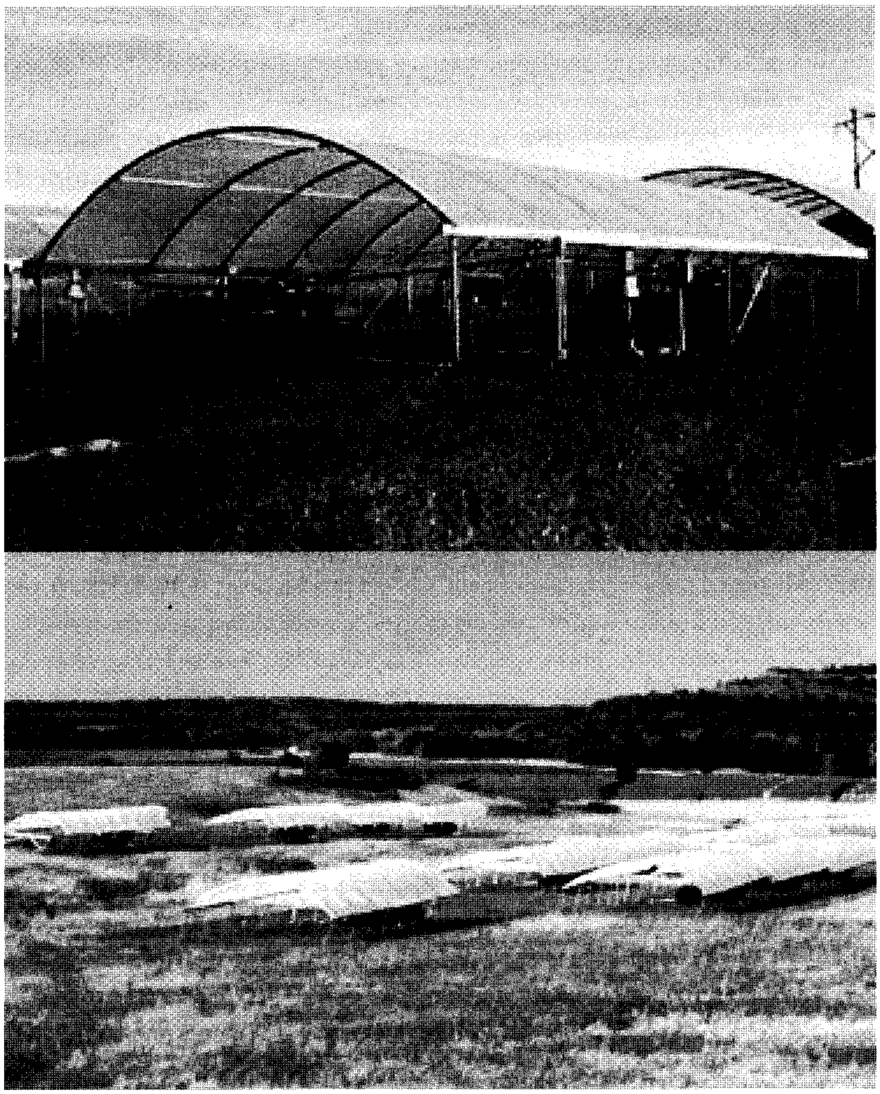

Figure 9.1. Rainfall manipulation plot study at the Konza Prairie Research Natural Area in northeastern Kansas.

quent rainfall inputs keep soil moisture relatively high, resulting in only sporadic periods of significant soil water deficit. Under a rainfall scenario of fewer, larger rainfall events, soil moisture would be more likely to cycle from saturation after infrequent but heavy rainfall inputs, to severe deficit during lengthy dry periods, to saturation again with the next large event. Plant physiological status (net photosynthesis, leaf water potential) and growth (aboveground and belowground production) would vary strongly with soil moisture patterns. Consequently, ANPP is predicted to decline, because extreme soil moisture variability would cause soils to be either too wet or too dry during critical periods for growth. Over time, these declines in ANPP might be reinforced by lowered average nitrogen availability because of reduced litter inputs and nitrogen mineralization.

In the long-term, species shifts might be expected to occur, as those species better adapted to the more severe rainfall regime would assume dominance, and the community would stabilize at a new composition with lower diversity, typical of present midgrass assemblages. This is a straightforward prediction to make if total rainfall quantity is reduced to that of the present midgrass prairie. The more fundamental question is whether similar vegetation changes can be driven simply by lengthened dry intervals between rainfall inputs. The answer to this question is less clear for native vegetation assemblages than for row-crop systems, where it is well known that an auspiciously timed rainfall can significantly boost production (Wittwer 1995). On one hand, rainfall amount would be the more critical factor in composition shifts if the generally diverse grassland community buffered the effects of variation in rainfall timing, because the assemblage would likely contain species that could take advantage of rainfall whenever it falls. Conversely, since the tallgrass prairies are dominated by a relatively small number of species (the C_4 grasses), which competitively exclude many other (largely C_3) species, rainfall properly timed for C_4 grasses should maintain their dominance. Mistimed rainfall, on the other hand, should reduce their dominance, and we would expect increased abundance of previously excluded species due primarily to altered timing of rainfall events. Changes in relative proportions of species among functional groups would then be likely to affect long-term patterns in productivity and compositional change (Tilman et al. 1997; Peterson et al. 1998).

Mesic Grassland Rainfall Manipulation Experiment

Tests of these hypotheses are perhaps best accomplished by field-scale experimental manipulation of rainfall patterns in intact native communities. To this end, the Rainfall Manipulation Plot (RaMP) study was initiated at Konza Prairie. Twelve rainfall manipulation shelters were constructed in 1998 on an annually burned site with a typical mix of warm-season C_4 grasses and C_3 forbs. Our objective was to conduct a 10-year field test of the relative importance of reduced growing season rainfall amount versus increased inter-rainfall dry periods as drivers of grassland ecosystem responses to rainfall.

Each rainfall manipulation shelter consists of a galvanized tubular steel frame, a clear plastic roof, gutters, 4,200 L polyethylene tanks for rainfall collection and storage, and an irrigation system for rainfall reapplication (fig. 9.2). The shelter sides and ends are open, and the tops are covered during the growing season (May–September) with 6 mil UV-transparent polyethylene. This arrangement excludes natural rainfall from a 9 by 14 m (128 m^2) area of undisturbed native tallgrass prairie, while maximizing air movement and minimizing temperature, relative humidity, and light artifacts. A 6 by 6 m area centered under each shelter is used to measure plant and soil responses to altered rainfall regimes. The core sampling area is surrounded by a 7.6 by 7.6 m perimeter barrier of 1.2 m deep galvanized sheet metal, which minimizes surface and subsoil water flow and root/rhizome penetration from outside the plot. The design and operation of these shelters is detailed further in Fay et al. (2000).

Experimental rainfall applications are conducted using a factorial combination of two treatments (n = 3 shelters per treatment): (a) altered growing season (May–September) rainfall amount, and (b) altered timing of growing season rainfall events, as follows:

1. Natural inter-rainfall dry interval and rainfall amount. This is the control treatment, which replicates the naturally occurring rainfall regime. Each time a natural rainfall event occurs, the amount of rain that fell is immediately applied to the plots.
2. Lengthened dry interval. Instead of applying rainfall immediately as it occurs, rainfall is withheld and accumulated to lengthen the dry interval by 50 percent. The accumulated rainfall is then applied as a single large event at the end of the dry interval. Over the season, the entire naturally occurring quantity of rainfall is applied, only the timing of rainfall inputs is altered.
3. Reduced amount. In this treatment, rainfall quantity is reduced by 30 percent, but is applied each time there is a natural rainfall. This imposes reduced amounts of rainfall without altering the timing of rainfall events.
4. Reduced amount and lengthened interval. Dry intervals are lengthened by 50 percent, and application quantity is reduced by 30 percent, imposing both reduced amounts and lengthened dry intervals.

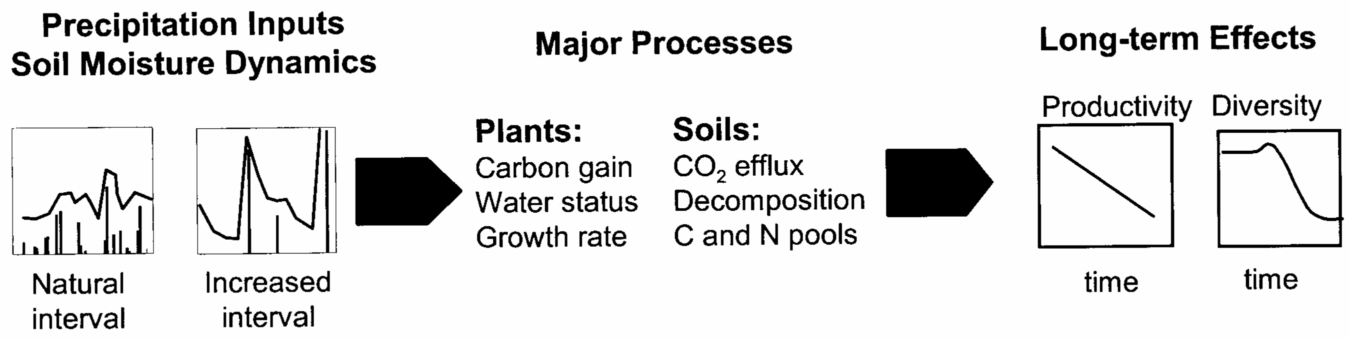

Figure 9.2. Conceptual model of the linkages between rainfall inputs, soil moisture dynamics, and plant, community, and ecosystem responses to lengthened inter-rainfall dry intervals in mesic tallgrass prairie.

These specific alterations of rainfall patterns were chosen because they are rare in current climatic patterns, but are predicted to become more common under some climate change scenarios for the Great Plains (Waggoner 1989; Easterling 1990; Houghton et al. 1990, 1996). A 30 percent reduction exceeds natural interannual variability in growing season rainfall at the RaMPs site (SD = 25 percent of the mean-based, 100-year record) and is typical of rainfall amounts presently occurring in midgrass prairies west of our study site. We based our rainfall manipulations on current rainfall patterns, rather than long-term average patterns, because year-to-year variability in rainfall is a dominant climatic characteristic of this grassland (Knapp, Briggs, et al. 1998a), making the study more realistic than if long-term averages were implemented.

In this chapter we will confine our examination of rainfall/soil moisture/plant responses to the natural interval/amount and the lengthened dry interval treatments (lengthened interval, lengthened interval/reduced amount). We chose these treatments in order to focus primarily on the impacts of altered timing, and because we expect them to exhibit the greatest impacts compared to the natural rainfall regime. Various climate, plant, and soil parameters are measured in the RaMPs experiment (Fay et al. 2000), but here we will focus on soil moisture dynamics (measured in the upper 30 cm of soil using time domain reflectometry methods; Topp et al. 1980), CO_2 flux, leaf water potential and photosynthesis, plant growth, and ANPP. Plant growth and physiological measurements focused on two species, the C_4 grass *Andropogon gerardii,* and a C_3 forb, *Solidago canadensis,* abundant members of the two dominant functional groups in the tallgrass prairie ecosystem.

The response variables that are most responsive to changes in soil moisture were measured weekly (soil moisture, soil CO_2 fluxes) or biweekly (leaf water potential and photosynthesis) from June through September. Growth of *A. gerardii* and *S. canadensis* was characterized with weekly measurements of plant height and leaf mass as plants approached peak growth (late July through September). ANPP was estimated from the dry weights of early November samples of current year standing crop. Data were summarized by calculating plot-level responses (since individual RaMPs are the experimental units), which were then used to calculate either date or growing season treatment means. All responses were measured on at least five samples per RaMP. Details of sampling techniques are in Knapp et al. (1993).

Grassland Responses to Rainfall

Rainfall and Soil Moisture Patterns

Total growing season rainfall for 1998 was about average, at 622 mm. From June through September, 27 natural rainfall events occurred (fig. 9.3), averaging 19.08 ± 3.82 mm (mean ± SE) of rainfall per event, with a rain event of at least 5 mm occurring every 8.9 ± 1.7 days. The natural rainfall regime included several large (~40 mm) storms, some occurring over several consecutive days in late June, late July, and mid- and late-September. This natural rainfall regime translated into five lengthened dry intervals averaging 25.3 ± 5.3 days, with precipitation applications following each dry period averaging 99.8 ± 34.9 mm. This nearly three-fold experimental increase in dry period length exceeded the target increase of 50 percent, because dry periods were defined using the most recent dry interval and rain events of at least 5 mm, and many of the shorter naturally occurring dry intervals also involved amounts <5 mm.

Lengthened dry intervals caused two main effects on soil moisture patterns (fig. 9.3). First, cycles of soil wetting and drying were uncoupled from the cycles associated with natural rainfall intervals. For example, during most of June, late July, and the latter half of September, naturally occurring peaks in soil moisture coincided with periods of low soil moisture caused by the experimentally lengthened dry intervals. The lengthened intervals also altered trajectories of soil moisture depletion. Soil water content fell rapidly during lengthened dry intervals in early June and mid- through late August. Rain applied at naturally occurring intervals during those same periods minimized or reversed soil moisture depletion, even with relatively small quantities (~20 mm). The lengthened dry interval/reduced amount treatment exhibited more extreme soil moisture depletion compared to the lengthened dry interval/natural quantity treatment (fig. 9.3). The lowest soil water content values (around 16 percent) were observed in the lengthened interval/reduced amount treatment in July and September after extended periods of meager rainfall. The lengthened dry interval/reduced amount treatment also reached slightly lower maximum soil water content values (43 percent) compared with the treatments receiving natural rainfall amounts (46 percent; fig. 9.3).

The ranges of dry period length and rainfall amount that exerted the most influence on soil moisture patterns during 1998 could be estimated from nonlinear regressions fit to plots of soil water content versus dry period length and rainfall amount (fig. 9.4a, b), composited from the control, lengthened

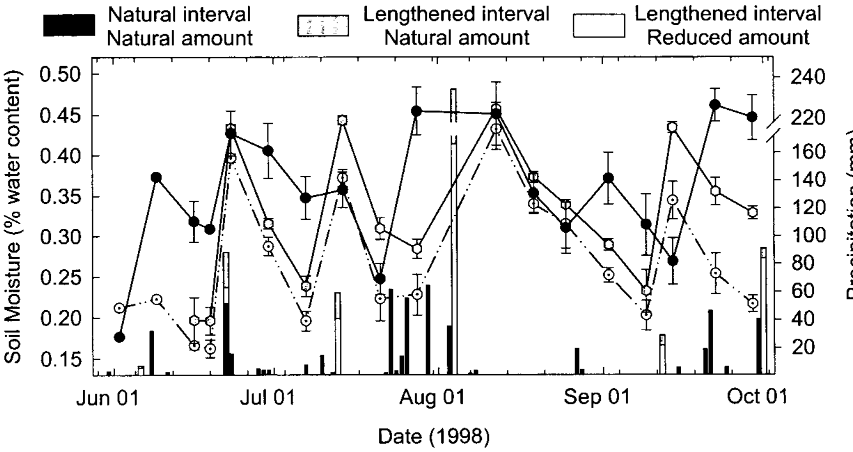

Figure 9.3. Soil moisture/rainfall relationships in native tallgrass prairie study plots during the 1998 growing season. See text for description of experimental treatments. Soil water contents (means ± SE, lines) were based on weekly time domain reflectometry measurements with 30 cm soil probes. Bars indicate rainfall applications. Figure redrawn from Fay et al. (2000).

interval, and lengthened interval/reduced amount treatments. Most soil drying occurred in the first 15 days without rainfall (fig. 9.4a), with slower soil water content reductions during longer dry periods, down to an estimated minimum of about 17.5 percent. This soil water content value is likely to represent depletion of most of the soil moisture that is readily available to plants (J. K. Koelliker, Kansas State University, pers. comm., August 1995). Soil water content increased rapidly with rainfall amount (fig. 9.4b) up to about 35 mm, suggesting that larger applications saturate the upper soil layers. This is consistent with our observations of runoff during very large applications, even when applied over two or three consecutive days to maximize infiltration (J. Carlisle, pers. obs.).

When averaged over the entire growing season, lengthened dry intervals, with no reduction in rainfall amount, caused a 9 percent reduction in soil water content compared to the rainfall applied in natural intervals and amounts (table 9.1). The lengthened dry interval/reduced amount treatment caused an average 25 percent reduction in soil water content.

Plant Responses

The reduced average soil moisture caused by the lengthened dry interval treatment was accompanied by increased plant stress and reduced growth

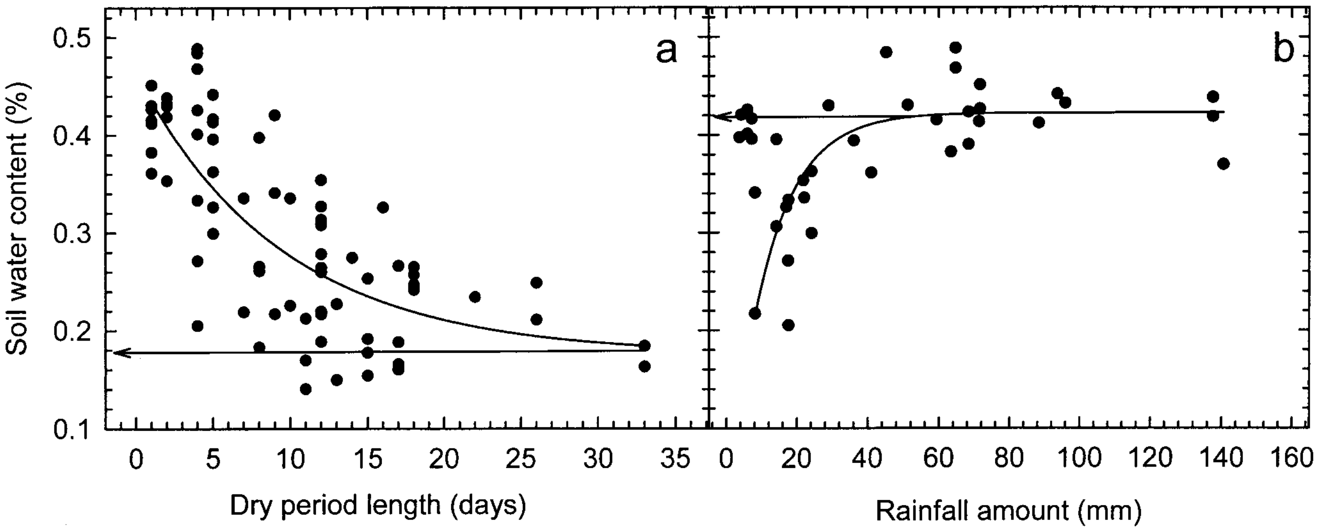

Figure 9.4. Nonlinear regressions of soil water content (swc) versus (a) days since a 5 mm or larger rain event or (b) rain event amount. Regression equations: (a) swc = $17.52 + 28.8e^{-10.46(\text{days})}$, $F_{2,70} = 46.76$, $R^2 = .572$, $P < .0001$; (b) swc = $42.25(1\text{-}e^{-.872(\text{mm})})$, $F_{1,30} = 31.25$, $R^2 = .510$, $P < .0001$. Arrows indicate estimated maximum/minimum swc during 1998. Data derived from figure 9.2 and Fay et al. (2000).

Table 9.1.

Soil, plant, and aboveground net primary productivity (ANPP) responses to rainfall manipulations, averaged (mean ± 1 SE) over the 1998 growing season. F and P values from Analysis of Variance. Letters denote significant differences between means, by least significant difference.

Rainfall Interval	Natural	Lengthened	Lengthened		
Rainfall Amount	Natural (100%)	Natural (100%)	Reduced (70%)	F (df)	P-value
% Soil water content	35.51 ± 1.85a	32.65 ± 2.15a	26.78 ± 1.90b	10.89 (2,32)	.0002
Soil CO_2 production (μmol m^{-2} s^{-1})	10.10 ± 0.86a	8.59 ± 0.89b	8.46 ± 0.80b	6.59 (2,27)	.0047
Andropogon gerardii (C_4 grass)					
Photosynthesis (μmol CO_2 m^{-2} s^{-1})	18.12 ± 1.32a	16.35 ± 1.95b	16.16 ± 1.61b	3.40 (2,18)	.0561
Stomatal conductance (mmol m^{-2} s^{-1})	273.11 ± 39.51	249.11 ± 48.09	236.79 ± 41.16	2.12 (2,18)	.1493
Leaf water potential (MPa)	-1.69 ± 0.07a	-1.83 ± 0.07b	-1.81 ± 0.06b	10.40 (2,25)	.0005
Plant height (cm)	73.26 ± 1.77a	65.57 ± 1.27b	61.01 ± 1.36	47.97 (2,16)	.0001
Specific leaf area (cm^2 g^{-1})	108.10 ± 10.46	111.22 ± 8.62	104.06 ± 8.18	2.89 (2,43)	.0666
Solidago canadensis (C_3 forb)					
Photosynthesis (μmol CO_2 m^{-2} s^{-1})	14.26 ± 0.92a	12.08 ± 1.09b	12.53 ± 1.23b	16.50 (2,16)	.0001
Stomatal conductance (mmol m^{-2} s^{-1})	749.51 ± 133.98a	578.48 ± 113.49b	520.74 ± 90.80b	9.74 (2,16)	.0017
Leaf water potential (MPa)	-1.25 ± 0.06	-1.31 ± 0.06	-1.27 ± 0.06	0.42 (2,25)	ns
Plant height (cm)	56.82 ± 1.79	55.36 ± 1.85	53.41 ± 1.24	1.22 (2,8)	ns
Leaf number	56.44 ± 4.80	57.86 ± 5.48	56.05 ± 4.63	1.02 (2,8)	ns
Specific leaf area (cm^2 g^{-1})	92.51 ± 2.61a	79.34 ± 1.98b	83.21 ± 1.76b	19.01 (2,43)	.0001
ANPP (g m^{-2})	639.80 ± 38.25	574.04 ± 14.79	536.66 ± 22.12	3.72 (2,8)	.0890

(table 9.1). For the dominant warm season C_4 grass *Andropogon gerardii,* photosynthetic carbon gain, leaf water potential, and plant height were reduced 8 to 11 percent compared with plants experiencing the natural rainfall regime. The C_3 forb *Solidago canadensis* experienced reductions of 8 to 15 percent in carbon gain and specific leaf area. At the system level, the cumulative effect of lengthened dry intervals was a 10 percent reduction in both ANPP and soil CO_2 flux.

The additional soil moisture deficit caused by the lengthened dry interval/reduced amount treatment caused further reductions in plant height of *Andropogon gerardii* (8 percent) and ANPP (12 percent), but no further decreases in other plant species responses or soil CO_2 flux.

Synthesis

The initial results from the RaMP experiment verified the importance of the primary elements of our conceptual model (fig. 9.1). Changes in the timing of rainfall inputs caused altered soil moisture patterns, increased plant stress, and reduced plant growth and ANPP. These plant and soil responses suggest that changes in the timing of rainfall events will play an important role in ecosystem responses to climate change.

Increased numbers of large rainfall events separated by extended dry intervals caused strong soil moisture cycles and reduced soil moisture when averaged over the season. This experimentally induced rainfall pattern appears to be rare in the recent climatic record. For example, in a recent 15-year period (1984–1997) at Konza Prairie, only 8 percent of rainfall events 5 mm were 15 or more days apart, and only 12 percent of storms were 35 mm or larger, the threshold for soil saturation from a single rainfall event. The responses observed so far in growth, physiology, and ANPP suggest several hypotheses about long-term responses to lengthened dry intervals.

Variability in ANPP

Long-term ANPP records from Konza Prairie suggest that climatic conditions during June and July may be critical in determining annual ANPP (P. Fay, unpublished data). With more strongly cyclical soil moisture patterns resulting from a regime of lengthened dry intervals and subsequent large rainfall events, the probability is increased that soils will be either too wet or too dry during such critical times for optimum production. Thus, year-to-year variation in ANPP is hypothesized to increase. However, the lower average soil moisture suggests greater overall water limitation of ANPP. Thus, we might expect stronger interannual rainfall/ANPP correlations than have been observed previously (Briggs and Knapp 1995). Considerable spatial variability in the rainfall/ANPP relationship also has been found in prairies in the Flint Hills (Briggs and Knapp 1995), with stronger correlations on shallow-soil upland sites than on deeper-soil lowland sites. Pronounced soil moisture cycles may also lead to a stronger ANPP/rainfall relationship on lowland sites like the RaMPs site, thus reducing spatial variability in ANPP.

Reduced Dominance by C_4 Grasses

Andropogon gerardii, a C_4 grass, was more negatively affected by lengthened dry intervals than was the C_3 forb, *Solidago canadensis. A. gerardii* plants were smaller and more stressed in lengthened dry interval treatments relative to controls. In contrast, *S. canadensis* growth was not reduced by lengthened dry intervals, despite reduced leaf-level carbon gain. The stress imposed on *Solidago* by lengthened dry intervals may have been partially offset by reductions in stomatal conductance. Since grasses are typically more shallow-rooted than forbs (Weaver 1958), they may be more sensitive to soil moisture changes in upper soil horizons. These results support the hypothesis that physiological acclimation in response to climate change may delay or reduce shifts in productivity or composition (Schimel 1993).

If the responses observed in *A. gerardii* and *S. canadensis* generally hold true for C_4 grasses and C_3 forbs, there may be a trend toward reduced competitive dominance by warm season grasses. This could have several possible consequences, such as increased forb contribution to ANPP, more rapid species turnover, increased susceptibility to invasions by exotics (Dukes and Mooney 1999; Smith and Knapp 1999), or flushes of annual forb production when large rainfall inputs coincide with favorable germination conditions.

Reduced Decomposition and Nutrient Availability

The primary sources of soil CO_2, root and microbial activity, are strongly responsive to soil moisture variation (Hayes and Seastedt 1987; Knapp, Briggs, et al. 1998; Rice et al. 1998a). The sensitivity of soil microbes to water deficits suggests possible long-term effects on nitrogen availability due to changes in rainfall timing, since soil microbes account for most nitrogen mineralization (Rice et al. 1998). Year-to-year variation in the severity of July moisture deficits may induce increased variation in nutrient supply, because July is a peak period for soil microbial activity (based on seasonal CO_2 flux patterns;

Knapp, Conard, and Blair 1998). Variability in soil microbial activity could either exacerbate or ameliorate increased yearly variation in ANPP (see above).

Future Research

Rainfall Amount

Reduced rainfall amount appears to have weaker effects than lengthened dry intervals on soil moisture, plant performance, and ANPP (Fay et al. 2000). Although we would expect reduced rainfall amounts to cause plant and soil responses in our experiment, a weak quantity effect will require more years to adequately assess compared to stronger rainfall timing effects. Also, since our treatments are based on current rainfall amounts and patterns, rather than long-term averages, there should be considerable year-to-year variation in the effects of a 30 percent reduction in rainfall amount on plant and soil characteristics, with greater effects in drier years. Soil depth and texture would also influence the effects of reductions in rainfall quantity (Fredeen et al. 1997). The RaMPs study is on deep and rather clayey soils; thus, reduced rainfall could have much stronger impacts on sites with shallower or sandier soils. On the other hand, GCM model predictions regarding growing season rainfall amount are less robust than predictions for temperature (Schneider 1993; Giorgi et al. 1994; Wittwer 1995; Karl et al. 1996). So, if rainfall amount continues to exert only minor influences on ecosystem characteristics compared with rainfall timing, then GCM uncertainties regarding specific changes in rainfall amounts will become a secondary issue, and the accuracy of GCM predictions regarding increased occurrence of convective rainfall events will be a greater concern.

Offsetting Effects of Elevated CO_2 on Changing Rainfall Regimes?

In future climates, predicted changes in rainfall patterns will not occur in isolation, but in concert with increases in atmospheric CO_2 concentrations. There are a variety of predicted effects of elevated CO_2 on ecosystems, including increased plant productivity, water use efficiency, soil moisture, and soil carbon storage, as well as decreased decomposition and nitrogen mineralization (Parton et al. 1995; Coughenour and Parton 1996; Mooney et al. 1999). For the Central Plains grasslands, altered rainfall patterns could potentially offset some CO_2 effects, because our preliminary results indicate that a lengthening of dry intervals is likely to decrease soil moisture and productivity. Thus, an important next step in unraveling the impacts of climate change on the conservation and sustainable use of grassland ecosystems would be a field-scale rainfall-times-CO_2 experiment, where the potential for rainfall patterns and elevated CO_2 to offset each other can be rigorously tested.

Climatic patterns, along with ungulate grazing and fire, are the three primary factors governing the structure and function of grassland ecosystems. Even in its early stages, the Rainfall Manipulation Plot experiment has provided useful insights into the impacts of altered precipitation patterns, and increased soil moisture variability, on fundamental characteristics of tallgrass prairie, an important temperate grassland ecosystem. The knowledge gained from this experiment over a long-term period will sharpen our understanding of the climatic context in which fire and grazing impacts occur. In addition, we expect to gain a greater appreciation of how precipitation variability may interact with other climatic and nonclimatic elements of global biological change.

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