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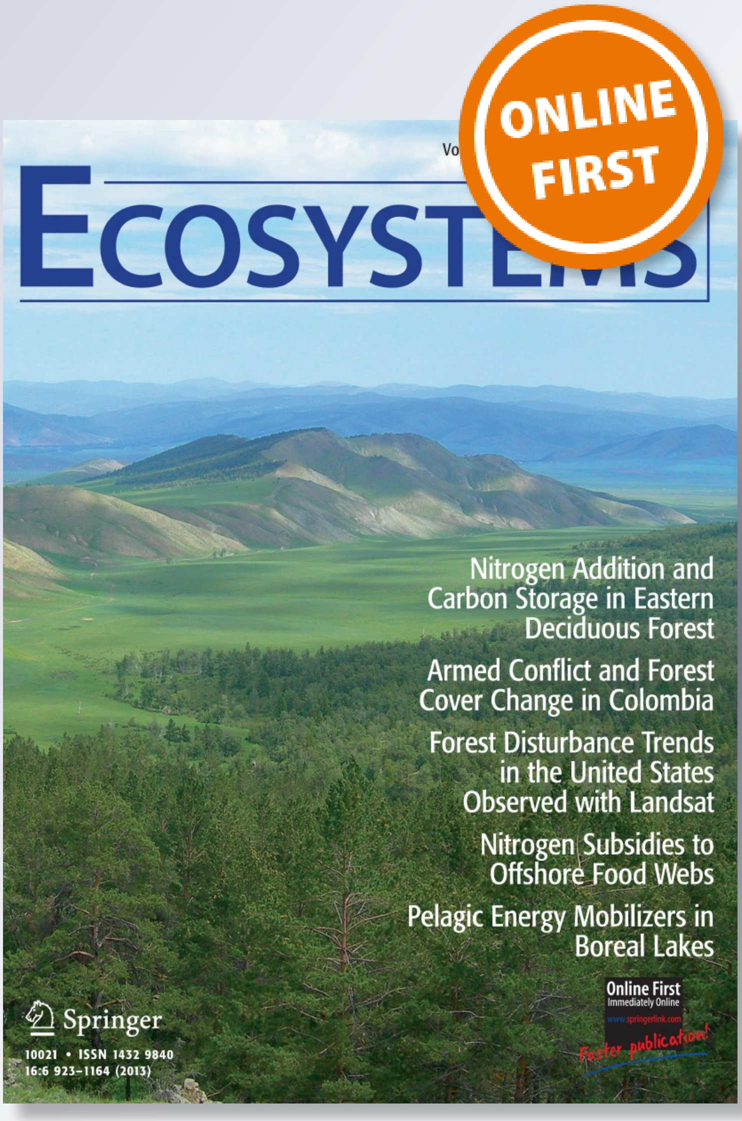

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Cessation of Burning Dries Soils Long Term in a Tallgrass Prairie

Joseph M. Craine* and Jesse B. Nippert

Division of Biology, Kansas State University, Manhattan, Kansas 66506, USA

ABSTRACT

Soil moisture is a critical variable in grassland function, yet how fire regimes influence ecohydrology is poorly understood. By altering productivity, species composition, and litter accumulation, fire can indirectly increase or decrease soil water depletion on a range of time scales and depths in the soil profile. To better understand how fire influences soil moisture in grasslands, we analyzed 28 years of soil moisture data from two watersheds in a central North American grassland which differ in their long-term fire frequency. Across 28 years, cessation of prescribed burning initially led to wetter soils, likely as litter accumulated and both transpiration and evaporation were suppressed. Long-term, cessation of burning led to soils drying more, especially at depths greater than 75 cm. The long-term drying of deep soils is consistent with the increase in woody species in the infrequently burned grassland as woody species likely have a greater reliance on soil water from deeper soil layers compared to co-occurring herbaceous species. Despite the ecohydrological changes associated with the cessation of prescribed burning, watersheds with different burn regimes responded similarly to short-term variation in climate variation. In both watersheds, low precipitation and high temperatures led to drier soils with greater responses in soil moisture to climate variation later in the season than earlier. There is no current evidence that the cessation of burning in this ecosystem will qualitatively alter how evapotranspiration responds to climate variation, but the use of deeper soil water by woody plants has the potential for greater transpiration during dry times. In all, modeling the depth-specific responses of soil moisture and associated ecosystem processes to changes in burn regimes will likely require including responses of plant community composition over short and long time scales.

Key words: fire; soil moisture; Konza Prairie; critical climate period; ecohydrology; evapotranspiration; woody species.

INTRODUCTION

Soil moisture availability is a central variable that controls ecosystem processes in grasslands (Weltzin and others 2003; Knapp and others 2008a; Jackson and others 2009; Wang and others 2012). By influencing the tension on water in plants, soil moisture is a key to determining plant carbon balance and productivity (Sala and others 1988; Sala and others 1992; Knapp and others 1993; Briggs and Knapp 1995; Knapp and others 2001; Morgan and others 2004). Soil moisture also impacts the activity of microbes, which determines the rates at which nutrients become available to plants as well as carbon dioxide and trace gas fluxes (Austin and others 2004; Risch and Frank 2007; Niboyet and others 2011). Ultimately, the energy balance of ecosystems is structured by soil moisture, determining the balance between sensible and latent

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**Corresponding author; e-mail:* jcraine@ksu.edu

heat flux (Miranda and others 1997; Bremer and Ham 1999). Vegetation-controlled evapotranspiration influences precipitation patterns (Trenberth 1998), no less short-term severe weather patterns (Raddatz and Cummine 2003) and long-term climate variability (Delire and others 2004).

In grasslands, fire controls soil moisture in complex ways that make predictions of its effects difficult. In the short-term, fire can increase soil moisture by directly reducing leaf area (Archibold and others 2003). The removal of litter layers by fire can either lead to net increases or decreases in soil moisture. On the one hand, litter layers decrease evaporation and transpiration (Bremer and Ham 1999), but they also intercept precipitation, reducing potential soil recharge (Seastedt 1985). Fire also impacts soil moisture indirectly by altering nutrient availability to plants. Fire promotes drying of soils by increasing the availability of nutrients such as phosphorus (Boerner 1982), which increases plant transpirational demand when plants are limited by these elements (Silva and others 2008). Yet, fire can also promote wetter soils when N is limiting. Fire volatilizes N at a relatively low temperature (Wan and others 2001), which can decrease N availability to plants long-term and potentially reduce plant demand for water as leaf area and leaf nitrogen concentrations are reduced (Seastedt and others 1991; D'Antonio and Vitousek 1992; Turner and others 1997).

Of all the changes in factors that affect soil moisture, the impact of fire on plant species composition might be the most important. Fire can disproportionately reduce the abundance of woody species over grasses (Scholes and Archer 1997; Sankaran and others 2005; Staver and others 2011). Woody species abundance in grasslands and savannas has a large impact on a number of ecosystem properties, including ecohydrology (Ludwig and others 2004; Huxman and others 2005; Brudvig and Asbjornsen 2009; Eldridge and others 2011; Wang and others 2012). There is no strong evidence yet on whether the presence of woody species consistently reduces or increases shallow soil moisture (Eldridge and others 2011). Regarding moisture at depth, woody species often have deeper roots than grasses (Schenk and Jackson 2002) and often rely on deeper soil moisture than grasses (Nepstad and others 1994; Breshears and Barnes 1999; Nippert and Knapp 2007; Ratajczak and others 2011; Throop and others 2012). Yet, the presence of deep roots does not always result in reliance on deep water (Verweij and others 2011) and there is uncertainty about under what conditions woody species would differentially dry deeper soil layers.

In all, how fire impacts soil moisture on different time scales in different parts of the soil profile is a complex question that requires long-term experiments with manipulations of fire frequency. The questions at stake are not just whether cessation of burning will alter the total quantity of water lost from ecosystems to the atmosphere, but also how water loss from ecosystems responds to climate variation. For example, cessation of fire might alter the plant community structure and favor species that are more physiologically drought tolerant or have deeper roots. A shift to these species may allow evapotranspiration to continue longer into and/or at a greater rate during droughts or heat waves, serving to buffer the increases in temperatures that occur during these events.

To better understand the consequences of the cessation of burning for the long-term trajectory of soil moisture and how soil moisture responds to climate variation, we analyzed 28 years of biweekly to monthly soil moisture data from two watersheds that differ in their burn history. One watershed was burned every spring over the 28 years whereas the other was only burned once. Long-term trends in soil moisture were assessed for both watersheds. A statistical technique (critical climate period analysis) (Craine and others 2012) was used to assess how climate variation at different times of year affected soil moisture in each watershed throughout the growing season. The critical climate period approach determines when during the year climate variability affects processes and separates the critical periods for climate variation from non-critical periods when climate variation has no significant impact on processes. With these data, we test the impacts of cessation of burning on soil moisture throughout the soil profile over long time periods. By examining patterns over almost 30 years, responses of soil moisture to changes in fire frequency can include the relatively slow changes in vegetation composition. If cessation of burning primarily impacts soil moisture by increasing litter layers and decreasing leaf area, then cessation of burning should lead to greater soil moisture at all depths. If cessation of burning increases woody species cover, cessation of burning could lead to drier soils, especially at depth because woody species can have deeper roots than herbaceous species. The balance of these (and other processes) over time should determine the temporal trend of soil moisture after cessation of burning, which has never been quantified over long time scales.

METHODS

Site Description and Measurements

The research on soil moisture and burning was conducted at the Konza Prairie Biological Station, a 3487-ha native tallgrass prairie located in northeastern Kansas (latitude = 39.08, longitude = − 96.56). Climate for the area typically consists of hot summers, cold winters, and moderately strong surface winds. Mean annual temperature is 13°C, with mean minimum and maximum monthly temperatures ranging from −3°C in January to 27°C in July. Annual precipitation for Konza Prairie averaged 833 mm from 1983–2010, with approximately 75% falling in the April to September growing season. All climate data used in this study were collected from a weather station located at Konza Prairie headquarters, approximately 5 km away from the watersheds studied here.

To study how fire affects the structure and function of grassland vegetation, Konza watersheds are used as large experimental units subjected to different long-term fire and grazing regimes. For this study, soil moisture was measured on two watersheds. The first is a 42-ha watershed (Watershed 1d) that had been ungrazed and burned annually in the spring (mid-to-late April) since the station was established in 1971 (Nippert and others 2011). The second is a 24-ha watershed (Watershed 20b) that is also ungrazed and has had no prescribed fire since 1975, but was burned once in a wildfire in April of 1991. Topographically, both watersheds consist of shallow xeric upland soils (cherty, silty clay loams overlying limestone and shale layers; Udic Argiustolls, Florence series), and mesic lowland soils (deeper colluvial and alluvial deposits; Pachic Argiustolls, Tully series). At the beginning of soil moisture measurements in 1983, vegetation on both topographic positions was dominated by perennial warm-season grasses, primarily *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*, with a high diversity but low abundance of other graminoids and perennial forbs. In 2010, vegetation in 1d was similar to 1983, but 20b had become dominated by woody species such as *Rubus ostryifolius* and *Cornus drummondii* throughout the watershed.

At two locations in the lowlands of both 1d and 20b, soil moisture was measured biweekly during the growing season and monthly the rest of the year since 1983. Soil moisture was measured with a neutron depth moisture gauge (Troxler Electronic Incorporated, Research Triangle Park, NC) in thin-walled aluminum access tubes buried 2 m deep. Readings were taken at 25 cm increments from 25–150 cm from 1983–2010. In January 1989, one of the access tubes in 20b became inaccessible below approximately 75 cm. Therefore, readings of soil moisture from 20b at 25 and 50 cm average between the two locations, but only one location for 75–150 cm.

In each watershed, species composition was determined in 20 permanently marked 10-m^2 circular plots evenly spaced along four randomly-located 50-m-long transects in the lowlands. At each plot, the canopy cover of vascular plants was visually estimated using a modified Daubenmire cover scale (Bailey and Poulton 1968) twice a year (late May–June; mid-August–September). Cover of a species in a given plot was then determined by converting each Daubenmire scale value to the midpoint of the cover range. The cover of each species in a plot was recorded as the maximum abundance at the plot level between the two time points. Cover for the species in the watershed was then averaged across the 20 plots for each year.

Aboveground biomass was measured at the end of each growing season in 20b by clipping 5 randomly selected quadrats (0.1 m^2) adjacent to each of four plant composition transect in the lowlands (n = 20 plots). Vegetation in the plots was clipped at ground level, biomass produced during the previous year, that is litter, was separated from live and dead biomass produced in the current year, and all biomass was oven-dried at 60°C before weighing. No measurable amounts of litter were present in 1d.

Analyses

Soil moisture data were expressed as an index of apparent field capacity (Briggs and Knapp 1995; Craine and others 2010). In 1998, a new neutron probe head was employed requiring that data be standardized for differences in maximum soil moisture before and after this date. To do this, the 90% quantile of all readings at each depth before and after 1998 were determined. All readings at a given depth for each time point were then divided by the respective value for the 90% quantile. The 10% of the soil moisture values greater than 1 were set to 1. This statistical technique standardizes soil moisture readings over time and across depths to have the same maximum value.

To test whether any trends in soil moisture were driven by changes in precipitation and/or temperature, or whether soil moisture had changed beyond what would have been expected from any shifts in climate, it was first necessary to determine how weather influenced soil moisture. A modification of critical climate period (CCP) analysis (Craine and others 2009; Craine and others 2010) was used to determine how the timing of climate variability affects soil moisture at different times of year. Standard critical climate period analysis determines precipitation sums or average temperatures over ranges of fixed dates each year. For example, standard CCP analysis could determine whether a given response is impacted more by variation in precipitation from day of year 100–130 or 105–135. Yet, soil moisture was not measured on the same day each year, so analyzing the impact of variation on precipitation from day of year 100–130 on soil moisture might be examining the impact of variation in precipitation 10 days before measurement of soil in some years and 20 days in other years. As such, we modified the CCP analysis to examine the impact of variation in climate over different periods before soil moisture was measured. More specifically, we calculated precipitation sums and average maximum temperatures over a range of dates relative to the measurement of soil moisture that year such that the timing relative to the measurement was constant across years within a given window of dates. The number of periods over which precipitation sums and average maximum temperatures were determined corresponds to all possible periods where the start date ranges from the day of the measurement to 50 days before the measurement, and the end date ranges from 10 days previous to 125 days previous to the event. With start and end dates incremented in 5-days steps (for example, day 0–10, 0–15, …5–15, 5–20…50–125), a total of 209 precipitation and temperature metrics were derived for each soil moisture measurement. For example, precipitation would be summed from June 3–13 for the 0–10 days index for a soil moisture measurement made on June 13, but from June 4–14 for the same index for a soil moisture measurement on June 14. The convention used here is for the start date of the relative CCP to be referenced later in the season and the end date earlier in the season, for example, for the 0–10 days index, the ‘‘start’’ date is the date soil moisture was measured and the ‘‘end’’ date 10-days before the measurement. Periods when precipitation significantly predicts soil moisture are referred to as critical precipitation periods. Critical temperature periods are analogous, but for average temperatures.

To aid in comparison of CCPs between watersheds, each month during the growing season (May–Sept) was divided in half, with values before the 16th being in the first half and values on or after the 16th in the second half of the month. Multiple linear regression was then used to determine whether the length of the CCP was associated with differences in depth and the time of growing season, using the mean day of year of measurements made for each half month.

Linear regression was used to examine relationships between depth and both average soil moisture and the coefficient of variation in soil moisture during the growing season. Paired t-tests were used to test for differences in soil moisture at a given depth and time between the two watersheds. To analyze how soil moisture in 20b changed relative to 1d, we calculated the difference in soil moisture between 1d and 20b at each time point for each depth. Data on the difference in soil moisture for each depth during May–September from 1983–2010 were then subjected to piecewise regression (Toms and Lesperance 2003). Because of the wildfire in 1991, which removed plant litter and partially reset the trajectory of community change, we examined how soil moisture changed before and after 1991 separately. For each depth, we determined the rate of change in soil moisture from 1983–1991, from 1991 to a model-determined inflection point, and then from that time point through 2010. This entailed determining an intercept for soil moisture at $t = 0$, the initial slope of soil moisture over time through 1991, the predicted soil moisture at the beginning of 1991, a second slope for soil moisture over time after 1991, the point in time after 1991 when the slope in soil moisture changed, and then the slope of soil moisture over time after this point.

To understand whether changes in the cover of woody species might be driving trends in soil moisture at individual depths, for each year in each watershed, total vegetation cover for each species derived from the long-term abundance plots was calculated and then summed into three functional groups: graminoids, herbaceous forbs, and woody species. Patterns of cover for the two watersheds were compared qualitatively with the timing of any changes in trends in soil moisture.

All statistics were calculated in JMP 9.0.3 (SAS Institute, Cary, NC).

RESULTS

For both the annually-burned (1d) and infrequently-burned (20b) watersheds, soil moisture declined at all depths as the growing season progressed ($P < 0.001$ for all depths in both watersheds). Minimum soil moisture for shallow depths was in early August, for example August 6 for 1d at 25 cm and August 5th for 20b at 25 cm (Figure 1). Soil moisture declined at deeper depths through the entire growing season and didn't reach minima until September. Soil moisture was greater and less variable at greater soil depths for both watersheds ($P < 0.04$ for all comparisons) (Figures 1, 2; Table 1).

Comparing soil moisture in the two watersheds (Table 1), in general, when soils were dry in 1d, they were also dry in 20b ($r = 0.87$, $P < 0.001$; Figure 3). Across the 5-month growing season, soils were on average wetter in 20b than 1d at 25 cm (0.85 ± 0.01 vs. 0.79 ± 0.01, $P < 0.001$) and 50 cm (0.88 ± 0.01 vs. 0.86 ± 0.01, $P < 0.001$), marginally drier in 20b than 1d at 100 cm (0.92 ± 0.01 vs. 0.93 ± 0.00, $P < 0.001$), and there was no significant difference in average soil moisture for 75, 125, and 150 cm. The wildfire that burned 20b in May 1991 led to much reduced soil moisture in 1991 compared to 1d at multiple depths (Figure 2), which appeared to persist during dry times through 1994.

As a first step in determining whether shifts in climate could explain trends in soil moisture, relationships between weather and soil moisture were determined for each watershed at different times of year. For both the annually burned 1d and infrequently burned 20b watersheds, soil moisture during the growing season increased with increasing precipitation during critical precipitation periods. In May, only 25% (5 of the 20) potential depth-time contrasts for the two watersheds had significant critical climate periods, that is in only 5 of the 20 combinations of depth and watershed for the two time windows was there a significant positive relationship between precipitation during some period before soil moisture was measured and soil moisture. In contrast, precipitation increased soil moisture in 60% of the comparisons in June and 100% for July, August, and September. Significant critical precipitation periods varied in length from 15 to 90 days, but were typically 65 days (median = 65 days) in length for both watersheds when significant. Soil moisture generally responded to precipitation in similar manners across depths and over the growing season in the two watersheds (Figure 4). When critical precipitation periods were significant for both watersheds, there were no differences in start dates, end dates, or length of the CCP between the two watersheds ($P > 0.75$) and the length of the CCP scaled at similar rates between the two watersheds (slope = 0.94, CI = 0.71 – 1.23; $P < 0.001$). Compared to deeper soils, moisture in shallow soils was more influenced by recent precipitation and integrated variation in precipitation over a shorter period (Figure 5). For 20b, the variation in soil

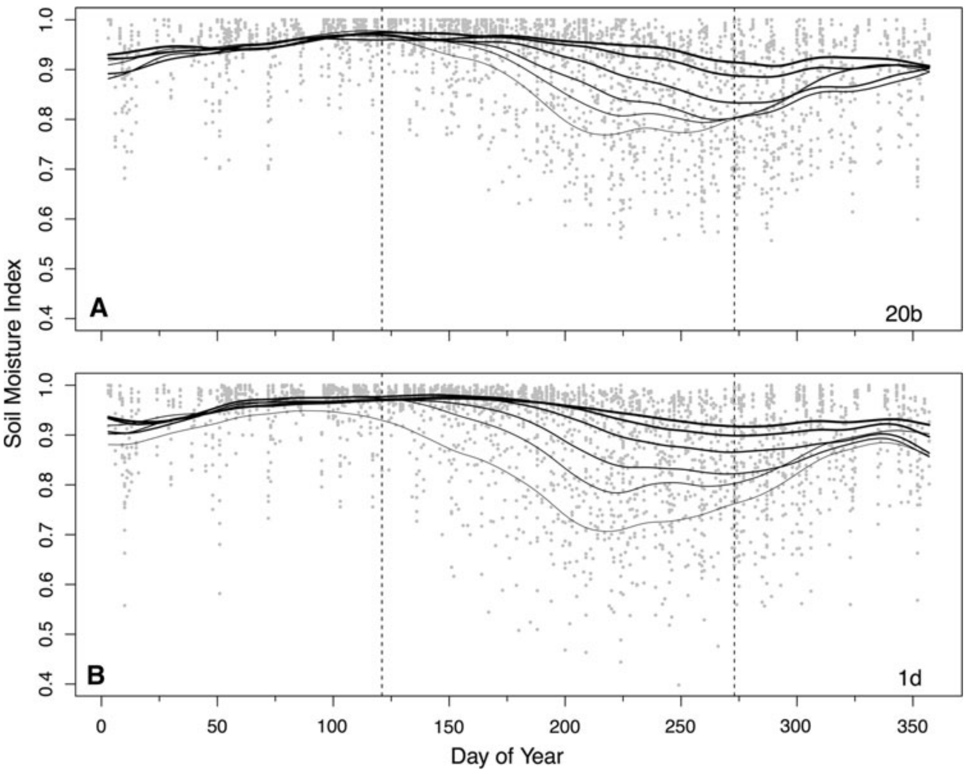

Figure 1. Seasonal patterns of an index of soil moisture (see text) over time for lowland soils in (**A**) a watershed burned every 20 years (20b) and (**B**) a watershed burned annually (1d). *Vertical dashed lines* denote May 1 to September 30. *Line thickness* increases with depth (25, 50, 75, 100, 125, 150 cm).

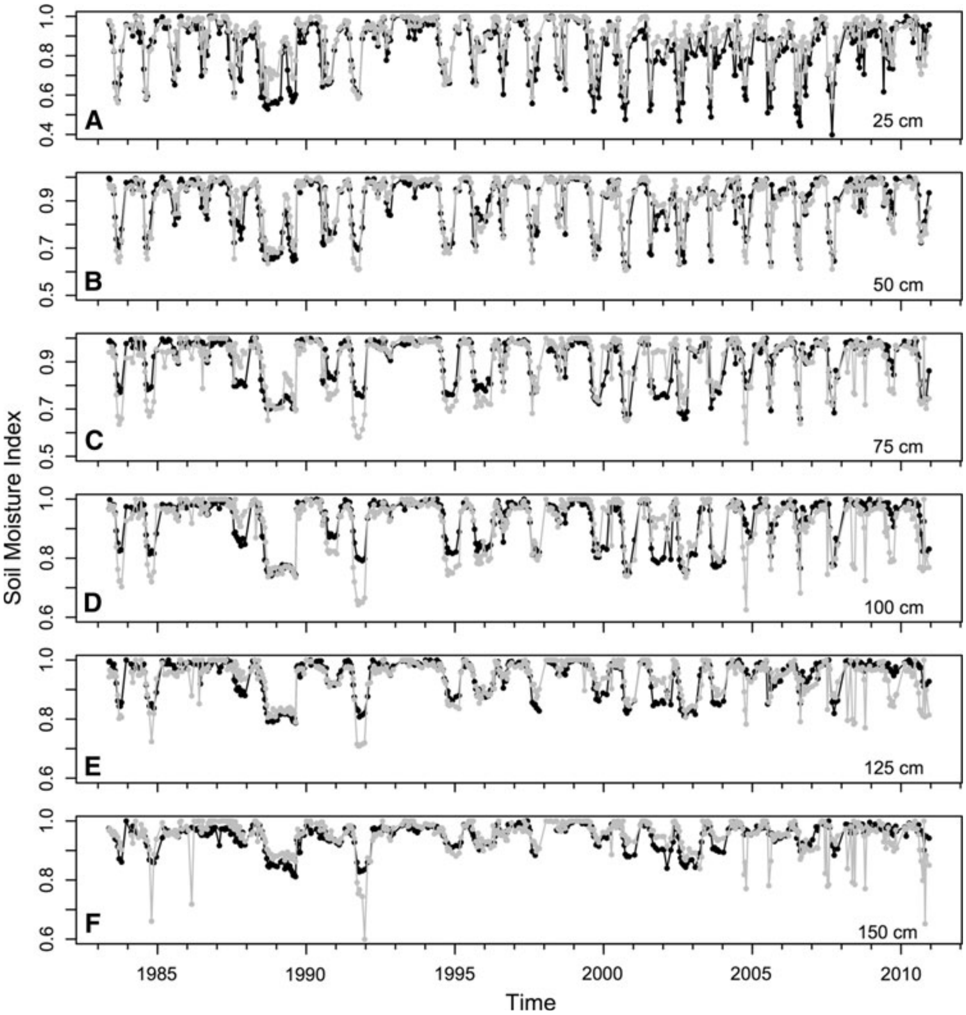

Figure 2. Soil moisture patterns from 1983–2010 for an annually burned watershed (1d; *black*) and a watershed burned every 20 years (20b; *gray*). Soil moisture was measured every 25 cm (**A**–**F**). Measurements were made an average of 9.5 times per year.

Table 1. Means (±S.E.) and Coefficient of Variation (CV) of Soil Moisture for Each Depth and Each Watershed Across 28 Years during the Growing Season

	Mean		CV	
	1d	20b	1d	20b
25	$0.79 \pm 0.01^{a*}$	0.85 ± 0.01^{a}	18.53	15.34
50	$0.86 \pm 0.01^{b*}$	0.88 ± 0.01^{b}	13.10	13.05
75	0.90 ± 0.01^{c}	0.89 ± 0.01^{b}	10.82	11.40
100	$0.93 \pm 0.00^{d*}$	0.92 ± 0.01^{c}	7.81	8.91
125	0.95 ± 0.00^{de}	0.95 ± 0.00^{d}	5.69	5.81
150	0.96 ± 0.00^{e}	0.96 ± 0.00^{d}	3.98	4.66

Superscript letters signify significant differences in soil moisture between two depths for a given watershed via Tukey's HSD.
Asterisk denotes significant difference in soil moisture at a given depth between the two watersheds ($P < 0.05$) assessed with paired t test.

moisture explained by variation in precipitation decreased with increasing soil depth (Figure 5). Reflecting the cumulative nature of soil water depletion, as the growing season progressed, variation in precipitation explained a greater proportion of the variation in soil moisture ($P < 0.001$).

When significant, soil moisture decreased with increasing temperature during temperature critical climate periods (17 of 17 cases). Temperature was generally a weaker predictor of soil moisture than precipitation, only significantly explaining soil moisture in 17 of the 120 contrasts in depth and time for the two watersheds. When signifi-

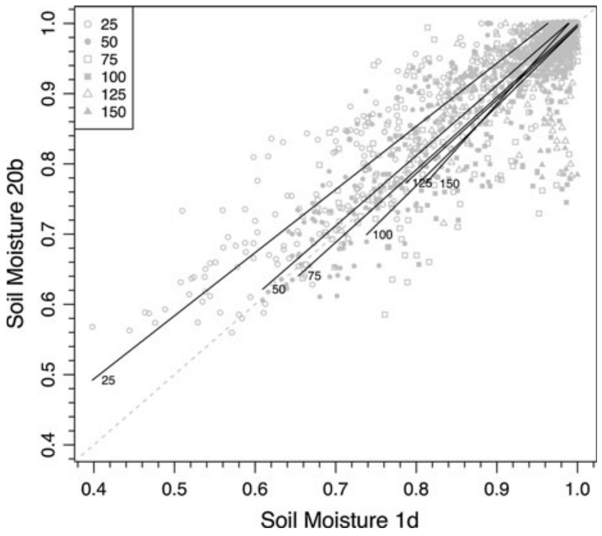

Figure 3. Comparison of soil moisture at specific points of time in the growing season between an infrequently burned watershed (20b) and an annually burned watershed (1d) at depths from 25 to 150 cm. All data from 1983–2010 are shown. Identity line presented for comparison (*dashed line*).

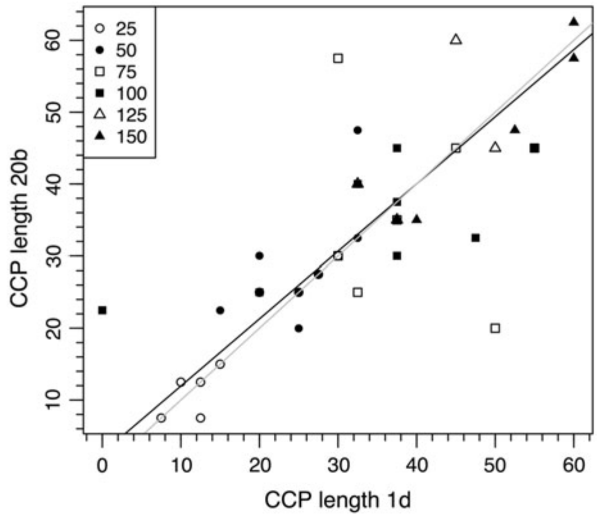

Figure 4. Relationship between the length of critical precipitation period for the annually burned watershed (1d) and the infrequently burned watershed (20b). Critical precipitation period lengths shown for significant bimonthly soil moisture from May to September. *Black line* is for orthogonal regression ($y = 2.59 + 0.94x$, $r = 0.77$). *Gray line* is identity line.

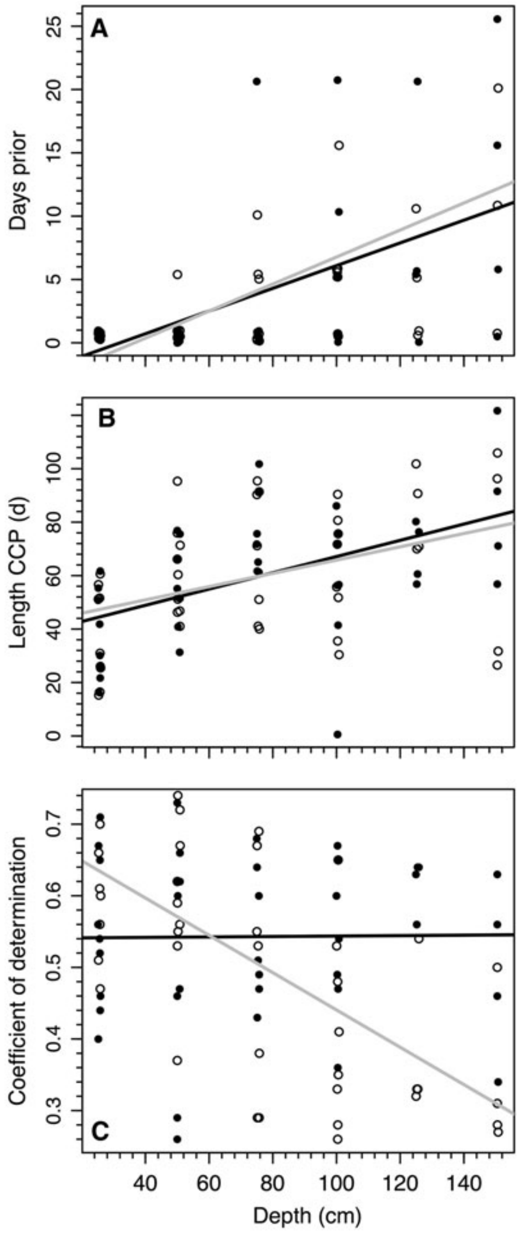

Figure 5. Relationships between soil depth and (**A**) number of days prior to measurement of soil moisture after which variation in precipitation did not impact soil moisture, (**B**) the length of the critical precipitation period during which variation in precipitation impacted soil moisture, and (**C**) the proportion of variation in soil moisture at a given time of year that is explained by variation in precipitation. Data presented for the annually burned watershed (1d; *closed circles*; *black line*) and the infrequently burned watershed (20b; *open circles*, *gray line*). A small error has been added to each point to better visualize density of data.

cant, temperature explained just 32% of the variation in soil moisture that precipitation did when significant. When significant, critical temperature periods were typically 25 days, more frequent in shallow depths (11 of 17 cases for 25 and 50 cm), and though not present in May, were well-distributed over the rest of the growing season.

Having determined the relationships between soil moisture and both temperature and precipitation at different times of year, any trends in soil moisture that might have occurred at a given depth and time for a watershed would not have changed as a result of trends in precipitation. Precipitation did not significantly increase or decrease from 1983–2010 during any of the significant precipitation or temperature periods ($P > 0.05$ for all contrasts). After accounting for variation in precipitation (and temperature when significant) during critical climate periods in the growing season, there were no significant overall linear trends in soil moisture from 1983 to 2010 for either watershed ($P > 0.05$ for all 120 comparisons across depth and time in the growing season for the two watersheds).

Relative to 1d, soil moisture in 20b increased at all depths from 1983–1991 and from 1991 to approximately 2002 (Table 2). Beginning in 2002, soils at all depths in 20b began to become more dry than 1d soils (Table 2; Figure 6). The decline in soil moisture at depth was most consistent with increases in woody species cover in the lowlands of 20b (Figure 7). In 20b, woody species cover increased from 1983 until the 1991 wildfire and then resumed increases in cover from 1992 onward. By 2002 woody species cover in permanent plots in 20b had reached approximately 30%. At that point, the most abundant woody species were *Symphoricarpos orbiculatus* (10.2%), *Rubus ostryifolius* (5.3%), and *Prunus americana* (5.0%) Since then, as deep soil moisture had continued to decline, woody species cover increased, reaching 70% total cover by 2010. Over that time, the most abundant woody species were *Cornus drummondii* (36.7%), *Rubus ostryifolius* (16.9%), and *Symphoricarpos orbiculatus* (10.2%). In contrast, in 1d woody species cover averaged less than 0.5%.

Although forb and grass cover in 20b has been changing along with woody cover, there is little to suggest changes in their cover would be responsible for the relative declines in deeper soil moisture in 20b. On average in 20b, from 1983–2010, forb cover had been linearly increasing 1.98 ± 0.4% y^{-1} ($P = 0.004$), yet has been declining at a rate of 4.00 ± 0.99% y^{-1} since 2004 ($P = 0.001$). Grass cover in 20b had been linearly decreasing 1.1 ± 0.4% y^{-1} over the same set of years ($P = 0.002$). In contrast, grass cover does not show an overall linear trend ($P = 0.12$) in 1d. Forb cover in 1d averaged 23%, and has increased on average 0.5% y^{-1}($P = 0.03$) with signs of similar potential decadal-scale cycles as 20b. Litter biomass in the lowlands of 20b averaged 544 ± 162 g m^{-2} exclusive of 1991 with no linear trends before or after 2002, or across all years ($P > 0.05$).

DISCUSSION

At Konza, long-term records of soil moisture reveal that the effects of cessation of burning on soil moisture change over time. In the infrequently burned watershed, there was no long-term directional trend in soil moisture because the cessation of burning caused soil moisture to increase short-term and decrease long-term. The lack of spring burning allows litter to accumulate, which by shading grasses and reducing evaporation, causes soil moisture to be depleted less during the growing season (Knapp and others 1993; Bremer and Ham 1999).

Although the short-term impacts of litter accumulation increased soil moisture, the long-term impacts of cessation of burning were to decrease soil moisture by removing the ecological filter (burning) that restricts woody expansion (Briggs and others 2005; Knapp and others 2008b). Woody species are not as constrained by litter as grasses

Table 2. Piecewise Linear Regression Results for the Difference in Soil Moisture (Scaled 0–1) Between 1d and 20b at Each Soil Depth Across 28 Years (cm)

Depth (cm)	b_0	m_1	b_{1991}	m_2	Inflection	m_3
25	−22.3 ± 4.9	0.011 ± 0.002*	−16.3 ± 2.6	0.008 ± 0.001*	2003.3 ± 0.8	−0.010 ± 0.002*
50	−17.5 ± 4.4	0.009 ± 0.002*	−8.1 ± 2.2	0.004 ± 0.001*	2002.4 ± 0.2	−0.009 ± 0.001*
75	−21.5 ± 5.5	0.011 ± 0.003*	−17.6 ± 3.5	0.009 ± 0.002*	2001.8 ± 0.7	−0.014 ± 0.002*
100	−9.2 ± 4.4	0.005 ± 0.002*	−14.9 ± 2.3	0.007 ± 0.001*	2001.7 ± 0.1	−0.016 ± 0.001*
125	−7.8 ± 3.7	0.004 ± 0.002*	−7.9 ± 2.3	0.004 ± 0.001*	2002.3 ± 0.6	−0.013 ± 0.002*
150	−6.8 ± 3.7	0.003 ± 0.002	−3.1 ± 2.2	0.002 ± 0.001	2002.6 ± 1	−0.009 ± 0.002*

b_0 is the soil moisture at $t = 0$, b_{1991} is the soil moisture at $t = 1991.0$; m_1, m_2, m_3 are the slopes of the relationships between time and the difference in soil moisture between the two watersheds for $x < 1991$, $x <$ inflection, and $x >$ inflection, respectively.

** Signifies slopes are significantly different from zero based on 95% confidence intervals. Negative slopes indicate greater drying in 20b than 1d during the window examined (and vice versa).*

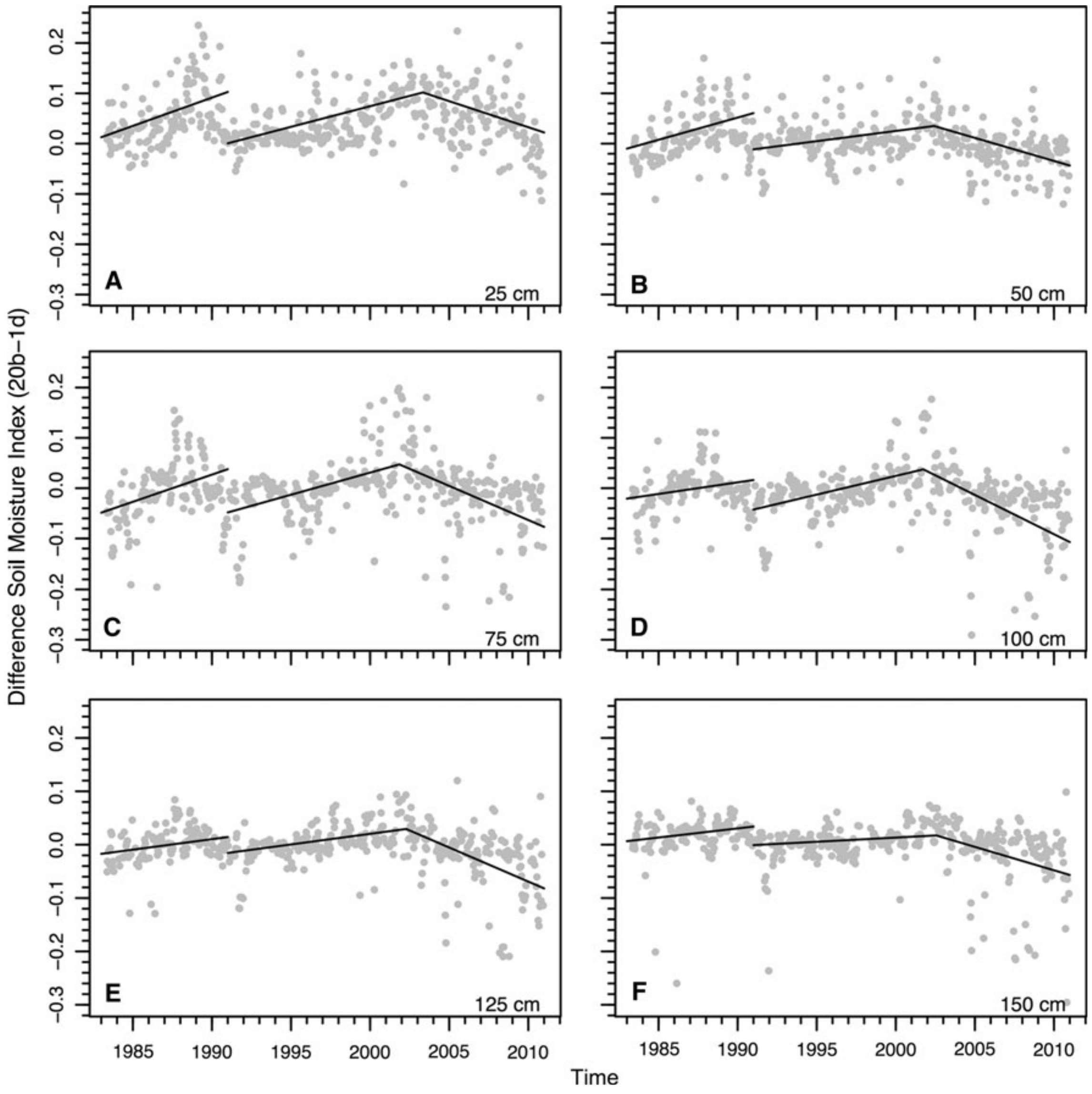

Figure 6. Difference in an index of soil moisture between an infrequently (20b) and annually burned (1d) watershed. Piecewise linear regression used to generate pattern of soil moisture at all depths over time.

and so may have greater acquisition of soil moisture. Yet surface soil moisture was largely similar between the two watersheds compared. The major impacts of increased woody cover were manifest on changes in intermediate to deep soil moisture (75–125 cm), but affected soil moisture at all depths. The differential depletion of deep soil moisture is unlikely to have been caused by reduced downward movement of water because soils were generally wet throughout the soil profile in the spring and surface soil moisture was similar during the growing season. Although the rooting depths for grasses can reach 2 m (Weaver 1968; Nippert and others 2012), many woody species and herbaceous species with woody roots are considered to preferentially depend on deeper soil water than grasses. In general, cessation of fire ultimately causing depletion of deep soil water supports observations of reliance of woody species on a functionally-separate source of water compared to coexisting herbaceous species (Walter 1979; Schulze and others 1996; Eggemeyer and others 2009).

At Konza, woody species are still increasing in abundance in 20b, but it is an open question as to whether the depletion of deep soil moisture will limit the further expansion of woody species or even cause them to decline during future droughts. In general, water-limited grasslands often have deep soil moisture that is thought to buffer community composition during dry years (Singh and

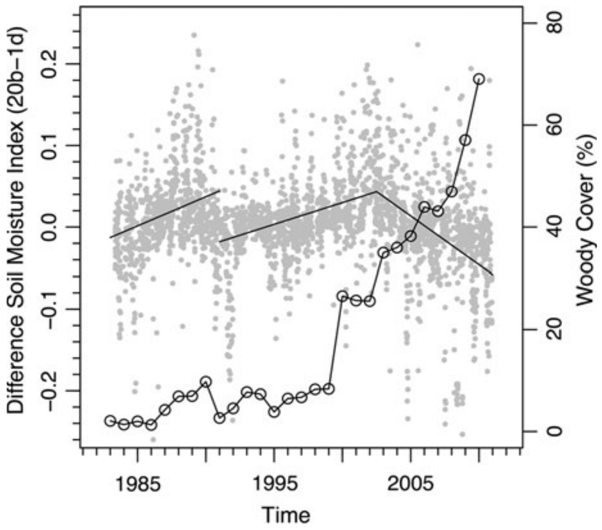

Figure 7. Overlay of woody species cover (*open circles*) and the difference in soil moisture between an infrequently (20b) and annually burned (1d) watershed. Soil moisture data presented for all depths from 25 to 150 cm. Piecewise linear regression used to generate pattern of soil moisture at all depths over time.

others 1998; Eggemeyer and others 2009). If woody species are effectively mining stored soil moisture during dry times, their expansion might be less sustainable, for example becoming more susceptible to droughts in the future. Another uncertainty is how vegetation in 20b will respond to any future fires. The wildfire in 1991 caused a large increase in productivity of the grasses in the lowlands of the unburned watershed 20b (La Pierre and others 2011) that led to a much greater reduction in soil moisture than in the annually-burned watershed. With the decline in grasses over time that accompanied the increase in woody species, whether a future fire would generate a similar subsequent flush in productivity and evapotranspiration is unknown.

Although the increase in woody species that accompanied cessation of fire led to declines in soil moisture, more time may be needed to determine whether the shift in vegetation would also alter the qualitative response of evapotranspiration to climate variability on the scale of days to weeks. In models of ecosystem function, the response of evapotranspiration to precipitation pulses is approximated as a decay rate (Williams and others 2009), which can differ among vegetation types (Teuling and others 2006), individual species within a given vegetation type (Huxman and others 2004), and seasonally as biomass accumulates (Lauenroth and Bradford 2006). Theoretically, the shift from grasses to woody species that access deeper soil water would alter seasonal dynamics of evapotranspiration because woody species produce a greater fraction of their leaf area early in the growing season whereas grasses continue to accumulate leaf area through a longer portion of the growing season. In addition, compared to adjacent grasslands, forests can have cooler surface temperatures, less variable evapotranspiration over the growing season that is more linearly related to soil water content, and generate lower rates of water infiltration and streamflow (Huxman and others 2005; Nosetto and others 2005; Scanlon and others 2005; Jackson and others 2009). These changes can happen as rapidly as a few years of introduction of woody species into grasslands (Nosetto and others 2005). Whether cessation of fire caused similar changes in the responsiveness to environmental variability is still unknown. There were too few years with high enough woody species cover to determine whether there were differences in the temporal responses of soil moisture to variability in temperature and precipitation between the infrequently and frequently burned watersheds.

In all, the unique multi-decadal time series of soil moisture from the frequently and infrequently burned watersheds reveal the differences between the short- and long-term impacts of cessation of burning. As fire regimes are changing in grasslands and savannas worldwide (Staver and others 2011), the consequences for evapotranspiration may take over a decade to develop. Although similar long-term research at other sites would be necessary to better generalize about long-term fire effects on soil moisture, the complexity of factors that impact the ultimate response of soil moisture to fire should not be underestimated. Considering the significant anthropogenic influence over fires (Bowman and others 2011) and the complexity of predicting changes in fire frequency (Moritz and others 2012), predicting water availability in future grasslands will be complicated, even without uncertainties in changes in climate. That said, the patterns laid out here reinforce general principles of the importance of considering changes in species composition when assessing the impacts of changes in disturbance regimes. For grasslands undergoing increases in woody species abundance, whether due to changes in fire regimes or not, deeper soil moisture is likely to become more depleted, which will have a range of cascading effects on everything from ecosystem resource exchange to streamflow (Jackson and others 2009). Hopefully, this long-term dataset will serve as an example of their importance and inspire similar monitoring in other ecosystems to increase our ability to generalize about the effects of fire and other disturbances on the functioning of grasslands.

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