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RESEARCH ARTICLE

Spatial versus temporal variation in precipitation in a semiarid ecosystem

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Abstract Spatial and temporal variations in precipitation are central features of semiarid ecosystems, influencing patterns of plant productivity and the distribution of native fauna. Although temporal variation in precipitation has been studied extensively, far less is known about the spatial scale and pattern of precipitation variability in semiarid regions. I used long-term precipitation records to examine spatial variation across the 63 km^2 Central Plains Experimental Range in northeastern Colorado, and across the 117,000 km^2 region of shortgrass steppe in eastern Colorado. Relative to temporal variation, spatial variation was low at scales <10 km, increased linearly across scales of 40–120 km, and was nearly equal in magnitude to temporal variation across distances of 120–160 km. Although I hypothesized that most spatial variation would be generated by early-summer convective thunderstorms in June, I found that the magnitude and spatial pattern of variation was similar for precipitation received in June compared to cumulative precipitation received during the full growing season. The degree of spatial autocorrelation in precipitation across all distances that I evaluated was similar for drought, dry, above-average and wet years. Across distances of 10–120 km, spatial variation within a single growing season was approximately two times greater than spatial variation in long-term mean growing-season precipitation, indicating spatial shifting in the locations of patches of high and low precipitation over multiple years. Overall, these findings suggest spatial variation at scales of 10–160 km may have been an important factor influencing vegetation patterns and migratory fauna of the shortgrass steppe, and have implications for livestock producers and future assessments of climate change.

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Introduction

Temporal variability in precipitation is a key factor influencing the structure and function of semiarid ecosystems (Knapp and Smith 2001; Austin et al. 2004; Collins et al. 2008), but far less is known about the scale and magnitude of spatial variation in precipitation in semiarid regions. Variation in mean annual precipitation (MAP) across gradients extending from arid to mesic regions has been quantified and related to ecosystem structure and function in many grasslands and savannas worldwide (e.g. McNaughton 1985; Williams et al. 1996; Lauenroth et al. 1999; Sankaran et al. 2005). However, the scale and magnitude of spatial variability within areas where long-term mean precipitation is relatively constant has rarely been quantified. Semiarid ecosystems are often characterized by vast expanses of flat to gently undulating topography, where orographics have minimal influence on precipitation patterns. Within these landscapes, spatial variability in precipitation inputs can be a consequence of local variation in the intensity and path of convective thunderstorms. Because water limitations influence nearly all aspects of semiarid ecosystem function, an understanding of spatial variation in precipitation inputs in these regions can provide insights to historic patterns of ecosystem function and potentially guide future approaches to ecosystem management and conservation.

In the grasslands of central North America, MAP decreases from east to west, while interannual variation in precipitation increases (Wiens 1972, 1974). The semiarid shortgrass steppe, located in the westernmost and driest portion of the central North American grasslands, is characterized by lower mean annual precipitation (MAP $\sim$ 300–550 mm) and higher interannual variation in precipitation [coefficients of variation (CV) $\sim$ 0.28] compared to mixed-grass and tallgrass prairie (MAP $\sim$ 500–730 cm, CV $\sim$ 0.23–0.26: Wiens 1972, 1974; Lauenroth and Milchunas 1992; Lauenroth et al. 1999). Considerable research in the shortgrass steppe has demonstrated the strong influence of temporal variation in precipitation at scales from days to years on plants and fauna (Wiens 1974; Sala and Lauenroth 1982; Milchunas et al. 1994; Milchunas et al. 1998; Derner et al. 2008). The Rocky Mountains that lie to the west of the shortgrass steppe influence climate and weather patterns due to the rain shadow they create (Pielke and Doesken 2008), but topographic variation east of the mountains, and its influence on movement of air masses, is minimal. Topography is characterized by gently undulating plains, with slopes typically 0–3%. For example, at the Central Plains Experimental Range in northeastern Colorado, typical catenas vary by 6–21 m in elevation over 1.6 km (Milchunas et al. 1989) and elevation varies by only 25–90 m over 10 km. Within this flat landscape, more than 70% of MAP falls during the growing season (April–September), and occurs during only 2–4% of the hours within a year (Pielke and Doesken 2008). Factors potentially contributing to spatial variation in precipitation include intense spring thunderstorms influenced by sharp temperature contrasts in air masses, and convective summer thunderstorms that bring high-intensity rainfall over small areas for short periods of time (Pielke and Doesken 2008). Despite the central role of moisture limitation in semiarid regions, I am unaware of studies that have examined the relative magnitude of spatial versus temporal variability in precipitation for these ecosystems.

Spatial variability in precipitation can potentially influence and interact with many aspects of ecosystem structure and function, but the influence may be particularly strong for organisms with the capacity to move across the landscape in response to spatial variation. My interest in spatial precipitation patterns was motivated by its implications for four aspects of the ecology and management of semiarid ecosystems. First, because bison were largely eliminated from central North American grasslands prior to the onset of ecological research, considerable speculation has surrounded their distribution, abundance and role in grassland dynamics (Bamforth 1987; Hart 2001; Lott 2002). Dry years were likely a primary determinant of bison distribution and abundance, and spatial variation in precipitation at scales of <10 km to >100 km may have influenced bison movement patterns, degree of herd aggregation, and population dynamics (Lott 2002). Second, drought is a key limitation for livestock management in semiarid regions today. Long-distance movement of livestock in response to spatially isolated rainfall has long been an important strategy in semiarid rangelands outside of North America (Coughenour 1991; McAllister et al. 2006). Understanding the spatial scale of precipitation variation during droughts can inform potential drought mitigation strategies for livestock producers. Third, bird communities in North American grasslands have been strongly influenced by precipitation patterns (Wiens 1974). Most bird species endemic to grasslands of central North America are migratory, hence can respond to large-scale spatial variation in precipitation, and are also undergoing population declines (Brennan and Kuvleskey 2005). The scale and magnitude of spatial variation in precipitation may be an important factor interacting with land use changes in grasslands (Samson et al. 2004), and could inform approaches for monitoring and mitigating declines in grassland bird species. Fourth, quantification of spatial patterns from long-term datasets can provide an important baseline for assessing the reliability of local precipitation predictions in unmeasured locations, and assessing future climate change. Research sites even in areas of flat topography that lack an on-site weather stations or rely on a single station often do not know how precipitation varies from station to research site, and precipitation can be a particularly difficult variable to predict with a sparse network of gauges (Hubbard 1994). Under future climate change, increases in inter- and intra-annual variability of precipitation are predicted (Meehl et al. 2007) but predictions are presented and discussed at the scale of regions within continents, and cannot address changes in spatial patterns across distances <1,000 km (Christensen and Hewiston 2007). Understanding both spatial and temporal patterns of variability in precipitation over the past half-century is essential to assessing future changes.

The objective of this study was to quantify the magnitude and scale of spatial variation in growing-season precipitation in the shortgrass steppe. The analysis focused on precipitation records collected at two spatial scales. First, I analyzed records from stations distributed across the USDA-Agricultural Research Service Central Plains Experimental Range in northeastern Colorado to examine spatial variation across distances of 1–8 km. Second, I analyzed records from stations distributed across eastern Colorado, which covers approximately 117,000 km^2 in the northern half of the shortgrass steppe ecosystem (Lauenroth and Milchunas 1992), to examine patterns across distances of 10–200 km. Specific objectives were to (1) test whether spatial variability in precipitation at local (1–8 km) and regional (10–200 km) scales is inversely related to the amount of growing-season precipitation, (2) compare the magnitude of spatial variation in precipitation across scales of 1–200 km to inter-annual variability, and (3) quantify the degree of patchiness in precipitation across spatial scales in the shortgrass steppe, and whether such patchiness differs between dry versus wet years.

Methods

Central plains experimental range

The Central Plains Experimental Range (CPER) encompasses approximately 62.8 km^2 of shortgrass steppe located northeast of Nunn, Colorado (40°49′N latitude, 107°47′W longitude). CPER was established in response to the abandonment of ranches and farms during the 1930s, and has supported rangeland research since 1939. Beginning in 1939, manual rain gauges were established at 27 different locations on the property, and have been monitored during May–September each year. Gauges were always checked within 60 h of a precipitation event, which limited losses to evaporation to less than 0.025 mm, but typically were checked 24 h after precipitation. Four additional gauge locations were added in the 1980s. I examined all precipitation records from 1939–2006, and removed records from any gauge that contained missing values for any week during a given year. I then identified all years for which complete records were available for at least 25 precipitation gauges. Only a subset of the gauges were monitored in the 1960s and 1970s, so the criterion of ≥25 gauges per year excluded 1960–1979 from analysis, and included a total of 31 years during 1939–1959 and 1971–2006.

For the 31 years with sufficient precipitation records, I calculated two metrics of spatial variation at two temporal resolutions for each of the 31 years. First, I calculated the magnitude of spatial variation as the mean difference in May–September precipitation among gauges separated by four distance classes: 0–2 km (35–80 pairs of gauges $year^{-1}$), 2–4 km (105–220 pairs $year^{-1}$), 4–6 km (86–196 pairs $year^{-1}$) and 6–8 km (33–78 pairs $year^{-1}$). Second, I measured the degree of patchiness in precipitation at different spatial scales by calculating Moran's I for each of the four separation distance classes described previously (Legendre and Fortin 1989). Calculations of both the magnitude of spatial variation and Moran's I were conducted for each individual year separately. I used Moran's I because it provides an index of the strength of autocorrelation in each distance class, where values approaching 1 indicate a complete lack of spatial variation within a distance class (i.e. a homogenous patch), values approaching −1 indicate maximum dissimilarity among locations within a distance class, and values near zero indicate no departure from random variation (Sokal and Oden 1978). I calculated Moran's I and evaluated its statistical significance (i.e. whether Moran's I differs significantly from zero for a given distance class) using the statistical package R (http://www.R-project.org). I calculated interannual variability as the average difference in precipitation between two consecutive years, averaged across all individual gauges and all pairs of years. For example, I first calculated the difference in precipitation received in 1939 versus 1940 for each gauge that have precipitation records for both years. I then averaged across all of those gauges to obtain a mean difference in precipitation between 1939 and 1940. I repeated this for all pairs of consecutive years in the dataset, and then calculated the overall mean interannual difference. I used this measure of interannual variation because it is the change between any two consecutive years (rather than, say the difference between 1939 and 1999) that influences the ecology and behavior of individual organisms such as herbivores, birds and humans in the shortgrass steppe.

I also classified each year in the dataset into one of four categories defined by the average amount of precipitation received in that year: drought years (<75% of long-term mean growing-season precipitation [MGSP], $N = 7$ years), dry years (75–100% of MGSP, $N = 9$), above-average years (100–125% of MGSP, $N = 9$) and wet years (>125% MGSP, $N = 6$). I then used two-way ANOVAs to examine whether the magnitude of spatial variation (absolute differences among gauges separated by different distances) and changes in the degree of spatial autocorrelation (Moran's I) varied in relation to drought category (drought, dry, above-average, and wet years) and spatial scale (10–40, 40–80, 80–120, 120–160 and 160–200 km).

In the shortgrass steppe, the greatest mean amount of monthly precipitation occurs in June, and precipitation in June often occurs as high-intensity, convective thunderstorms that affect smaller areas for shorter periods of time (Pielke and Doesken 2008). I hypothesized that spatial variation may be significantly greater in June compared to May–September cumulative rainfall, and therefore conducted all analyses for the full growing season (May–September cumulative precipitation for each of the 31 years) as well as for June precipitation only. For the June analysis, I excluded data from 1980 (when no precipitation occurred in June) so results are based on 30 years of precipitation records.

Eastern Colorado

Previous analyses of precipitation in the Great Plains have primarily focused on the large-scale gradient from the shortgrass steppe in the west to the tallgrass praires in the east. The objective was to evaluate spatial heterogeneity within the shortgrass steppe as defined by Lauenroth and Milchunas (1992). Specifically, I examined variation within an approximately 450 km (N–S) by 260 km (E–W) portion of the shortgrass steppe defined by the northern, eastern and southern boundaries of Colorado, and on the west by the base of the Rocky Mountains. I obtained total monthly precipitation data from the National Climatic Data Center (www.ncdc.noaa.gov) for those weather stations that are members of the cooperative observing network in the United States, and are in counties east of the Rocky Mountains in Colorado. I excluded stations west of Interstate 25 in order to remove locations located in the foothills or at the immediate base of the mountains. For analyses, I used those stations ($N = 64$) with $\geq$25 years of complete April–September precipitation records during the period 1951–2005. Earlier decades were not included because fewer stations were available prior to 1951. I focused on April–September precipitation because these months encompass the growing season, are when most precipitation occurs in the shortgrass steppe, and are least affected by the variance involved in recording snow. I included April precipitation in this analysis because data for eastern Colorado were available, and April precipitation can be important for production of cool-season grasses in the shortgrass steppe (Milchunas et al. 1994). Latitude and longitude for each station were converted to Universal Transverse Mercator units in order to calculate distances among all pairs of weather stations for spatial analyses.

For all years during 1951–2005, I calculated the magnitude of spatial variation in eastern Colorado as the mean difference in April–September precipitation among gauges separated by five distance classes: 0–40 km (21–56 pairs of gauges year^{-1}), 40–80 km (90–170 pairs year^{-1}), 80–120 km (119–264 pairs year^{-1}), 120–160 km (134–302 pairs year^{-1}), and 160–200 km (138–278 pairs year^{-1}). Calculations were performed for each individual year separately. As with the analysis for CPER, I also calculated Moran's I and evaluated its deviation from zero for each distance class each year to obtain an index of the degree of patchiness in precipitation at different spatial scales. I calculated interannual variability using the same method as for the CPER dataset.

I then classified the years into four categories defined by the average amount of precipitation received in that year, again using the same criteria as described for the CPER analysis. This gave 6 drought years, 23 dry years, 21 above-average years, and 5 wet years. I again used two-way ANOVAs to test whether the magnitude of spatial variation (absolute differences among gauges separated by different distances) and spatial pattern of variation (Moran's I) differed among drought categories and among spatial scales. To illustrate changes in spatial patterns of precipitation in eastern Colorado, I also generated kriged maps of precipitation based on the 64 precipitation gauges used in the analyses. I used GS + (Version 7.0; Gamma Design Software 2006) to construct semivariograms for each dataset, to identify best-fit models for the semivariograms (exponential, spherical, Gaussian or linear) and to use the fitted model to generate maps using ordinary block kriging (Robertson and Gross 1994) with 9 km^2 blocks.

Results

Small-scale (1–8 km) spatial variation in precipitation

At CPER, mean growing-season (May–September) precipitation for the 31 years in which ≥25 gauges were measured was 202 mm. The magnitude of spatial variation in growing-season precipitation increased from an average of only 15 mm (18% of temporal variation) across distances <2 km to an average of 31 mm (37% of temporal variation) across distances of 6–8 km. Spatial variation at all separation distances was substantially lower than the mean inter-annual variation of 83 mm (Fig. 1a). When the absolute magnitude of spatial variation in precipitation was analyzed in relation to drought classes (drought, dry, above-average vs. wet years) and the distance separating gauges, I found no interaction between drought class and separation distance ($F_{9,108} = 0.54$, $P = 0.84$; Fig. 1b). The magnitude of spatial variation increased significantly with increasing separation distance ($F_{3,108} = 14.02$, $P < 0.0001$) and was greater in years with more overall rainfall ($F_{3,108} = 19.01$; $P < 0.0001$; Fig. 1b). However, reduced spatial variation in drought versus wet years was proportional to the

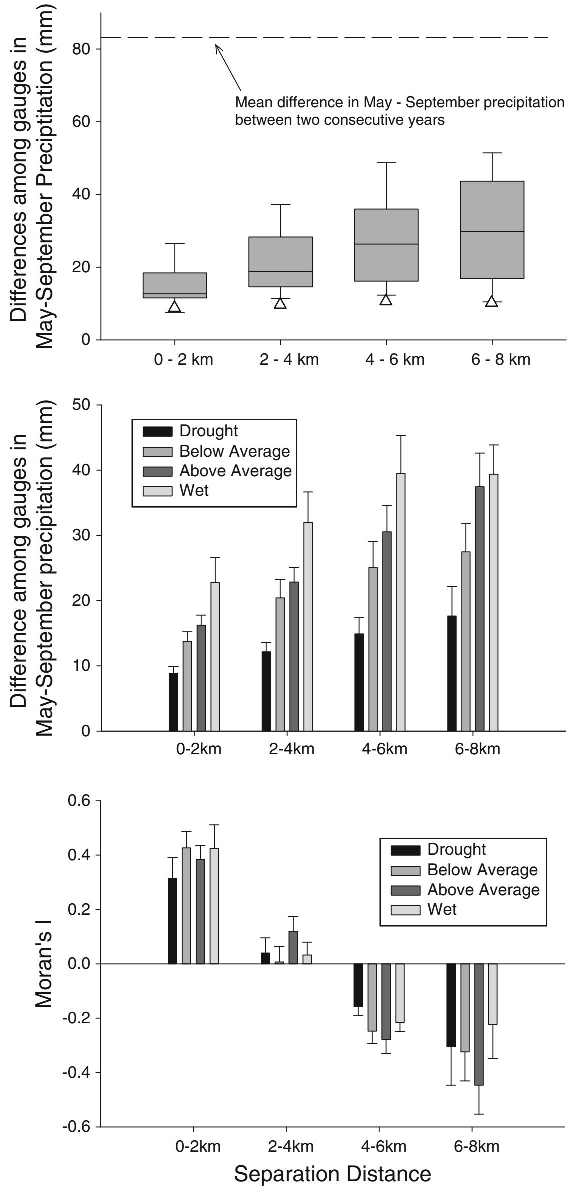

Fig. 1 Relationship between the distance separating precipitation gauges at the Central Plains Experimental Range in northeastern Colorado and **a** variation in growing-season precipitation (boxplots for $N = 31$ years with sufficient precipitation records during 1941–2006), **b** variation in growing-season precipitation for drought, below-average, above-average and wet years (mean + 1SE), and **c** the degree of spatial autocorrelation in growing-season precipitation for different types of years as measured by Moran's I (mean + 1 SE). Boxplots in **a** depict the within-year spatial variation for 31 different years, while the *open triangles* show spatial variation among gauges in long-term mean growing-season precipitation

reduction in mean precipitation in drought versus wet years, such that the coefficient of variation among gauges was not significantly correlated with mean precipitation received in a given year ($P > 0.15$).

The degree of spatial autocorrelation in precipitation (Moran's I) did not interact with the amount of rainfall received in a growing season (drought class × separation distance interaction, $F_{9,108} = 0.80$, $P = 0.62$; Fig. 1c). Although mean Moran's I declined significantly with increasing separation distance class ($F_{3,108} = 70.9$, $P < 0.001$, Fig. 1c) there was no variation in Moran's I among years with different amounts of rainfall received ($F_{3,108} = 0.38$, $P = 0.77$). Rainfall was positively and significantly aggregated at the <2 km scale in 25 of 31 years, and exhibited no consistent spatial pattern at a scale of 2–4 km (Fig. 1c). This implies that variation in precipitation among locations separated by 2–4 km was roughly equivalent to the total amount of variation within the 63 km^2 property. Locations separated by 4–6 km showed significant negative spatial autocorrelation (i.e. received significantly different rainfall amounts than expected by random as measured by Moran's I) in 13 of 31 years, and locations separated by 6–8 km were negatively autocorrelated in 16 of 31 years (Fig. 1c).

Spatial patterns were strikingly similar for rainfall received in 1 month (June) as compared to May–September cumulative rainfall (Figs. 1 vs. 2). In June, I again found no interaction between drought class and separation distance ($F_{9,104} = 0.24$, $P = 0.99$; Fig. 2b). The magnitude of spatial variation increased significantly with increasing separation distance ($F_{3,104} = 6.84$, $P = 0.0003$) and was greater in years with more overall rainfall. ($F_{3,104} = 20.85$, $P = 0.0001$; Fig. 2b). Although the magnitude of spatial variation increased with separation distance, spatial variation at 6–8 km was still substantially lower than variation between any two consecutive years (Fig. 2a).

Overall, these results show that the general spatial pattern of precipitation at CPER consists of portions of the landscape separated by 4–8 km receiving significantly different levels of rainfall in approximately 50% of the years, and conversely no significant spatial variability occurring at this scale for the remaining years. The magnitude of spatial variability across distances of 4–8 km varied from 15 to 18 mm in drought years to 39 mm in wet years.

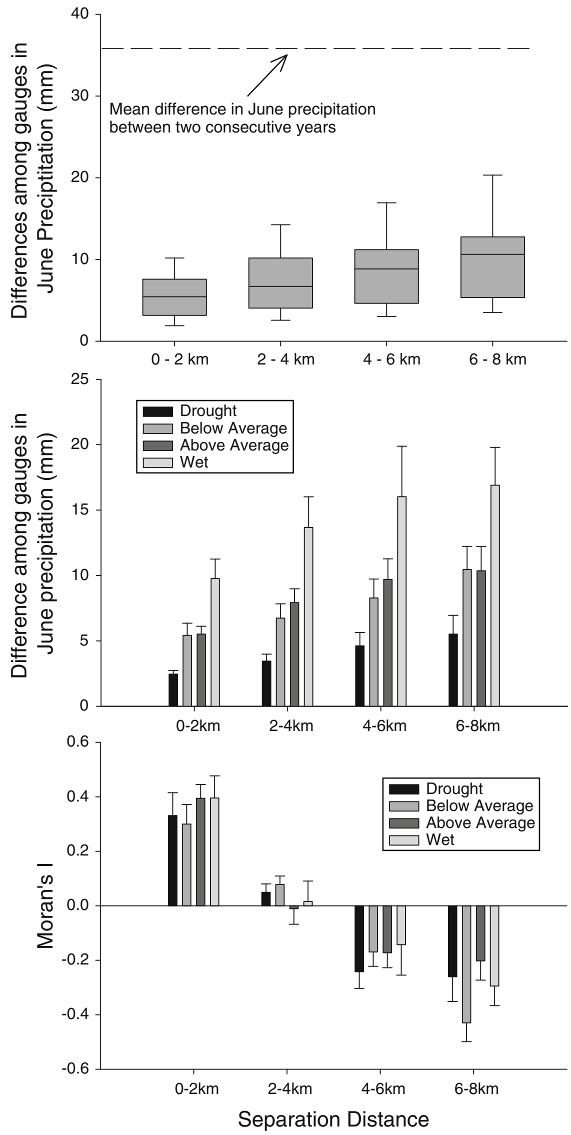

Fig. 2 Relationship between the distance separating rain gauges at the Central Plains Experimental Range in northeastern Colorado and **a** variation in June precipitation (boxplots for $N = 30$ years during 1941–2006), **b** variation in growing-season precipitation for drought, below-average, above-average and wet years (mean + 1 SE), and **c** the degree of spatial autocorrelation in growing-season precipitation for different types of years as measured by Moran's I (mean + 1 SE)

Large-scale (>10 km) spatial variation in precipitation

Mean cumulative precipitation during April–September based on all gauges in eastern Colorado with at least 25 years of precipitation records during

1951–2005 was 293 mm. Spatial variation in growing-season precipitation increased from an average of 54 mm (56% of temporal variation) across distances <40 km to 86 mm (89% of temporal variation) across distances >120 km (Fig. 3a). I found no significant interaction between separation distance and the degree of drought in terms of the magnitude of spatial variation ($F_{12,255} = 0.15$, $P = 0.99$; Fig. 3b). The magnitude of spatial variation increased substantially with increasing separation distance class ($F_{4,255} = 54.6$, $P < 0.0001$) and was greater in wet versus drought years ($F_{3,255} = 41.87$, $P < 0.0001$; Fig. 3b). Spatial variation increased approximately linearly across scales from <40 km to 120–160 km, such that mean spatial variation within the 120–160 km distance class was nearly as great as inter-annual variability (96 mm; Fig. 3a). An asymptote in spatial variability was reached at the 120–160 km separation distance, such that variability was similar for the 120–160 km and the 160–200 km distance classes (Fig. 3a–c). I also found no significant interaction between separation distance and the degree of drought in terms of the spatial pattern of variation (Moran's I: $F_{12,255} = 0.23$, $P = 0.99$; Fig. 3c). Moran's I declined significantly with increasing separation distance across distances of <40 to 120–160 km ($F_{3,255} = 0.23$, $P < 0.0001$) and was slightly lower in the wettest years compared with dry and drought years ($F_{4,255} = 0.23$, $P = 0.047$). Rainfall was positively and significantly aggregated at distances <40 km in 51 of 55 years, and was positively and significantly aggregated at 40–80 km in 47 of 55 years. Rainfall exhibited substantially lower spatial autocorrelation at scales of 80–200 km (Fig. 3c).

For illustration purposes, kriged maps of precipitation patterns for eastern Colorado were derived for a drought year (2002; MGSP = 169 mm) and subsequent average precipitation year (2003; MGSP = 263 mm). These maps are simply presented to show shifts in the magnitude and scale of spatial variation in growing-season precipitation over time (Fig. 4). The years 2002 and 2003 were selected because they illustrate how spatial variation across distances of 120–160 km within both a drought and an average year can be as substantial as the difference between a drought

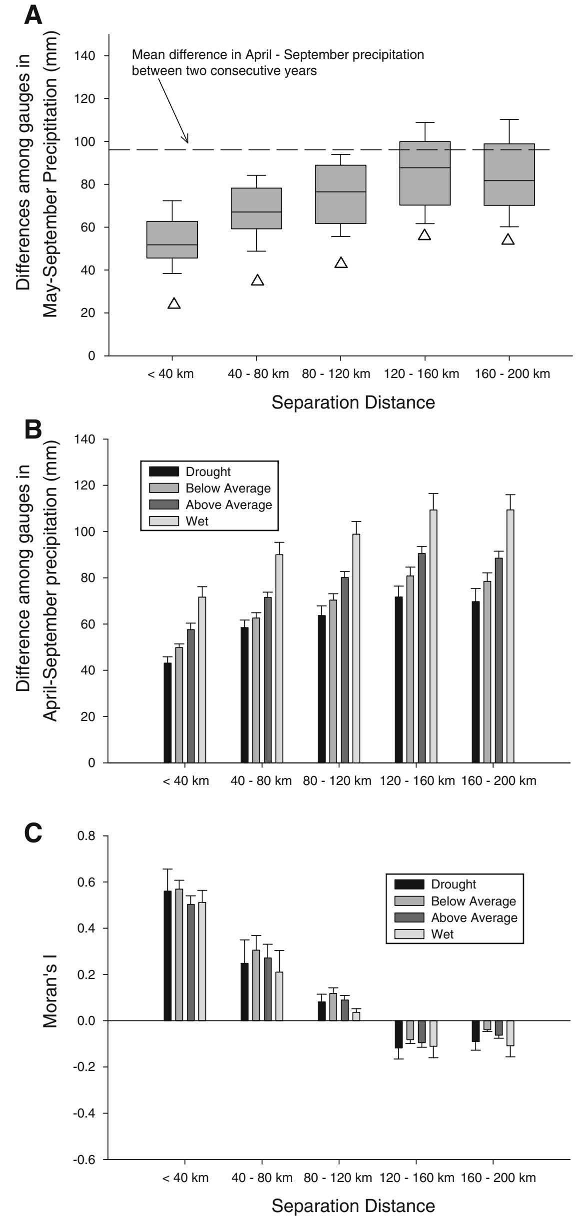

Fig. 3 Relationship between the distance separating rain gauges in the shortgrass steppe of eastern Colorado and **a** variation in growing-season precipitation for 55 years (1951–2005), **b** variation in growing-season precipitation for drought, below-average, above-average and wet years (mean + 1 SE), and **c** the degree of spatial autocorrelation in growing-season precipitation as measured by Moran's I (mean + 1SE). Boxplots in **a** show the within-year spatial variation for 55 different years, while the *open triangles* show spatial variation among gauges in long-term mean growing-season precipitation

and a subsequent average year in any given location (Fig. 4a vs. b).

One finding from this study is that spatial variation in any given year (boxplots in Fig. 3a for all 55 years; Fig. 4a, b for 2 representative years) is significantly greater than spatial variation in long-term MAP (open triangles in Fig. 3a; map in Fig. 4c). Across eastern Colorado, this is particularly evident at separation distances of 10–40 km, where spatial variation is 2.3 times greater in individual years compared to the long-term mean (Fig. 3a, boxplots vs. open triangles). This difference diminished with increasing separation distances, such that at distances greater than 120 km, spatial variation was 1.6 times greater in individual years compared to the long-term mean (Fig. 3a). The opposite trend was found in the CPER analysis. At this local scale, spatial variation across distances of 6–8 km in any given year was 3.1 times greater than spatial variation in the long-term mean; that ratio declined with decreasing separation distances such that spatial variation in individual years was only 1.7 times greater at distances of 0–2 km (Fig. 1a boxplots vs. open triangles). These results indicate that areas receiving high and low

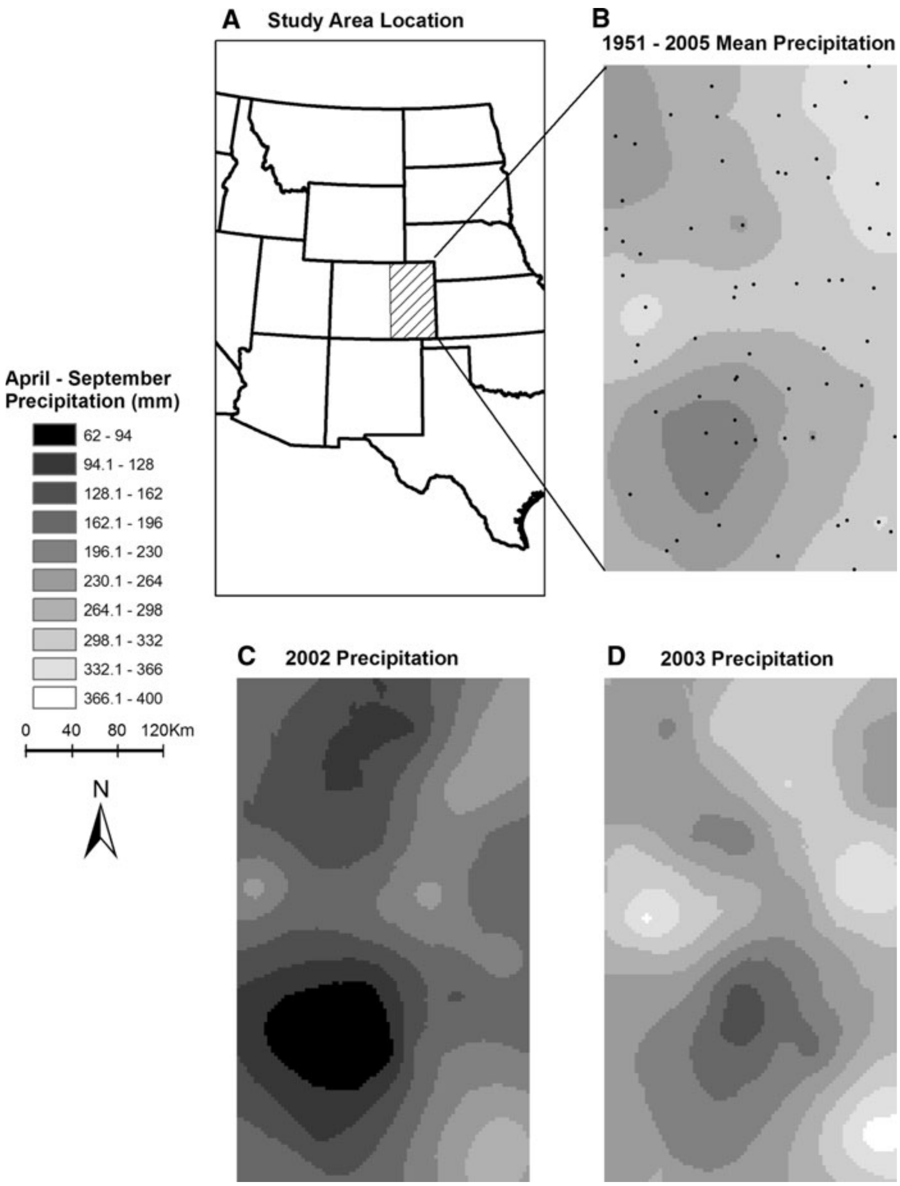

Fig. 4 Location of the study area in eastern Colorado (**a**) and kriged maps of spatial variation in growing-season precipitation in the shortgrass-steppe of eastern Colorado for a drought year (2002) and a subsequent year of near-average precipitation (2003), as compared to spatial variation in long-term (1951–2005) mean precipitation (**b**–**d**). Each map is bounded on the north, east and south by the Colorado state line, and on the west by the base of the Rocky Mountains. *Black dots* in **b** show the locations of rain gauges used in the analyses. The *maps* illustrate the greater degree of spatial variation in individual years (**c**, **d**) as compared to the long-term mean (**b**), and spatial shifts among years in the locations of patches of high and low precipitation (**c** vs. **d**)

levels of precipitation in any given year shift over time (example in Fig. 4a vs. b).

Spatial patterns for eastern Colorado were similar for June alone compared to April–September cumulative precipitation (Figs. 3 vs. 5). However, mean spatial variation at 120–160 km (31 mm) in June was only 76% of mean variation between any two consecutive years (Fig. 5a). There was no interaction between separation distance and drought class either for the magnitude of spatial variation ($F_{12,255} = 0.04$, $P = 1.0$; Fig. 5b) or the pattern of spatial variation ($F_{12,255} = 1.25$, $P = 0.26$). The magnitude of spatial variation in June increased significantly with increasing separation distances ($F_{4,255} = 7.92$, $P < 0.001$) and was greater in years with more precipitation ($F3,255 = 16.09$, $P < 0.001$; Fig. 5b). The degree of spatial autocorrelation in June declined with increasing separation distance ($F4,255 = 64.84$, $P < 0.0001$), and was significantly lower in years with high levels of precipitation in June (>125% of long-term mean June precipitation) compared with years when June precipitation was less than the long-term mean ($F4,255 = 3.21$, $P = 0.024$; Fig. 5c).

Discussion

A central finding of this analysis is that relative to interannual variation, spatial variation in growing-season precipitation in the shortgrass steppe is low across distances of <10 km, increases substantially across distances of 40–80 km (71% of inter-annual variability), and is nearly equivalent (87–89%) in magnitude to inter-annual variability across distances >120 km. Furthermore, the magnitude of spatial variation is significantly higher in wet compared to dry years (Figs. 3b, 5b), but the spatial pattern of that variation (i.e. the scale and homogeneity of wet versus dry patches) is similar in dry and wet years (Figs. 3c, 5c). Greater spatial variability in wet years may be related to increased inputs from high-intensity precipitation events because precipitation events larger than 5 mm account for more than 50% of inputs in wet years, while the amount of precipitation received in events generating less than 5 mm is similar in both wet and dry years (Sala et al. 1992). The rate of increase in spatial variation across distances of 1–8 km (based on the CPER analysis) cannot be compared directly with the rate of increase

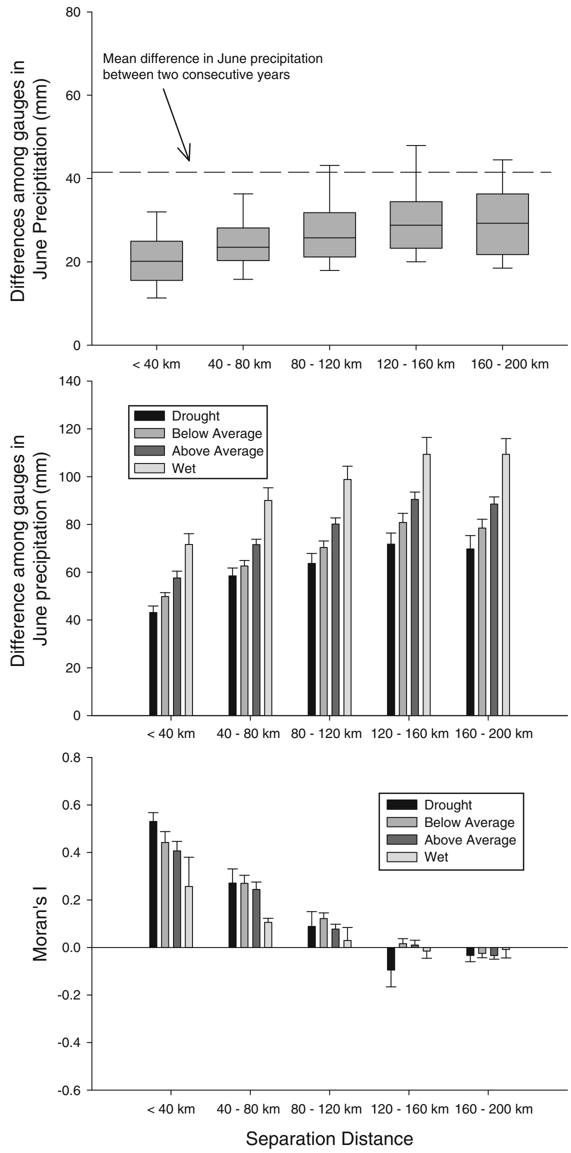

Fig. 5 Relationship between the distance separating rain gauges in the shortgrass steppe of eastern Colorado and **a** variation in June precipitation for 55 years (1951–2005), **b** variation in June precipitation for drought, below-average, above-average and wet years (mean + 1 SE), and **c** the degree of spatial autocorrelation in June precipitation as measured by Moran's I (mean + 1 SE)

across distances of 40–160 km (based on the eastern CO analysis) due to differences in the methods and timing of data collection, but the two analyses are consistent in showing a linear increase in spatial variation across all scales from 1 to 160 km, with variation reaching an asymptote for separation distances greater than 160 km.

The fact that the eastern CO analysis showed the strongest positive autocorrelation at a scale of 10–40 km (indicating homogenous patches at this scale relative to variation across all of eastern CO) is consistent with the finding that significant negative spatial autocorrelation occurs at scales of 6–8 km within the CPER property in 50% of the years. In other words, an area with a diameter of approximately 8 km will typically encompass a boundary between two distinct patches of high versus low precipitation in approximately 50% of the years. In the remaining years, an area the size of CPER is entirely contained within a patch of high or low precipitation. When viewed at the scale of all of eastern Colorado, these patches are most homogenous at scales of 10–40 km. Patches of this size are likely the result of inputs from intense, localized thunderstorms during the growing season (Fig. 6), which are overlaid on the more homogenous distribution of precipitation received from slow-moving storm systems that affect broader areas. Thunderstorm patterns can be driven by different factors in different seasons, with spring storms influenced by the polar jet stream, early-summer thunderstorms affected by more localized air mass boundaries, and late-summer storms influenced by the North American monsoons (Pielke and Doesken 2008).

Although I hypothesized that localized early-summer thunderstorms may produce the high spatial variation in June, I found that cumulative precipitation over the full growing season was just as spatially variable as June precipitation. These results emphasize the importance of spatial variability in weather patterns throughout the growing season. One contributing factor may be localized feedbacks whereby areas receiving moisture at the beginning of the growing season are more likely to receive subsequent rainfall, as enhanced evaporation and transpiration in a locality provides additional energy to fuel future thunderstorms (Pielke et al. 1999).

Spatial variation increased linearly across distances of 10–160 km. Patterns discussed previously emphasize the role of isolated thunderstorms at scales of 10–40 km. At larger separation distances, increasing variation may be the result of multiple contributing factors. In particular, high spatial variation at 120–160 km may result from the combination of localized thunderstorm patterns overlaid on more temporally consistent spatial gradients associated with broad elevation gradients (e.g. the Arkansas and South Platte river drainages) and the west to east gradient created by the rain shadow of the Rocky Mountains along the western border of the study area.

Across distances of 6–8 km, the mean spatial variation of 30 mm is low relative to interannual variation, but can still significantly influence plant production in this region where growing-season precipitation averages only 202 mm. Actual plant production will depend on numerous local site conditions including topography, soils and grazing intensity, but long-term analyses of plant production at CPER (Lauenroth and Sala 1992; Milchunas et al. 1994) suggest that a difference of 30 mm precipitation during May–September is equivalent to $\sim$40–50 kg ha^{-1} in above-ground plant production. Across distances of 120–160 km, variation in growing-season precipitation could induce variation in plant production on the order of 110–140 kg/ha (Lauenroth and Sala 1992; Milchunas et al. 1994). When variation in soil types and texture across the shortgrass steppe is coupled with spatial variation in precipitation, they could together contribute to even greater spatial variation in soil moisture availability and plant production. In addition, variability in plant production is likely to exceed variation predicted from simple regression relationships because time lags and precipitation event size distribution also affect plant productivity (Lauenroth and Sala 1992; Heisler-White et al. 2008), and because plant production increases to a greater degree in wet years than it declines in dry years (Knapp and Smith 2001; Derner et al. 2008).

Fig. 6 Example of spatially variable growing-season thunderstorms in the semiarid, western region of the central North American grasslands. Photo credit: Sam Cox

Spatial variability in rainfall could have been one factor affecting mobile fauna in this region prior to European settlement. For example, one-way bison migrations in Wyoming and Utah are on the order of 22–45 km (Berger 2004; Bruggeman et al. 2007) and migratory movements >100 km are undertaken by several other large ungulate species (Berger 2004). Thus, bison movements in response to the substantial spatial variation in precipitation that I documented at scales of 40–160 km could clearly have been energetically feasible. Movements in response to spatial variability in forage resources can reduce the effect of temporal variability on density-dependence in ungulate populations, as has been shown for elk and bison populations in montane habitats (Wang et al. 2006). Although field assessments of how spatial precipitation variability affects on grazer movements are not possible, spatially explicit ecosystem models that simulate vegetation dynamics, ungulate foraging decisions, and movement patterns (e.g. Christensen et al. 2003; Plumb et al. 2009) may be an effective means to explore the consequences of spatial precipitation patterns that I documented for large-scale herbivore movement. Responses of migratory bird populations to spatial variability in precipitation have also been of considerable interest to ecologists (Wiens 1974), and today have direct implications for the design of grassland reserve networks. For example, two smaller properties separated by 40–80 km experience more than twice the variation in precipitation than a single large property. When combined with information on how at-risk bird species shift breeding locations among years, such information can assist in the effective allocation of conservation efforts.

Ranches on the order of 50–100 km^2 can span distances of 7–10 km, and ranches with separate parcels can be distributed over even larger distances. My findings concerning high spatial variability in precipitation at scales of 120–160 km suggest that movement of livestock over such distances through collaborative networks of livestock producers may be one means to mitigate temporal variation in precipitation. Recent discussions between U.S. and African livestock producers have emphasized the value of large-scale livestock mobility (Curtin and Western 2008), and such 'agistment' networks are most effective where spatial variation in resource availability is high (McAllister et al. 2006). I also note that the National Grasslands in the shortgrass steppe each encompass $\sim$440–1800 km^2 of public rangeland that present substantial opportunities for large-scale shifts in cattle stocking rates in response to spatially variable precipitation patterns.

Another practical use of this analysis concerns the reliability of using precipitation records from an off-site weather station to represent a nearby, unmeasured location. While this will depend on the application of the data, my analysis across spatial scales of 1–8 km at CPER found that variation across distances of as little as 2–4 km is similar in magnitude to variation across the entire 63 km^2 property. Where accurate measures of precipitation for a local study are important, my results suggest gauges should be within 2 km of the study site. At the same time, the magnitude of variation across the 63 km^2 property was small compared to interannual variability, so for some applications, using measurements from a single gauge may be reasonably reliable for distances up to 8 km away. Beyond this, the potential difference in precipitation between a gauge and an unmeasured location increases linearly up to a separation distance of 160 km (Fig. 3a).

Within the expansive and topographically homogenous shortgrass steppe, my analysis emphasizes the importance of spatially variable precipitation at all scales. In particular, spatial variation is equivalent in magnitude to inter-annual variation at scales of 120–160 km. Management and conservation strategies for semiarid rangelands can be increasingly effective by recognizing and incorporating this source of spatial variation.

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