

Heterogeneity of Thermal Extremes: Driven by Disturbance or Inherent in the Landscape

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Abstract Ecologists are beginning to recognize the effect of heterogeneity on structure and function in arid and semiarid ecosystems. Additionally, the influences of temperature on ecosystems are widely documented, but landscape temperature patterns and relationships with vegetation are rarely reported in ecological studies. To better understand the importance of temperature patterns to the conservation and restoration of native ecosystems, we designed an experiment to investigate relationships among soil surface temperature, landscape heterogeneity, and grazing intensity. Grazing intensity did influence the vegetation structure and composition. Heavy treatments had the greatest bare ground and the least vertical structure. Ungrazed treatments had the most litter and live grass cover. However, average temperatures among the three grazing treatments were not different and ranged less than 2°C during midday summer periods. The temperature difference between riparian and upland landscapes within grazing treatments was 21°C. Landscape position (riparian vs. upland) did have a significant influence on soil surface temperature and produced a variation in temperature 11 times greater than grazing intensities. Thermal heterogeneity did not differ among grazing treatments. Lower soil surface temperatures (associated with riparian areas) may provide a critical thermal refuge for many animals in arid and semiarid ecosystems on hot summer days, when air temperatures can exceed 37°C. Riparian zones, specifically

riparian vegetation, are an important component in ecosystem management.

Keywords Soil temperature · Riparian · Landscape variability · Thermal refugia · Global climate change

Introduction

Heterogeneity has been described as the root of biological diversity at all levels of ecological organization and should serve as the foundation for conservation and ecosystem management (Christensen 1997; Ostfeld and others 1997; Wiens 1997). Ecologists are beginning to recognize the role of heterogeneity in ecological systems and acknowledging its influence on population dynamics and biodiversity (MacArthur and Pianka 1966; Wiens 1976; Turner and Gardner 1991; Sarnelle and others 1993). Heterogeneity is largely associated with spatial and temporal variability, resulting in scale dependency, and can be influenced by such factors as grazing and topoedaphic features (Fuhlendorf and Smeins 1996; 1999). Often it is in reference to vegetation structure, but other factors may include spatially oriented disturbances influencing such things as evapotranspiration, water infiltration, and microclimate temperature.

Temperature influences the rate of chemical reactions and processes that occur within and around living organisms. Below ground, relatively low temperatures slow microbial activity, which in turn reduces the speed at which carbon and nitrogen cycle (Mielnic and Dugas 2000; Tschерko and others 2001; Luo and others 2001; Frank and others 2002). Inversely, above ground, increased temperatures can inhibit plant growth by increasing

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photorespiration (Bliss 1956; Billings and Mooney 1968; Berry and Bjorkman 1980; Nilsen and Orcutt 1996). Unlike plants, animals have the ability to seek out optimal thermal environments and refuge from thermal extremes. Animals balance foraging behavior and predator avoidance with thermal refuge and are therefore dependent on heterogeneity and thermal patterns. Animals that efficiently utilize microhabitats to conserve energy gain advantage by re-locating these reserves to other vital processes (Walsberg 1985, 1986, 1993; Webb and Rogers 1988). Specific microclimates within a species' range can have profound effects on population dynamics (survival, movements, and fitness) and may dictate habitat utilization throughout the year (Sedgeley 2001; Sharp and Van Horne 1999). Within semiarid and arid ecosystems it is critical that we understand thermal patterns, especially in light of global climate change.

Vegetation characteristics (i.e., availability and distribution of food, structure, and cover) dictate habitat selection for many wildlife species (Ostfeld 1985; Kendigh and Fawver 1981; Pierson and Wight 1991) and serve as a critical moderator of local temperature extremes (Pianka 1988). Herbaceous biomass removal (livestock grazing) is an influential process that governs changes in vegetation structure and composition (Milchunas and Lauenroth 1993). Temperature and livestock grazing can have both direct and indirect influences on ecosystem function by influencing the distribution and abundance of animal species including insects, birds, and mammals, especially in arid and semiarid environments (Bock and others 1984; Dennis and others 1998, Ritchie 2000).

The influence of temperature on biotic communities is widely documented (Loik and others 2000; Roads and others 1994; Daubenmire 1974), but landscape temperature patterns are infrequently reported in ecological studies (Chen and others 1996). Interactions between air temperature and livestock grazing can influence soil moisture, photosynthetic, respiration, and decomposition rates, creating unique habitat conditions that ultimately influence distribution and abundance of plant and animal populations (Geiger 1965; Daniel and others 1979; Perry 1994). Consequently, landscape-level temperature gradients may have a profound effects on the distribution and abundance of biological communities, especially those occupying more arid environments (Schleucher 1999; Karr and Freemark 1983). As global warming continues, quantifying relationships between landscapes and the thermal environment will likely play an increasing role in conservation and restoration of many ecological systems. To better understand the ecological importance of these relationships to conservation and restoration of our native ecosystems, we designed an experiment to document relationships among temperature, landscape heterogeneity, and grazing

intensity. Specifically we hypothesized that (1) grazing intensity will alter vegetation structure and composition; (2) increased grazing intensity would increase soil temperature; (3) grazing intensity will alter soil surface temperature more than landscape position (upland or riparian); (4) riparian soil temperature will be cooler than upland temperature and (5) moderate grazing intensity will increase temperature heterogeneity, i.e., "patchiness" and variability.

Methods

This study was located on the Marvin Klemme Range Research Station (35°25' N; 99°05' W) of the Oklahoma Agricultural Experiment Station. This area is located approximately 15 km south of Clinton, Oklahoma, in the Rolling Red Plains Resource Area of the southern Great Plains. Average annual precipitation was 77 cm and ranged from 51 to 82 cm (Fuhlendorf and others 2001). The 600-ha research station is largely rolling uplands cut by several steep drainages, with a mean elevation of 490 m. Vegetation is classified as mixed-grass prairie, with species such as *Bouteloua curtipendula*, *Bouteloua gracilis*, and *Schizachyrium scoparium* occurring on upland sites. Riparian woodland, comprising 5% of the total land area, were dominated by *Populus deltoides*, *Ulmus americana*, *Bumelia lanuginosa*, and *Sapindus Drummondii*. Taxonomic nomenclature follows Hatch and others (1990).

In 1989, the research site was divided into 10 pastures to study the importance of variable grazing intensities to rangeland condition. These long-term treatments were randomly assigned to pastures and have been adjusted to represent replicated moderate and heavy grazing, where livestock are given access to pastures from approximately 1 May until the middle of September. Moderate grazing represents stocking rates that approximate USDA Natural Resource Conservation Service recommendations for the specific site, whereas heavy grazing is nearly twice the moderate stocking rates.

Replicated treatments were established on ca. 45-ha plots that were subjected to heavy ($n = 2$), moderate ($n = 2$), and ungrazed ($n = 2$) treatments. We established two 100-m transects in each replication that started at the center of a riparian zone and extended perpendicular from the riparian zone in opposite directions onto the adjacent upland, so that the effects of topographic position (upland, riparian) and spatial patterns of variability would be maximized for each transect. Transect locations were selected to minimize the differences in physical features (slope, aspect, and soil type) among grazing treatments. To quantify relationships between vegetation structure and

Table 1 Comparison of vegetation characteristics (percentage ground cover, percentage composition of plant functional groups, angle of obstruction, and vegetation height) among grazing treatments on the Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000

Note. Superscript letters within rows represent statistical difference ($p \leq 0.05$)

Vegetation characteristic	Heavy			Moderate			Ungrazed		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
Bare ground	400	35.6 ^c	32.4	400	23.5 ^b	30.1	399	11.8 ^a	23.7
Leaf litter	400	1.9 ^a	10.3	400	10.5 ^b	24.6	399	19.4 ^c	31.5
Grass	400	50.9 ^a	34.3	400	53.7 ^{ab}	34.4	399	56.5 ^b	38.5
Forb	400	23.8 ^a	22.8	400	24.8 ^a	22.4	399	26.6 ^a	25.9
Sedge	400	2.1 ^b	13.9	400	2.2 ^b	14.0	399	0.0 ^a	0.0
Shrub	400	2.6 ^a	14.5	400	3.2 ^a	15.5	399	2.7 ^a	13.9
Vegetation height (cm)	400	27.7 ^a	22.6	400	36.6 ^b	31.9	400	52.9 ^c	36.0
Angle of obstruction (deg)	400	45.6 ^a	37.2	400	53.5 ^b	36.5	400	72.6 ^c	29.7

temperature, we recorded the maximum plant vegetation height from the center of each quadrat and determined the angle of obstruction (Harrell and Fuhlendorf 2002) along eight radii at 45° compass intervals. Additionally, bare ground and cover of grass, forb, shrub and litter, and litter were estimated. All upland measurements were recorded on slopes <3°. Riparian zones were trenched drainages with an east-west orientation, with the relatively steep slope of >5° at the margin.

Soil surface temperatures (hereafter referred to as temperature) were recorded using an Omegascope OS531 hand-held infrared thermometer placed 3 cm above the surface of the ground. We recorded four temperature measurements 6 cm from each 0.25 × 0.25-m quadrat corner and one directly in the center, totaling five measurements per quadrat at 1-m intervals along each transect. Measurements were recorded during the period of greatest physiological stress (August) for plant and animal communities in this region. We restricted collection times to between 1100 and 1700 h, when the temperature and light intensity were maximized (i.e., 0% cloud cover) and randomized the treatment and replication sampling in order to reduce any time of day and grazing treatment interaction.

Stepwise regression analysis (SPSS 2000) was used to determine relationships between vegetation structure and temperature. Variables selected for inclusion in the model were considered significant when $p \leq 0.15$ (Hosmer and Lemeshow 1989; Sams and others 1996; Cody and Smith 1997). One-way analysis of variance (ANOVA) (SPSS 2005) was used to determine temperature differences between grazing treatments. To determine the spatial autocorrelation of temperature, one form of pattern, we created a semivariogram of the temperatures for each transect within grazing treatments (Clark 1980; Turner and others 1991). The mean nugget, sill, and range for the two 100-m transects per replication were determined using GS+ software (Gamma Design Software 2004). ANOVA was used to determine if differences occurred among grazing treatments. Differences were considered significant at $p \leq 0.05$.

Results

Grazing altered the vegetation composition and cover of this semiarid ecosystem. The amount of bare ground increased with grazing and was 3-fold greater in heavy than in ungrazed pastures (Table 1). In contrast, litter decreased with grazing intensity and was nearly 10-fold greater in ungrazed sites (Table 1). Cover of grass was higher in ungrazed than in heavy grazed sites, but there was no difference in forb or shrub cover between grazing treatments (Table 1). Vegetation height and angle of obstruction were greatest in ungrazed sites and decreased with grazing intensity (Table 1).

Mean temperatures did vary across grazing treatments, with moderate grazing producing lower temperatures (47.4°C) than ungrazed conditions (49.1°C; Fig. 1) ($p \leq 0.05$). However, the difference is less than 2°C and likely due to slight variations in riparian and upland site sizes. To evaluate similar landscape positions, data were

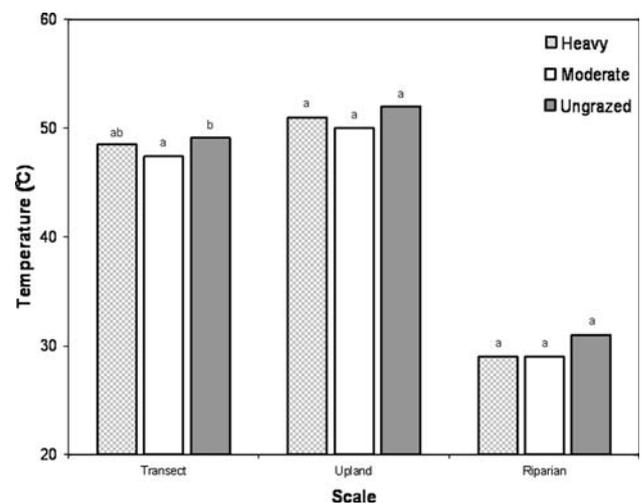


Fig. 1 Mean soil surface temperature (°C) for different grazing intensities and topographic positions, along 100-m transects on Marvin Klemme Range Research Station, Bessie, Oklahoma, summer 2000. Letters within scale categories represent statistical difference ($p \leq 0.05$)

grouped by upland and riparian and compared across treatments. Temperatures did not differ among grazing treatments when separated landscape position ($p \leq 0.05$) (Fig. 1). Data were pooled across treatments to evaluate differences between landscape positions (upland and riparian). Results showed that upland temperatures (51.0°C) were higher ($p \leq 0.001$) than those within the riparian area (30.1°C). The average difference between riparian and upland temperatures across all grazing treatments was 21°C. This is a nearly 11 times greater range in temperature across landscape positions versus grazing treatments.

Best-fit multiple regression models that predicted soil surface temperature from vegetation characteristics within the riparian ($R^2 = 0.09$, $F = 2.43$, $p = 0.121$, two-variable model) and uplands ($R^2 = 0.22$, $F = 12.27$, $p = 0.001$, three-variable model) explained only a small percentage of the variation in soil surface temperature (Table 2). On uplands, bare ground was the best predictive variable, accounting for only 12% of the variation in soil surface temperature (Table 1), where increases in bare ground and litter were associated positively with temperature. Grass cover and vegetation height were correlated negatively with soil surface temperature. Although significant correlations existed between community parameters (bare ground, cover of litter, cover of grass, and vegetation height) and soil surface temperature, all correlation coefficients were low ($r < 0.34$; Table 2), resulting in the rejection of our first hypothesis.

Semivariance of temperature was spatially dependent and rose continuously with lag distance in all grazing treatments, indicating a high degree of continuity (Fig. 2). The mean nugget for the heavy, moderate, and ungrazed treatments was 46.76, 9.23, and 11.45 m, respectively, but did not differ statically ($p < 0.05$). The sill for the heavy, moderate, and ungrazed treatments was 82.82, 100.30, and 130.04, respectively, and did not differ ($p < 0.05$). The range (effective temperature patch size) for the heavy,

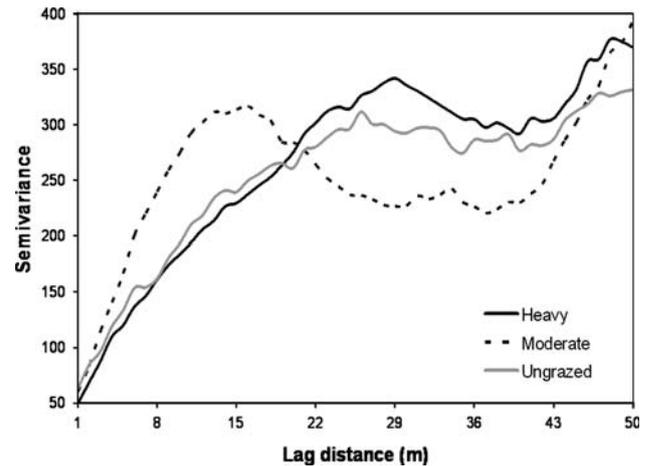


Fig. 2 Semivariograms based on soil surface temperatures for heavy, moderate, and ungrazed treatments during August on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000

moderate, and ungrazed treatments was 26.37, 35.01, and 21.31 m and did not differ ($p < 0.05$) among treatments.

Discussion

With the recent increase in global awareness and landscape modifications, understanding human impacts on climate is critical. Climate change resulting in increase temperatures heightens the importance of understanding thermal patterns across the landscape. Significant variations in soil heat flux can occur in regions where vegetation cover is clumped, with large areas of exposed soil (conditions that are common on our upland study sites) and temperature variability is highest during the midafternoon hours (Kustas and others 2000; Saunders and others 1998). Therefore, it was reasonable to expect landscape soil surface temperatures to be highly variable across multiple spatial scales at our study site. Temperatures $\geq 50^\circ\text{C}$ are capable of destroying vital proteins that are essential for life support (Calder and King 1974; Daubenmire 1974; Larcher 1991). Hence, thermal patterns of landscape variability may be a critical habitat feature capable of limiting the distribution and abundance of plant and animal species throughout the day, especially in hot, arid environments. Thus, consideration of management-induced and landscape-level thermal patterns may be a critical component to understanding ecological processes associated with biodiversity and conservation at multiple spatial and temporal scales.

Grazing intensity can have profound influences on the plant species composition and vertical height and structure of the associated vegetation (Cingolani and others 2005; Fuhlendorf and Smeins 1997; Biondini and others 1998; Hartnett and others 1996; Hart and others 1993; Dyksterhuis 1949; Ellison 1960), and variables associated

Table 2 Vegetation characteristics selected by a stepwise multiple regression analysis to predict soil surface temperatures on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000

Landscape position	Variable	Parameter estimate	SE	Partial R^2	p
Upland	Intercept	49.12	0.51	–	<0.001
	Bare ground	0.10	0.01	0.12	<0.001
	Litter	0.13	0.01	0.09	<0.001
	Height	–0.03	0.01	0.01	<0.001
Riparian	Intercept	28.06	0.70	–	<0.001
	Grass	0.03	0.02	0.07	0.054
	Angle of obstruction	0.02	0.02	0.02	0.121

with vegetation or ground cover can explain differences in soil surface temperatures in some ecosystems (Saunders and others 1998). However, cover of vegetation <0.5 m tall is generally a poor predictor of soil-surface temperature (Saunders and others 1998). We recorded similar relationships and found vegetation characteristics to be poor predictors of soil surface temperature. This resulted in minimal differences in temperature among grazing treatments. Consistent with other studies (Milchunas and others 1989), increased grazing intensity decreased litter abundance and increased bare ground, while ungrazed treatments had the inverse relationship. Large-scale land cover changes do have the potential to alter soil surface temperatures. Changes in ground cover caused a 4°C temperature shift between overgrazed areas in Sonora, Mexico, and properly grazed areas in Arizona, USA (Balling 1988, 1989; Bryant and others 1990). However, in our study the total cover of live, photosynthetically active “green” plants was relatively unchanged among the grazing intensities. Transpiration has a cooling effect on leaf tissue (Clum 1926) which may moderate environmental temperatures including that at the soil surface (Daubenmire 1974; Larcher 1991). This is further emphasized when looking at the percentage of bare ground and litter cover. Increases in both had positive correlations with increased temperatures.

Animals do not graze uniformly (Senft and others 1987), so we expected grazing to have an influence on the spatial arrangement of vegetation (McNaughton 1984; Glenn and others 1992; Fuhlendorf and Smeins 1997, 1998; Adler and Lauenroth 2000). However, we found the influence of grazing on thermal heterogeneity to be negligible, largely because the grazing influence is on vegetation <0.5 m tall. Heterogeneity associated with grazing is most often in reference to vertical structure, which is related to plant height, bare ground, and litter. However, vertical structure is not an indication of the actual amount of “green” plant material, which may be more dependent on landscape variability than grazing intensity.

The importance of riparian zones and, specifically, riparian vegetation for landscape integrity is well understood and often incorporated into ecosystem management (Naiman and Decamps 1997). Avian species have a high affinity for riparian corridors for breeding, brood rearing, and feeding habitat (Saab 1999). Diurnal organisms must balance foraging demands with thermal stress. Canopy shading from riparian trees reduces the amount of solar radiation at the soil surface (Larcher 1991; Belsky 1994; D’Odorico and others 2007). This shading had a major influence in that 96% of all riparian soil surface temperatures were $\leq 39^\circ\text{C}$, while 94% of upland soil surface temperatures were $\geq 40^\circ\text{C}$ during the heat of the day. Furthermore, soil surface temperatures in wooded riparian

areas were on average 20°C below upland temperatures. Even though riparian habitats were a minor component of these landscapes (<5%), they may be a critical habitat component as thermal refugia during the heat of the day.

Conclusion

Most previous studies of landscape heterogeneity have focused on variability of vegetation components with clear discontinuities that are often created by soil, topographic variation, or disturbances associated with vegetation. But relationships among vegetation structure, topographic position, grazing, and microclimate act in concert to shape grassland ecosystems and habitats. Lower soil surface temperatures (associated with riparian areas) may provide critical thermal refugia for many animals on hot summer days, when the air temperatures can exceed 37°C. Patterns of thermal heterogeneity were not directly related to any one vegetation variable, hence landscape patterns based on vegetation parameters alone are limited in their use since patterns of thermal variability are likely influenced by the integration of vegetation and environmental variables. Increased temperatures associated with global climate change increase the importance of riparian zones for thermal refuge. We recommend that ecologists who are interested in conservation or restoration evaluate biotic ecosystem components while simultaneously considering abiotic components.

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