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Guretzky, John A.; Dunn, Cheryl; and Hillhouse, Heidi L., "Long-term Sandhills prairie responses to precipitation, temperature, and cattle stocking rate" (2016). *Agronomy & Horticulture -- Faculty Publications*. 1033.

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Long-term Sandhills prairie responses to precipitation, temperature, and cattle stocking rate

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Abstract

Understanding of Sandhills prairie, the most expansive sand dune region stabilized by perennial grasses in the Western Hemisphere, is limited by lack of long-term vegetation data. We used a 26-year dataset to evaluate Sandhills prairie responses to year-to-year variation in precipitation, temperature, and cattle stocking rate. Basal cover, a measurement that is constant seasonally and used to detect long-term changes in bunchgrass vegetation, was measured in 38–40 permanent plots positioned along four transects spanning 769 ha from 1979 to 2007. Across this period, total basal cover averaged 2.4 % and was dominated by warm-season grasses (81.1 %). *Schizachyrium scoparium* (little bluestem), the dominant warm-season bunchgrass, consisted of 60.0 % relative basal cover. Warm-season grass and total basal cover responded positively to lag 3-year growing season precipitation indicating delayed responses to improved growing season conditions, but these variables also were positively associated with stocking rate. The positive responses may be due to slow spread of warm-season grasses by vegetative structures in response to favorable growing conditions in light to moderately stocked rangeland. Despite its dominance, however, warm-season grass cover had no influence on cover of other functional groups providing weak support for

competition as regulator of Sandhills prairie composition. Forb cover was best related in a negative manner to 3-year running mean total precipitation, a surprising result that maybe signaling factors governing basal responses in prairie remain largely unresolved. Woody species cover, however, was positively associated with mean growing season temperatures indicating potential of these to spread under warming scenarios.

Keywords: Basal cover, Climate change, Cool-season grasses, Grasslands, Great plains, Warm-season grasses

Introduction

Climate variability and change is expected to alter ecosystem structure and function (Easterling et al. 2000; Weltzin et al. 2003; Smith et al. 2009; Cleland et al. 2013; Hoover et al. 2014). A hierarchy of responses from changes in plant growth and function, to simplification of plant communities, and invasion of exotic species are possible (Tilman and El Haddi 1992; Smith et al. 2009). These responses by the plant community are dependent on the magnitude, duration, and timing of the climatic stress (Hoover et al. 2014). Periods of below average precipitation or drought in the

past have led to a decrease in basal cover of dominant warm-season bunchgrasses (Weaver and Albertson 1936; Herbel et al. 1972; Fuhlendorf and Smeins 1997; Biondini et al. 1998). Resilience, i.e., capacity for recovery of ecosystem function (Hoover et al. 2014), however, was demonstrated when subsequent increases in growing season rainfall returned basal cover of the dominant warm-season grass species to near pre-drought levels despite changes in plant community composition (Herbel et al. 1972; Fuhlendorf and Smeins 1997; Biondini et al. 1998).

In the central U.S., the presence of dominant perennial warm-season grasses enhances resilience to climatic extremes (Hoover et al. 2014) through investment in traits such as belowground reserves that supply carbohydrate when photosynthesis and growth is limited and basal meristems that remain protected from disturbances such as grazing (Coughenour 1985; Ott and Hartnett 2011). Warm-season grasses also adjust osmotically, fold or roll leaves, and modify stomatal conductance to maintain photosynthetic and metabolic activities during low moisture stress (Sala et al. 1982; Knapp 1985). Deeply penetrating, widely branching, and depth-segregated rooting systems also help perennial warm-season grasses tolerate drought (Weaver and Albertson 1936), and spread of vegetative structures contributes to population recovery after drought (Hendrickson and Briske 1997; Benson et al. 2004).

Although there has been much focus on evaluating grassland responses to extreme climatic events in recent years (Fay et al. 2002, 2003, 2008; Knapp et al. 2002; Heisler-White et al. 2008; Hoover et al. 2014), the presence of long-term datasets also can be valuable in assessing plant community responses to climate variability (Sherry et al. 2012), but these responses have not been examined in Nebraska Sandhills prairie. The Sandhills, a \approx 4.8 million ha region in north central Nebraska, is the most expansive sand dune region in the Western Hemisphere currently stabilized by perennial warm-season grasses and supported by soils that rapidly absorb precipitation (Bleed and Flowerday 1998; Schacht et al. 2000). The Sandhills supports about 720 vascular plant species, including 670 native species and 50 introduced species (Kaul 1998), and is one of the largest, contiguous grasslands remaining in the Great Plains region of North America (Samson et al. 2004). Although prairie vegetation currently provides stability, wide-scale

wind erosion occurred during the Holocene, and it has been projected that a shift toward a warmer climate may cause grassland death and allow dunes to move (Mangan et al. 2004).

In 1926, a long-term study was established at the Nebraska National Forest to investigate Sandhills prairie responses to cattle grazing. At the time, grazing was being used to shift prairie vegetation from a taller, *S. scoparium*, to a shorter, *Bouteloua hirsuta* (hairy grama), dominated bunchgrass community to create a natural firebreak and protect adjacent forest from wildfire. Frequency of occurrence of plant species among permanent plots was evaluated across a period spanning from 1926 to 2004 and reported in Stubbendieck and Tunnell (2008). However, data collected on plant basal cover from 1979 to 2007 have not been summarized, analyzed, or reported. Basal cover, a measure of ground area covered by crowns and shoots, has often been evaluated in long-term studies (Albertson and Tomanek 1965; Herbel et al. 1972; Fuhlendorf and Smeins 1997; Fuhlendorf et al. 2001; Gillen and Sims 2006) and is considered an appropriate metric to evaluate disturbances related to weather functions in bunchgrass-dominated communities because of its stability within and across growing seasons (Herbel et al. 1972; Havstad and Herrick 2003) and power to detect ecologically significant changes (Brady et al. 1995).

Our objectives were to use the long-term data on basal cover to describe relative species composition and examine responses of most abundant plant species and functional groups in Sandhills prairie to year-to-year variation in precipitation, temperature, and cattle stocking rate. We hypothesized that (1) total basal cover would increase with greater temperature and precipitation due to positive responses of warm-season grasses (e.g., Knapp 1985); (2) perennial forb cover would be resistant to precipitation and temperature variability because forbs can obtain water from different soil depths (e.g., Nippert and Knapp 2007); (3) an increase in cattle stocking rate would reduce warm-season grass cover due to negative grazing effects on *S. scoparium* (e.g., Butler and Briske 1988; Derner et al. 1994); and (4) an increase in *S. scoparium* would negatively affect cover of other species due to greater competition as bunchgrasses concentrate soil resources and occupy space (e.g., Derner and Briske 2001).

Methods

Study area

The study was located in Sandhills prairie on sands ecological sites at the Nebraska National Forest Bessey Ranger District—Bessey Unit (41°52'N; 100°21'W), 1.6 km west of Halsey in Thomas County, NE (Fig. 1). The Bessey Unit encompassed 36,638 ha including 7913 ha of the largest plantation forests of *Pinus ponderosa* (ponderosa pine) and *Juniperus virginiana* (eastern red cedar) in the United States (US Forest Service

2009). Grassland consisted of 28,139 ha of the Bessey Unit and was characterized historically as a mixture of tallgrass and mixed-grass prairie (Pool 1913; Tolstead 1942; Schacht et al. 2000). Soils were Valentine fine sands with a parent material of quartz sand (Keech and Bentall 1971).

Established in 1926, the permanently marked plots in this study were originally used to evaluate the feasibility of using heavy grazing (i.e., a cattle stocking rate of 2.2 animal unit months (AUM) ha⁻¹, where one AU = 450 kg live weight) to establish a firebreak near the forest. After being monitored through 1938 and

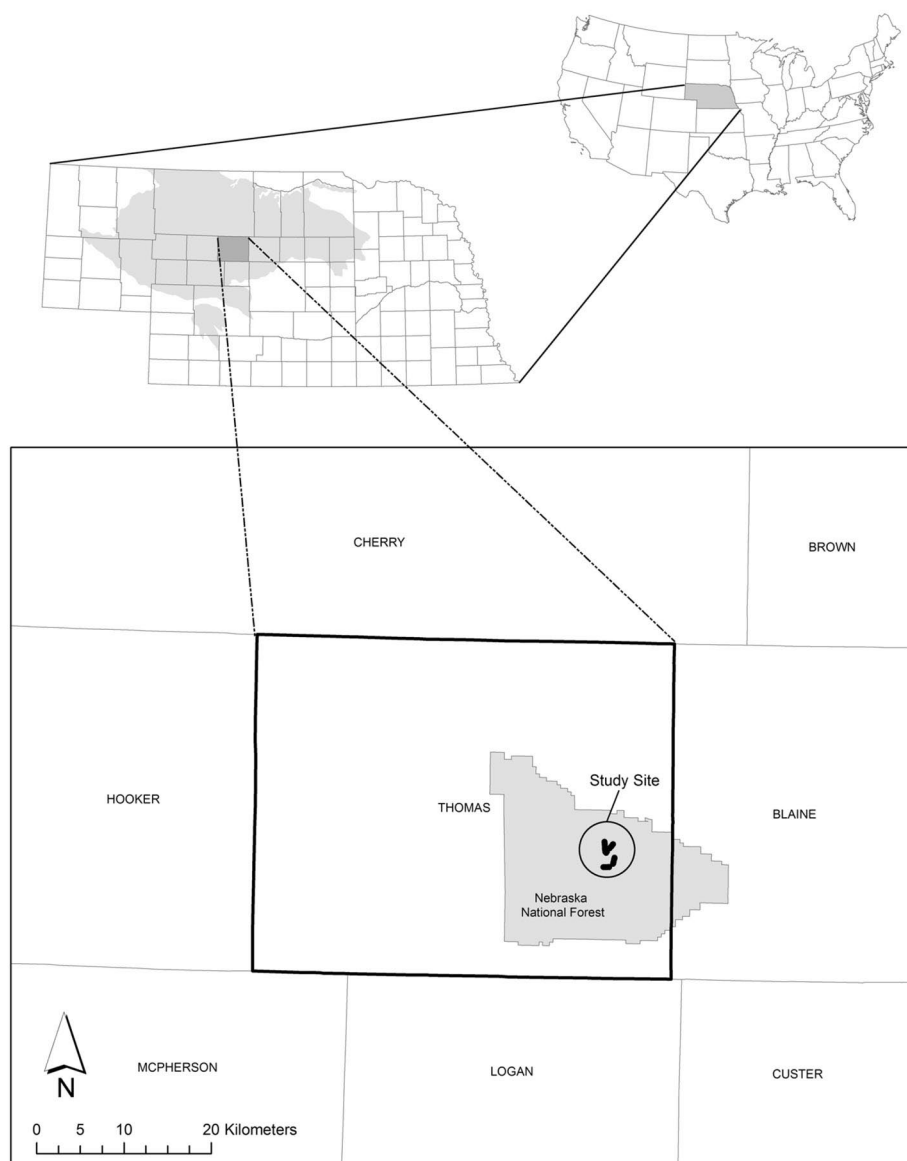


Figure 1 Location of long-term monitoring plots in Sandhills prairie at the Nebraska National Forest in Thomas County, Nebraska. The extent of Sandhills prairie in Nebraska is indicated by the light gray shading in the statewide map

briefly by the US Forest Service in the 1940s, data were not collected from the plots until 1979 when this study was initiated. The 48 plots established in 1926 were arranged along four transects covering a range of topographic positions (dune tops, slopes, and interdunes/terraces) and slope directions (Fig. 2). By 1979, eight plots could no longer be located, and some of the remaining plots were difficult to find consistently. Of the remaining 40 plots, twenty-nine had data collected every year, eight were missing data from either 1 or 2 years, and three were missing data from more than 2 years. Most of the plots were in Valentine fine sand with rolling and hilly, 9–60 % slopes with the exception of half of transect 4 which was in Valentine fine sand with rolling, 9–24 % slopes (Fig. 2). Heavy grazing following establishment of the plots in 1926 was successful in shifting botanical composition, but due to increased weed invasion and improvements in fire control equipment, a moderate grazing regime was implemented and *S. scoparium* was again the dominant species by 1979

(Stubbendieck and Tunnell 2008). From 1979 to 2007, all plots experienced the same cattle stocking rate each year (mean = 0.85 AUM ha⁻¹), but this varied with grazing allotments established annually between ranchers and the U.S. Forest Service and was not closely associated with climatic variables (Appendix in Table 5).

Data collection and analysis

Basal cover was measured annually in August or September 1979–2007, except from 2000 to 2002 (Appendix in Table 4). Each plot had two permanent markers that allowed square frames to be consistently placed on the same 1-m² area. After placing a 1-m² square frame in the designated position, basal cover was measured using the line intercept method. A ruler was placed across the frame at nine pre-determined locations for a maximum basal cover of 9000 mm. Basal cover was recorded by measuring the distance (mm) in which the basal part of the

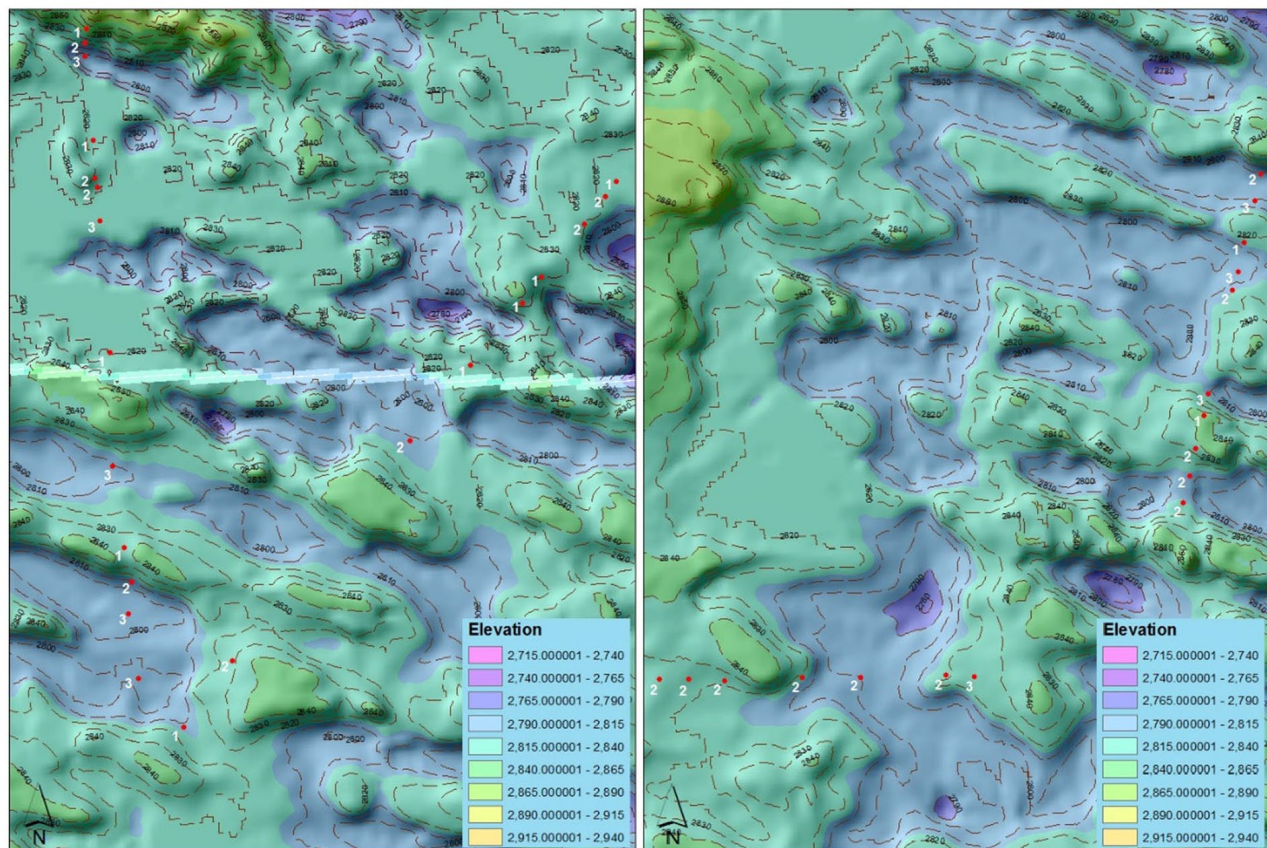


Figure 2 Distribution of long-term monitoring plots along four transects traversing dune top (1), slope (2), and interdunal/terrace (3) topographic positions in Sandhills prairie at the Nebraska National Forest in Thomas County, Nebraska

plant intersected the ruler. Through the study period, 92 plant species were recorded, but most of these species were absent from plots across several years. The 14 species that made up 95 % of the total cover and present in nearly all 25 years of the study (Appendix in Table 4) were used in analyses to describe relative species composition and examine relationships of mean plot basal cover to climatic and stocking rate variables (Appendix in Table 5). Relationships of mean plot basal cover to climatic and stocking rate variables also were examined by functional groups which included warm season grasses, cool-season grasses, sedges, succulents, forbs, and woody species computed from the 92 species recorded in the 26 years of the study.

A series of stepwise multiple regression analyses were used to examine relationships of actual basal cover of the 14 most abundant species, their functional groups, and total basal cover with climate data, cattle stocking rates, and basal cover of *S. scoparium* and warm-season grasses as a whole based on a priori knowledge of their dominance in Sandhills prairie (Pool 1913; Schacht et al. 2000; Stubbendieck and Tunnell 2008). The use of stepwise regressions helped eliminate multicollinearity issues with the climate data by adding independent variables one at a time. The model with the lowest Akaike's Information Criteria value was selected as the most suitable model out of all the models generated. Annual and monthly climate data were obtained from the National Climatic Data Center (2013) and the High Plains Regional Climate Center (2012). Weather stations were located at or within 48 km of Halsey, NE. Climatic variables included total precipitation (Total PPT), mean annual temperature (Mean Ann Temp), minimum temperature (Min Temp), maximum temperature (Max Temp), and the Palmer drought severity index (PDSI) which combines precipitation and temperature and produces a number that is either negative or positive relating to dry or wet periods, respectively (Heddinghaus and Sabol 1991). The growing season (April–September) means of most variables were separated from the data, and total precipitation was also divided into early growing season (April–June) and late growing season (July–Sept). Total precipitation during the growing season of the previous year (Lag 1-year PPT), a 3 year lag (Lag 3-year PPT), and a three-year running mean (3-year running mean PPT), as well as a three-year lag late growing season (July–Sept) were also added. All statistical analyses were conducted with SPSS statistical

package (version 22.0, SPSS Incorporated, Chicago, IL). Normal distribution of data was assessed by a Kolmogorov–Smirnov goodness of fit test. Statistical significance was declared at $P \leq 0.05$.

Results

Relative species composition

Total basal cover had a mean \pm SD of 2.4 ± 1.0 % across the study period of 1979–2007. Of this cover, 81.1 ± 9.6 and 8.9 ± 7.3 % consisted of warm- and cool-season grasses, respectively. *Schizachyrium scoparium* and *B. hirsuta* were the most abundant warm season grasses, and *Dichanthelium oligosanthes* (Scribners panicum) and *Hesperostipa comata* (needle- and thread) were the most abundant cool-season grasses (Table 1). A total of 45 species of forbs were recorded with a combined basal cover of 1.9 ± 1.5 %, and woody species, which included subshrubs, shrubs, and a tree, had a combined basal cover of 1.6 ± 1.2 %. *Ambrosia psilostachya* (western ragweed) comprised approximately half of the forb cover, while *Rosa arkansana* (prairie rose) and *Amorpha canescens* (leadplant) were the most abundant woody plants (Table 1). Two genera of sedges, *Carex* and *Cyperus*, comprised 4.5 ± 2.7 % of basal cover while succulents, represented by three species in the *Opuntia* genus, had a basal cover of 2.1 ± 2.5 %. *Opuntia fragilis* (little prickly pear) accounted for over half of the succulent cover.

Climatic conditions and cattle stocking rate

Climatic variables that had the greatest influence on basal cover included mean growing season (April–September) temperature and precipitation, mean growing season maximum temperature, mean dormant season (October–March) temperature, mean late growing season (July–September) precipitation, and total annual precipitation (Fig. 3). From 1979 to 2007, mean \pm SD growing season temperature was 17.5 ± 1.0 °C while mean \pm SD growing season maximum temperature was 25.2 ± 1.3 °C. Meanwhile, growing season precipitation accounted for the majority of total annual precipitation (Fig. 3), which averaged 440 ± 90 and 578 ± 116 mm, respectively. Most precipitation fell early in the growing season (April–June) but late growing season precipitation had more impact on basal cover responses. Across the study, PDSI had a mean \pm SD of 1.9 ± 2.7 indicating a slightly wetter period overall (Appendix in Table 5).

Table 1 Relative basal cover of plant species that occurred in C50 % of plots in Sandhills prairie at the Nebraska National Forest Bessey Ranger District near Halsey, Nebraska from 1979 to 2007

| Scientific name and authority | Common name | Functional group | Relative basal cover (%) |
|---|-------------------------|-------------------|--------------------------|
| <i>Ambrosia psilostachya</i> DC. | Western ragweed | Forb | 0.7 |
| <i>Andropogon hallii</i> Hack | Sand bluestem | Warm-season grass | 2.0 |
| <i>Artemisia ludoviciana</i> Nutt. | Cudweed sagewort | Forb | 0.1 |
| <i>Bouteloua hirsuta</i> Lag. | Hairy grama | Warm-season grass | 8.3 |
| <i>Calamovilfa longifolia</i> (Hook.) Scribn. | Prairie sandreed | Warm-season grass | 1.8 |
| <i>Carex</i> and <i>Cyperus</i> spp. | Sedges | Sedge | 4.6 |
| <i>Dichanthelium oligoanthos</i> (Schult.) Gould | Scribners panicum | Cool-season grass | 2.8 |
| <i>Dichanthelium wilcoxianum</i> (Vasey) Freckmann | Wilcox panicum | Cool-season grass | 0.3 |
| <i>Eragrostis spectabilis</i> (Pursh) Steud. | Purple lovegrass | Warm-season grass | 0.7 |
| <i>Eragrostis trichodes</i> (Nutt.) A.W. Wood | Sand lovegrass | Warm-season grass | 4.0 |
| <i>Helianthus annuus</i> L./ <i>Helianthus petiolaris</i> Nutt. | Annual/Plains sunflower | Forb | 0.1 |
| <i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth | Needle-and-thread | Cool-season grass | 3.1 |
| <i>Koeleria macrantha</i> (Ledeb.) Schult. | Prairie junegrass | Cool-season grass | 0.6 |
| <i>Opuntia fragilis</i> (Nutt.) Haw. | Little prickly pear | Succulent | 1.3 |
| <i>Paspalum setaceum</i> Michx. | Sand paspalum | Warm-season grass | 0.7 |
| <i>Panicum virgatum</i> L. | Switchgrass | Warm-season grass | 2.2 |
| <i>Poa pratensis</i> L. | Kentucky bluegrass | Cool-season grass | 0.4 |
| <i>Rosa arkansana</i> Porter ex Porter & J.M. Coult. | Prairie rose | Woody | 1.2 |
| <i>Schizachyrium scoparium</i> (Michx.) Nash | Little bluestem | Warm-season grass | 60.0 |
| <i>Sorghastrum nutans</i> (L.) Nash | Indiangrass | Warm-season grass | 0.3 |
| <i>Sporobolus cryptandrus</i> (Torr.) A. Gray | Sand dropseed | Warm-season grass | 1.8 |
| <i>Vulpia octoflora</i> (Walter) Rydb. | Sixweeks fescue | Cool-season grass | 0.1 |

Basal cover responses

Climatic variables explained basal cover responses of 10 of 14 species (Table 2). For these ten species, the variation explained (adjusted R^2) ranged from 18.1 to 68.1 %. Basal cover of *S. scoparium*, despite being the dominant species and highly competitive for soil resources (Derner and Briske 2001), did not show a significant response to climatic variables. *Schizachyrium scoparium* only explained basal cover responses of two species; *S. scoparium* was positively correlated with *Paspalum setaceum* (sand paspalum) basal cover and negatively correlated with *R. arkansana* basal cover. Meanwhile, growing season and total precipitation were negatively related to basal cover responses of several species including *A. psilostachya*, *B. hirsuta*, *Calamovilfa longifolia* (prairie sandreed), *Eragrostis*

trichodes (sand lovegrass), and *H. comata* as demonstrated by significant b coefficients for the 3-year running means for April–September, July–September, and total precipitation, as well as simply total precipitation (Table 2). Late growing season precipitation, both in terms of lag 3-year and total precipitation, also contributed to improved understanding of *B. hirsuta* responses.

Either current year mean April–September temperature or mean April–September maximum temperature were strong positive predictors of *Andropogon hallii* (sand bluestem), *B. hirsuta*, *R. arkansana*, and *Sporobolus cryptandrus* (sand dropseed) basal cover. *Opuntia fragilis* was the only species that had a negative response to growing season maximum temperature. However, as PDSI decreased, meaning the combination of precipitation and temperature was having a drying effect, *O. fragilis* and *P. virgatum* increased in

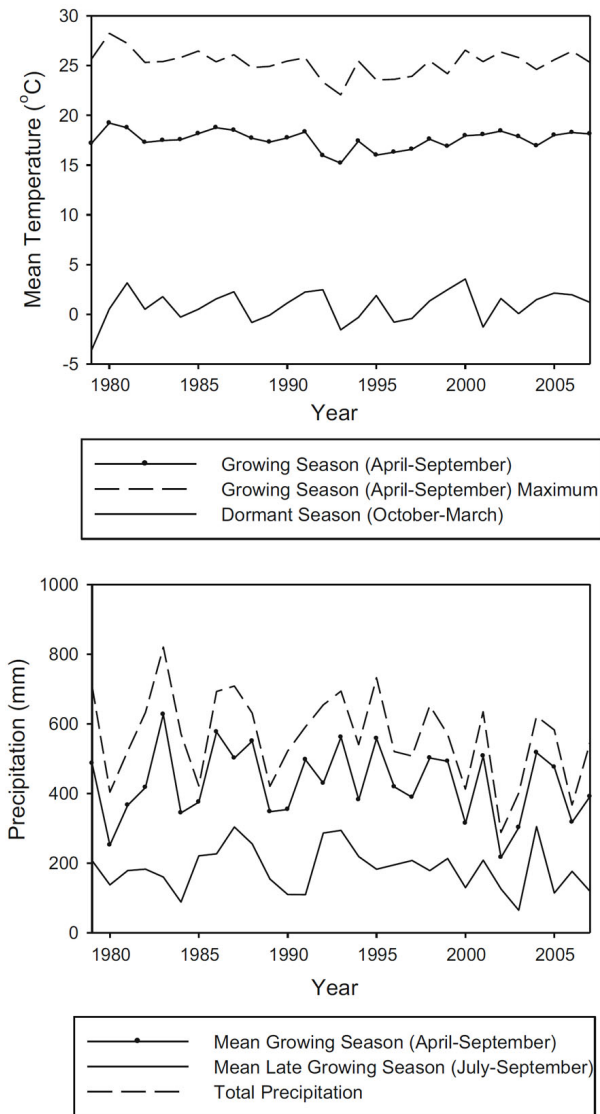


Figure 3 Temperature and precipitation variables that influenced plant species and functional group composition in Sandhills prairie at the Nebraska National Forest Bessey Ranger District near Halsey, Nebraska from 1979 to 2007

basal cover, while *H. comata* decreased. In two models, stocking rate was found to be a strong predictor variable (Table 2). Stocking rate was negatively correlated with *O. fragilis* cover but positively correlated with *A. psilostachya* cover.

Climatic variables and stocking rate explained from 0 to 31.4 % of functional group variation (Table 3). The 3-year running mean total precipitation had a negative relationship with forb basal cover, while growing season temperature was positively related to woody species basal cover. Meanwhile, as PDSI decreased,

succulent basal cover increased. Basal cover of warm-season grasses had the same predictor variables as total cover, responding positively to stocking rate and lag 3-year growing season precipitation. Basal cover of cool-season grasses was negatively influenced by an increase in total precipitation, but basal cover of sedges showed no response to climatic variables or stocking rate.

Discussion

Relative species composition

Relative species composition compared well with historical vegetation composition on sands ecological sites, indicating the prairie was in good to excellent condition (Pool 1913; Tolstead 1942; Schacht et al. 2000; Stubbendieck and Tunnell 2008). Principal dominants historically included tall and mid-height warm-season grasses including *A. hallii*, *C. longifolia*, and *S. scoparium*. Subdominant grass species included *Achnatherum hymenoides* (Indian ricegrass), *D. oligoanthes*, *H. comata*, *H. spartea* (porcupinegrass), *P. virgatum*, *S. cryptandrus*, and either *B. hirsuta* or *B. gracilis* (blue grama). With exception of *A. hymenoides* and *B. gracilis*, all of these species were found in the prairie. Areas where the prairie differed from the historical vegetation composition was in terms of warm-season grass and forb cover. Historically, the plant community consisted of 85 % grasses and grasslike plants, 10 % forbs, and 5 % shrubs (including succulents) by weight (USDA-NRCS 2016). In contrast, average basal cover in this Sandhills prairie consisted of 95 % grasses and grass-like plants, 2 % forbs, and 4 % shrubs (including succulents). Of warm-season grasses, 60 % of relative basal cover was *S. scoparium* compared to 2 % each for *A. hallii* and *C. longifolia*, which may be artifacts of sampling methods that elevate measures of crown-forming bunchgrasses such as *S. scoparium* relative to rhizomatous species with widely dispersed tiller populations (Cullan et al. 1999). With regard to forbs, *Artemisia dracuncululus* (tarragon) and *Cirsium sp.* (thistle) were not found in the prairie but were there historically (USDA-NRCS 2016).

Topography as it relates to soil depth and moisture availability also can influence Sandhills prairie composition (Schacht et al. 2000). Vegetation surveys have found the presence of *S. scoparium* and cool

Table 2 Stepwise multiple regressions for basal cover of plant species in Sandhills prairie from 1979 to 2007 relative to variables including *Schizachyrium scoparium* (SCSC) cover, precipitation (PPT), temperature (Temp), and the Palmer drought severity index (PDSI)

| Species | Adjusted R^2 | F value | P value | Independent variable | B | P value | β |
|-----------------------------------|----------------|---------|-----------|-------------------------------|-----------|-----------|---------|
| <i>Ambrosia psilostachya</i> | 0.542 | 10.86 | <0.001 | Constant | -313.427 | 0.168 | |
| | | | | 3-year running mean total PPT | -9.938 | <0.001 | -0.602 |
| | | | | Mean Apr–Sept max temp | 6.996 | 0.020 | 0.342 |
| | | | | Stocking rate | 152.453 | 0.027 | 0.323 |
| <i>Andropogon hallii</i> | 0.28 | 10.714 | 0.003 | Constant | -1749.833 | 0.006 | |
| | | | | Mean Apr–Sept temp | 29.868 | 0.003 | 0.556 |
| <i>Bouteloua hirsuta</i> | 0.681 | 11.679 | <0.001 | Constant | -7166.763 | 0.017 | |
| | | | | Mean Apr–Sept max temp | 192.235 | <0.001 | 0.787 |
| | | | | 3-year running mean PPT | -187.918 | <0.001 | -0.732 |
| | | | | Apr–Sept | | | |
| | | | | Mean Oct–Mar temp | -147.778 | <0.001 | -0.720 |
| | | | | Lag 3-year PPT July–Sept | 92.783 | 0.004 | 0.447 |
| <i>Calamovilfa longifolia</i> | 0.523 | 10.141 | <0.001 | Constant | 1290.623 | <0.001 | |
| | | | | 3-year running mean PPT | -39.602 | 0.001 | -0.554 |
| | | | | Apr–Sept | | | |
| | | | | Total PPT | -13.798 | 0.018 | -0.402 |
| | | | | Total PPT July–Sept | -19.327 | 0.047 | -0.322 |
| <i>Carex spp.</i> | NS | | | | | | |
| <i>Dichanthelium oligosanthes</i> | NS | | | | | | |
| <i>Eragrostis trichodes</i> | 0.435 | 10.635 | 0.001 | Constant | 965.001 | 0.001 | |
| | | | | 3-year running mean PPT | -58.401 | 0.001 | -0.627 |
| | | | | July–Sept | | | |
| <i>Hesperostipa comata</i> | 0.582 | 9.701 | <0.001 | Lag 3-year PPT Apr–Jun | 34.196 | 0.001 | 0.610 |
| | | | | Constant | 2421.465 | <0.001 | |
| | | | | Total PPT | -39.860 | <0.001 | -0.892 |
| | | | | Mean PDSI | 56.296 | 0.001 | 0.750 |
| | | | | 3-year running mean total PPT | -45.471 | 0.001 | -0.637 |
| | | | | Lag 1-year PPT Apr–Sept | -19.385 | 0.016 | -0.393 |
| <i>Opuntia fragilis</i> | 0.613 | 14.191 | <0.001 | Constant | 1311.688 | 0.004 | |
| | | | | Mean PDSI | -21.493 | <0.001 | -0.662 |
| | | | | Stocking rate | -528.273 | <0.001 | -0.597 |
| | | | | Mean Apr–Sept max temp | -13.022 | 0.021 | -0.340 |
| <i>Panicum virgatum</i> | 0.181 | 6.527 | 0.017 | Constant | 214.141 | <0.001 | |
| | | | | Mean PDSI | -22.007 | 0.017 | -0.462 |
| <i>Paspalum setaceum</i> | 0.141 | 5.114 | 0.033 | Constant | 20.494 | 0.344 | |
| | | | | SCSC cover | 0.008 | 0.033 | 0.419 |
| <i>Rosa arkansana</i> | 0.402 | 9.420 | 0.001 | Constant | -960.023 | 0.007 | |
| | | | | Mean Apr–Sept temp | 17.054 | 0.003 | 0.523 |
| | | | | SCSC cover | -0.006 | 0.034 | -0.353 |
| <i>Schizachyrium scoparium</i> | NS | | | | | | |
| <i>Sporobolus cryptandrus</i> | 0.201 | 7.279 | 0.013 | Constant | -2726.764 | 0.018 | |
| | | | | Mean Apr–Sept max temp | 37.272 | 0.013 | 0.482 |

In these regressions, the adjusted R^2 described fit of the model to the data, the first P value indicated significance of the model, B was the unstandardized coefficient, the second P value indicated significance of independent variable in the model, and β was the standardized coefficient.

Table 3 Stepwise multiple regression results for basal cover of functional groups in Sandhills prairie from 1979 to 2007 relative to variables including warm-season grass cover, precipitation (PPT), temperature (temp), and the Palmer drought severity index (PDSI)

| Functional group | Adjusted R ² | F value | P value | Independent variable | B | P value | β |
|---------------------|-------------------------|---------|---------|-------------------------------|------------|---------|--------|
| Forbs | 0.244 | 9.074 | 0.006 | Constant | 524.826 | 0.001 | |
| | | | | 3-year running mean total PPT | -17.361 | 0.006 | -0.524 |
| Woody plants | 0.260 | 9.768 | 0.005 | Constant | -1331.052 | 0.008 | |
| | | | | Mean Apr–Sept temp | 22.831 | 0.005 | 0.538 |
| Succulents | 0.314 | 6.73 | 0.005 | Constant | 352.432 | <0.001 | |
| | | | | Stocking rate | -539.215 | 0.011 | -0.461 |
| | | | | Mean PDSI Apr–Sept | -16.499 | 0.018 | -0.423 |
| Warm-season grasses | 0.313 | 6.708 | 0.005 | Constant | -4380.236 | 0.199 | |
| | | | | Stocking rate | 17,762.878 | 0.006 | 0.515 |
| | | | | Lag 3-year PPT Apr–Sept | 331.338 | 0.019 | 0.423 |
| Cool-season grasses | 0.154 | 5.545 | 0.027 | Constant | 1397.363 | <0.001 | |
| | | | | Total PPT | -33.246 | 0.027 | -0.433 |
| Sedges | NS | | | | | | |
| Total basal cover | 0.289 | 6.091 | 0.008 | Constant | -0.009 | 0.396 | |
| | | | | Stocking rate | 0.051 | 0.007 | 0.506 |
| | | | | Lag 3-year PPT Apr–Sept | 0.001 | 0.028 | 0.401 |

In these regressions, the adjusted R^2 described fit of the model to the data, the first P value indicated significance of the model, B was the unstandardized coefficient, the second P value indicated significance of independent variable in the model, and β was the standardized coefficient.

season grasses such as *H. comata* and *Koeleria macrantha* (prairie junegrass) to be positively associated with north-facing slopes, while warm-season grasses such as *C. longifolia* and *A. hallii* were positively associated with south-facing slopes (Schacht et al. 2000). While some of our species were aligned with the same topographic positions [e.g., *B. hirsuta* and dune tops; *Poa pratensis* (Kentucky bluegrass) and interdunes] as in Schacht et al. (2000), limitations on plot numbers assigned to various topographic positions prevented a robust analysis of plant species-topographic associations in our study (data not shown).

Basal cover responses to precipitation and temperature

Seasonal or total precipitation variables influenced basal cover responses of 5 of the 14 species we analyzed, as well as total basal cover, but for the most part, species responses were individualistic and noisy as observed in other long-term studies (e.g., Fuhlen-dorf and Smeins 1997; Gillen and Sims 2006; Tilman et al. 2006; Adler and HilleRisLambers 2008). Arid and semi-arid grasslands often contain a large number of annual species that are particularly responsive

to changes in precipitation (O'Connor and Roux 1995; Hobbs et al. 2007; Cleland et al. 2013). Of the 9 species that did not respond to year-to-year fluctuations in seasonal or total precipitation, 7 of these were grasses or sedges and their basal responses were likely delayed by slow spread and contraction of vegetative structures and crowns in response to current climatic conditions. As a group, warm-season grass and total basal cover responded positively to 3-year lag growing season precipitation, results supportive of our first hypothesis and other long-term studies that have found basal cover of perennial warm-season grasses to be responsive to changes in precipitation (Albertson and Tomanek 1965; Fuhlendorf et al. 2001), though responses depended on a lag period (e.g., Sherry et al. 2012).

Temperature variability influenced basal cover responses of 6 of the 14 species but not total basal cover. The warm-season grasses, *A. hallii*, *B. hirsuta*, and *S. cryptandrus*, responded positively to mean growing season temperatures (Table 2), responses consistent with our first hypothesis and the four carbon photosynthetic pathway (C4) of these species (Knapp 1985). Indeed, warm-season rhizomatous grasses responded positively to growing season temperatures (Table 3). Positive responses of *R. arkansana* and woody species to mean growing season temperature also were observed. Woody species exhibit plasticity in depth of water uptake relative to warm-season grasses during drought (Eggemeyer et al. 2008), which may contribute to tolerance of higher growing season temperatures.

Although the majority of forbs did not respond to temperature variables, the increase of *A. psilostachya* to increasing mean growing season maximum temperatures is partially supported by Alward et al. (1999) who found forbs increased with increasing minimum growing season temperatures and by Adler and HilleRisLambers (2008) who observed population growth of prairie forbs to be more responsive to changes in mean temperatures than either precipitation or species composition. The increase of *A. psilostachya* with stocking rate also was consistent with previous reports about grazing responses in Sandhills prairie (Reece et al. 2004). On the other hand, we also found forb basal cover to have a negative relationship with the 3-year running mean for total annual precipitation, a result not easily explained. The mechanisms and determinants for why forbs would respond negatively to precipitation amount or not at all as observed by

others remain unresolved (Briggs and Knapp 2001), though it is interesting to note that forb basal cover responses were not as closely associated with mean growing season precipitation as the 3-year running mean total precipitation.

Depending on greenhouse gas emission scenarios, recent projections have average temperatures increasing from 1 to 3 °C and winter to spring precipitation increasing 5 to 15 % by 2099 in the central U.S. (US Global Change Research Program 2009; Polley et al. 2013). With increased temperatures, we might expect to find *S. scoparium* and warm-season grasses as a whole continue to account for the majority of basal cover in Sandhills prairie but also observe increased basal cover of woody species such as *R. arkansana* and forbs such as *A. psilostachya*. Changes in precipitation patterns, on the other hand, would most likely impact basal cover of forbs, warm-season grasses, and cool season grasses as a whole. Nonetheless, despite having long-term observations on basal cover, extrapolating results to predict climatic responses of Sandhills prairie remains difficult due in part to uncertainties associated with future climatic changes and to species-specific responses to climatic and management conditions (Weltzin et al. 2003; Mangan et al. 2004; Adler and HilleRisLambers 2008).

Basal cover, stocking rate, and warm-season grass competition

With regard to our third hypothesis, we found stocking rate influenced warm-season grass responses, but results were opposite to that which we predicted. We hypothesized basal cover of warm season grasses would decrease with increased stocking rate as heavy grazing intensities have been known to negatively impact basal cover of *S. scoparium* (Butler and Briske 1988; Derner et al. 1994). The use of conservative stocking rates to achieve 50 % rangeland utilization annually in all plots, however, likely did not produce strong enough defoliation intensities to have a negative influence on *S. scoparium* basal cover and, indeed, likely produced defoliation intensities that encourage spread, and therefore, overall greater basal cover of warm season grasses. Increases in basal cover, tiller densities, and frequency of occurrence of perennial warm-season grasses have been observed with light to moderate grazing intensities in the Sandhills (Reece et al. 1988; Stephenson et al. 2013). Implementation

of heavier grazing intensities where utilization approaches 75 % or more may reduce basal cover of warm-season grasses and contribute to shifting of grassland vegetation from taller to shorter species (Fuhlendorf and Smeins 1997; Fuhlendorf et al. 2001). Indeed, the latter was observed during early years of this study with the shift from *S. scoparium* to *B. hirsuta* dominance (Stubbendieck and Tunnell 2008) when stocking rates averaged 2.2 AUM ha⁻¹ compared to an average of 0.85 AUM ha⁻¹ from 1979 to 2007. As stocking rate increases, both the percentage of tillers defoliated and the number of tillers defoliated multiple times per growing season increase, thereby weakening *S. scoparium* (Derner et al. 1994).

Lastly, we hypothesized that an increase in basal cover of *S. scoparium* and warm-season grasses as a whole would have a negative effect on basal cover of other species and functional groups. This hypothesis was based on the view that biotic and abiotic processes can regulate population responses to climatic variability (Symstad and Tilman 2001; Adler and HilleRisLambers 2008; Levine et al. 2010). The decline in forb basal cover with the 3-year running mean for total annual precipitation, a response opposite of those grasses, also suggests a potential role of competitive interactions in regulating their dynamics (Briggs and Knapp 2001). Despite their dominance, however, basal cover of *S. scoparium* and warm season grasses as a whole had minimal influence on basal cover of other species and functional groups. This might have been different if species and functional groups responses to *S. scoparium* and warm-season grasses were evaluated in terms of foliar cover and herbage production; however, current results suggest competition has a weak influence on basal cover in Sandhills prairie. Interestingly, Symstad and Tilman (2001) found *S. scoparium* increased reproductive output and aboveground biomass but did not respond in terms of recruitment in an experiment in which its competitors were removed suggesting it may itself have minimal influence on other species. Root systems that facilitate water uptake from different depths may be a mechanism by which forbs avoid competition and coexist with dominant warm-season grasses such as *S. scoparium* (Nippert and Knapp 2007). Forb interactions with warm-season grasses also may be more important in terms of recruitment of propagules than in regulating cover of existing plants (Adler and HilleRisLambers 2008).

Conclusions

Across the 26-year study, results showed that growing season precipitation and temperature, as well as cattle stocking rate, explained the most variability in basal cover responses of individual plant species and functional groups in Sandhills prairie. Stocking rate and lag 3-year growing season precipitation was particularly important to explaining variability of warm-season grasses, which consisted of the majority of total basal cover. The use of light to moderate stocking rates combined with greater precipitation across a few growing seasons would contribute to increased warm season grass and total basal cover, presumably through spread of vegetative structures and enlarging of crowns of bunchgrasses. With regard to forbs and woody plants, subtle deviations from the use of light to moderate stocking rates and growing season precipitation are not likely to have an impact on basal cover of these functional groups, although an increase in stocking rate would promote greater cover of *A. psilostachya*. As a whole, however, understanding of factors that explain forb basal cover in Sandhills prairie remain largely unresolved. Woody species basal cover, on the other hand, would be expected to increase with greater warming in Sandhills prairie. With regard to cool season grasses, they were a smaller component of basal cover in this Sandhills prairie, and similar to that of forbs, we do not have strong conclusions about factors governing their responses, although total precipitation may have a role. Improvement in understanding of variability of cool-season grass basal cover would need further investigation. Lastly, despite their dominance, we found *S. scoparium* and warm-season grass cover as a whole did not explain basal cover responses of most other species and functional groups, providing weak support for competition as a factor that regulates plant community composition in Sandhills prairie.

Appendix – See Tables 4 and 5.

Table 4 Basal cover (mm m⁻²) of species that made up 95 % of total cover and present in nearly all 26 years and their respective functional groups in Sandhills prairie at the Nebraska National Forest near Halsey, NE

| Year | Total | Amps | Anha | Bohi | Calo | Casp | Diol | Ertr | Heco | Opfr | Pase | Pavi | Roar | Scsc | Spccr | FO | WO | SU | WS | CS | SG |
|------|-------|------|------|------|------|------|------|------|------|------|------|------|------|-------|-------|------|-----|------|-------|------|------|
| 1979 | 392.0 | 0.8 | 2.5 | 60.5 | 2.0 | 13.1 | 5.2 | 0.0 | 5.6 | 0.6 | 3.5 | 2.2 | 1.6 | 246.9 | 4.4 | 2.2 | 2.7 | 0.6 | 360.3 | 13.1 | 13.1 |
| 1980 | 411.9 | 1.5 | 8.9 | 35.4 | 9.0 | 19.4 | 8.4 | 9.5 | 7.3 | 1.3 | 5.7 | 5.6 | 3.8 | 256.4 | 13.5 | 3.9 | 5.0 | 5.6 | 357.8 | 20.2 | 19.4 |
| 1981 | 301.7 | 1.4 | 3.1 | 22.9 | 6.9 | 7.2 | 2.3 | 11.0 | 1.4 | 0.8 | 1.1 | 2.7 | 1.1 | 214.8 | 5.9 | 3.2 | 1.7 | 0.8 | 283.0 | 5.8 | 7.2 |
| 1982 | 247.9 | 3.1 | 4.8 | 33.7 | 5.1 | 15.6 | 2.0 | 10.0 | 5.9 | 1.7 | 0.0 | 2.0 | 2.3 | 139.3 | 9.2 | 5.0 | 2.7 | 4.0 | 211.7 | 8.8 | 15.6 |
| 1983 | 125.5 | 1.5 | 4.4 | 23.5 | 5.8 | 10.1 | 3.0 | 9.0 | 1.3 | 1.5 | 0.0 | 1.5 | 1.6 | 49.4 | 3.2 | 3.3 | 2.1 | 1.9 | 101.3 | 6.9 | 10.1 |
| 1984 | 146.8 | 1.2 | 4.2 | 20.5 | 2.6 | 10.1 | 6.3 | 10.8 | 4.6 | 0.5 | 0.1 | 1.1 | 3.1 | 72.4 | 2.2 | 3.6 | 3.9 | 0.8 | 114.6 | 13.8 | 10.1 |
| 1985 | 231.5 | 0.3 | 6.8 | 30.8 | 7.1 | 32.0 | 8.6 | 8.1 | 13.8 | 1.5 | 1.2 | 6.1 | 3.6 | 79.4 | 19.0 | 2.9 | 6.3 | 4.5 | 159.3 | 26.4 | 32.0 |
| 1986 | 152.5 | 1.1 | 7.5 | 12.4 | 2.2 | 14.0 | 8.1 | 17.5 | 4.9 | 1.8 | 0.6 | 7.2 | 5.8 | 55.2 | 2.3 | 3.4 | 6.9 | 1.8 | 109.8 | 16.6 | 14.0 |
| 1987 | 80.2 | 1.6 | 3.0 | 5.0 | 2.9 | 5.1 | 3.6 | 2.8 | 1.4 | 1.6 | 0.8 | 5.0 | 2.7 | 34.3 | 2.0 | 2.5 | 3.0 | 7.6 | 56.4 | 5.6 | 5.1 |
| 1988 | 133.6 | 2.1 | 2.5 | 19.4 | 1.4 | 3.8 | 3.0 | 4.9 | 1.3 | 0.6 | 0.9 | 3.3 | 3.9 | 81.3 | 0.9 | 3.2 | 5.0 | 2.6 | 114.7 | 4.4 | 3.8 |
| 1989 | 129.8 | 1.1 | 3.4 | 9.7 | 0.8 | 5.1 | 4.8 | 7.9 | 0.1 | 4.6 | 0.9 | 4.7 | 2.1 | 76.4 | 0.9 | 3.3 | 2.7 | 6.1 | 106.6 | 6.1 | 5.1 |
| 1990 | 158.1 | 0.5 | 3.4 | 9.5 | 1.6 | 3.5 | 2.5 | 4.4 | 3.1 | 6.9 | 2.1 | 2.9 | 1.0 | 104.4 | 1.2 | 3.4 | 1.5 | 10.6 | 129.9 | 9.2 | 3.5 |
| 1991 | 129.6 | 0.1 | 1.5 | 4.4 | 2.2 | 4.2 | 1.9 | 6.6 | 4.8 | 9.6 | 1.3 | 3.2 | 1.9 | 80.3 | 1.7 | 0.5 | 2.2 | 9.6 | 102.0 | 11.2 | 4.2 |
| 1992 | 138.0 | 0.0 | 1.4 | 5.2 | 1.2 | 4.4 | 5.1 | 10.9 | 8.6 | 5.2 | 1.2 | 0.9 | 1.2 | 81.8 | 2.0 | 0.7 | 1.6 | 8.9 | 104.6 | 17.1 | 4.4 |
| 1993 | 129.8 | 0.1 | 2.0 | 2.9 | 0.5 | 2.8 | 3.7 | 8.0 | 7.7 | 2.0 | 1.8 | 2.2 | 0.2 | 88.5 | 0.6 | 1.0 | 0.4 | 3.0 | 107.5 | 14.8 | 3.1 |
| 1994 | 210.3 | 0.5 | 1.8 | 5.7 | 0.7 | 4.1 | 4.8 | 7.7 | 6.2 | 1.6 | 1.0 | 1.7 | 1.1 | 167.6 | 0.9 | 1.4 | 1.4 | 2.6 | 188.7 | 12.1 | 4.1 |
| 1995 | 303.8 | 0.4 | 3.1 | 13.3 | 1.2 | 7.4 | 6.5 | 4.8 | 4.2 | 0.3 | 1.2 | 1.9 | 0.8 | 253.5 | 0.6 | 1.4 | 1.0 | 2.6 | 280.0 | 11.3 | 7.4 |
| 1996 | 331.8 | 0.2 | 1.2 | 6.3 | 0.7 | 9.3 | 5.3 | 2.0 | 4.2 | 0.6 | 0.5 | 1.9 | 0.7 | 287.2 | 0.7 | 1.0 | 1.5 | 1.8 | 301.8 | 16.5 | 9.3 |
| 1997 | 330.9 | 0.7 | 1.2 | 1.9 | 1.4 | 13.5 | 11.0 | 4.5 | 8.8 | 2.3 | 2.6 | 2.8 | 1.1 | 262.5 | 2.1 | 1.5 | 1.5 | 3.3 | 278.9 | 32.4 | 13.5 |
| 1998 | 316.0 | 0.2 | 1.5 | 4.5 | 0.4 | 8.2 | 8.5 | 7.5 | 4.5 | 1.6 | 4.1 | 1.5 | 0.2 | 260.6 | 0.9 | 1.2 | 0.2 | 2.5 | 283.1 | 20.5 | 8.2 |
| 1999 | 185.4 | 1.5 | 1.3 | 4.4 | 3.8 | 5.8 | 4.0 | 4.8 | 2.7 | 0.6 | 2.7 | 3.5 | 2.2 | 134.0 | 9.0 | 2.4 | 2.6 | 0.6 | 164.3 | 9.7 | 5.9 |
| 2003 | 272.6 | 3.0 | 4.0 | 26.5 | 17.8 | 14.9 | 6.5 | 13.0 | 20.0 | 1.1 | 0.0 | 11.5 | 4.8 | 134.1 | 6.5 | 3.7 | 5.2 | 1.6 | 214.2 | 32.9 | 14.9 |
| 2004 | 224.3 | 3.2 | 5.1 | 39.6 | 3.1 | 14.4 | 8.8 | 22.9 | 9.7 | 2.1 | 4.5 | 11.7 | 3.8 | 78.4 | 6.0 | 9.7 | 6.1 | 2.1 | 173.0 | 19.1 | 14.4 |
| 2005 | 179.1 | 4.5 | 5.2 | 32.2 | 7.0 | 11.2 | 9.1 | 4.2 | 15.2 | 2.8 | 1.4 | 5.8 | 2.9 | 58.2 | 5.2 | 10.4 | 4.8 | 3.1 | 119.6 | 30.1 | 11.2 |
| 2006 | 255.8 | 2.6 | 3.2 | 13.6 | 3.6 | 5.3 | 10.9 | 0.2 | 7.2 | 0.4 | 1.4 | 9.5 | 2.8 | 175.1 | 2.8 | 4.9 | 3.3 | 0.6 | 218.7 | 22.8 | 5.4 |
| 2007 | 258.8 | 3.3 | 10.0 | 20.8 | 10.2 | 8.9 | 7.0 | 0.0 | 18.9 | 0.0 | 0.6 | 11.5 | 2.3 | 147.7 | 0.8 | 7.3 | 3.3 | 0.7 | 201.8 | 33.9 | 9.0 |

Amps, *Ambrosia psilostachya*; Anha, *Andropogon hallii*; Bohi, *Bouteloua hirsuta*; Calo, *Calamovilfa longifolia*; Casp, *Carex* species; Diol, *Dichanthelium oligosanthes*; Ertr, *Eragrostis trichodes*; Heco, *Hesperostipa comata*; Opfr, *Opuntia fragilis*; Pase, *Paspalum setaceum*; Pavi, *Panicum virgatum*; Roar, *Rosa arkansana*; Scsc, *Schizachyrium scoparium*; and Spccr, *Sporobolus cryptandrus*; FO forbs, WO woody plants, SU succulents, WS warm-season grasses, CS cool-season grasses and SG sedges

Table 5 Precipitation (PPT), temperature (temp), Palmer drought severity index (PDSI), and stocking rate variables for the Nebraska National Forest near Halsey, NE

| Year | PPT Apr- Sept | Mean Apr- Sept temp | Mean ann temp | Total PPT | Mean Apr-Sept max temp | Mean Apr-Sept min temp | PPT Apr- June | PPT Jul- Sept | Mean ann. max temp | Mean ann.min temp | Lag 1 year PPT Apr- Sept | Total Oct- Mar | Mean mean Mar temp | PDSI Apr- Sept | Mean rate | Stocking |
|------|---------------------|------------------------------|---------------------|--------------|------------------------------|------------------------------|---------------------|---------------------|-----------------------------|-------------------------|--------------------------------|----------------------|-----------------------------|----------------------|--------------|----------|
| 1979 | 486 | 17.2 | 7.8 | 708 | 25.7 | 8.8 | 279 | 207 | 15.8 | -0.1 | 393 | 165 | -3.6 | 3.2 | 3.3 | 1.14 |
| 1980 | 252 | 19.2 | 10.3 | 404 | 28.2 | 10.2 | 114 | 137 | 18.6 | 1.9 | 486 | 260 | 0.5 | -1.3 | -0.2 | 1.04 |
| 1981 | 366 | 18.8 | 10.7 | 522 | 27.3 | 10.2 | 188 | 179 | 18.8 | 2.5 | 252 | 93 | 3.2 | -1.8 | -1.4 | 1.14 |
| 1982 | 417 | 17.3 | 8.7 | 633 | 25.3 | 9.2 | 235 | 182 | 16.5 | 1.0 | 366 | 136 | 0.5 | 1.3 | 1.8 | 0.77 |
| 1983 | 627 | 17.5 | 8.9 | 821 | 25.4 | 9.5 | 467 | 160 | 15.9 | 1.9 | 417 | 264 | 1.8 | 6.2 | 5.5 | 0.81 |
| 1984 | 344 | 17.6 | 9.3 | 571 | 25.8 | 9.3 | 256 | 88 | 16.7 | 1.9 | 627 | 205 | -0.3 | 5.1 | 4.8 | 0.52 |
| 1985 | 375 | 18.2 | 8.5 | 421 | 26.5 | 9.9 | 154 | 221 | 16.1 | 0.9 | 344 | 153 | 0.5 | 1.9 | 2.4 | 0.44 |
| 1986 | 577 | 18.8 | 11.2 | 693 | 25.4 | 11.6 | 351 | 226 | 17.9 | 4.3 | 375 | 69 | 1.5 | 3.2 | 3.3 | 0.52 |
| 1987 | 502 | 18.5 | 10.1 | 709 | 26.1 | 10.9 | 198 | 304 | 17.2 | 3.0 | 577 | 200 | 2.3 | 3.9 | 3.9 | 0.79 |
| 1988 | 550 | 17.7 | 8.7 | 631 | 24.8 | 10.6 | 295 | 255 | 15.7 | 1.6 | 502 | 127 | -0.8 | 2.8 | 2.1 | 0.84 |
| 1989 | 347 | 17.3 | 8.4 | 420 | 24.9 | 9.1 | 193 | 154 | 16.1 | 0.4 | 550 | 83 | -0.1 | -3.2 | -2.7 | 0.99 |
| 1990 | 354 | 17.7 | 9.6 | 522 | 25.5 | 10.0 | 244 | 109 | 17.6 | 1.8 | 347 | 82 | 1.1 | -2.9 | -2.8 | 0.77 |
| 1991 | 497 | 18.3 | 10.1 | 591 | 25.8 | 10.8 | 388 | 109 | 17.2 | 2.0 | 354 | 134 | 2.2 | -1.7 | -1.2 | 0.00 |
| 1992 | 429 | 16.0 | 9.0 | 654 | 23.4 | 8.6 | 143 | 286 | 16.3 | 1.7 | 497 | 233 | 2.5 | 1.3 | 1.7 | 0.81 |
| 1993 | 562 | 15.2 | 6.9 | 694 | 22.1 | 8.4 | 268 | 294 | 13.7 | 0.0 | 429 | 109 | -1.6 | 5.3 | 5.1 | 0.94 |
| 1994 | 382 | 17.4 | 9.0 | 540 | 25.5 | 9.3 | 163 | 218 | 16.8 | 1.2 | 562 | 117 | -0.3 | 4.5 | 4.9 | 0.89 |
| 1995 | 558 | 16.0 | 8.6 | 733 | 23.6 | 8.4 | 376 | 182 | 16.4 | 0.8 | 382 | 206 | 1.9 | 6.1 | 5.5 | 0.86 |
| 1996 | 419 | 16.3 | 7.1 | 520 | 23.6 | 9.1 | 224 | 195 | 14.5 | -0.2 | 558 | 146 | -0.8 | 4.0 | 4.3 | 0.86 |
| 1997 | 389 | 16.6 | 9.0 | 507 | 23.9 | 9.2 | 181 | 207 | 16.4 | 1.5 | 419 | 65 | -0.4 | 3.1 | 3.3 | 0.86 |
| 1998 | 502 | 17.6 | 9.6 | 652 | 25.5 | 9.9 | 324 | 178 | 17.2 | 1.9 | 389 | 137 | 1.3 | 3.5 | 3.7 | 0.86 |
| 1999 | 493 | 16.9 | 10.0 | 570 | 24.2 | 9.7 | 279 | 213 | 18.0 | 2.1 | 502 | 174 | 2.5 | 4.8 | 3.2 | 0.86 |
| 2003 | 302 | 17.9 | 9.5 | 401 | 25.8 | 9.8 | 237 | 65 | 17.5 | 1.5 | 216 | 103 | 0.1 | -2.2 | -2.5 | 0.94 |
| 2004 | 517 | 16.9 | 9.3 | 622 | 24.6 | 9.3 | 213 | 305 | 17.0 | 1.5 | 302 | 101 | 1.5 | -2.0 | -1.5 | 1.04 |
| 2005 | 475 | 18.0 | 10.0 | 582 | 25.6 | 10.5 | 362 | 114 | 17.8 | 2.2 | 517 | 77 | 2.1 | 2.0 | 1.0 | 1.04 |
| 2006 | 317 | 18.3 | 9.9 | 367 | 26.5 | 10.1 | 141 | 176 | 18.1 | 1.8 | 475 | 97 | 2.0 | -1.7 | -0.8 | 1.04 |
| 2007 | 391 | 18.1 | 9.6 | 544 | 25.3 | 11.0 | 272 | 119 | 16.9 | 2.2 | 317 | 123 | 1.2 | 3.6 | 3.2 | 1.04 |

Precipitation (mm) and temperature (°C) variables were computed on annual (ann), growing season (Apr-Sept), early growing season (Apr-June), dormant season (Oct-Mar), and 1-year lag bases. Stocking rate is measured in animal unit months (AUM) ha⁻¹

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