

Regional productivities of plant species in the Great Plains of the United States

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Abstract

Few studies have analyzed the production of plant species at regional scales in grassland ecosystems, due in part to limited availability of data at large spatial scales. We used a dataset of rangeland surveys to examine the productivities of 22 plant species throughout the Great Plains of the United States with respect to three environmental factors: temperature, precipitation and soil texture. Productivity of plant species was obtained from Natural Resource Conservation Service (NRCS) range site descriptions. We interpolated climate data from 296 weather stations throughout the region and used soil texture data from NRCS State Soil Geographic (STATSGO) databases. We performed regression analyses to derive models of the relative and absolute production of each species in terms of mean annual temperature (MAT), mean annual precipitation (MAP), and percentage SAND, SILT and CLAY.

MAT was the most important factor for 55% of species analyzed; MAP was most explanatory for 40% of the species, and a soil texture variable was most important for only one species. Production of C₃ species tended to be negatively related to MAT, MAP and positively related to CLAY. Production of C₄ shortgrasses, in general, was positively related to MAT and negatively related to MAP and SAND, whereas C₄ tallgrass productivity tended to be positively associated with MAP and SAND, and was highest at intermediate values of MAT. Our results indicate the extent to which functional types can be used to represent individual species. The regression equations derived in this analysis can be important inclusions in models that assess the effects of climate change on plant communities throughout the region.

Introduction

Environmental changes can potentially alter plant communities in a variety of ways. Species that are positively affected could increase productivity and increase in importance within plant communities, as well as extend their ranges into new areas. Species negatively impacted could decrease productivity, decline in importance within communities and exhibit reductions in distribution. Extinction is also possible if environmental conditions change sufficiently (Melillo et al. 1992; Esser 1992). One step toward predicting the impact of climate change on species abundances and distributions is to improve our understanding of how productivities of species are related to current environmental conditions.

Constructing productivity patterns of plant species at large scales is limited by the availability of data (Smith et al. 1993) and can be especially difficult in areas where most native vegetation has been replaced by crops. Pollen data have been used to approximate the spatial and temporal patterns of tree species abundances at regional and continental scales (Prentice 1992). However, approximately 25% of terrestrial vegetation is composed of grasslands (Singh et al. 1983), and pollen data do not provide accurate resolution below the family level for grasses (Brown 1993). Opal phytoliths, a potential indicator of native vegetation structure for grasslands, cannot distinguish grasses to the genus or species level (Brown 1993). These techniques therefore have limitations in their applicability to grassland studies. The lack of data is at least a par-

tial explanation for why there have not been many studies addressing species dynamics in grasslands at large scales. Studies utilizing data on grass species for large areas in North America have used either floristic data (Teeri & Stowe 1976) or density, cover or biomass measurements (Nicholson & Hulett 1969, Sims et al. 1978, Boutton et al. 1980; Snaydon 1991; Paruelo & Lauenroth 1996) from a relatively small number of sites.

Only recently have scientists tapped an existing source of data that can be used to examine grass species production at large spatial scales in the United States. Rangeland surveys are a valuable source of species productivity data for states containing lands managed for grazing. These data have been used to examine abundance patterns for several plant species (Brown & Gersmehl 1985; Brown 1989, 1993). They have also been used to relate the production of species to environmental factors for eastern Colorado (Fan 1993). However, they have not previously been used to relate species productivities to environmental conditions at a regional spatial scale.

It remains to be seen whether production of species relate to environmental factors at the regional scale. It is possible that patterns of species abundances are not strongly related to abiotic variables at this scale (Brown & Gersmehl 1985). Other controls such as biotic interactions may be important in determining species production. When grass species have been grouped by photosynthetic pathway into C_3 and C_4 functional types, their frequency, production and distribution have been related with environmental factors such as temperature, precipitation and soil texture at regional to continental scales (Teeri & Stowe 1976; Sims et al. 1978; Paruelo & Lauenroth 1996; Epstein et al. 1997). Although functional types can be used to represent properties of plant community structure (Smith et al. 1993), knowledge of individual species provide detailed insight into community dynamics. Additionally, species within a functional group may exhibit different relationships with environmental factors.

We examined relationships between environmental factors and the abundance of 22 of the most important plant species in terms of production for the Great Plains of the United States. Our objectives were to (1) develop regression models for the production of each species using environmental variables as predictors, (2) determine whether species with similar attributes, such as photosynthetic pathway and stature, have similar relationships with environmental factors.

Methods

We formulated quantitative relationships between the productivities of plant species and three environmental factors for the Great Plains of the United States. We analyzed species production in terms of both absolute aboveground net primary production (ANPP) and relative ANPP (percentage of community ANPP accounted for by the species). Absolute production represents the abundance of the species, whereas relative production is an indicator of species dominance. The environmental factors used in the analysis were mean annual temperature (MAT), mean annual precipitation (MAP) and soil texture (percentage sand, silt and clay in the surface soil layer). We selected environmental variables that have substantial gradients within the Great Plains and that have been shown to relate to plant species or functional type production (Sims et al. 1978; Boutton et al. 1980; Fan 1993; Paruelo & Lauenroth 1996; Epstein et al. 1997).

We constructed a spatial database of plant species production and environmental variables for the Great Plains of the United States. Plant species production data were collected from USDA Natural Resource Conservation Service (NRCS) range site descriptions. NRCS range sites represent the potential native plant community of well-managed rangeland in the absence of disturbances and other management regimes. NRCS determines the potential plant community by evaluating otherwise undisturbed vegetation under varying degrees of grazing pressure. The excellent condition range sites used in this analysis have not been deteriorated by excessive grazing. Range sites are essentially 'the product of all abiotic and biotic factors responsible for their development' and are unique in the combination of total annual yield and plant community composition (USDA 1967). Range site descriptions include the relative production (%) attributed to each species in the plant community, as well as total community production in favorable, normal and unfavorable years. These data are based on total growth during a single growing season and determined by harvesting plant material at various growth stages (USDA 1967). We calculated absolute production (g m^{-2}) for each species by multiplying the proportion of production for that species by the total site production for normal climate years.

Range site descriptions were spatially located using NRCS State Soil Geographic (STATSGO) databases, organized in a geographic information system (GIS) (ARC/INFO Version 6.1.1. Environmental Systems Research Institute, Inc. 1992. Redlands, CA). These

databases aggregate county soil survey maps to represent soil patterns at the scale of a state or region (1:250 000) (USDA 1991). The databases are used primarily for large-scale resource management and monitoring. In STATSGO databases, states are divided into polygons, or Soil Associations (SA), representing areas of similar aggregate soil characteristics. The minimum size of an SA is 625 ha. Each SA is composed of a number of range sites, which can be related to range site descriptions. The database includes the areal extent of each range site within each SA so that production for an SA can be calculated as the weighted average of the production values for the component range sites. Data were only used for SAs in which every component was related to a valid range site description; approximately 65% of the SAs were considered usable. The degree of aggregation in STATSGO makes this dataset appropriate for regional-scale studies (Lathrop et al. 1995, Davidson 1995).

The use of rangeland survey data limited the database to states in which at least some land is managed as rangeland. For the purpose of this analysis, it was also essential that range site descriptions included the relative production of each species in the plant community. The database for this study included Kansas, Nebraska, North Dakota, South Dakota, Texas, and the Great Plains portions of Colorado, Montana, New Mexico and Wyoming. Oklahoma has approximately 37.5% of its area as rangeland (Lauenroth et al. 1994), but NRCS range site descriptions for the state did not include the relative production of individual species. Therefore, Oklahoma data were not included in the analysis.

The lack of species productivity estimates throughout the Great Plains makes it difficult to independently evaluate the quality of the dataset at the species level. However, range site representations of total aboveground net primary production, as well as productivity of C₃ and C₄ functional types, compared favorably to field data compiled from studies throughout the Great Plains (Paruelo & Lauenroth 1996; Paruelo et al. 1997; Epstein et al. 1997).

We used climate data from 296 weather stations throughout the region (Figure 1) (CLIMATEDATA 1988). For each station, daily values of precipitation, and daily minimum and maximum temperatures were collected for the period 1969 to 1988. Annual precipitation and average annual temperature were calculated for each station by year and averaged over the 20-year period. The GIS was used to generate MAT isotherms of 0.25 °C intervals and MAP isohyets of 1 cm intervals

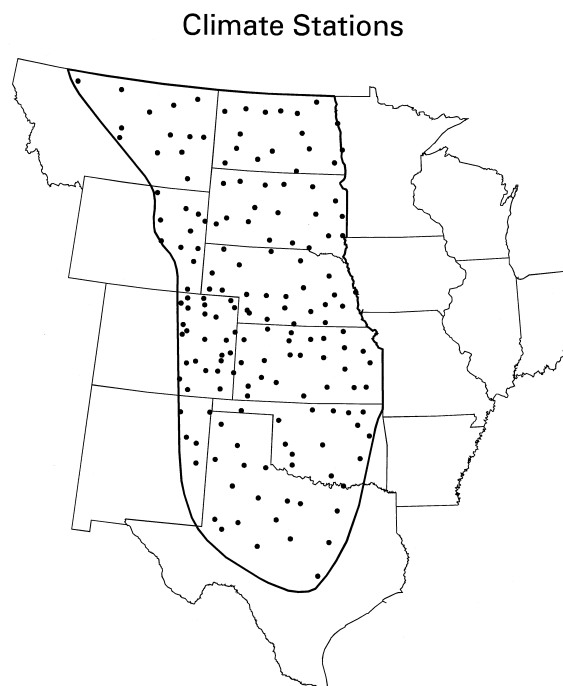


Figure 1. The distribution of 296 weather stations used to derive the regional climatic variables.

for the region. Values for areas between contours were determined by the midpoint of the surrounding contours. Soil texture data (percentage sand, silt and clay) were generated from the texture classification of the soil surface layer for each STATSGO polygon (Burke et al. 1991). Thus, any geographic point in the Great Plains could be associated with the relative and absolute production of each species, and values for MAT, MAP and soil texture.

A set of approximately 200 random points was generated from the database to represent the geographic space of the region and the environmental space of the three abiotic factors (Figure 2). Stepwise multiple regression analyses were performed on the relative and absolute production of 22 plant species (Tables 1a and 1b) with respect to five environmental variables: MAT, MAP, percentage sand (SAND), percentage silt (SILT) and percentage clay (CLAY). Quadratic terms for mean annual temperature (MAT2) and mean annual precipitation (MAP2) were added to models of species that exhibited parabolic functions of productivity with respect to MAT or MAP. All three soil texture percentages were used in the analysis to ensure finding the most concise relationships with soil texture; no equation, however, was allowed to have more than two of

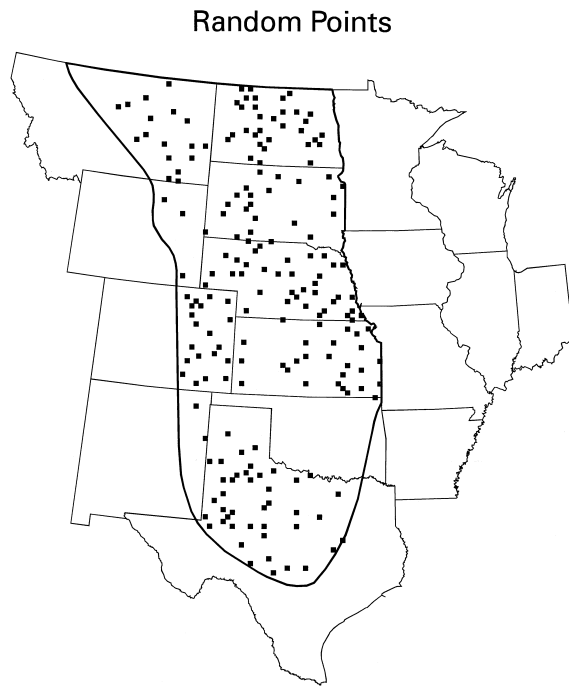


Figure 2. The 202 spatially random points used in the stepwise regression analyses of species productivities. Species productivity data were not available for Oklahoma.

the texture variables so that all variables remained independent. A significance level of 0.001 was required for variables to enter and remain in the models. This relatively strict level of significance was used so that only the most important variables would be included. Given a large sample size of 200 points, the stepwise regression would otherwise be quite lenient in its admittance of independent variables.

Of the 22 species analyzed, 9 were C_3 grasses and 13 were C_4 grasses. Maps of the relative and absolute production of the 22 species based on the NRCS range site data are included in Appendix A. Many of the species are dominant in plant communities throughout the Great Plains. *Agropyron dasystachyum* (Hook.) Scribn., *Agropyron smithii* Rydb., *Bouteloua gracilis* (H.B.K.) Lag. ex Steud., *Calamovilfa longifolia* (Hook.) Scribn., *Koeleria pyramidata* (Lam.) Beauv., *Poa secunda* Presl, *Stipa comata* Trin. & Rupr. and *Stipa viridula* Trin. are important components of communities throughout the northern mixed prairie (Coupland 1992). These plant communities are found in eastern Montana and Wyoming, and western North and South Dakota. *Agropyron smithii*, *Bouteloua curtipendula* (Michx.) Torr., *Bouteloua eriopoda*

(Torr.) Torr., *Bouteloua gracilis*, *Buchloë dactyloides* (Nutt.) Engelm., *Hilaria belangeri* (Steud.) Nash, *Hilaria jamesii* (Torr.) Benth. and *Hilaria mutica* (Buckl.) Benth. can be important plants in shortgrass steppe communities (Lauenroth & Milchunas 1992). Shortgrass steppe is located in eastern Colorado and New Mexico, and western Kansas, Oklahoma and Texas. *Agropyron smithii*, *Aristida longiseta* Steud., *Bouteloua curtipendula*, *Bouteloua gracilis*, *Buchloë dactyloides*, *Koeleria pyramidata*, *Schizachyrium scoparium* (Michx.) Nash, *Sitanion hystrix* (Nutt.) J. G. Smith and *Stipa leucotricha* Trin. & Rupr. are important grasses in southern mixed prairie plant communities (Coupland 1992). Southern mixed prairie is generally located in western Nebraska and central Kansas, Oklahoma and Texas. *Andropogon gerardii* Vitman, *Panicum virgatum* L., *Schizachyrium scoparium*, *Sorghastrum nutans* (L.) Nash and *Stipa spartea* Trin. are the prominent grasses in the tallgrass prairie (Kucera 1992), found in eastern North Dakota, South Dakota, Nebraska, Kansas, Oklahoma and Texas. Nomenclature follows Flora of the Great Plains (Great Plains Flora Association 1986).

Results and discussion

Environmental gradients

There are strong gradients of MAT and MAP in the Great Plains (Lauenroth & Burke 1995). MAT increases from 4 °C near the border between the U.S. and Canada to 20 °C in south-central Texas (Figure 3a). While there are exceptions (Björkman et al. 1975, Caldwell et al. 1977), the optimum temperature for photosynthetic rate in C_4 plants is generally higher than for C_3 plants (Black 1973, Ehleringer 1978). Thus, temperature variables should influence the distribution and production of plant species with different photosynthetic pathways. MAP increases from less than 30 cm in the western part of the region to 120 cm in the southeast (Figure 3b). MAP is strongly related to ANPP in the region (Sala et al. 1988). The importance of plant attributes such as height, root distribution and drought tolerance varies with precipitation. Along a gradient of increasing precipitation, belowground competition for soil water becomes less important, and aboveground competition for light increases (Tilman 1988; Lauenroth & Coffin 1992). Shortgrasses, which allocate less biomass aboveground, are found predominantly in the drier parts of the region, whereas

Table 1a. Species list

Species Name	Species Code	Season	Relative Height	Max. Importance *
<i>Agropyron dasystachyum</i>	AGDA	cool	medium	nmp
<i>Agropyron smithii</i>	AGSM	cool	medium	nmp
<i>Andropogon gerardii</i>	ANGE	warm	tall	tgp
<i>Aristida longiseta</i>	ARLO	warm	medium	smp
<i>Bouteloua curtipendula</i>	BOCU	warm	medium	smp
<i>Bouteloua eriopoda</i>	BOER	warm	short	sgs
<i>Bouteloua gracilis</i>	BOGR	warm	short	sgs
<i>Buchloë dactyloides</i>	BUDA	warm	short	sgs
<i>Calamovilfa longifolia</i>	CALO	warm	medium	nmp
<i>Hilaria belangeri</i>	HIBE	warm	short	sgs
<i>Hilaria jamesii</i>	HIJA	warm	short	sgs
<i>Hilaria mutica</i>	HIMU	warm	short	sgs
<i>Koeleria pyramidata</i>	KOPY	cool	medium	nmp
<i>Panicum virgatum</i>	PAVI	warm	tall	tgp
<i>Poa secunda</i>	POSE	cool	medium	nmp
<i>Schizachyrium scoparium</i>	SCSC	warm	tall	tgp
<i>Sitanion hystrix</i>	SIHY	cool	medium	sgs
<i>Sorghastrum nutans</i>	SONU	warm	tall	tgp
<i>Stipa comata</i>	STCO	cool	medium	nmp
<i>Stipa leucotricha</i>	STLE	cool	medium	smp
<i>Stipa spartea</i>	STSP	cool	tall	tgp
<i>Stipa viridula</i>	STVI	cool	medium	nmp

* nmp - Northern Mixed Prairie
 sgs - Shortgrass Steppe
 smp - Southern Mixed Prairie
 tgp - Tallgrass Prairie

Table 1b. Species ranked by production

Species Name	Maximum average production (g/m ²)
<i>Schizachyrium scoparium</i>	249
<i>Andropogon gerardii</i>	190
<i>Agropyron smithii</i>	111
<i>Bouteloua gracilis</i>	98
<i>Stipa viridula</i>	98
<i>Bouteloua curtipendula</i>	94
<i>Panicum virgatum</i>	86
<i>Sorghastrum nutans</i>	82
<i>Stipa comata</i>	79
<i>Buchloë dactyloides</i>	53
<i>Calamovilfa longifolia</i>	47
<i>Stipa leucotricha</i>	44
<i>Hilaria mutica</i>	39
<i>Bouteloua eriopoda</i>	38
<i>Stipa spartea</i>	33
<i>Agropyron dasystachyum</i>	28
<i>Hilaria belangeri</i>	26
<i>Hilaria jamesii</i>	22
<i>Koeleria pyramidata</i>	10
<i>Sitanion hystrix</i>	5
<i>Aristida longiseta</i>	4
<i>Poa secunda</i>	4

tallgrasses dominate the humid areas (Weaver 1954; Sims 1988).

There is a wide range of soil textures in the Great Plains. The western portion of the region contains large

areas of eolian sand deposited from the Rocky Mountains (Muhs & Maat 1993), which yields a general gradient of decreasing sand content from west to east (Burke et al. 1991); there is more local heterogeneity in

Table 2a. Individual species relative production

	INT	R ²	P	Independent Variables	Regression Coefficient	Partial R ²	P
C3 grasses							
AGSM	33.93	0.56	0.0001	MAT	-1.026	0.30	0.0001
				CLAY	0.239	0.15	0.0001
				MAP	-0.265	0.09	0.0001
				SAND	-0.112	0.02	0.0020
STCO	11.36	0.54	0.0001	MAT	-0.915	0.47	0.0001
				SAND	0.067	0.07	0.0001
STVI	12.97	0.46	0.0001	MAT	-0.681	0.27	0.0001
				CLAY	0.186	0.13	0.0001
				MAP	-0.107	0.06	0.0001
AGDA	5.45	0.18	0.0001	MAP	-0.060	0.10	0.0001
				SAND	-0.036	0.08	0.0001
POSE	0.76	0.15	0.0001	MAT	-0.025	0.11	0.0001
				MAP	-0.006	0.04	0.0029
KOPY	2.19	0.34	0.0001	MAT	-0.183	0.31	0.0001
				MAP	0.012	0.03	0.0077
SIHY	-0.47	0.22	0.0001	MAP	-0.016	0.07	0.0002
				MAT	0.197	0.06	0.0003
				MAT ²	-0.007	0.05	0.0008
				SILT	0.008	0.04	0.0046
STLE	-0.72	0.29	0.0001	MAT	0.065	0.25	0.0001
				CLAY	0.008	0.04	0.0021
STSP	-4.25	0.40	0.0001	MAT	-0.350	0.19	0.0001
				MAP	0.270	0.13	0.0001
				MAP ²	-0.002	0.08	0.0001
C4 grasses							
BOGR	0.08	0.31	0.0001	MAP	-0.298	0.16	0.0001
				MAT ²	-0.152	0.09	0.0001
				MAT	4.148	0.06	0.0001
BUDA	3.08	0.39	0.0001	MAT	0.723	0.22	0.0001
				MAP	-0.120	0.13	0.0001
				SAND	-0.044	0.04	0.0002
BOER	0.24	0.22	0.0001	MAT	0.347	0.12	0.0001
				MAP	-0.057	0.10	0.0001
HIBE	-0.91	0.13	0.0001	MAT	0.071	0.10	0.0001
				CLAY	0.015	0.03	0.0065
HIMU	-0.58	0.06	0.0007	MAT	0.076	0.06	0.0007
HIJA	1.58	0.04	0.0031	MAP	-0.022	0.04	0.0031
BOCU	-12.31	0.62	0.0001	MAT	1.132	0.45	0.0001
				MAP ²	-0.004	0.07	0.0001
				SAND	-0.073	0.06	0.0001
				MAP	0.414	0.04	0.0001
PAVI	-13.88	0.63	0.0001	MAP	0.147	0.34	0.0001
				MAT ²	-0.079	0.15	0.0001
				MAT	1.614	0.10	0.0001
				SAND	0.052	0.03	0.0001
SCSC	-4.04	0.30	0.0001	MAP	0.259	0.30	0.0001
ANGE	-31.85	0.73	0.0001	MAP	0.414	0.49	0.0001
				MAT ²	-0.160	0.13	0.0001
				MAT	3.080	0.07	0.0001
				SILT	0.140	0.04	0.0001
SONU	-7.46	0.65	0.0001	MAP	0.168	0.63	0.0001
				SAND	0.022	0.02	0.0022
CALO	-8.18	0.56	0.0001	SAND	0.160	0.42	0.0001
				MAT ²	-0.058	0.11	0.0001
				MAT	0.982	0.03	0.0027
APIO	NS						

Table 2b. Individual species absolute production

	INT	R ²	P	Independent Variables	Regression Coefficient	Partial R ²	P
C3 grasses							
AGSM	40.26	0.41	0.0001	MAT CLAY	-3.156 0.559	0.31 0.10	0.0001 0.0001
STCO	26.94	0.49	0.0001	MAT SAND	-2.183 0.158	0.43 0.06	0.0001 0.0001
STVI	21.59	0.31	0.0001	MAT CLAY	-1.864 0.304	0.24 0.07	0.0001 0.0001
AGDA	6.87	0.18	0.0001	MAP SAND	-0.077 -0.043	0.11 0.07	0.0001 0.0001
POSE	1.05	0.13	0.0001	MAT MAP	-0.036 -0.008	0.10 0.03	0.0001 0.0082
KOPY	-0.97	0.41	0.0001	MAT MAP MAP ² CLAY	-0.466 0.248 -0.001 -0.035	0.22 0.14 0.03 0.02	0.0001 0.0001 0.0012 0.0075
SIHY	-0.53	0.21	0.0001	MAP MAT MAT ² SILT	-0.017 0.217 -0.008 0.009	0.07 0.06 0.04 0.04	0.0002 0.0001 0.0012 0.0044
STLE	-1.91	0.20	0.0001	MAT	0.234	0.20	0.0001
STSP	-15.53	0.37	0.0001	MAP MAT MAP ²	0.867 -1.025 -0.005	0.19 0.11 0.07	0.0001 0.0001 0.0001
C4 grasses							
BOGR	3.44	0.21	0.0001	MAP MAT ² MAT	-0.361 -0.187 5.204	0.09 0.06 0.06	0.0001 0.0002 0.0004
BUDA	3.83	0.37	0.0001	MAT MAP SAND	1.506 -0.209 -0.085	0.25 0.08 0.04	0.0001 0.0001 0.0009
BOER	0.46	0.19	0.0001	MAT MAP	0.690 -0.114	0.10 0.09	0.0001 0.0001
HIBE	-1.65	0.10	0.0001	MAT	0.202	0.10	0.0001
HIMU	-1.16	0.07	0.0002	MAT	0.151	0.07	0.0002
HIJA	1.65	0.04	0.0052	MAP	-0.023	0.04	0.0052
BOCU	-19.76	0.50	0.0001	MAT SILT	2.574 0.182	0.46 0.04	0.0001 0.0001
PAVI	-52.14	0.69	0.0001	MAP MAT ² MAT SAND	0.695 -0.261 5.082 0.141	0.50 0.07 0.07 0.05	0.0001 0.0001 0.0001 0.0001
SCSC	-45.63	0.48	0.0001	MAP	1.441	0.48	0.0001
ANGE	-143.07	0.77	0.0001	MAP MAT ² MAT SILT	2.113 -0.624 11.526 0.489	0.58 0.12 0.05 0.02	0.0001 0.0001 0.0001 0.0001
SONU	-31.68	0.71	0.0001	MAP	0.773	0.71	0.0001
CALO	-14.12	0.56	0.0001	SAND MAT ² MAT	0.347 -0.120 2.035	0.45 0.09 0.02	0.0001 0.0001 0.0018
ARLO	NS						

soil texture than in climate. Soil texture can affect the temporal and spatial availability of soil moisture in different layers of the soil profile (Noy-Meir 1973), which can influence the production of species with different root distributions (Walter 1971; Walker & Noy-Meir 1982; Soriano & Sala 1983; Liang et al. 1989; Sala et al. 1989) and, potentially, different growing seasons (Barnes & Harrison 1982; Lane 1995).

Species productivities vs environmental variables

All species were significantly related to environmental variables ($p < 0.01$) (Tables 2a and 2b) with the exception of *Aristida longiseta*, a C_4 bunchgrass found in soils of all textures and common in disturbed areas (Stubbendieck et al. 1992). The number of independent variables in the models ranged from one to four. A climatic variable (MAT or MAP) was the most important factor in 95% of the significant models. MAT was present in 81% of the models, and it was the most important factor in 55%. MAP was present in 67% of the models and was the most important factor in 40%. A soil texture variable appeared in 57% of the models, but was the most important factor for only one species, *Calamovilfa longifolia* (prairie sandreed); percentage sand was the most explanatory variable for the relative and absolute production of this species.

Temperature appears to be the most important factor controlling the regional distribution and production of C_3 vs C_4 functional types (Teeri and Stowe 1976, Epstein et al. 1997); it is therefore likely that temperature is also important in controlling the regional productivities of C_3 and C_4 species. Some species in the Great Plains, such as those dominating the shortgrass steppe, have relatively low productivity potentials; however, the species that dominate the tallgrass prairie can be highly productive given enough soil water (Lauenroth and Sala 1992; Kucera 1992; Huston 1997). The spatial patterns of productivity for all of the tallgrass species examined in this study (*A. gerardii*, *P. virgatum*, *S. scoparium*, *S. nutans*, *S. spartea*) were consistent with a regional precipitation gradient; the productivities of these species were therefore strongly related to MAP.

C_3 species dominate in the northwestern portion of the Great Plains, an area with low temperatures and low precipitation. MAT was the most explanatory variable in 72% of the models for C_3 species. Production of 6 of 9 C_3 species was negatively correlated with MAT. This was expected considering that photosynthetic rates of C_3 species can be constrained at high temperatures

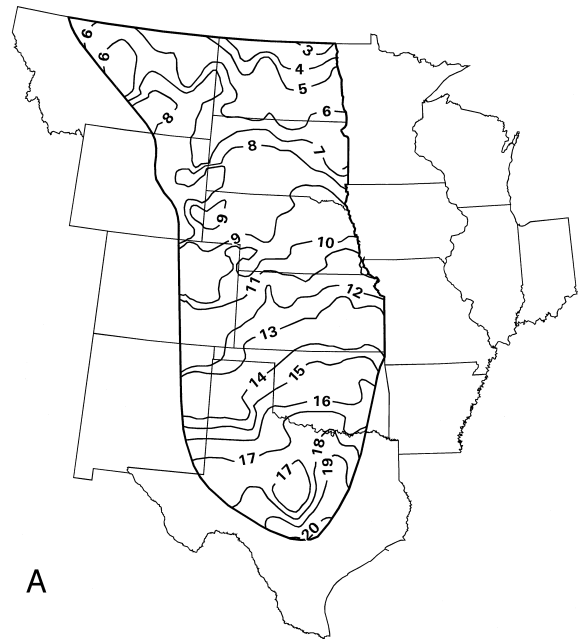


Figure 3a. Isotherms of mean annual temperature ($^{\circ}\text{C}$).

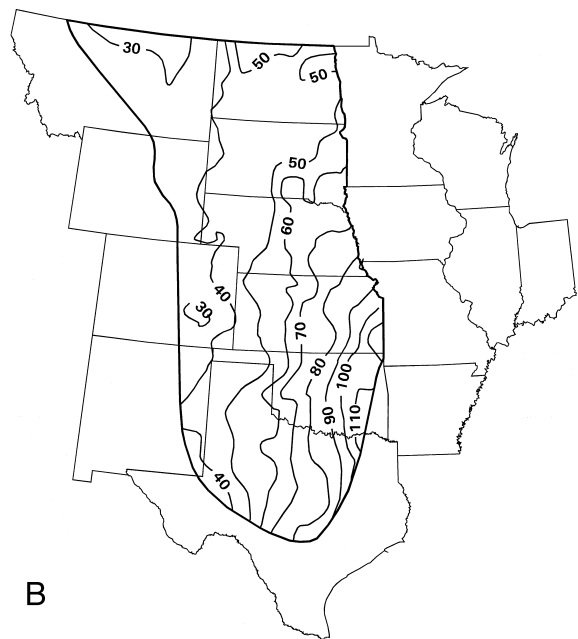


Figure 3b. Isohyets of mean annual precipitation (cm) for the Great Plains of the United States.

(Black 1973; Ehleringer & Björkman 1977; Ehleringer 1978). *Stipa leucotricha*, a C_3 grass with a winter growing season, is found mainly in Oklahoma and Texas and had a positive relationship with MAT. *Sitanion hystrix*

was most abundant at intermediate values of MAT, and *Agropyron dasystachyum* did not have a significant relationship with MAT.

MAP was present in 67% of the models for C₃ species and was negatively correlated with production for 67% of the models in which it appeared. This tendency reflects a relationship also exhibited by C₃ grasses as a group (Epstein et al. 1997). Two species showed exceptions to this pattern. *Koeleria pyramidata* exhibited an increase in relative production with increasing MAP, and absolute production of *K. pyramidata* had maximum values at intermediate levels of MAP. Relative and absolute production of *Stipa spartea*, a C₃ tallgrass, also had maxima at intermediate levels of precipitation.

Although associations between soil texture and C₃ species production were mixed, the most common patterns were either a positive relationship with CLAY or a negative relationship with SAND. *Agropyron dasystachyum*, *Agropyron smithii*, *Stipa leucotricha* and *Stipa viridula* all exhibited these relationships. Conversely, absolute production of *Koeleria pyramidata* had a negative relationship with CLAY, and production of *Stipa comata* was positively related to SAND. Production of *Sitanion hystrix* was positively correlated with SILT. Clay content in soils was shown to be positively related to the production of C₃ species in eastern Colorado (Fan 1993) and to the total production of C₃ grasses in the Great Plains (Epstein et al. 1997). Fine-textured soils could be advantageous to C₃ species, by holding more water than coarse-textured soils during the C₃ growing season when evaporative demand is low (Barnes & Harrison 1982; Lane 1995). Under moist microclimatic conditions, the higher water holding capacities of clay soils also yield greater nitrogen mineralization rates (Van Veen et al. 1985; Schimel & Parton 1986). High nitrogen turnover could lead to increased productivity for C₃ species with high tissue nitrogen demand (Wedin & Tilman 1990).

C₄ grasses dominate in the southern and eastern portions of the Great Plains. C₄ shortgrasses dominate in the southwestern portion of the region with a decrease in production to the north where temperatures are cooler and to the east as precipitation increases. Decreases in the productivities of C₄ shortgrasses with increasing precipitation are likely due to competition with taller grasses (Epstein et al. 1996). C₄ tallgrasses are found in the eastern portion of the Great Plains, and their north-south distributions in the United States range from North Dakota to Texas.

MAT was present in 75% of the significant models for C₄ species and was the most important factor in 42% of the models. The models where MAT was the most explanatory variable were either for shortgrasses or mid-height grasses. MAT was positively related to the production of 4 out of 6 C₄ shortgrasses analyzed and *Bouteloua curtipendula*, a C₄ mid-height grass common in the southern mixed prairie. An exception was *Bouteloua gracilis*, a C₄ bunchgrass which dominates in most of the shortgrass steppe and is important over much of the northern and southern mixed prairies (Lauenroth & Milchunas 1992; Coupland 1992). *B. gracilis* had maximum production at intermediate values of MAT. *Calamovilfa longifolia*, a dominant grass in the sandhills region of Nebraska, also had maximum production at intermediate MAT. *Hilaria jamesii*, a C₄ shortgrass common in the southwest, did not have a significant relationship with MAT.

None of the C₄ tallgrasses had MAT as the most explanatory factor. *Andropogon gerardii* and *Panicum virgatum* were most abundant at intermediate values of MAT; these MAT values are found geographically in eastern Kansas and Oklahoma. Production of these C₄ species presumably decreased to the north due to decreasing temperatures, and to the south because of high evapotranspiration and competition from woody species. *Schizachyrium scoparium* and *Sorghastrum nutans*, the other two C₄ tallgrasses analyzed, did not have significant relationships with MAT.

MAP was present in 71% of the significant models for C₄ grasses and was the most explanatory variable in 50% of the models. MAP was negatively correlated with the production of 4 out of 6 C₄ shortgrasses. This is likely because taller species are able to replace the shortgrasses as MAP increases, due to their greater ability to compete for light or nitrogen (Tilman 1988; Lauenroth & Coffin 1992; Olff 1992). *Bouteloua gracilis* was the only shortgrass species that had MAP as the most important factor in its models. *Hilaria belangeri* and *Hilaria mutica* did not have significant relationships with MAP. For mid-height C₄ species, *Calamovilfa longifolia* did not have a significant relationship with MAP, and *Bouteloua curtipendula* had maximum relative production at intermediate MAP.

MAP was the most important factor in the models for all four C₄ tallgrasses analyzed. MAP was positively related to the production of *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium* and *Sorghastrum nutans*. Productivity patterns of C₄ tallgrasses are similar to patterns of MAP and total ANPP in the region, increasing from west to east. It is

therefore not surprising that MAP was the most explanatory variable in the models for these species.

Soil texture variables were significant in 50% of the models of C₄ species. The most common correlation was a positive relationship with SAND. SAND was the most important variable for *Calamovilfa longifolia* and was positively related to the production of this species. Additionally, SAND was positively associated with the production of two C₄ tallgrasses, *Panicum virgatum* and *Sorghastrum nutans*. Coarse-textured soils hold soil water further down in the soil profile, potentially below the rooting zone of shallow-rooted species, where deeper-rooted species can take advantage of it (Noy-Meir 1973). The production of *Buchloë dactyloides*, a relatively shallow-rooted species was negatively related to SAND. Relative production of *Bouteloua curtipendula* was also negatively associated with sand content, and CLAY had a positive effect on the relative production of *Hilaria belangeri*. Total production of C₄ grasses has been shown to be positively related to sand content in eastern Colorado (Fan 1993) and throughout the Great Plains (Epstein et al. 1997).

Analysis of models

The relationships between species productivities and the three environmental factors used in the analysis were highly variable. Compared to relationships found in a separate study when species were grouped into C₃ and C₄ functional types (Epstein et al. 1997), the associations were relatively weak. Coefficients of determination ranged from 0.04 for the production of *Hilaria jamesii*, a C₄ shortgrass common in the southwestern Great Plains, to 0.77 for the absolute production of *Andropogon gerardii*, a dominant C₄ tallgrass. Only 7 of the 22 species analyzed had over 50% of the variation in relative production explained by these variables, and only 5 species had over 50% of absolute production explained.

The species that had the most variation in production explained by these models were C₄ tallgrasses and mid-height grasses, and two dominant C₃ grasses, *Agropyron smithii* and *Stipa comata*. Much of the variation in ANPP in the Great Plains is accounted for by MAP (Sala et al. 1988). Productivity patterns of C₄ tallgrasses correspond spatially to patterns of MAP and ANPP, all increasing from west to east. It is therefore reasonable that the environmental factors used in this analysis, especially MAP, would be related to the production of C₄ tallgrasses. Tallgrasses, in general, are not tolerant of dry conditions and tend to dominate in

humid regions, where they can outcompete shorter species for sunlight or nitrogen (Tilman 1988; Lauenroth & Coffin 1992).

In general, the species with the strongest relationships were those that attain dominance in at least one of the major grassland types. Dominant C₃ species in the northern mixed prairie, such as *Agropyron smithii* and *Stipa comata*, achieve greater production and have more extensive ranges than less important C₃ species (Coupland 1992). They should therefore be expected to have stronger relationships than less widespread species with the coarse environmental variables used in this analysis.

There could be several explanations for the weak relationships. The productivity patterns of species may not be largely controlled by climate at the regional scale. Brown & Gersmehl (1985) found that migration dynamics explained the spatial patterns of species in the Great Plains better than climate. Additionally, the environmental factors examined in this study are relatively coarse; the temporal patterns of growing season rainfall, maximum and minimum temperatures, or soil moisture status might be better indicators of the productivities of C₃ or C₄ species (Hattersley 1983; Cavagnaro 1988; Briggs & Knapp 1995). The functions relating species production to environmental factors may also not be completely captured by linear and quadratic terms. While these terms illustrate the important trends, they may not yield high coefficients of determination. Last, and potentially most important, is that the weakest relationships were found for the species with lowest abundances. It is a general problem that there is greater uncertainty associated with less abundant species. It is also possible that less common species are influenced less by spatial variability in climate than more abundant species (Collins & Glenn 1990).

Many of the species in this study show the same general relationships with environmental variables that are exhibited by the functional group to which they belong (Epstein et al. 1997). There are however exceptions; species or subtypes may have distinct productivity patterns that do not coincide with the patterns of their associated functional group (Ellis et al. 1980; Hattersley 1983). One important example illustrated here is the divergence of C₄ shortgrasses and C₄ tallgrasses in their relationships with temperature, precipitation and soil texture. C₄ shortgrass species had relationships with soil texture and precipitation opposite those of total C₄ grasses (Epstein et al. 1997). While total production of C₄ grasses is positively related to MAT

(Epstein et al. 1997), productivities of C₄ tallgrass species either had maxima at intermediate MAT or were not significantly related to MAT. This study provides a framework for the extent to which functional types should be used to represent individual species.

Conclusion

MAT and MAP were important in explaining the productivity patterns of many plant species in the Great Plains; soil texture variables were less important. Some common trends were found in these relationships. MAT was generally the most important variable in the models for C₃ species. Production of C₃ species commonly decreased with MAT and MAP. The most common relationships between C₃ species and soil texture were either a positive relation with clay content or a negative association with sand.

MAT was also the most important variable in the models for C₄ shortgrasses. Production of C₄ shortgrasses was, in general, positively related to MAT and negatively related to MAP. C₄ shortgrasses and mid-sized grasses most commonly had negative relationships with sand content. MAP was the most important variable in explaining the production of C₄ tallgrasses. C₄ tallgrasses were positively related to MAP, and were most productive at intermediate values of MAT or were not significantly related to MAT. The most common relation between C₄ tallgrasses and soil texture was a positive relationship with sand content.

The models derived in this study express the influence of both physiology and competitive interactions on species productivities in response to regional-scale environmental factors. Although quite simple, these models can be used to hypothesize how changes in the environment could potentially alter plant communities throughout the Great Plains.

Acknowledgements

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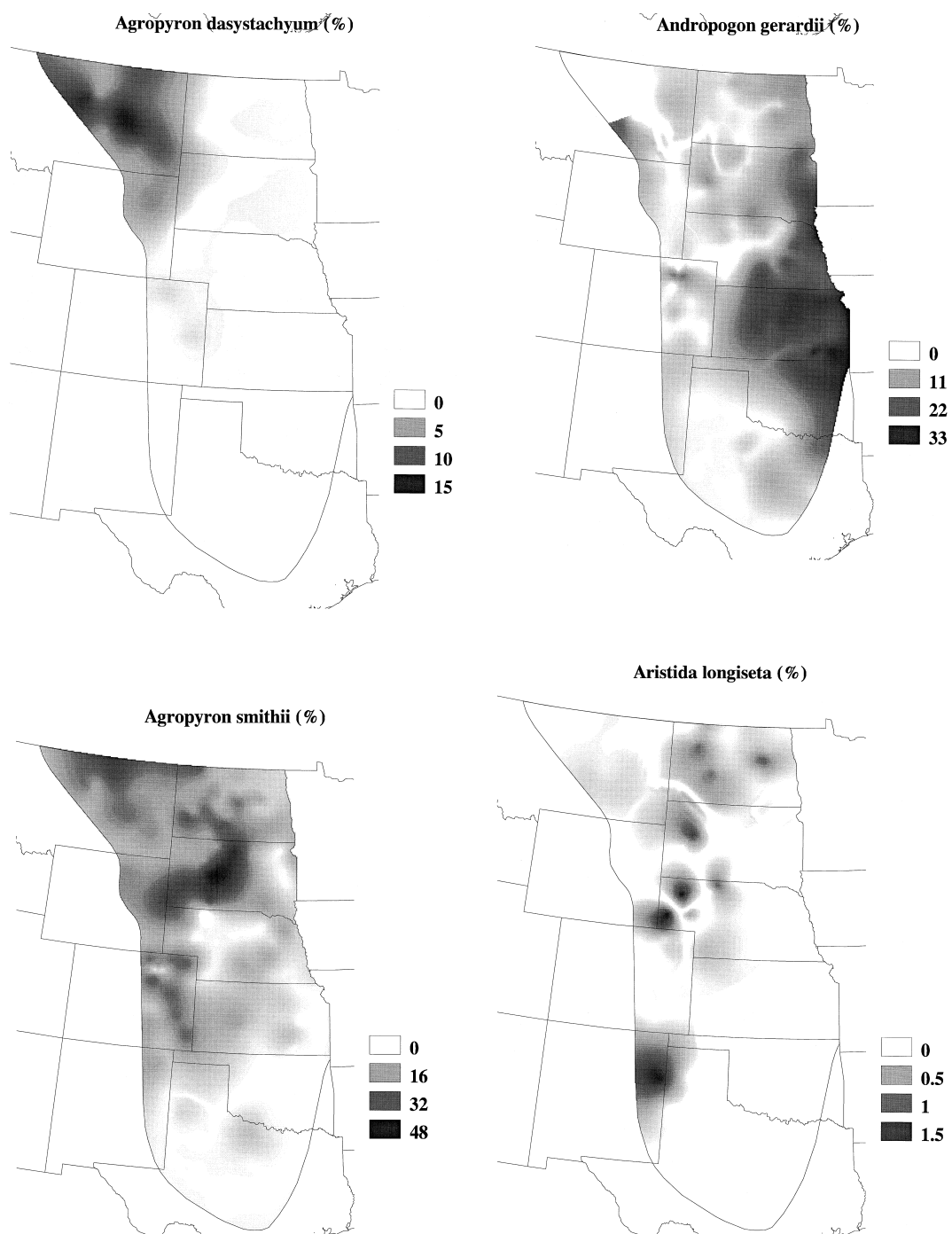
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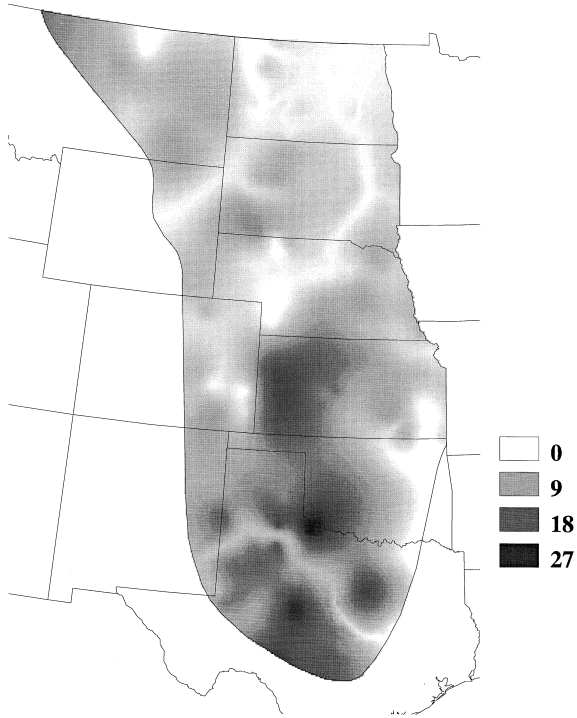
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Appendix A.

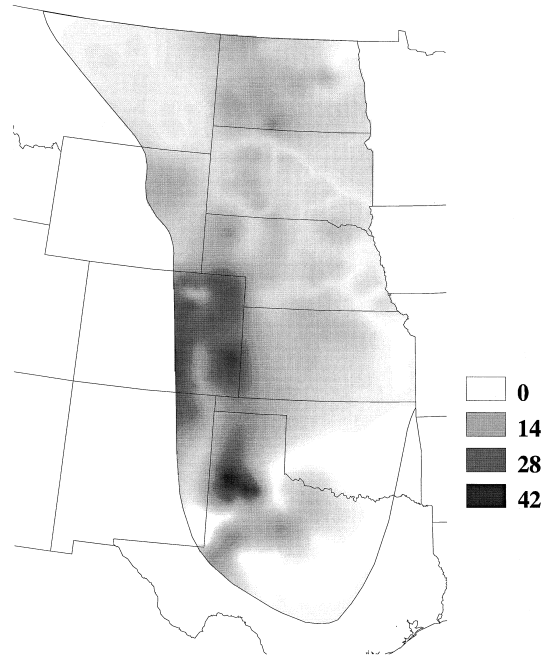
Maps of relative (%) and absolute (g m^{-2}) production of plant species in the Great Plains from NRCS range site descriptions.



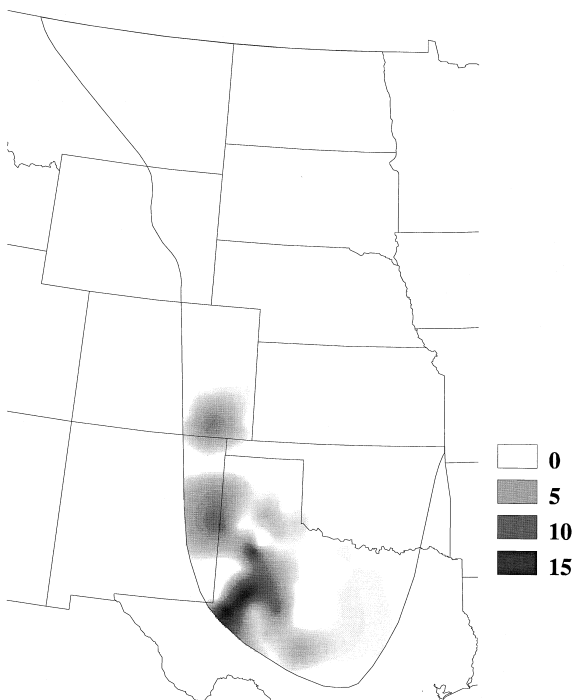
***Bouteloua curtipendula* (%)**



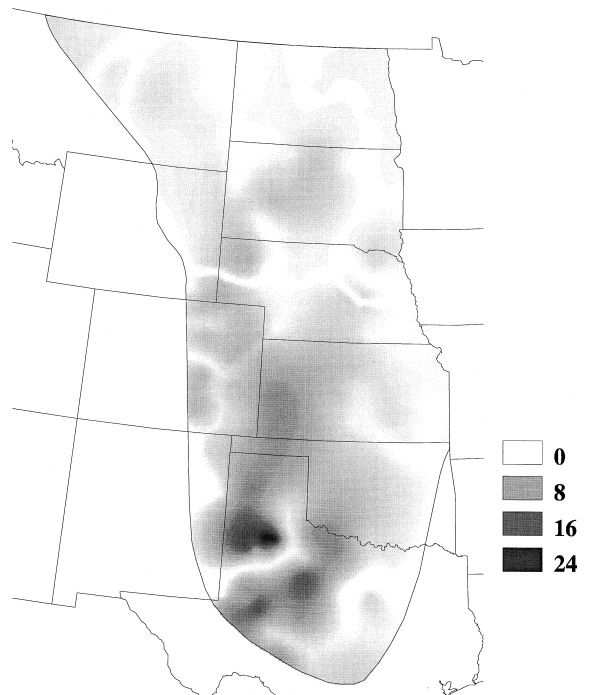
***Bouteloua gracilis* (%)**



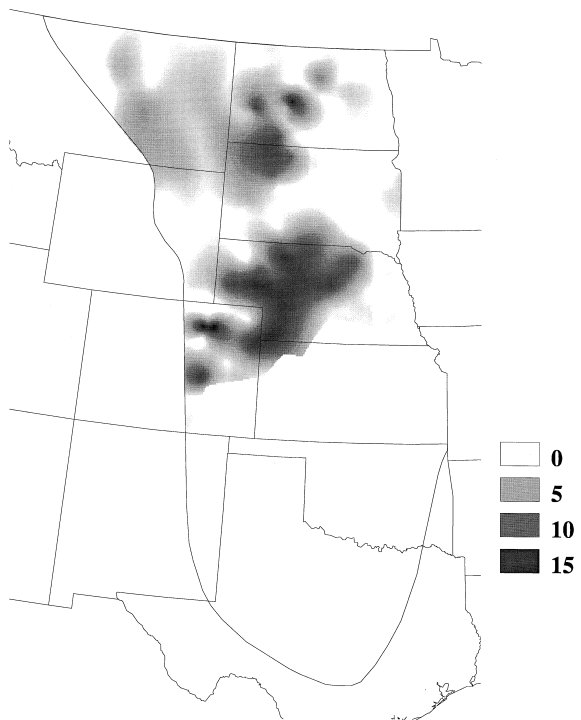
***Bouteloua eriopoda* (%)**



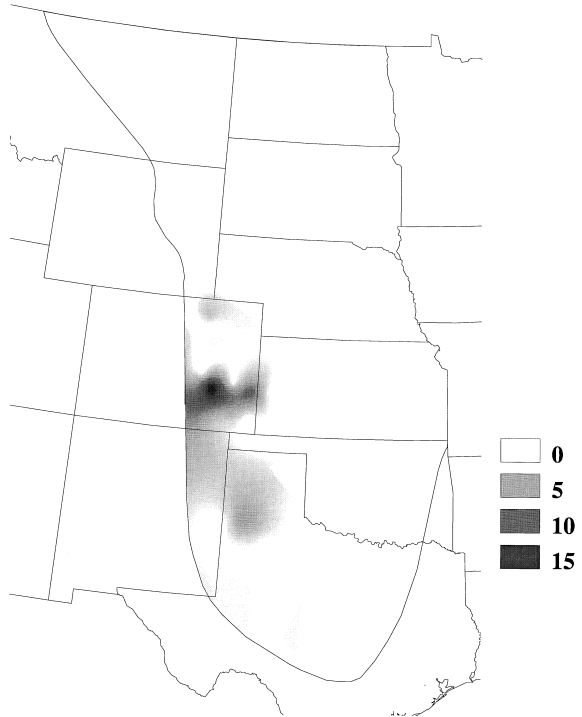
***Buchloe dactyloides* (%)**



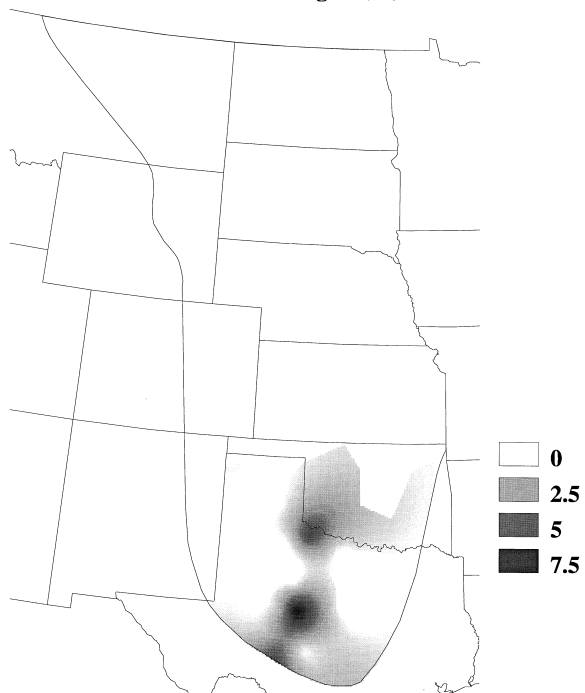
Calamovilfa longifolia (%)



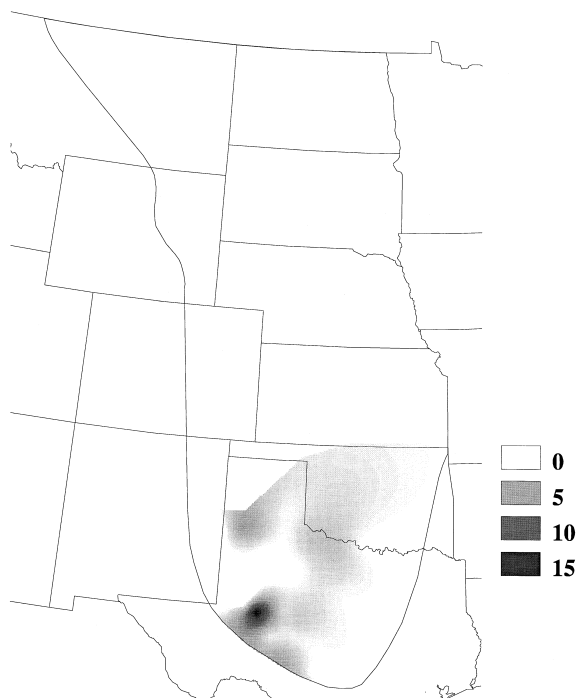
Hilaria jamesii (%)



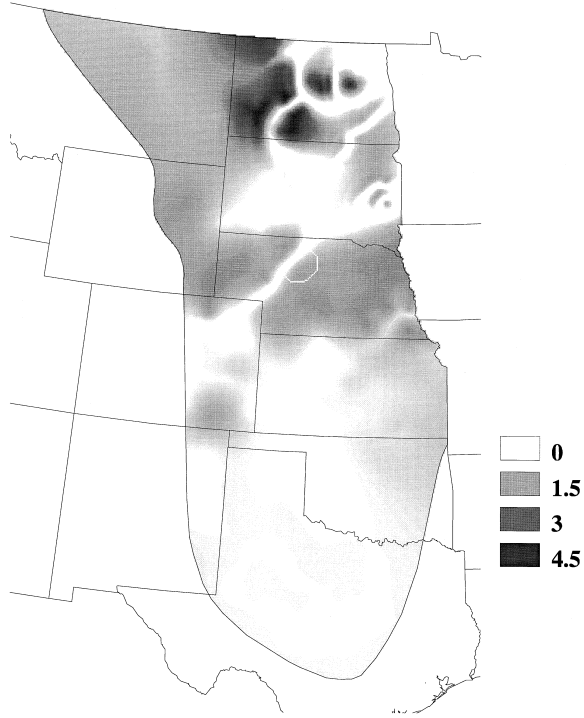
Hilaria belangeri (%)



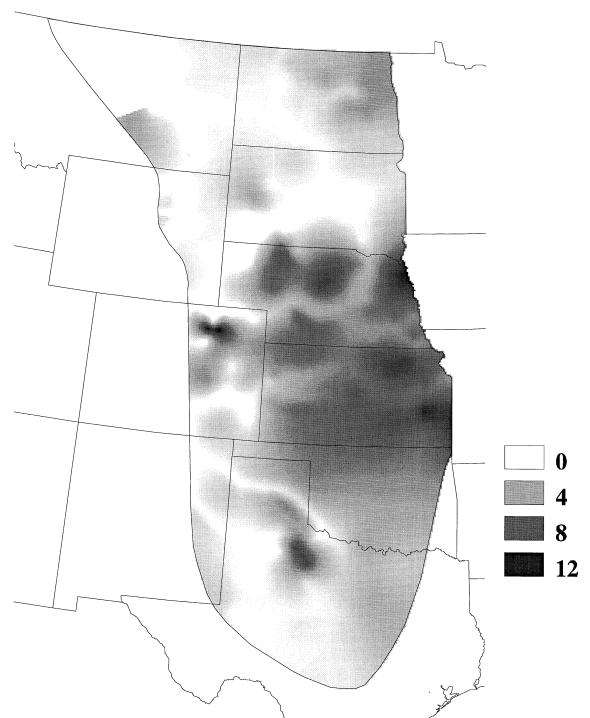
Hilaria mutica (%)



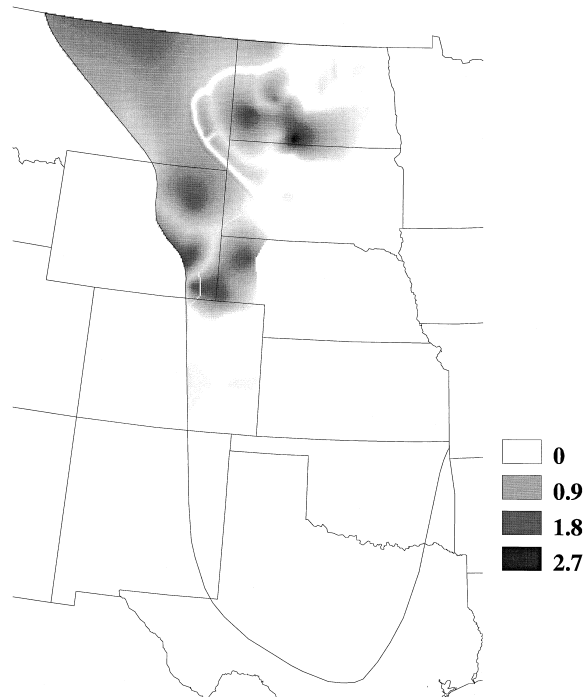
***Koeleria pyramidata* (%)**



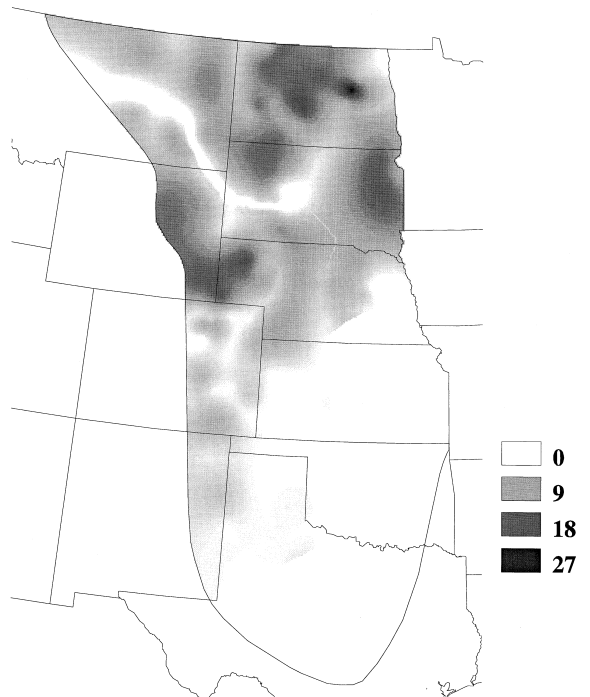
***Panicum virgatum* (%)**



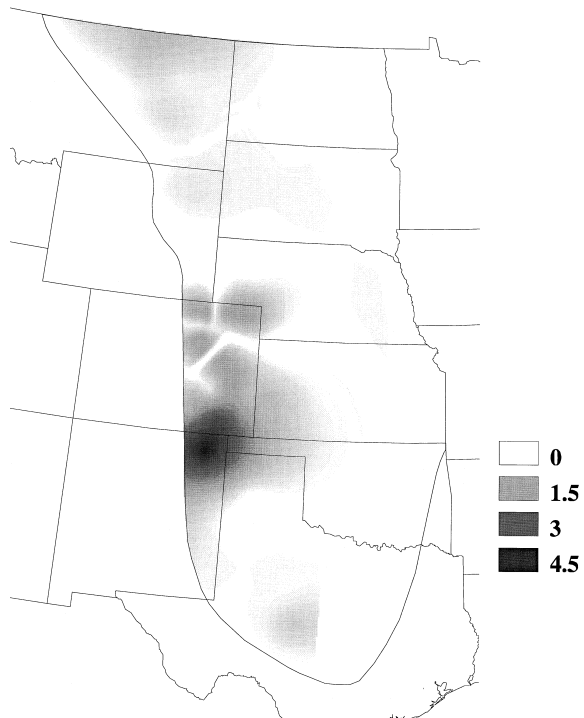
***Poa secunda* (%)**



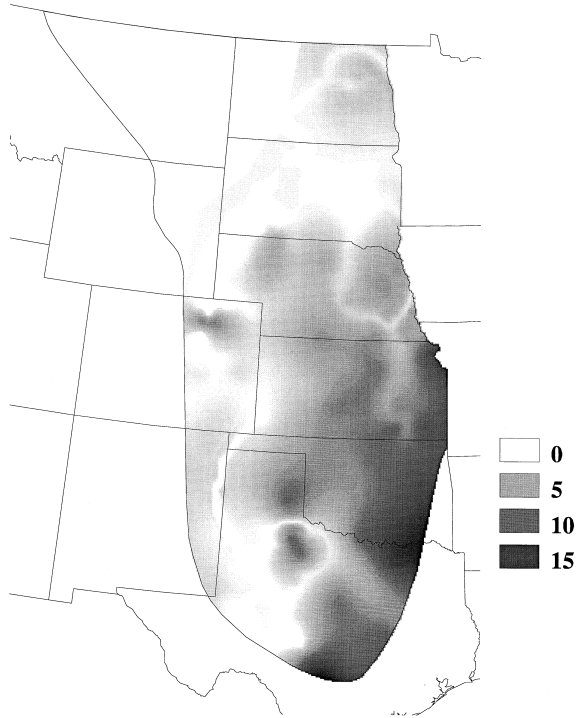
***Stipa comata* (%)**



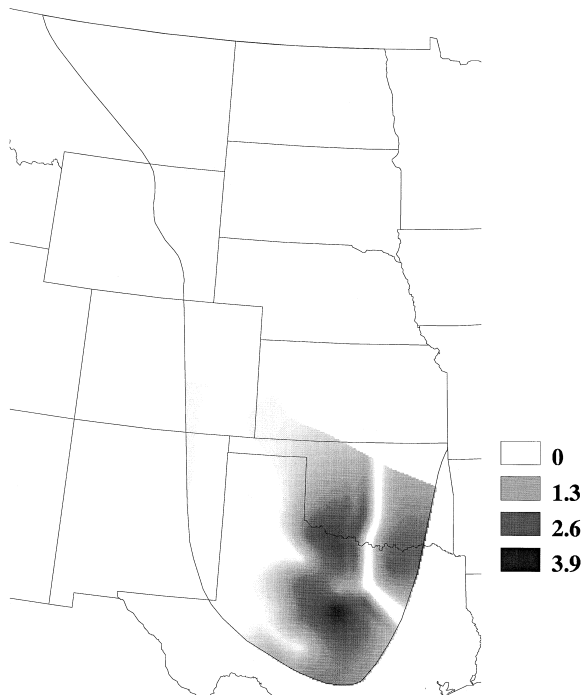
***Sitanion hystrix* (%)**



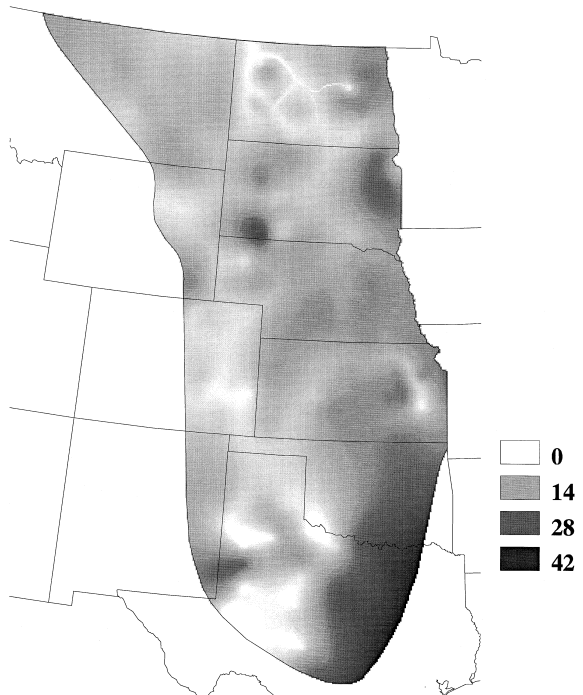
***Sorghastrum nutans* (%)**



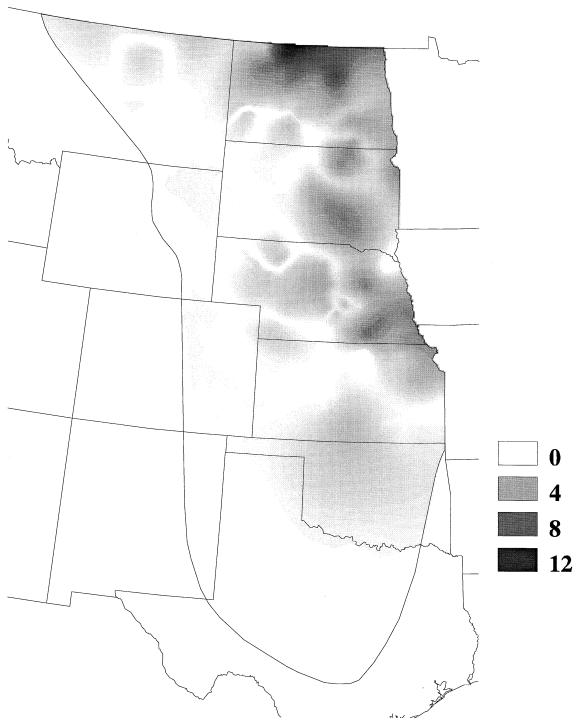
***Stipa leucotricha* (%)**



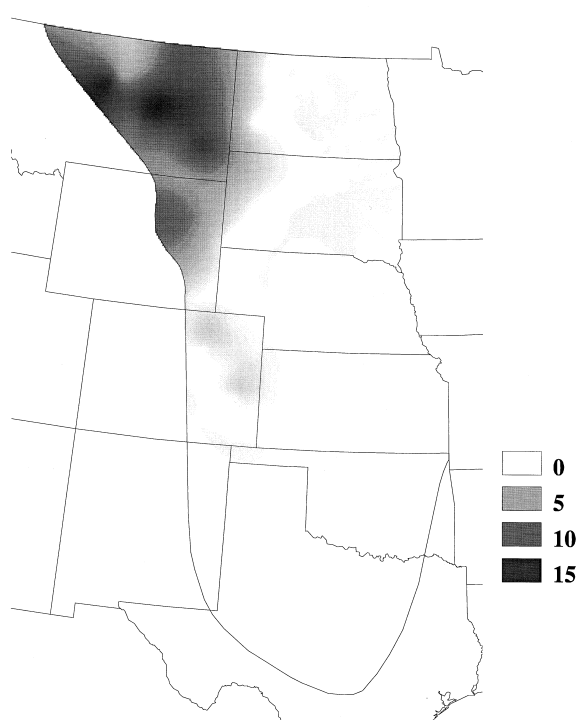
***Schizachyrium scoparium* (%)**



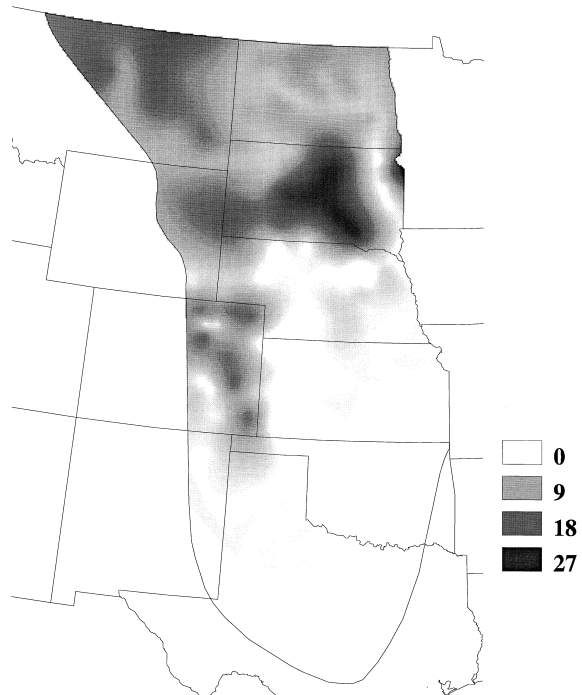
Stipa spartea (%)



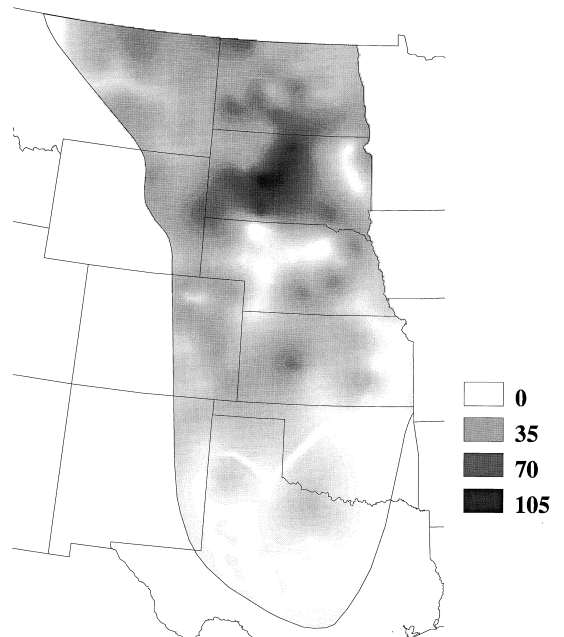
Agropyron dasystachyum (g/m²)



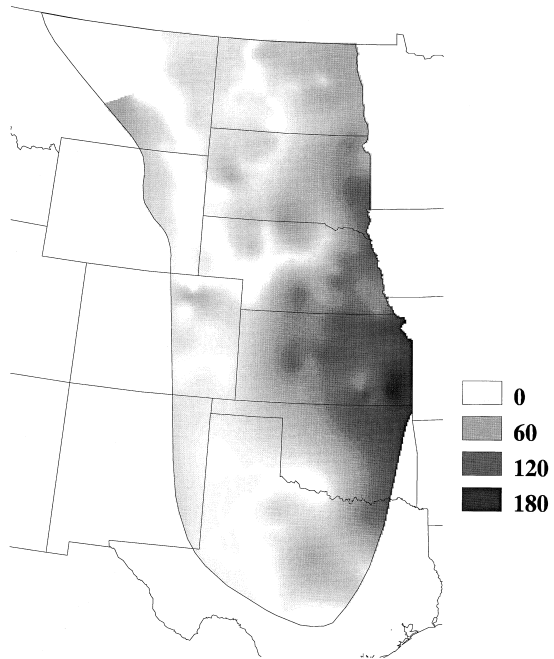
Stipa viridula (%)



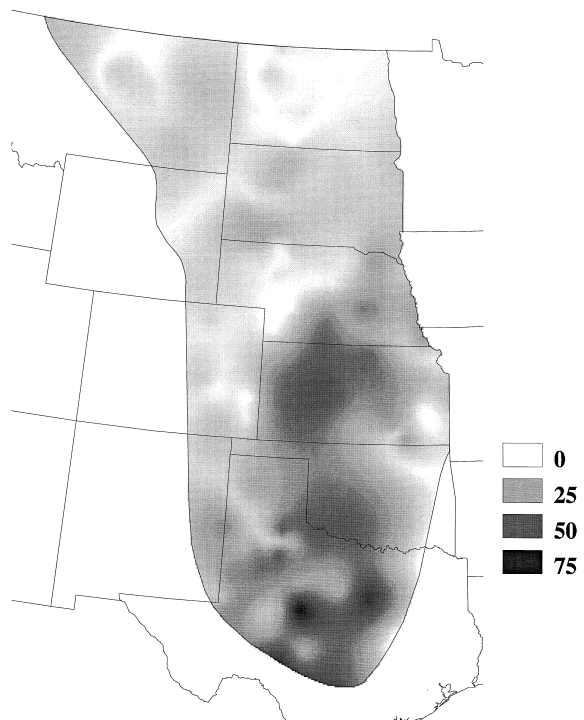
Agropyron smithii (g/m²)



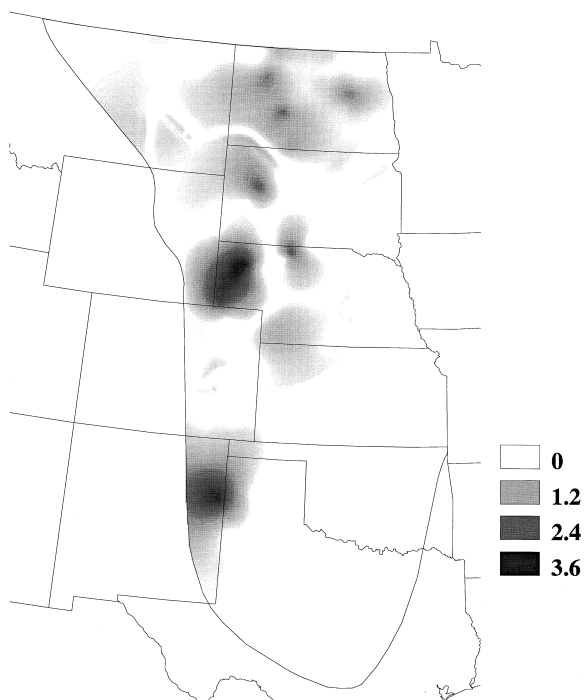
***Andropogon gerardii* (g/m²)**



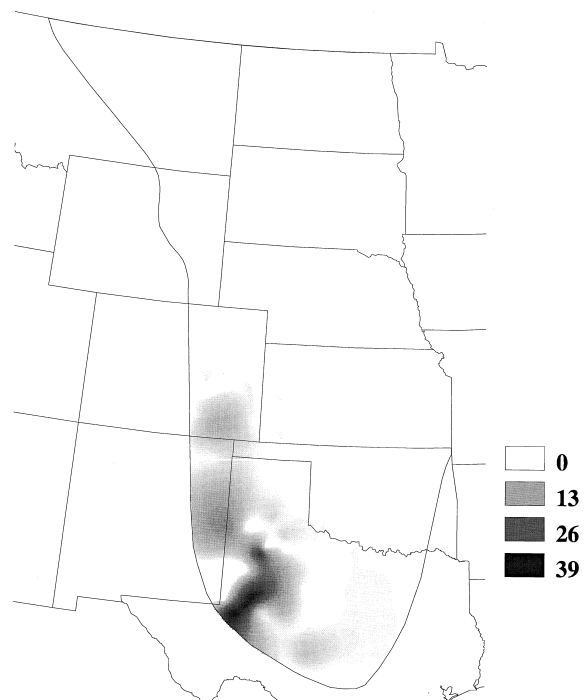
***Bouteloua curtipendula* (g/m²)**



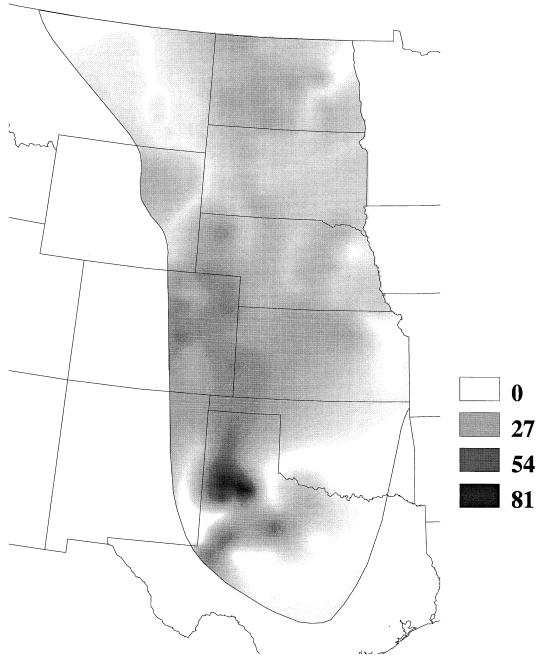
***Aristida longiseta* (g/m²)**



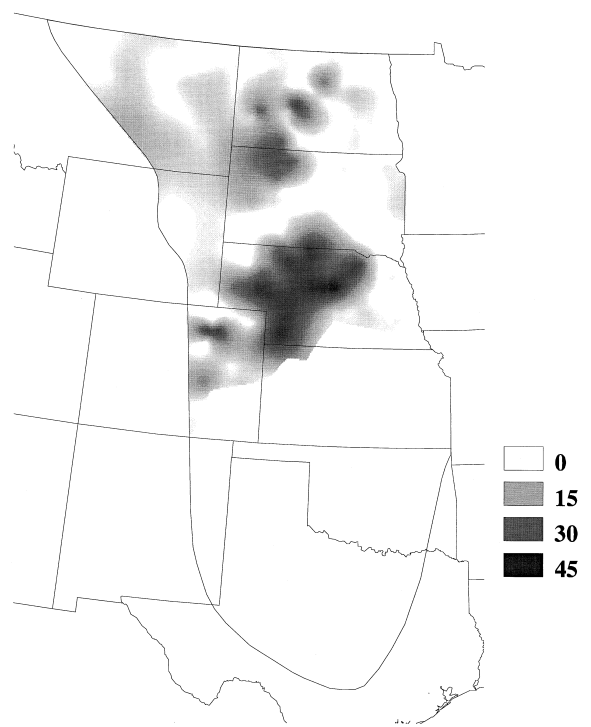
***Bouteloua eriopoda* (g/m²)**



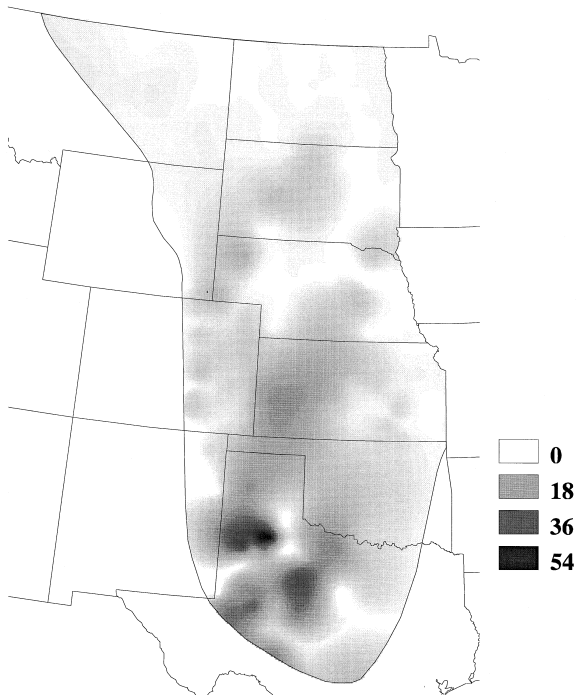
***Bouteloua gracilis* (g/m²)**



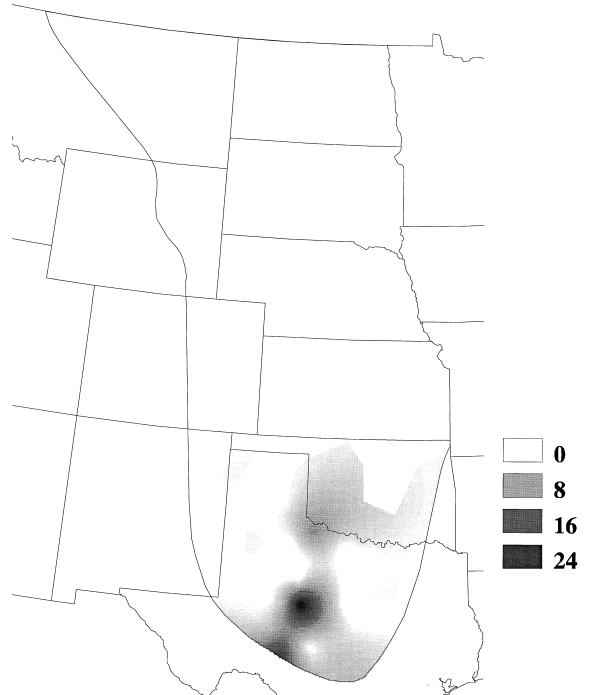
***Calamovilfa longifolia* (g/m²)**



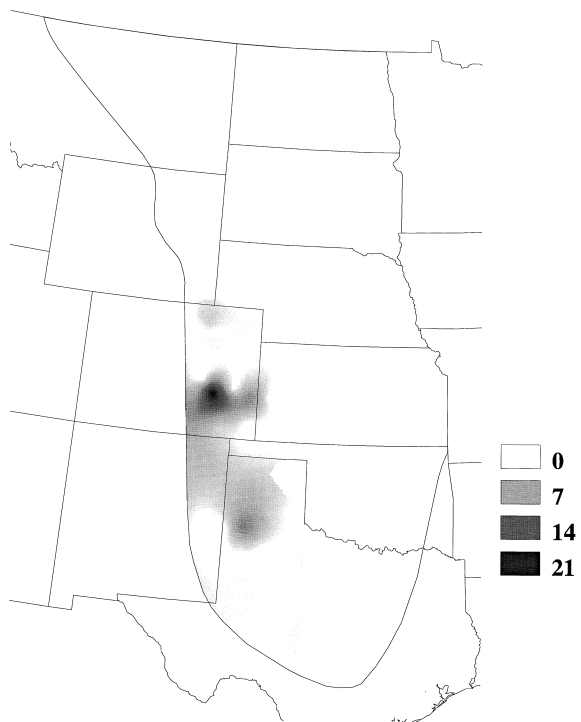
***Buchloe dactyloides* (g/m²)**



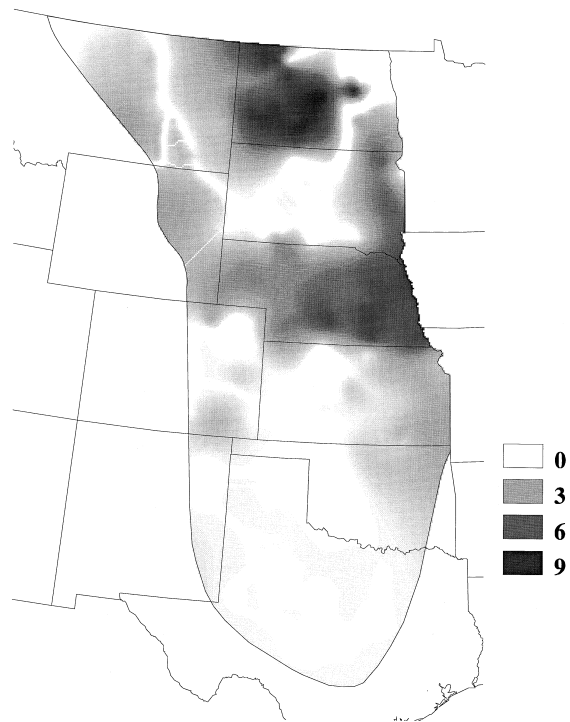
***Hilaria belangeri* (g/m²)**



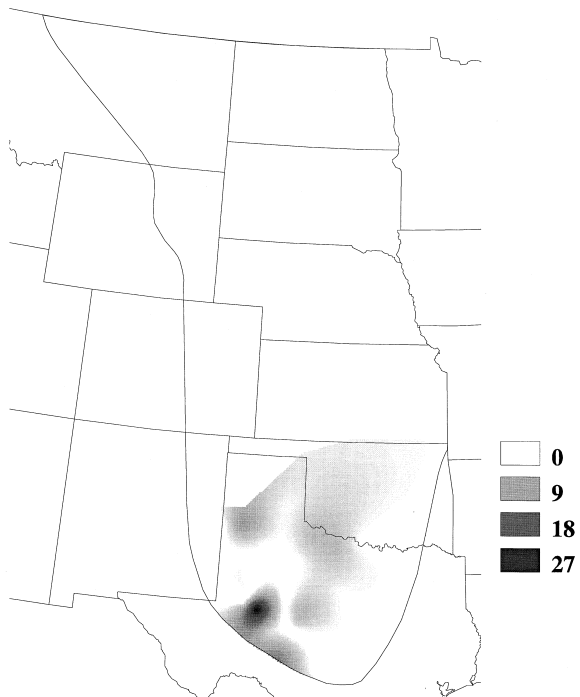
***Hilaria jamesii* (g/m²)**



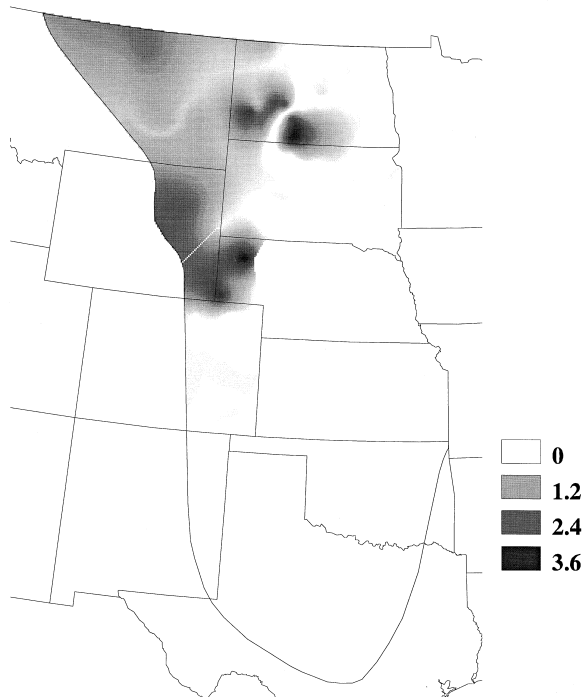
***Koeleria pyramidata* (g/m²)**



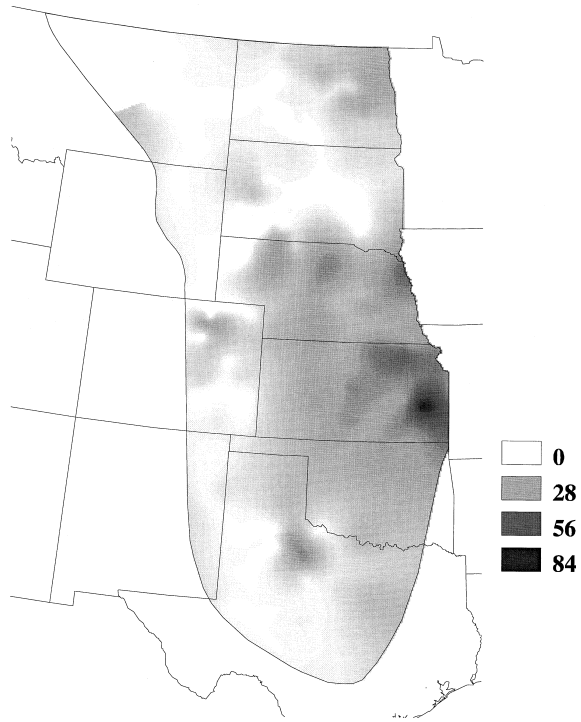
***Hilaria mutica* (g/m²)**



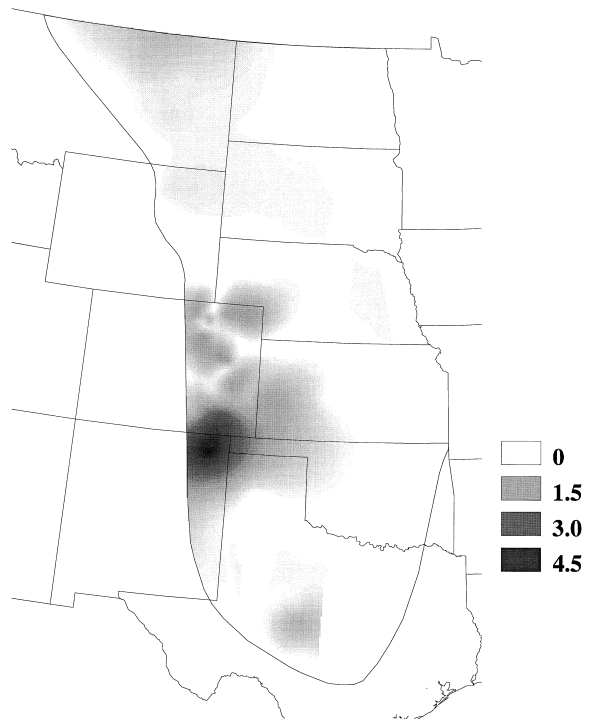
***Poa secunda* (g/m²)**



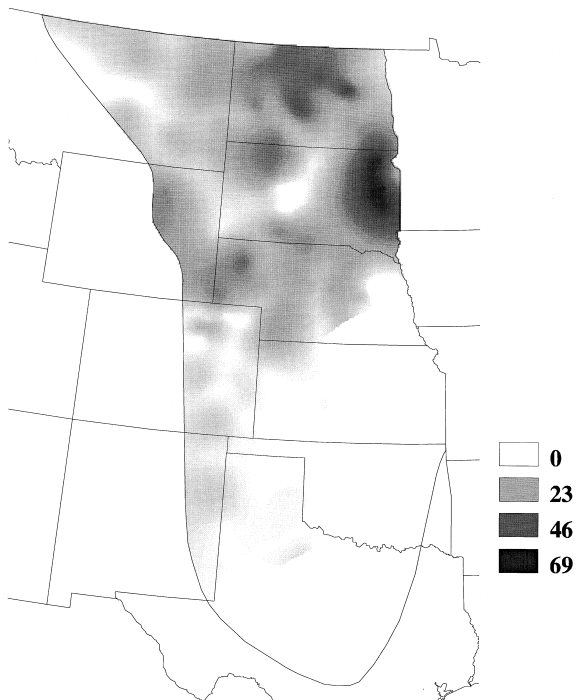
***Panicum virgatum* (g/m²)**



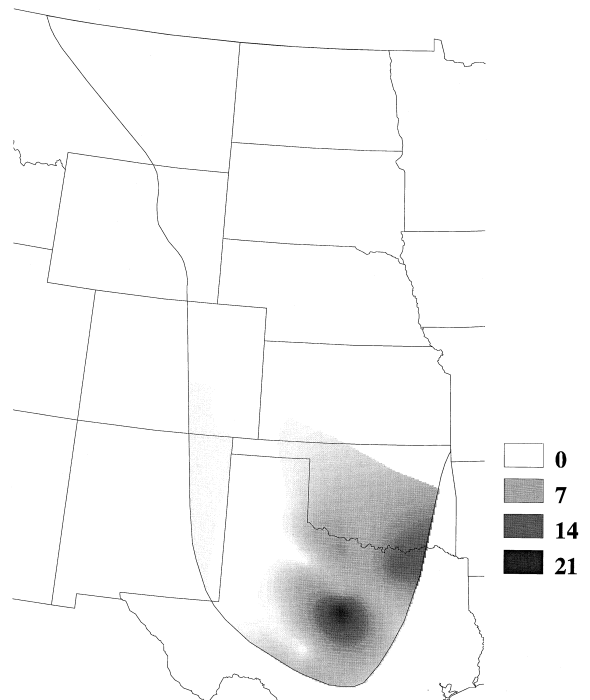
***Sitanion hystrix* (g/m²)**



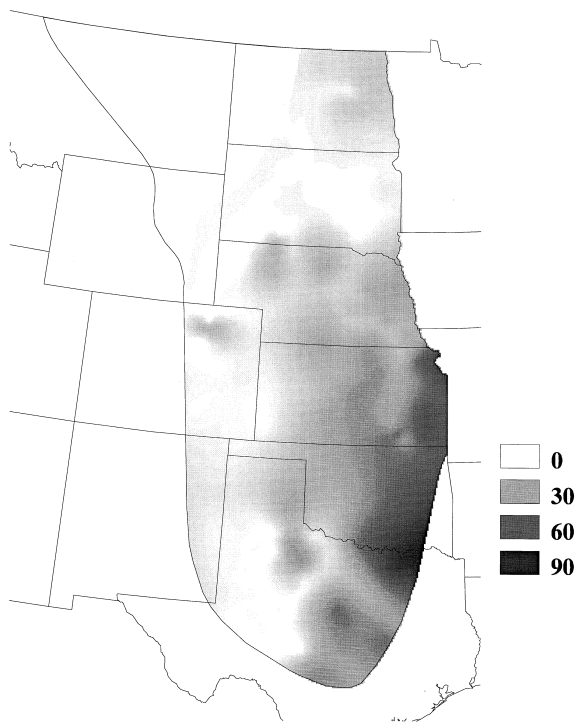
***Stipa comata* (g/m²)**



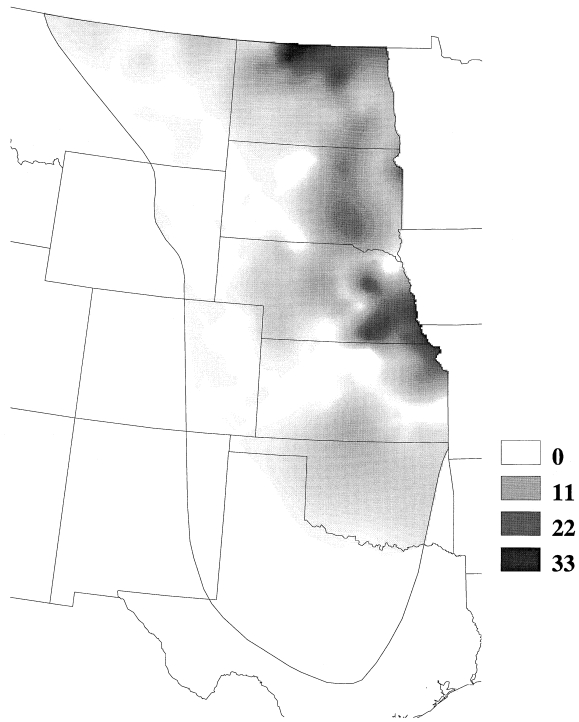
***Stipa leucotricha* (g/m²)**



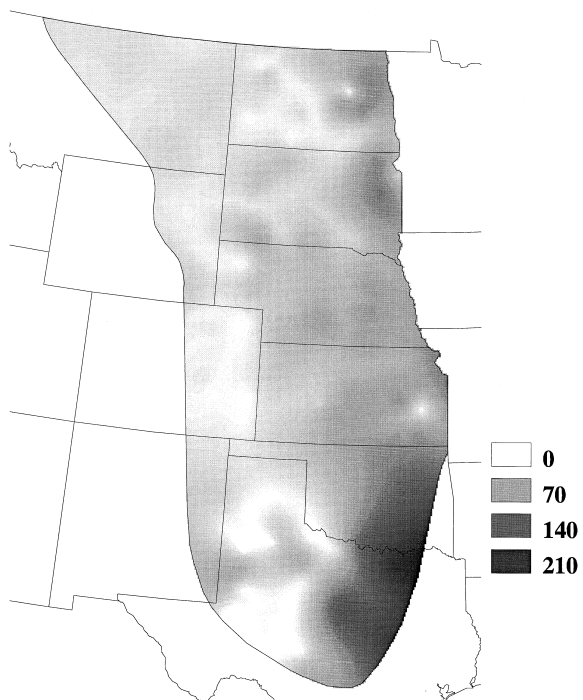
Sorghastrum nutans (g/m²)



Stipa spartea (g/m²)



Schizachyrium scoparium (g/m²)



Stipa viridula (g/m²)

