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RELATIVE ABUNDANCE OF PLANT FUNCTIONAL TYPES IN GRASSLANDS AND SHRUBLANDS OF NORTH AMERICA¹

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Abstract. We analyzed the geographic distribution and climatic controls of the distribution of plant functional types (PFT) in temperate grasslands and shrublands of North America. It has been widely accepted that temperature is the principal control on the distribution of C₃ and C₄ species. Our results show that precipitation and its seasonal distribution are also important. C₄ grass distribution was positively related to three climatic variables: mean annual precipitation, mean annual temperature, and the proportion of the precipitation falling in summer. These variables accounted for 66% of the total variability of this functional type. C₃ grass abundance decreased with mean annual temperature and increased with the proportion of the precipitation falling during winter ($r^2 = 0.37$). Sixty-two percent of the variability in the relative abundance of shrubs was explained by mean annual precipitation and the proportion of winter precipitation.

Latitude and longitude explained a substantial portion of the variability of the distribution of the relative abundance of shrubs, C₃ grasses, and C₄ grasses (53, 46, and 61%, respectively). Along a given longitude, C₃ grasses increased with latitude. As one moves westward, C₄ grasses are replaced by shrubs. The relative abundance of C₄ grasses reached a maximum at southern latitudes and eastern longitudes. Succulents showed a marginal decreasing trend with latitude. No relationship with geographic variables was detected for forbs.

Key words: biogeography; C₃ and C₄ grasses; climatic controls; plant functional types (PFT); shrubs.

INTRODUCTION

A common characteristic of most environmental problems that the world confronts at the end of the 20th century is their large spatial scale. Predictive models developed at the site level are not easily scaled up to the regional or global level. Intersite comparisons are a powerful tool for constructing models of the patterns of structure or function of ecosystems at large scales (Peters et al. 1991). Regional analyses of the controls on aboveground primary production and soil carbon storage and loss in the central grassland region of North America (Sala et al. 1988, Burke et al. 1989b), and of the determinants of herbivore biomass in Africa and South America (McNaughton et al. 1989, Oesterheld et al. 1992), are good examples of this approach. Several models relating climate and vegetation have been developed at a global scale (Holdridge 1947, Box 1981, Prentice et al. 1992), but regional models have received less attention.

A group of species that share traits (morphological and physiological attributes) and play a similar role in

an ecosystem can be referred to as a functional type (Hawkins and MacMahon 1989), a guild (Root 1967), or a functional group (Lauenroth et al. 1978). Plant functional types (PFT) provide a logical link between physiological and life history strategies at the plant level and processes at the ecosystem level (Chapin 1993). The definition of PFT is currently receiving a lot of attention in ecology (Walker 1992, Leishman and Westoby 1992, Boutin and Keddy 1993, Golluscio and Sala 1993, Chapin 1993).

Previous studies of the regional distribution of PFTs has focused on C₃ and C₄ plants (Teeri and Stowe 1976, Stowe and Teeri 1978, Hattersley 1983). One exception is the analysis of Cook and Irwin (1992), who studied the distribution of shrubs, graminoids, and forbs in relation to climatic variables in the western Great Plains and the eastern portion of the Great Basin. Other studies have analyzed the distribution of C₃ and C₄ grasses, but at local scales (i.e., Werger and Ellis 1981). Many authors have analyzed the distribution of these functional types along elevation gradients (Chazdon 1978, Meinzer 1978, Tieszen et al. 1979, Boutton et al. 1980, Rundel 1980, Cavagnaro 1988). Epstein (1995) analyzed the climatic controls on primary production of C₃ and C₄ grasses on the Central Grasslands of USA. Except for the studies by Boutton et al. (1980) and Epstein (1995), all of these analyses have been based

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on the number, or the proportion, of C_3 and/or C_4 species in the local floras. The number of species is a poor indicator of the abundance of a particular PFT. For example, at the Central Plains Experimental Range in Northcentral Colorado (USA), C_3 grasses account for 59% of the total number of grass species, however they only account for 10% of grass biomass (see Appendix).

The objectives of our study were to analyze: (1) the geographic distribution of PFTs in temperate grasslands and shrublands of central North America, and (2) the climatic controls of their regional distribution. The analyses were based on field estimates of relative abundance of each PFT. The hypothesis underlying the analyses is that resource levels control the relative abundance of PFT, and that for grasslands and shrublands climate is the main determinant of resource availability at a regional scale. We expect that the quantitative relationships between climate and the relative abundance of PFTs will provide a tool to generate maps of their potential distribution.

We defined PFTs based on morphological, structural, and functional attributes: shrubs, C_3 grasses, C_4 grasses, succulents, and forbs (nongraminoid herbs). The differentiation between C_3 and C_4 plants is important in the framework of global change because their responses to CO_2 and climate change are different (Ehleringer 1978, Carson and Bazzaz 1982, Carter and Peterson 1983, Pearcy and Ehleringer 1984, Curtis et al. 1990, Polley et al. 1992, 1993, Kimball et al. 1993). Despite the fact that separation into C_3 and C_4 species could be useful for shrubs and forbs, the lack of data prevented this differentiation.

METHODS

We selected 73 sites across the temperate zone of central North America, from 119.55° to 93.20° W longitude and from 29.58° to 52.13° N latitude (Fig. 1). This region includes most of the grasslands and shrublands of the continent. To be included in the analyses sites had to be areas with relatively low human impact (National Parks, National Grasslands, Experimental Stations, research sites, etc.). Also, the sites were selected based on the availability of actual vegetation data. We discarded azonal vegetation, such as wetlands or halophilous communities. The species from each site were classified into the different functional types. We classified grass species into C_3 and C_4 categories on the basis of the photosynthetic pathways in the different tribes of the Poaceae (Smith and Brown 1973, Tieszen et al. 1979, Gould and Shaw 1983). We classified dicot species as shrubs or forbs according to the information presented in McGregor and Barkley (1986) and Stubbendieck et al. (1992). The succulent functional type included the species of the Cactaceae family. Relative importance values (Appendix) were calculated as the proportion of total plant cover, biomass, or above-ground primary production data corresponding to each PFT. Within the context of our objectives we assumed

that the relative importance values derived from these three indicators of the abundance were equivalent (Heitschmidt et al. 1985, Lauenroth et al. 1986, Yong-Hong 1989).

For each site, we obtained the geographic coordinates and climatic data for the nearest weather station. The climatic variables were mean annual temperature (MAT), mean annual precipitation (MAP), thermal amplitude (AMP) (temperature in July minus temperature in January), and the proportion of the precipitation that falls in the periods December–February (DJF/MAP) and June–August (JJA/MAP). These variables were calculated from long-term averages of monthly values of maximum and minimum temperature, and precipitation, taken from the Earthinfo (1993) climatic database. The selected sites cover a range of MAT from 2°C to 21.2°C and a range of precipitation (MAP) from 117 to 1011 mm (Appendix).

The relative abundances of the five functional types were the dependent variables in two stepwise regression analyses (Kleinbaum and Kupper 1978). One of the regression analyses included geographic coordinates (latitude and longitude) and their quadratic and logarithmic transformations as independent variables. The other analysis included the climatic variables, their quadratic and logarithmic transformations, and the two-way interactions among the untransformed MAT, MAP, and AMP. For C_3 and C_4 grasses we included a dummy variable representing the biome (grassland = 1 or shrubland = 2). Sites were classified as grassland or shrubland according to Küchler's map (Küchler 1964). The boundary between grasslands and shrublands roughly corresponded to a proportion of shrubs of 20%. To analyze possible biases associated with the points included in the analyses, we randomly selected 7 of the 73 points, removed them from the data set, and recalculated the regression models. We repeated this procedure five times. We compared the coefficient of determinations, the y intercepts, and the coefficients of each of the variables included in the models for the five subsets of data ($n = 66$) and for the complete data set ($n = 73$) for C_4 grasses, C_3 grasses, and shrubs.

A map of the potential distribution of three of the functional types (shrubs, C_3 grasses, and C_4 grasses) was generated from the regression models and a climatic database (Leemans and Cramer 1991). This database was constructed from actual climatic data for 2583 stations worldwide. Weather records were interpolated to a grid with a resolution of 0.5° of latitude and longitude. The database includes average monthly temperature, precipitation, and cloudiness. From the maps of relative abundance of each functional type (layers) we produced a false color composite image of physiognomy (proportion of functional types) displaying simultaneously the three layers. Data were processed in ARC-INFO (ESRI, Redlands, California) and ERDAS (ERDAS, Atlanta, Georgia).

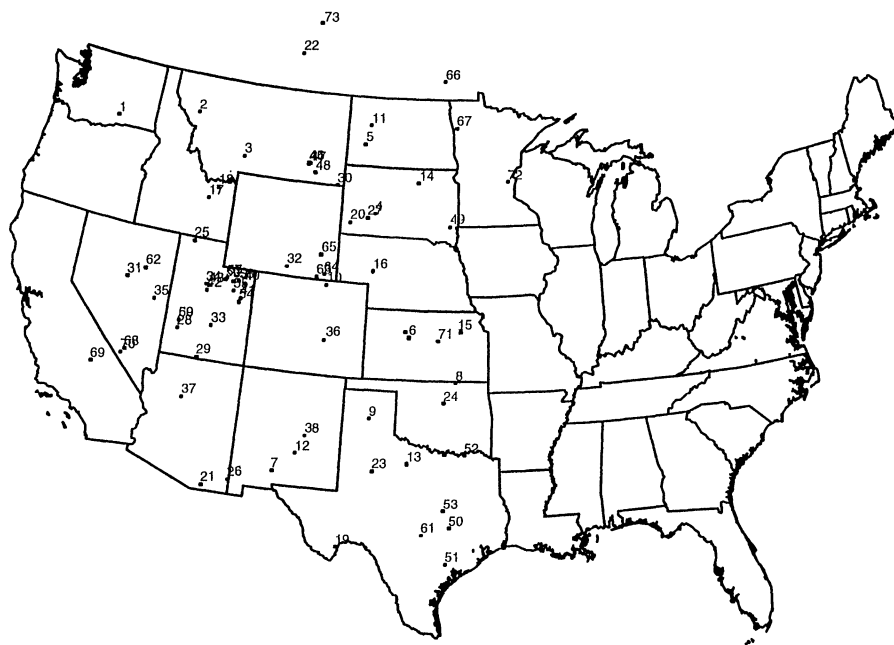


FIG. 1. Map of the study sites used in the plant functional type analyses. Latitude and longitude are expressed in centesimal degrees. The references in parentheses are to papers with descriptions of the study sites. 1. ALE, Washington, 119.55° W, 46.40° N (Sims et al. 1978); 2. Bison, Montana, 114.27° W, 47.32° N (Sims et al. 1978); 3. Bridger, Montana, 110.78° W, 45.78° N (Sims et al. 1978); 4. Cottonwood, South Dakota, 101.87° W, 43.95° N (Sims et al. 1978); 5. Dickinson, North Dakota, 102.82° W, 46.90° N (Sims et al. 1978); 6. Hays, Kansas, 99.38° W, 38.87° N (Sims et al. 1978); 7. Jornada, New Mexico, 106.75° W, 32.62° N (Sims et al. 1978); 8. Osage, Oklahoma, 96.55° W, 36.95° N (Sims et al. 1978); 9. Pantex, Texas, 101.53° W, 35.30° N (Sims et al. 1978); 10. CPER, Colorado, 104.60° W, 40.82° N (Sims et al. 1978); 11. Fort Berthold Indian Reservation, North Dakota, 102.50° W, 47.75° N (Redmann 1975); 12. Fort Stanton Experimental Ranch, New Mexico, 105.55° W, 33.48° N (Pieper et al. 1971); 13. Texas Experimental Range, Texas, 99.23° W, 33.33° N (Pluhar et al. 1987); 14. S. H. Ordway Memorial Prairie, South Dakota, 99.10° W, 45.33° N (Ode and Tieszen 1980); 15. Konza Prairie, Kansas, 96.60° W, 39.10° N (Abrams and Hulbert 1987); 16. Arapaho, Nebraska, 101.80° W, 41.55° N (Barnes et al. 1983); 17. Idaho National Engineering Laboratory, Idaho, 112.67° W, 43.73° N (Anderson and Shumar 1986); 18. U.S. Sheep Experimental Station, Idaho, 112.15° W, 44.25° N (Murray 1988); 19. Black Gap Wildlife Management Area, Texas, 102.92° W, 29.58° N (Aide and Van Auken 1985); 20. Wind Cave National Park, South Dakota, 103.45° W, 43.53° N (Forde et al. 1984); 21. Appleton-Whittel Research Ranch, Arizona, 110.50° W, 31.60° N (Bock et al. 1984); 22. Matador, Canada, 107.72° W, 50.70° N (Singh et al. 1983); 23. Snyder, Texas, 101.18° W, 32.97° N (McPherson et al. 1988); 24. Oklahoma State University Agricultural Research, Oklahoma, 97.23° W, 36.05° N (Ewing and Engle 1988); 25. Curlew Valley, Utah, 113.08° W, 41.87° N (West 1985); 26. Portal, Arizona, 109.12° W, 32.00° N (Chew 1982); 27. Badlands National Park, South Dakota, 102.33° W, 43.75° N (Uresk 1990); 28. Escalante desert, Utah, 113.25° W, 38.17° N (Germano and Lawhead 1986); 29. Glen Canyon, Utah, 111.87° W, 37.10° N (Rasmussen and Brotherson 1986); 30. Alzada, Montana, 104.47° W, 45.03° N (MacCracken et al. 1983); 31. Grass Valley, Nevada, 116.75° W, 39.82° N (Young et al. 1986); 32. SSHA, Wyoming, 107.17° W, 41.42° N (Burke et al. 1989a); 33. Capitol Reef National Park, Utah, 111.30° W, 38.52° N (Player and Urness 1982); 34. Provo, Utah, 111.95° W, 40.17° N (Brotherson and Brotherson 1981); 35. Lowry Spring, Nevada, 114.90° W, 39.16° N (Everett and Koniak 1981); 36. El Paso, Colorado, 104.50° W, 38.55° N (Kinraide 1984); 37. Coconino County, Arizona, 112.35° W, 35.27° N (Hessing et al. 1982); 38. Lincoln County, New Mexico, 105.08° W, 34.28° N (Beavis et al. 1982); 39. Uinta Basin 1—Duchesne, Utah, 110.38° W, 40.47° N (Brotherson and Brotherson 1979); 40. Uinta Basin 2—Vernal, Utah, 109.65° W, 40.45° N (Brotherson and Brotherson 1979); 41. Uinta Basin 3—Sleep Ridge, Utah, 109.75° W, 39.88° N (Brotherson and Brotherson 1979); 42. Utah Lake Shadscale, Utah, 111.87° W, 39.92° N (Brotherson et al. 1986); 43. Utah Lake Grasewood, Utah, 111.75° W, 40.12° N (Brotherson et al. 1986); 44. Hay Coulee, Montana, 106.48° W, 45.82° N (Singh et al. 1983); 45. Kluver West, Montana, 106.48° W, 45.87° N (Singh et al. 1983); 46. Kluver North, Montana, 106.47° W, 45.88° N (Singh et al. 1983); 47. Kluver East, Montana, 106.37° W, 45.85° N (Singh et al. 1983); 48. Fort Howes, Montana, 106.00° W, 45.48° N (Lauenroth et al. 1984); 49. Eastern South Dakota, South Dakota, 97.00° W, 43.50° N (Blankespoor 1987); 50. Fayette, Texas, 96.83° W, 30.58° N (Diamond and Smeins 1985); 51. UCP, Texas, 97.00° W, 29.00° N (Diamond and Smeins 1985); 52. Blackland prairie, Texas, 96.00° W, 33.75° N (Diamond and Smeins 1985); 53. San Antonio prairie, Texas, 97.17° W, 31.33° N (Diamond and Smeins 1985); 54. Hill Creek, Utah, 109.83° W, 39.66° N (Brotherson and Brotherson 1979); 55. Wells Drawn, Utah, 110.25° W, 40.08° N (Brotherson and Brotherson 1979); 56. Red Creek, Utah, 110.83° W, 40.50° N (Brotherson and Brotherson 1979); 57. Rock Creek, Utah, 110.75° W, 40.58° N (Brotherson and Brotherson 1979); 58. Strawberry Creek, Utah, 110.00° W, 40.50° N (Brotherson and Brotherson 1979); 59. Pine valley (Sagebrush), Utah, 113.25° W, 38.50° N (Yorks et al. 1992); 60. Pine valley (Spiny hopsage), Utah, 113.25° W, 38.50° N (Yorks et al. 1992); 61. Edwards Plateau, Texas, 98.33° W, 30.25° N (Fowler and Dunlap 1986); 62. Elko County, Nevada, 115.75° W, 40.33° N (Tueller and Eckert 1987); 63. Pole Mountain, Wyoming, 105.28° W, 41.12° N (Boutton et al. 1980); 64. Cheyenne, Wyoming, 104.82° W, 41.25° N (Boutton et al. 1980); 65. Wheatland, Wyoming, 105.12° W, 42.07° N (Boutton et al. 1980); 66. Winnipeg, Canada, 97.50° W, 49.87° N (Levin and Keleher 1969); 67. Red River Valley, Minnesota, 96.62° W, 47.75° N (Smeins and Olsen 1970); 68. Nevada Test Site, Nevada, 116.08° W, 36.83° N (Beatley 1975); 69. Death Valley, California, 117.83° W,

RESULTS

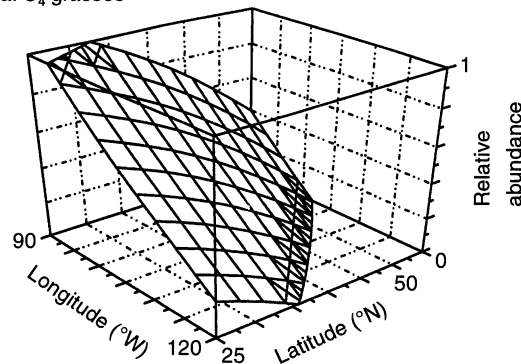
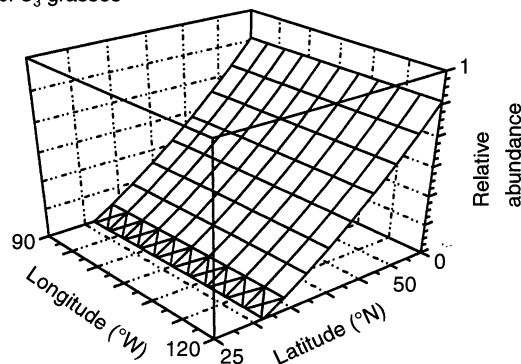
For the whole region, geographic coordinates explained 61, 46, and 53% of the variability of C_4 grasses, C_3 grasses, and shrubs, respectively (Fig. 2). The relative abundance of C_4 grasses decreased with both latitude and longitude (Fig. 2a) ($r^2 = 0.61$, $F = 55$, $df = 2, 70$, $P < 0.0001$) and was, therefore, highest at southern latitudes and eastern longitudes. Along a given longitude, C_3 grasses increased with latitude (Fig. 2b) ($r^2 = 0.46$, $F = 59$, $df = 2, 70$, $P < 0.0001$). As one moves westward, C_4 grasses are replaced by shrubs. Shrub relative abundance increased with longitude and decreased with latitude (Fig. 2c) ($r^2 = 0.53$, $F = 40$, $df = 2, 70$, $P < 0.0001$). Succulent relative abundance had a weak negative relationship with latitude ($SUC = 0.3651 - 0.0962 \ln LAT$, $r^2 = 0.07$, $F = 5.58$, $df = 1, 71$, $P < 0.03$). The relative abundance of forbs did not show a significant relationship with either latitude or longitude.

The relative abundance of C_4 grasses increased with increases in three climatic variables: MAP, MAT, and JJA/MAP (Fig. 3) ($r^2 = 0.66$, $F = 44$, $df = 3, 69$, $P < 0.0001$). Mean annual precipitation (MAP) showed the highest partial r^2 , followed by mean annual temperature (MAT) (0.35 and 0.17, respectively). The seasonality of precipitation (JJA/MAP) explained 14% of the total variance (r^2 partial = 0.14).

The abundance of C_3 grasses decreased with mean annual temperature (MAT) and increased with the proportion of total precipitation falling in winter (DJF/MAP) ($r^2 = 0.37$, $F = 17$, $df = 3, 69$, $P < 0.0001$) (Fig. 4). The biome (grassland or shrubland) also had a significant effect on the relationship (Fig. 4a, b). Most of the variance in the distribution of the relative abundance of C_3 grasses was explained by MAT (r^2 partial = 0.26). The biome and the distribution of precipitation accounted for 7 and 4% of the total variance, respectively.

Precipitation and its seasonal distribution accounted for 62% of the variability in the regional distribution of the shrubs (Fig. 5) ($r^2 = 0.62$, $F = 59$, $df = 2, 70$, $P < 0.0001$). Shrub abundance was negatively related to precipitation (Fig. 5), which is the same result reported by Cook and Irwin (1992) for a band on each side of the Rocky Mountains. Shrubs showed a positive relationship with the proportion of annual precipitation falling in winter, which explained most of the variance in their distribution (r^2 partial = 0.47).

Climatic variables explained a small proportion of the variability in the relative abundance of forbs and succulents (15 and 13%, respectively). The relative abundance of forbs tended to increase with MAP and

a. C_4 grassesb. C_3 grasses

c. Shrubs

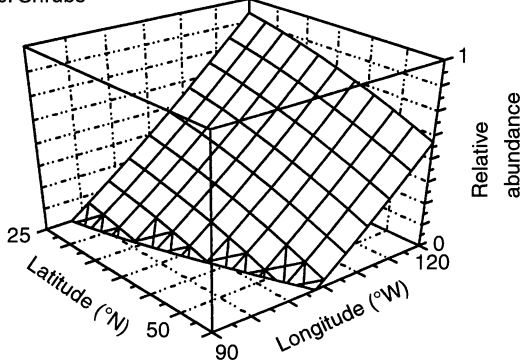
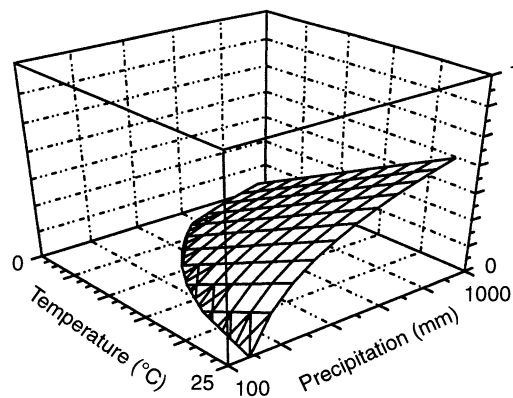


FIG. 2. Relationships between the geographic coordinates and the relative abundances of C_4 grasses (C_4G), C_3 grasses (C_3G), and shrubs (SHR). $C_4G = 15.9339 - 3.2460 \ln LONG - 0.0003072LAT^2$ ($r^2 = 0.61$, $F = 55$, $df = 2, 70$, $P < 0.0001$). $C_3G = -0.4075 + 0.000415LAT^2$ ($r^2 = 0.46$, $F = 59$, $df = 1, 71$, $P < 0.0001$). $SHR = -1.3364 - 0.000139LAT^2 + 0.000163LONG^2$ ($r^2 = 0.53$, $F = 40$, $df = 2, 70$, $P < 0.0001$).

←

36.00° N (Bradley 1970); 70. Rock Valley, Nevada, 116.25° W, 36.67° N (Turner and McBrayer 1970); 71. Salina, Kansas, 97.62° W, 38.75° N (Piper and Gernes 1988); 72. Cedar Creek, Minnesota, 93.20° W, 45.40° N (Inouye et al. 1987, Tilman 1987); 73. Kernen Prairie, Canada, 106.63° W, 52.13° N (Pylypec 1986).

a. Proportion of precipitation
in summer (JJA/MAP) = 0.15



b. Proportion of precipitation
in summer (JJA/MAP) = 0.45

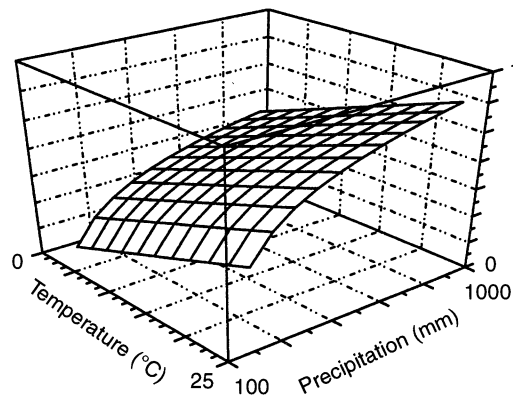


FIG. 3. Relationship between the relative abundance of C_4 grasses and mean annual precipitation (MAP), and mean annual temperature (MAT) for two values of the proportion of precipitation falling in summer (JJA/MAP) (a. 0.15, b. 0.45): $C_4G = -0.9837 + 0.000594MAP + 1.3528JJA/MAP + 0.2710 \ln MAT$ ($r^2 = 0.66$, $F = 44$, $df = 3, 69$, $P < 0.0001$).

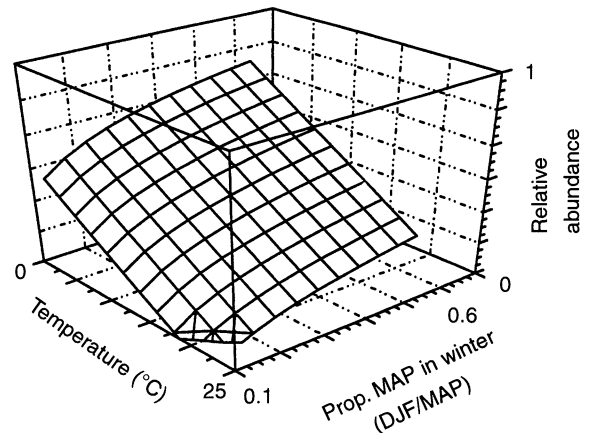
to decrease with MAT ($FRB = -0.2035 + 0.07975 \ln MAP - 0.0623 \ln MAT$, $r^2 = 0.15$, $F = 6$, $df = 2, 70$, $P < 0.0037$). For succulents, relative abundance decreased with the thermal amplitude (AMP) and the proportion of precipitation falling in winter [SUC = $(1.20246 AMP^{-0.0689} DJF/MAP^{-0.0322}) - 1$, $r^2 = 0.13$, $F = 6.3$, $df = 2, 70$, $P < 0.0031$].

The percentage of the variance explained and the values of both the y intercept and the coefficients of the variables included were similar among the models fit to five different subsets of the data (Table 1). Our conclusion from this analysis is that there was a small amount of bias associated with the specific sites included in our analyses.

DISCUSSION

Precipitation and its seasonal distribution are important controls, in addition to temperature, on the dis-

a. Grassland areas



b. Shrubland areas

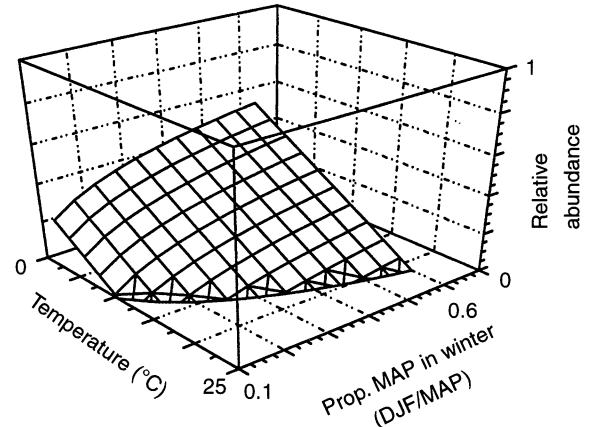


FIG. 4. Relationship between the relative abundance of C_3 grasses and mean annual temperature (MAT) and the proportion of precipitation falling in winter (DJF/MAP) for grasslands (BIOME = 1) (a) and shrublands (BIOME = 2) (b). $C_3G = 1.1905 - 0.02909MAT + 0.1781 \ln DJF/MAP - 0.2383BIOME$ ($r^2 = 0.37$, $F = 17$, $df = 3, 69$, $P < 0.0001$).

tribution of the relative abundance of C_3 and C_4 grasses. In a recent analysis, Epstein (1995) described the relationship between the relative abundance of C_4 grasses and mean annual precipitation for the Central Grassland region of USA. Although the importance of changes in precipitation seasonality in causing vegetation shifts from C_3 - to C_4 -dominated ecosystems has been suggested (Quade et al. 1989), the importance of this factor as a determinant of the present distribution of C_3 and C_4 grasses has not been quantified previously. Moreover, most of the regional or global analyses of C_4 grass distributions under global change scenarios have been based on relationships that explain the number of species of this plant functional type from temperature (see Henderson et al. [1994] for Australia and Lloyd and Farquhar [1994] for the terrestrial biosphere). In our analyses, the regional distribution of the relative abundance of C_4 grasses was positively

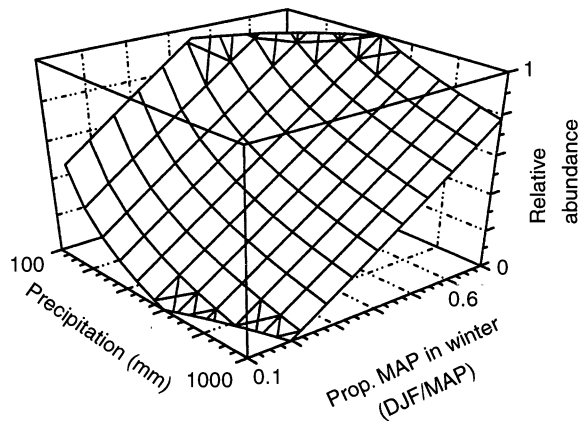


FIG. 5. Relationship between the relative abundance of shrubs and mean annual precipitation (MAP) and the proportion of precipitation falling in winter (DJF/MAP). $\text{SHR} = 1.7105 + 1.5451\text{DJF/MAP} - 0.2918 \ln \text{MAP}$ ($r^2 = 0.62$, $F = 56$, $df = 2, 70$, $P < 0.0001$).

related with three climatic variables: mean annual precipitation, mean annual temperature, and the proportion of the precipitation falling in summer. These variables accounted for 66% of the total variability of this functional type. Temperature accounted for only 25% of the variance explained by climatic variables. The remaining 75% was associated with mean annual precipitation and its seasonality.

C_3 grass abundance decreased with mean annual tem-

perature and increased with the proportion of precipitation falling during winter, however the coefficients differed between biomes (Fig. 4). The relative abundance of shrubs was controlled not only by the amount of precipitation but also by the proportion of winter precipitation. This functional type has, in general, deeper roots than grasses (Fernández and Paruelo 1988, Lee and Lauenroth 1994) and should be able to use water stored deep in the soil profile (Walter 1971, Walker and Noy-Meir 1982, Knoop and Walker 1985, Sala et al. 1989). A winter distribution of precipitation increases the amount of water stored deep in the soil (Paruelo and Sala 1995, Sala et al. 1996).

For the temperate zone of North America, MAP and MAT have an almost orthogonal distribution (Jenny 1980). MAT decreases with increasing latitude (from South to North) ($r = -0.84$, $P < 0.01$), and MAP decreases with longitude ($r = -0.73$, $P < 0.01$) (from East to West). Consequently, latitude and longitude can be used as surrogate variables for the main climatic dimensions of the area (MAT and MAP, respectively). C_3 grass relative abundance showed a significant relationship with latitude (Fig. 2b) because the main climatic control of its distribution, MAT, varied in a North–South direction. At 31°N the relative abundance of this PFT is predicted to be zero (Fig. 7). C_4 grass relative abundance was correlated with both latitude and longitude (Fig. 2a). The significant relationship with both geographic coordinates arises from the de-

TABLE 1. Coefficient of determination (r^2), y intercept, and coefficients of the variables included in the models for the complete data set ($n = 73$) and for five subsets ($n = 66$). The five subsets of data were produced by randomly deleting seven points. The numbers in parentheses are standard errors. MAP: mean annual precipitation, MAT: mean annual temperature, JJA/MAP: proportion of total precipitation falling in summer (June, July, and August), DJF/MAP: proportion of total precipitation falling in winter (December, January, and February), and Biome: grassland (1) or shrubland (2).

C_4 grasses							
	r^2	y intercept		MAP coeff.		JJA/MAP coeff.	
Complete set	0.66	-0.98	(0.125)	0.00059	(0.000107)	1.35	(0.212)
Set 1	0.67	-0.92	(0.125)	0.00063	(0.000104)	1.21	(0.211)
Set 2	0.65	-0.96	(0.130)	0.00059	(0.000116)	1.40	(0.217)
Set 3	0.65	-0.98	(0.132)	0.00055	(0.000113)	1.33	(0.222)
Set 4	0.67	-0.99	(0.129)	0.00054	(0.000114)	1.43	(0.226)
Set 5	0.68	-1.07	(0.134)	0.00055	(0.000116)	1.48	(0.229)
C_3 grasses							
	r^2	y intercept		MAT coeff.		ln DJF/MAP coeff.	
Complete set	0.37	1.19	(0.230)	-0.029	(0.00534)	0.18	(0.0891)
Set 1	0.35	1.05	(0.251)	-0.027	(0.00543)	0.12	(0.0938)
Set 2	0.35	1.11	(0.238)	-0.028	(0.00578)	0.15	(0.0897)
Set 3	0.35	1.18	(0.253)	-0.029	(0.00575)	0.18	(0.0956)
Set 4	0.37	1.16	(0.243)	-0.029	(0.00546)	0.16	(0.0929)
Set 5	0.34	1.2985	(0.2784)	-0.03004	(0.0005945)	0.2219	(0.10304)
Shrubs							
	r^2	y intercept		DJF/MAP coeff.		ln MAP coeff.	
Complete set	0.62	1.71	(0.374)	1.55	(0.276)	-0.29	(0.0557)
Set 1	0.64	1.68	(0.286)	1.63	(0.286)	-0.29	(0.0561)
Set 2	0.61	1.78	(0.401)	1.51	(0.288)	-0.30	(0.0603)
Set 3	0.58	1.70	(0.395)	1.44	(0.295)	-0.29	(0.0590)
Set 4	0.67	1.72	(0.404)	1.78	(0.304)	-0.30	(0.0597)
Set 5	0.57	1.59	(0.420)	1.55	(0.297)	-0.27	(0.0630)

pendence of the relative abundance of C_4 grasses on MAP, MAT and JJA/MAP. The relative abundance of C_4 grasses was maximum at southern latitudes and eastern longitudes (Fig. 6) and it is predicted to be zero in the northwestern corner of the study region (Fig. 7). As one moves westward there is a replacement of C_4 grasses by shrubs (Fig. 6). The predicted point of zero relative abundance of shrubs occurs at lower longitudes in the southern than in the northern part of the region (Fig. 7).

Teeri and Stowe (1976) related the regional distribution of the number of species of C_4 grasses in North America with temperature and Boutton et al. (1980) found that temperature was the main control of the distribution of C_3 and C_4 species along an elevation gradient where precipitation and temperature covaried. The data used by Teeri and Stowe (1976) (number of species in local floras), and the high covariance of temperature and precipitation in the Boutton et al. (1980) analysis, would lead to an underestimation of the effect of precipitation on the distribution of C_3 and C_4 species. We used point climatic data for a region where temperature and precipitation have a near orthogonal distribution in space. This allowed for a better analysis of the relative importance of temperature and precipitation on the distribution of the plant functional types.

Forbs comprise a heterogeneous functional type where species with widely varying characteristics are included (Golluscio and Sala 1993). The relative abundance of this PFT is also highly variable with grazing (Milchunas et al. 1989). Their heterogeneous composition and its dependence on local biotic factors could explain the low proportion of the variability accounted for by climate for this functional type. Because succulents and forbs are minor components of the biomass and productivity of most arid and semiarid plant communities in temperate North America, the error associated with estimating relative abundance from different values of importance (cover, biomass, annual net primary production) will be higher than for the other functional types. This error term could account for a substantial portion of the unexplained variance of these PFTs.

C_4 -grass-dominated vegetation (green areas in Fig. 6) occupies most of the southeastern portion of the grassland and shrubland areas of North America. Those areas are characterized by high temperature and high precipitation with a summer distribution. Toward the

northeastern portion of the region, grasslands become codominated by C_4 and C_3 grasses. Decreases in both precipitation and temperature explain this pattern (blue areas in Fig. 6). The western portion of the region is clearly dominated by shrubs (red areas in Fig. 6). Except for southeastern Arizona and western New Mexico, C_3 grasses are the codominant functional type on the portion of the grassland and shrubland areas west of the Rocky Mountains. Low precipitation and a winter concentration of precipitation are responsible for this pattern.

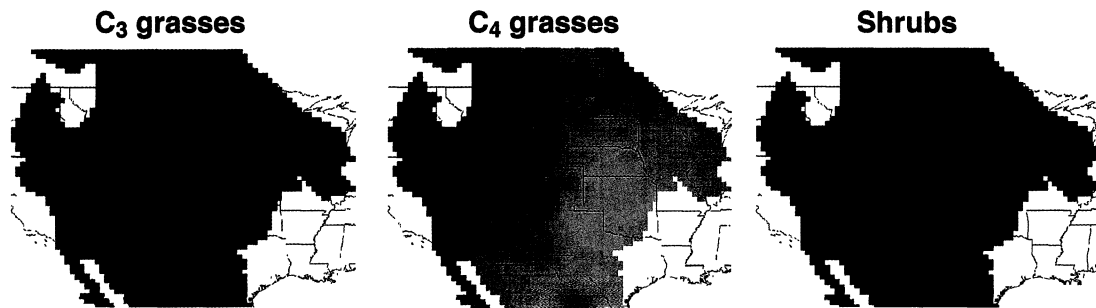
CONCLUSIONS AND APPLICATIONS

Quantitative models of the relationships between PFTs and geographic and climatic variables provide new insights into the regional distribution of vegetation in central North America. (1) Temperature has been recognized as an important control on the distribution of numbers of species of C_3 and C_4 grasses, but our results suggest that when relative abundance is considered precipitation and its seasonal distribution are also important controls. The effect of these variables at a regional scale is consistent with previous knowledge about the ecophysiology and phenology of C_3 and C_4 grasses. (2) The amount of winter precipitation is an important control on the relative abundance of shrubs as hypothesized by others (Stoddart et al. 1975, West 1983). As the proportion of winter precipitation increases, the amount of water stored deep in the soil profile also increases (Paruelo and Sala 1995). This agrees with the two-layer hypothesis proposed to explain the relative proportion of grasses and woody plants (Walter 1971). (3) On a regional basis, climatic variables were more strongly correlated with the distribution of C_4 grasses and shrubs than with C_3 grasses, forbs, or succulents.

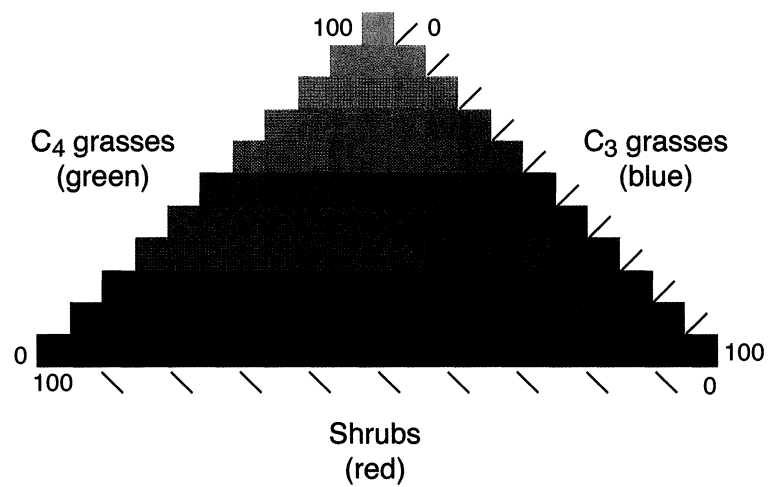
A proper description of the spatial distribution of the relative abundance of PFTs is critical in relation with some aspects of global change research at continental scales. PFT composition affects the exchange of energy, matter, and momentum between the surface and the atmosphere (Walker 1994), and changes in the relative abundance of grasses and shrubs will affect ecosystem processes such as nutrient availability (Barendse et al. 1987, 1994, Pastor et al. 1993), soil water dynamics (Sala et al. 1989, Paruelo and Sala 1995), primary productivity (Sala et al. 1989), soil carbon accumulation (Archer et al. 1988, Schlesinger et al.

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FIG. 6. Maps showing the distribution of the relative abundance of C_3 grasses, C_4 grasses, and shrubs (upper maps) and the physiognomies resulting from combining these three variables for the grassland and shrublands areas of North America. Each variable (relative abundance of C_3 grasses, C_4 grasses, and shrubs) was assigned to a band (blue, green, red) and displayed as composite color raster image (larger map). For the single-variable maps (small maps) the value of each variable increases with the intensity of the color from 0 to 100% relative abundance. The bottom triangle shows the colors resulting from combining the different bands in the composite. The areas corresponding to shrublands and grasslands were defined based on Küchler (1964) and Dodd (1979). Relative abundances were calculated using the equations in Figs. 3, 4, and 5, and a climatic database (Leemans and Cramer 1991).



Relative abundance code



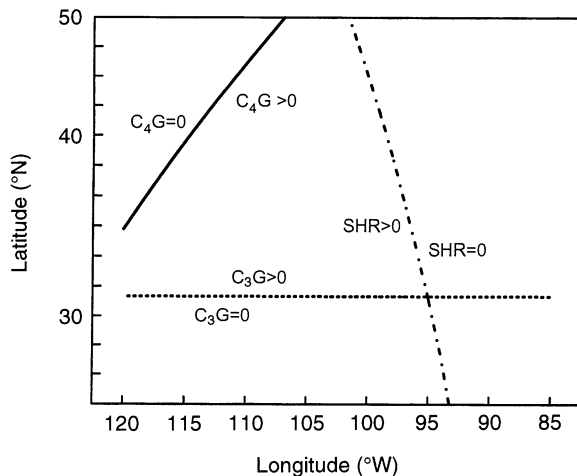


FIG. 7. Latitude and longitude for which the relative abundance of C_3 grasses (C_3G), C_4 grasses (C_4G), and shrubs (SHR) is predicted to be zero. Lines were calculated from the models in Fig. 2.

1990), and horizontal and vertical resource patterning (Belsky 1994). The relative abundance of different PFTs also affects albedo and roughness (Aguiar et al., *in press*). Incorporation of structural characterization of the vegetation in mesoscale atmospheric models is, consequently, crucial. Correlative models also allow predictions about the relative impact of land use on mesoclimate (Pielke et al. 1991). However, it is important to point out the uncertainties associated with the use of these relationships outside the domain for which they were generated, i.e., higher CO_2 concentrations (Woodward 1993).

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APPENDIX

Relative abundance of C₃ grasses (C₃G), C₄ grasses (C₄G), shrubs (SHR), forbs (FRB), and succulents (SUC); and mean annual precipitation (mm) (MAP), mean annual temperature (°C)(MAT), and proportion of precipitation falling in summer (JJA/MAP) and winter (DJF/MAP) for 73 sites from the grassland and shrubland areas of temperate North America.

Sites	C ₃ G	C ₄ G	SHR	FRB	SUC	MAP	MAT	JJA/ MAP	DJF/ MAP
ALE	0.65	0.00	0.29	0.06	0.00	199	12.4	0.12	0.45
Bison	0.65	0.00	0.00	0.35	0.00	469	7.5	0.24	0.29
Bridger	0.76	0.01	0.04	0.19	0.00	536	7.2	0.24	0.20
Cottonwood	0.75	0.18	0.03	0.04	0.00	476	8.2	0.35	0.15
Dickinson	0.33	0.28	0.07	0.31	0.00	484	4.8	0.40	0.14
Hays	0.03	0.83	0.01	0.14	0.00	623	12.0	0.40	0.11
Jornada	0.00	0.31	0.43	0.25	0.01	259	14.5	0.47	0.17
Osage	0.02	0.87	0.00	0.10	0.00	969	15.3	0.30	0.14
Pantex	0.05	0.72	0.00	0.08	0.16	542	13.9	0.44	0.13
CPER	0.05	0.44	0.08	0.36	0.07	421	8.5	0.31	0.14
Fort Berthold Indian Reservation	0.36	0.41	0.05	0.18	0.00	446	5.1	0.41	0.15
Fort Stanton Experimental Ranch	0.00	0.50	0.35	0.14	0.00	376	11.2	0.51	0.17
Texas Experimental Range	0.21	0.70	0.01	0.08	0.00	661	17.8	0.27	0.16
S.H. Ordway Memorial Prairie	0.51	0.25	0.09	0.14	0.00	575	6.1	0.36	0.16
Konza Prairie	0.07	0.78	0.02	0.12	0.00	885	12.9	0.37	0.12
Arapaho	0.29	0.70	0.00	0.01	0.00	556	8.6	0.38	0.12
Idaho National Eng. Laboratory	0.05	0.00	0.91	0.04	0.00	344	6.6	0.18	0.35
U.S. Sheep Experimental Station	0.13	0.00	0.65	0.21	0.00	415	6.0	0.22	0.33
Black Gap Wildlife Management Area	0.00	0.31	0.23	0.08	0.38	347	18.9	0.41	0.12
Wind Cave National Park	0.65	0.13	0.00	0.22	0.00	575	5.3	0.36	0.13
Appleton-Whittel Research Ranch	0.00	0.76	0.14	0.10	0.00	477	13.9	0.50	0.22
Matador	0.89	0.00	0.05	0.06	0.00	370	3.5	0.45	0.19
Snyder	0.08	0.30	0.49	0.13	0.00	537	16.7	0.32	0.12
Oklahoma State University of Agricultural Research	0.47	0.37	0.00	0.16	0.00	870	15.4	0.29	0.15
Curlew Valley	0.00	0.00	1.00	0.00	0.00	356	7.3	0.18	0.31
Portal	0.00	0.42	0.42	0.16	0.00	570	12.2	0.42	0.24
Badlands National Park	0.21	0.48	0.02	0.28	0.00	457	8.8	0.36	0.13
Escalante desert	0.29	0.00	0.70	0.01	0.00	327	9.5	0.16	0.31
Glen Canyon	0.35	0.31	0.27	0.07	0.00	176	13.8	0.25	0.28
Alzada	0.28	0.40	0.25	0.04	0.04	345	6.4	0.46	0.14
Grass Valley	0.45	0.00	0.50	0.05	0.00	405	5.9	0.40	0.12
SSHA	0.31	0.00	0.55	0.14	0.00	375	5.7	0.16	0.29
Capitol Reef National Park	0.02	0.11	0.75	0.12	0.00	231	12.1	0.29	0.21
Provo	0.49	0.00	0.31	0.20	0.00	723	11.2	0.14	0.34
Lowry Spring	0.36	0.00	0.39	0.25	0.00	365	6.9	0.15	0.31
El Paso	0.01	0.95	0.01	0.01	0.02	373	11.5	0.35	0.18
Coconino County	0.00	0.60	0.36	0.04	0.00	733	9.4	0.23	0.37
Lincoln County	0.00	0.84	0.08	0.07	0.00	351	11.7	0.45	0.18
Uinta Basin 1—Duchesne	0.63	0.00	0.27	0.08	0.02	244	7.2	0.20	0.29
Uinta Basin 2—Vernal	0.03	0.00	0.79	0.17	0.00	244	7.2	0.20	0.29
Uinta Basin 2—Sleep Ridge	0.07	0.00	0.77	0.16	0.00	207	7.2	0.22	0.28

APPENDIX. Continued.

Sites	C ₃ G	C ₄ G	SHR	FRB	SUC	MAP	MAT	JJA/ MAP	DJF/ MAP
Utah Lake Shadscale	0.12	0.00	0.25	0.64	0.00	646	10.0	0.11	0.36
Utah Lake Grasewood	0.36	0.00	0.27	0.37	0.00	593	11.0	0.13	0.35
Hay Coulee	0.63	0.15	0.12	0.10	0.00	409	7.5	0.30	0.20
Kluver West	0.86	0.03	0.00	0.11	0.00	409	7.5	0.30	0.20
Kluver North	0.47	0.12	0.30	0.11	0.00	409	7.5	0.30	0.20
Kluver East	0.58	0.05	0.28	0.09	0.00	409	7.5	0.30	0.20
Fort Howes	0.68	0.02	0.01	0.29	0.00	495	7.9	0.32	0.17
Eastern S Dakota	0.71	0.11	0.00	0.18	0.00	717	7.5	0.34	0.15
Fayette	0.06	0.76	0.00	0.18	0.00	935	20.7	0.23	0.22
UCP	0.04	0.86	0.00	0.10	0.00	976	21.2	0.29	0.18
Blackland Prairie	0.14	0.71	0.00	0.16	0.00	1011	17.7	0.23	0.19
San Antonio prairie	0.06	0.80	0.00	0.14	0.00	823	19.5	0.20	0.21
Hill Creek	0.34	0.00	0.65	0.01	0.00	207	7.2	0.22	0.28
Wells Drawn	0.31	0.00	0.68	0.01	0.00	321	6.5	0.19	0.35
Red Creek	0.21	0.00	0.45	0.33	0.00	418	5.9	0.20	0.38
Rock Creek	0.69	0.00	0.28	0.03	0.00	418	5.9	0.20	0.38
Strawberry Creek	0.48	0.00	0.39	0.13	0.00	270	6.9	0.21	0.27
Pine valley (Sagebrush)	0.02	0.00	0.94	0.04	0.00	327	9.5	0.16	0.31
Pine valley (spiny hopsage)	0.08	0.28	0.58	0.06	0.00	327	9.5	0.16	0.31
Edwards Plateau	0.11	0.63	0.14	0.12	0.00	841	20.1	0.23	0.22
Elko County	0.11	0.00	0.86	0.03	0.00	332	7.8	0.12	0.40
Pole Mountain	0.23	0.17	0.30	0.29	0.01	421	3.9	0.29	0.18
Cheyenne	0.18	0.66	0.01	0.12	0.03	527	7.4	0.28	0.16
Wheatland	0.05	0.68	0.00	0.26	0.01	430	9.5	0.27	0.16
Winnipeg	0.19	0.24	0.09	0.48	0.00	512	2.0	0.42	0.12
Red River Valley	0.48	0.40	0.00	0.13	0.00	611	4.2	0.39	0.16
Nevada test site	0.02	0.05	0.79	0.11	0.02	169	17.1	0.28	0.32
Death Valley	0.00	0.04	0.96	0.00	0.00	180	15.1	0.10	0.49
Rock Valley	0.00	0.00	1.00	0.00	0.00	117	18.1	0.21	0.39
Saline	0.07	0.80	0.01	0.11	0.01	789	12.9	0.34	0.13
Cedar Creek	0.31	0.39	0.13	0.18	0.00	892	6.6	0.35	0.15
Kernen Prairie	0.72	0.01	0.14	0.13	0.00	352	2.0	0.46	0.14