



Relative Abundance of Plant Functional Types in Grasslands and Shrublands of North America

Jose M. Paruelo, W. K. Lauenroth

Ecological Applications, Volume 6, Issue 4 (Nov., 1996), 1212-1224.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Ecological Applications is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Ecological Applications

©1996 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

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

JOSÉ M. PARUELO²

Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins, Colorado 80523 USA

W. K. LAUENROTH

Department of Rangeland Ecosystem Science and Natural Resource and Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA

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

¹ Manuscript received 26 June 1995; revised and accepted 28 November 1995; final version received 29 January 1996.

² Departamento de Ecología, Facultad de Agronomía, Universidad de Buenos Aires, Avenida San Martín 4453-(1417) Buenos Aires, Argentina.

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, Percy 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).

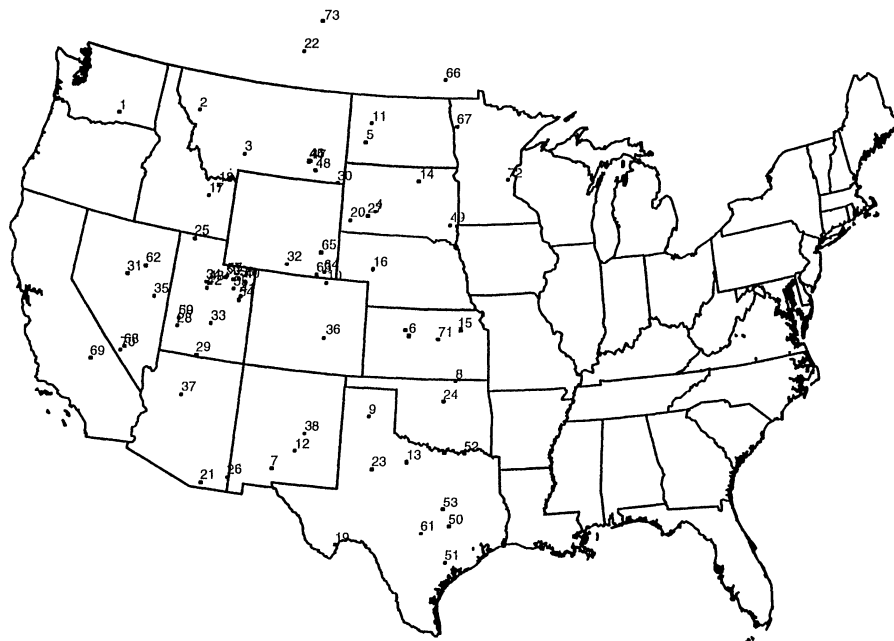


FIG. 1. Map of the study sites used in the plant functional type analyses. Latitude and longitude are expressed in centesimal degrees. The references in parentheses are to papers with descriptions of the study sites. 1. ALE, Washington, 119.55° W, 46.40° N (Sims et al. 1978); 2. Bison, Montana, 114.27° 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 (Brotherson 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

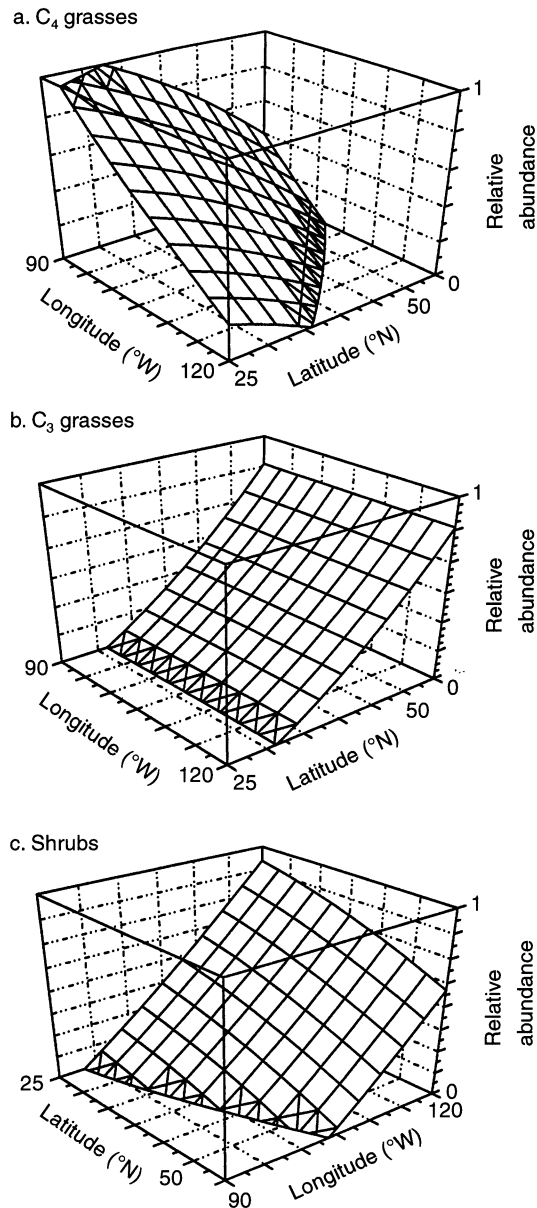


FIG. 2. Relationships between the geographic coordinates and the relative abundances of C_4 grasses (C_4G), C_3 grasses (C_3G), and shrubs (SHR). $C_4G = 15.9339 - 3.2460 \ln LONG - 0.0003072LAT^2$ ($r^2 = 0.61$, $F = 55$, $df = 2, 70$, $P < 0.0001$). $C_3G = -0.4075 + 0.000415LAT^2$ ($r^2 = 0.46$, $F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

←

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. Kern Prairie, Canada, 106.63° W, 52.13° N (Pylypec 1986).

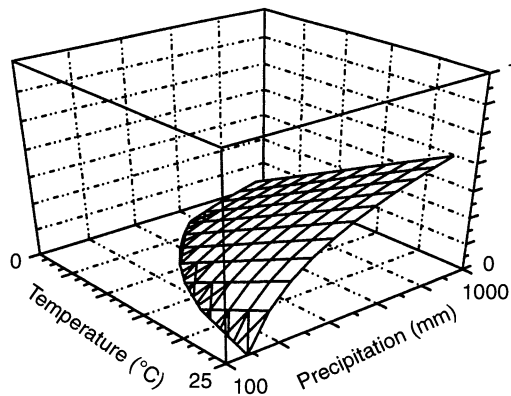
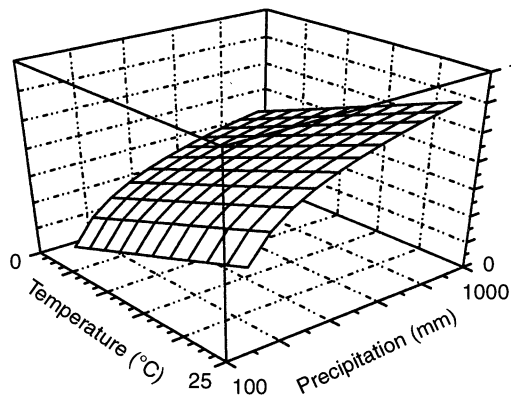
a. Proportion of precipitation
in summer (JJA/MAP) = 0.15b. Proportion of precipitation
in summer (JJA/MAP) = 0.45

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): $C_4G = -0.9837 + 0.000594MAP + 1.3528JJA/MAP + 0.2710 \ln MAT$ ($r^2 = 0.66$, $F = 44$, $df = 3, 69$, $P < 0.0001$).

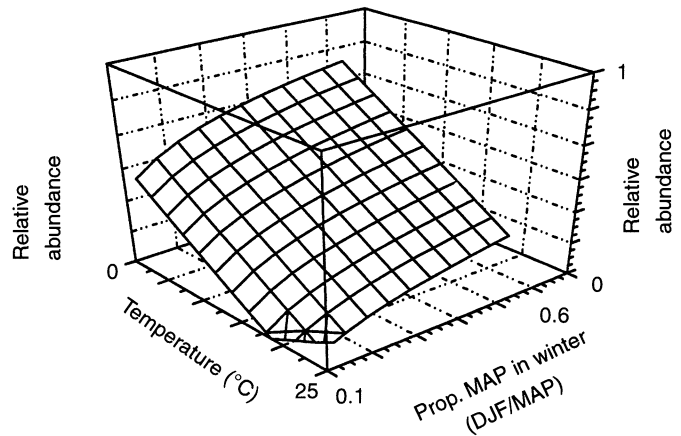
to decrease with MAT (FRB = $-0.2035 + 0.07975 \ln MAP - 0.0623 \ln MAT$, $r^2 = 0.15$, $F = 6$, $df = 2, 70$, $P < 0.0037$). For succulents, relative abundance decreased with the thermal amplitude (AMP) and the proportion of precipitation falling in winter [SUC = $(1.20246 AMP^{-0.0689} DJF/MAP^{-0.0322})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

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

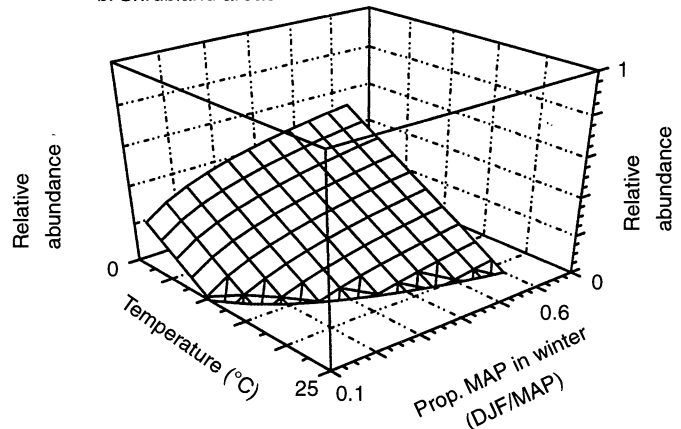


FIG. 4. Relationship between the relative abundance of C_3 grasses and mean annual temperature (MAT) and the proportion of precipitation falling in winter (DJF/MAP) for grasslands (BIOME = 1) (a) and shrublands (BIOME = 2) (b). $C_3G = 1.1905 - 0.02909MAT + 0.1781 \ln DJF/MAP - 0.2383BIOME$ ($r^2 = 0.37$,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

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

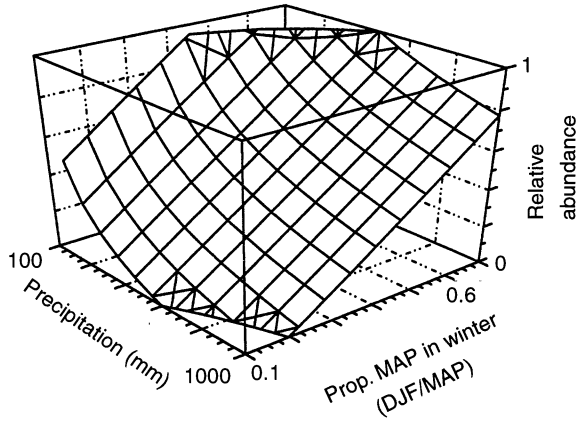


FIG. 5. Relationship between the relative abundance of shrubs and mean annual precipitation (MAP) and the proportion of precipitation falling in winter (DJF/MAP). $SHR = 1.7105 + 1.5451DJF/MAP - 0.2918 \ln MAP$ ($r^2 = 0.62$, $F = 56$, $df = 2, 70$, $P < 0.0001$).

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.

C₃ 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). C₃ 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). C₄ 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.	ln MAT coeff.	
Complete set	0.66	-0.98	(0.125)	0.00059 (0.000107)	1.35 (0.212)	0.27 (0.0467)	
Set 1	0.67	-0.92	(0.125)	0.00063 (0.000104)	1.21 (0.211)	0.25 (0.0462)	
Set 2	0.65	-0.96	(0.130)	0.00059 (0.000116)	1.40 (0.217)	0.25 (0.0485)	
Set 3	0.65	-0.98	(0.132)	0.00055 (0.000113)	1.33 (0.222)	0.28 (0.0496)	
Set 4	0.67	-0.99	(0.129)	0.00054 (0.000114)	1.43 (0.226)	0.28 (0.0498)	
Set 5	0.68	-1.07	(0.134)	0.00055 (0.000116)	1.48 (0.229)	0.31 (0.0520)	
C ₃ grasses							
	r^2	y intercept		MAT coeff.	ln DJF/MAP coeff.	Biome coeff.	
Complete set	0.37	1.19	(0.230)	-0.029 (0.00534)	0.18 (0.0891)	-0.24 (0.0714)	
Set 1	0.35	1.05	(0.251)	-0.027 (0.00543)	0.12 (0.0938)	-0.22 (0.0747)	
Set 2	0.35	1.11	(0.238)	-0.028 (0.00578)	0.15 (0.0897)	-0.22 (0.0739)	
Set 3	0.35	1.18	(0.253)	-0.029 (0.00575)	0.18 (0.0956)	-0.23 (0.0765)	
Set 4	0.37	1.16	(0.243)	-0.029 (0.00546)	0.16 (0.0929)	-0.24 (0.0727)	
Set 5	0.34	1.2985	(0.2784)	-0.03004 (0.0005945)	0.2219 (0.10304)	-0.26 (0.0833)	
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.

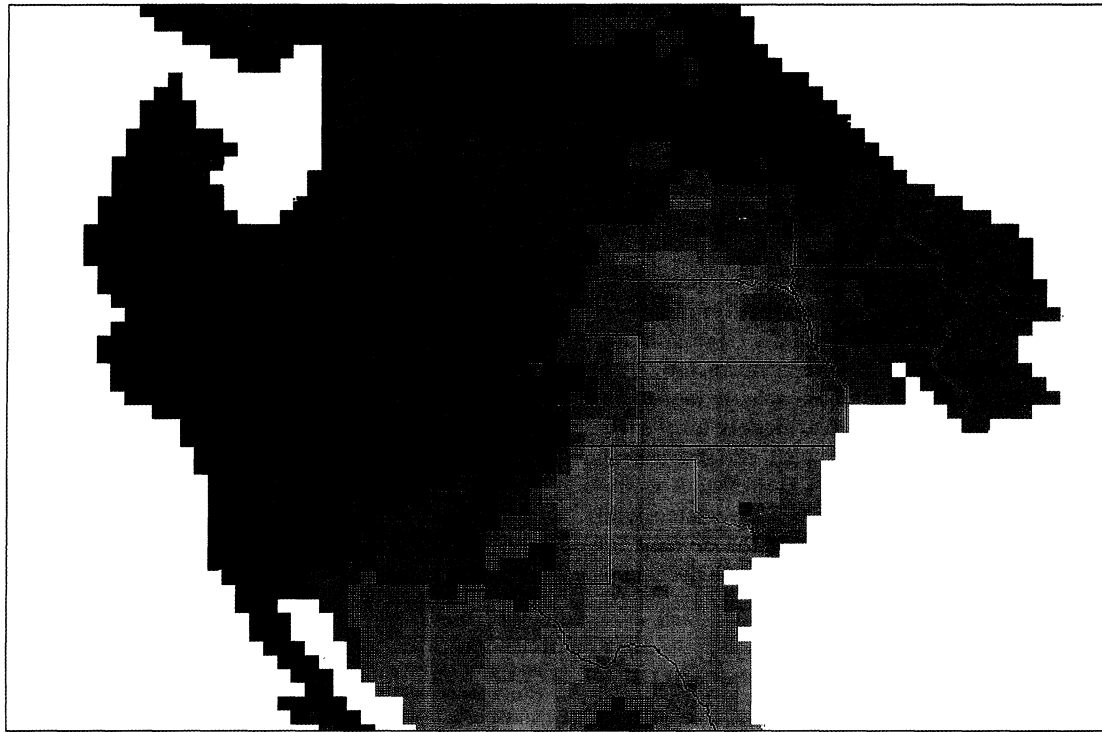
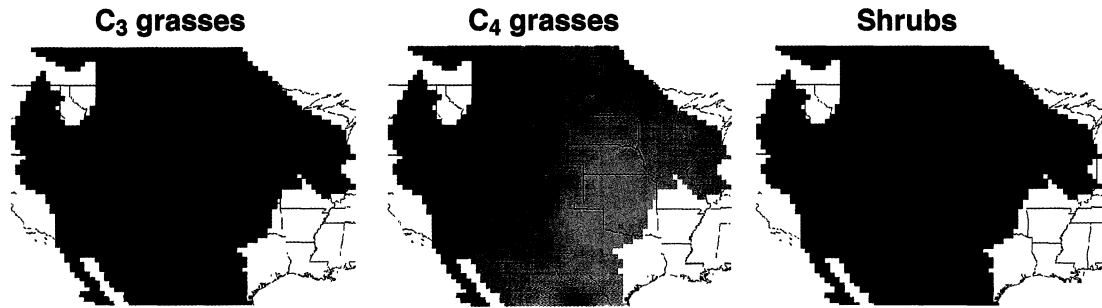
CONCLUSIONS AND APPLICATIONS

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.

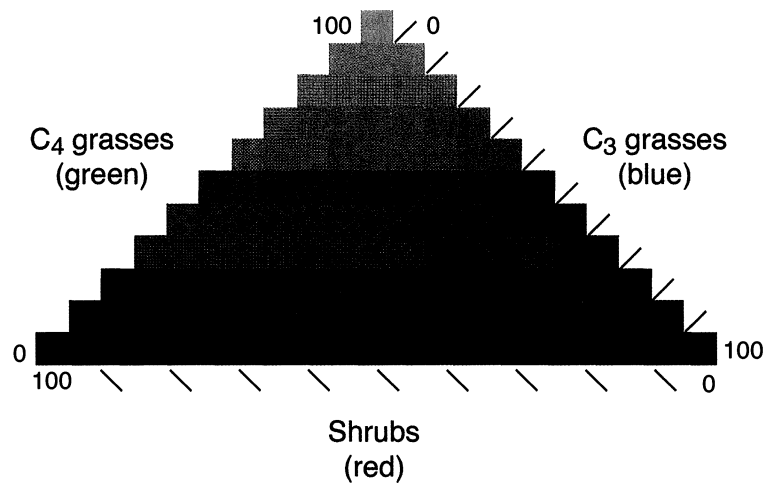
A proper description of the spatial distribution of the relative abundance of PFTs is critical in relation with some aspects of global change research at continental scales. PFT composition affects the exchange of energy, matter, and momentum between the surface and the atmosphere (Walker 1994), and 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.

→

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



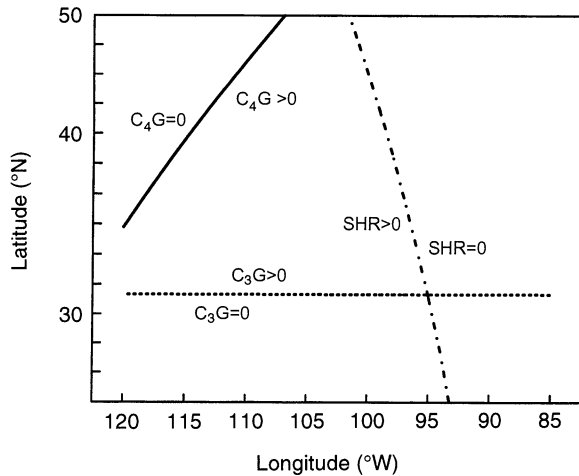


FIG. 7. Latitude and longitude for which the relative abundance of C_3 grasses (C_3G), C_4 grasses (C_4G), and shrubs (SHR) is predicted to be zero. Lines were calculated from the models in Fig. 2.

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).

ACKNOWLEDGMENTS

This study was funded by the LTER-NSF grant BSR 90-11659. JMP was supported by the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET) and the University of Buenos Aires. This work contributes to the Global Change and Terrestrial Ecosystems (GCTE) Core Project of the International Geosphere-Biosphere Programme (IGBP).

LITERATURE CITED

- Abrams, M. D., and L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tall-grass prairie in Northeast Kansas. *American Midland Naturalist* **117**:442–445.
- Aguiar, M. R., J. M. Paruelo, O. E. Sala, and W. K. Lauenroth. *In press*. Ecosystem consequences of plant functional types changes in a semiarid grassland. *Journal of Vegetation Science*.
- Aide, M., and W. Van Auken. 1985. Chihuahuan desert vegetation of limestone and basalt slopes in west Texas. *Southwestern Naturalist* **30**:533–542.
- Anderson, J. E., and M. L. Shumar. 1986. Impacts of black-tailed jackrabbits at peak population densities on sagebrush-steppe vegetation. *Journal of Range Management* **39**:152–155.
- Archer, S., C. Scirifes, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* **58**:111–127.
- Barnes, P. W., L. L. Tieszen, and D. J. Ode. 1983. Distribution, production, and diversity of C_3 and C_4 dominated communities in a mixed prairie. *Canadian Journal of Botany* **61**:741–751.
- Beatley, J. C. 1975. Climates and vegetation pattern across the Mojave/Great Basin desert transition of Southern Nevada. *American Midland Naturalist* **93**:53–70.
- Beavis, W. D., J. C. Owens, J. A. Ludwig, and E. W. Huddleston. 1982. Grassland communities of east-central new Mexico and density of the range caterpillar, *Hemileuca oliviae* (Lepidoptera: Saturniidae). *Southwestern Naturalist* **27**:335–343.
- Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* **75**:922–932.
- Berendse, F., B. Berg, and E. Bosatta. 1987. The effect of lignin and nitrogen on the decomposition of litter in nutrient-poor ecosystems: a theoretical approach. *Canadian Journal of Botany* **65**:1116–1120.
- Berendse, F., M. Schmitz, and W. de Wissler. 1994. Experimental manipulation of succession in heathland ecosystems. *Oecologia* **100**:38–44.
- Blankespoor, G. W. 1987. The effects of prescribed burning on a tall-grass prairie remnant in eastern South Dakota. *Prairie Naturalist* **19**:177–188.
- Bock, C. E., J. H. Bock, W. R. Kenney, and V. M. Hawthorne. 1984. Responses of birds, rodents, and vegetation to livestock exclusion in a semidesert grassland site. *Journal of Range Management* **37**:239–242.
- Boutin, C., and P. A. Keddy. 1993. A functional classification of wetland plants. *Journal of Vegetation Science* **4**:591–600.
- Boutton, T. W., A. T. Harrison, and B. N. Smith. 1980. Distribution of biomass of species differing in photosynthetic pathway along an altitudinal transect in southeastern Wyoming grassland. *Oecologia* **45**:287–298.
- Box, E. O. 1981. Predicting physiognomic vegetation types with climate variables. *Vegetatio* **45**:127–139.
- Bradley, W. G. 1970. The vegetation of Saratoga Springs, Death Valley National Monument, California. *Southwestern Naturalist* **15**:111–129.
- Brotherson, J. D., and K. J. Brotherson. 1979. Ecological and community relationships of *Eriogonum corymbosum* (Polygonaceae) in the Uinta Basin, Utah. *Great Basin Naturalist* **39**:177–191.
- Brotherson, J. D., and W. T. Brotherson. 1981. Grazing impacts on the sagebrush communities of Central Utah. *Great Basin Naturalist* **41**:335–340.
- Brotherson, J. D., L. L. Rasmussen, and R. D. Black. 1986. Comparative habitat and community relationships of *Atriplex confertifolia* and *Sarcobatus vermiculatus* in Central Utah. *Great Basin Naturalist* **46**:348–357.
- Burke, I. C., W. A. Reiners, and R. K. Olson. 1989a. Topographic control of vegetation in a mountain big sagebrush steppe. *Vegetatio* **84**:77–86.
- Burke, I. C., C. M. Yonker, W. J. Parton, C. V. Cole, K. Flach, and D. S. Schimel. 1989b. Texture, climate, and cultivation effects on soil organic content in US grassland soils. *Soil Science Society of America Journal* **53**:800–805.
- Carson, R. W., and F. A. Bazzaz. 1982. Photosynthetic and growth response to fumigation with SO_2 at elevated CO_2 for C_3 and C_4 plants. *Oecologia* **54**:50–54.
- Carter, D. R., and K. M. Peterson. 1983. Effects of a CO_2 -enriched atmosphere on the growth and competitive interaction of a C_3 and a C_4 grass. *Oecologia* **58**:188–193.
- Cavagnaro, R. 1988. Distribution of C_3 and C_4 grasses at different altitudes in a temperate arid region of Argentina. *Oecologia* **76**:273–277.
- Chapin, F. S. 1993. Functional role of growth forms in ecosystem and global processes. Pages 287–312 in J. R. Eh-

- Irlinger and C. B. Field, editors. Scaling physiological processes. Academic Press, San Diego, California, USA.
- Chazdon, R. L. 1978. Ecological aspects of the distribution of C_4 grasses in selected habitats of Costa Rica. *Biotropica* **10**:265–269.
- Chew, R. M. 1982. Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in Southeastern Arizona. *American Midland Naturalist* **108**: 159–169.
- Cook, J. G., and L. L. Irwin. 1992. Climate-vegetation relationships between the Great Plains and Great Basin. *American Midland Naturalist* **127**:316–326.
- Curtis, P. S., L. M. Balduman, B. G. Drake, and D. F. Whigham. 1990. Elevated atmospheric CO_2 effects on below-ground processes in C_3 and C_4 estuarine marsh communities. *Ecology* **71**:2001–2006.
- Diamond, D. D., and F. E. Smeins. 1985. Composition, classification and species response patterns of remnant Tallgrass Prairies in Texas. *American Midland Naturalist* **113**: 294–309.
- Dodd, J. L. 1979. North American grasslands map. In N. R. French, editor. *Perspectives in grassland ecology*. Springer Verlag, New York, New York, USA.
- EarthInfo. 1993. National Climate Data Center summary of the day. Earthinfo, Boulder, Colorado, USA.
- Ehleringer, J. R. 1978. Implications of quantum yield differences on the distributions of C_3 and C_4 grasses. *Oecologia* **31**:255–267.
- Epstein, H. E. 1995. Environmental controls of plant species and plant functional type productivity in the Great Plains. Master's thesis. Colorado State University, Fort Collins, Colorado, USA.
- Everett, R. L., and S. Koniak. 1981. Understory vegetation in fully stocked pinyon-juniper stands. *Great Basin Naturalist* **41**:467–475.
- Ewing, A. L., and D. M. Engle. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist* **120**:212–223.
- Fernández, R. J., and J. M. Paruelo. 1988. Root systems of two patagonian shrubs: a quantitative description using a geometrical method. *Journal of Range Management* **41**: 220–223.
- Forde, J. D., N. F. Sloan, and D. A. Shown. 1984. Grassland habitat management using prescribed burning in Wind Cave National Park, South Dakota. *Prairie Naturalist* **16**:97–110.
- Fowler, N. L., and D. W. Dunlap. 1986. Grassland vegetation of the eastern Edwards Plateau. *American Midland Naturalist* **115**:146–155.
- Germano, D. J., and D. N. Lawhead. 1986. Species diversity and habitat complexity: does vegetation organize vertebrate communities in the Great Basin? *Great Basin Naturalist* **46**: 711–720.
- Golluscio, R. A., and O. E. Sala. 1993. Plant functional types and ecological strategies in Patagonian forbs. *Journal of Vegetation Science* **4**:839–846.
- Gould, F. W., and R. B. Shaw. 1983. *Grass systematics*. Second edition. Texas A&M University Press, College Station, Texas, USA.
- Hattersley, P. W. 1983. The distribution of C_3 and C_4 grasses in Australia in relation to climate. *Oecologia* **57**:113–128.
- Hawkins, C. P., and J. A. MacMahon. 1989. Guilds: the multiple meanings of a concept. *Annual Review of Entomology* **34**:423–451.
- Heitschmidt, R. K., S. L. Dowhower, R. A. Gordon, and D. L. Price. 1985. Response of vegetation to livestock grazing at the Texas Experimental Ranch. Texas Agricultural Experiment Station B-1515. Texas A&M University, College Station, Texas, USA.
- Henderson, S., P. Hattersley, S. von Caemmerer, and C. B. Osmond. 1994. Are C_4 pathway plants threatened by global climatic change? Pages 529–549 in E. D. Schulze and M. M. Caldwell, editors. *Ecophysiology of photosynthesis*. Springer-Verlag, Berlin, Germany.
- Hessing, M. B., C. D. Johnson, and R. P. Balda. 1982. Early secondary succession of a pinyon-juniper woodland in a northern Arizona powerline corridor. *Southwestern Naturalist* **27**:1–9.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* **105**:367–368.
- Inouye, R. S., N. J. Huntly, D. Tilman, J. R. Tester, M. Stillwell, and K. C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. *Ecology* **68**:12–26.
- Jenny, H. 1980. The soil resource, origin and behavior. *Ecological Studies* **37**.
- Kimball, B. A., J. R. Mauney, F. S. Nakayama, and S. B. Idso. 1993. Effects of increasing atmospheric CO_2 on vegetation. *Vegetatio* **104/105**:65–75.
- Kinraide, T. B. 1984. The influence of soil texture on the vegetation of a grazed, short grass prairie in Colorado. *Southwestern Naturalist* **29**:277–287.
- Kleinbaum, D. G., and L. L. Kupper. 1978. *Applied regression analysis and other multivariate methods*. Duxbury, North Scituate, Massachusetts, USA.
- Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* **73**:235–253.
- Küchler, A. W. 1964. *The potential natural vegetation of the conterminous United States*. American Geographical Society, New York, New York, USA.
- Lauenroth, W. K., J. J. Dodd, and P. L. Sims. 1978. The effects of water and nitrogen induced stress on plant community structure in a semiarid grassland. *Oecologia* **36**: 211–222.
- Lauenroth, W. K., J. L. Leatham, D. G. Milchunas, and J. L. Dodd. 1984. The Plains region and experimental sites. Pages 11–43 in W. K. Lauenroth and E. M. Preston, editors. *The effects of SO_2 on a grassland*. *Ecological Studies* **45**.
- Lauenroth, W. K., H. W. Hunt, D. M. Swift, and J. S. Singh. 1986. Estimating aboveground net primary productivity in grasslands: a simulation approach. *Ecological Modelling* **33**:297–314.
- Lee, C. A., and W. K. Lauenroth. 1994. Spatial distribution of grass and shrub root systems in the shortgrass steppe. *American Midland Naturalist* **132**:117–123.
- Leemans, R., and W. Cramer. 1991. The IIASA database for mean monthly values of temperature, precipitation, and cloudiness on a global terrestrial grid. Research Report RR-91-18. International Institute of Applied Systems Analysis, Luxemburg.
- Leishman, M. R., and M. Westoby. 1992. Classifying plants into groups on the basis of associations of individual traits—evidence from Australian semi-arid woodlands. *Journal of Ecology* **80**:417–424.
- Levin, M. H., and G. M. Keleher. 1969. Vegetation of a prairie near Winnipeg, Manitoba. *Canadian Field Naturalist* **83**:113–122.
- Lloyd, J., and G. D. Farquhar. 1994. ^{13}C discrimination during CO_2 assimilation by the terrestrial biosphere. *Oecologia* **99**:201–215.
- MacCracken, J. G., D. W. Uresk, and R. M. Hansen. 1983. Plant community variability on a small area in southeastern Montana. *Great Basin Naturalist* **43**:660–668.
- McGregor, R. L., and T. M. Barkley, editors. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas, USA.
- McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341**: 142–144.
- McPherson, G. R., H. A. Wright, and D. B. Wester. 1988.

- Patterns of shrub invasion in semiarid Texas grasslands. *American Midland Naturalist* **120**:391–397.
- Meinzer, F. C. 1978. Observaciones sobre la distribución taxonómica y ecológica de la fotosíntesis C_4 en la vegetación del noroeste de Centroamérica. *Revista de Biología Tropical* **26**:359–369.
- Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* **80**:11–23.
- Murray, R. B. 1988. Response of three shrub communities in southern Idaho to spring-applied tebuthiuron. *Journal of Range Management* **41**:16–22.
- Ode, D. J., and L. L. Tieszen. 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. *Ecology* **61**:1304–1311.
- Oesterheld, M., O. E. Sala, and S. J. McNaughton. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* **356**:234–236.
- Paruelo, J. M., and O. E. Sala. 1995. Water losses in the Patagonian Steppe: a modelling approach. *Ecology* **76**:510–520.
- Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forest of Isle Royale National Park. *Ecology* **74**:467–480.
- Pearcy, R. W., and J. Ehleringer. 1984. Comparative ecophysiology of C_3 and C_4 plants. *Plant, Cell and Environment* **7**:1–13.
- Peters, R. H., J. J. Armesto, B. Boeken, J. J. Cole, C. T. Driscoli, C. M. Duarte, T. M. Frost, J. P. Grime, J. Kolasa, E. Prepas, and W. G. Sprules. 1991. On the relevance of comparative ecology to the larger field of ecology. Pages 46–64 in J. Cole, G. Lovett, and S. Findlay, editors. *Comparative analyses of ecosystems*. Springer-Verlag, New York, New York, USA.
- Pielke, R. A., G. Dalu, J. S. Snook, T. J. Lee, and T. G. F. Kittel. 1991. Nonlinear influence of mesoscale land use on weather and climate. *Journal of Climate* **4**:1053–1069.
- Pieper, R. D., J. R. Montoya, and V. L. Groce. 1971. Site characteristics on pinyon-juniper and blue grama ranges of South Central New Mexico. *New Mexico State University Agricultural Experimental Station Bulletin* **573**.
- Piper, J. K., and M. C. Gernes. 1988. Vegetation dynamics of three tallgrass prairie sites. In T. B. Bragg and J. Stubbendieck, editors. *Proceedings of the 11th North American Prairie Conference*. Lincoln, Nebraska, USA.
- Player, R. L., and P. J. Urness. 1982. Habitat manipulation for reestablishment of Utah prairie dogs in Capitol Reef National Park. *Great Basin Naturalist* **42**:517–523.
- Pluhar, J. J., R. W. Knight, and R. K. Heitschmidt. 1987. Infiltration rates and sediment production as influenced by grazing systems in the Texas Rolling Plains. *Journal of Range Management* **40**:240–243.
- Polley, H. W., H. B. Johnson, B. D. Marino, and H. S. Mayeux. 1993. Increase in C_3 plant water-use efficiency and biomass over Glacial to present CO_2 concentrations. *Nature* **361**:61–64.
- Polley, H. W., H. B. Johnson, and H. S. Mayeux. 1992. Carbon dioxide and water fluxes of C_3 annuals and C_3 and C_4 perennials at subambient CO_2 concentrations. *Functional Ecology* **6**:693–703.
- Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* **19**:117–134.
- Pylypec, B. 1986. The Kernan prairie—a relict fescue grassland near Saskatoon, Saskatchewan. *Blue Jay* **44**:222–231.
- Quade, J., T. E. Cerling, and J. R. Bowman. 1989. Development of Asian monsoon revealed by marked ecological shift during the late Miocene in northern Pakistan. *Nature* **342**:163–166.
- Rasmussen, L. L., and J. D. Brotherson. 1986. Response of winterfat (*Ceratoides lanata*) communities to release from grazing pressure. *Great Basin Naturalist* **46**:148–155.
- Redmann, R. E. 1975. Production ecology of grassland plant communities in western North Dakota. *Ecological Monographs* **45**:83–106.
- Root, R. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. *Ecological Monographs* **37**:317–350.
- Rundel, P. W. 1980. The ecological distribution of C_4 and C_3 grasses in the Hawaiian Islands. *Oecologia* **45**:354–359.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* **81**:501–505.
- Sala, O. E., W. K. Lauenroth, and R. A. Golluscio. 1996. Plant functional types in temperate arid regions. In T. M. Smith, I. A. Woodward, and H. H. Shugart, editors. *Plant functional types*. Cambridge University Press, Cambridge, England, *in press*.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* **69**:40–45.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* **247**:1043–1048.
- Sims, P., J. S. Singh, and W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands. *Journal of Ecology* **66**:251–285.
- Singh, J. S., W. K. Lauenroth, R. K. Heitschmidt, and J. L. Dodd. 1983. Structural and functional attributes of the vegetation of northern mixed prairie of North America. *Botanical Review* **49**:117–149.
- Smeins, F. E., and D. E. Olsen. 1970. Species composition and production of a native Northwestern Minnesota tall grass prairie. *American Midland Naturalist* **84**:398–410.
- Smith, B. N., and W. V. Brown. 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratio. *American Journal of Botany* **60**:505–513.
- Smith, T. M., H. H. Shugart, F. I. Woodward, and P. J. Burton. 1993. Plant functional types. Pages 272–291 in A. M. Solomon and H. H. Shugart, editors. *Vegetation dynamics and global change*. Chapman and Hall, New York, New York, USA.
- Steuter, A. A. 1987. C_3/C_4 production shift on seasonal burns—Northern Mixed Prairie. *Journal of Range Management* **40**:27–31.
- Stoddard, L. A., A. D. Smith, and T. W. Box. 1975. *Range management*. McGraw Hill, New York, New York, USA.
- Stowe, L. G., and J. A. Teeri. 1978. The geographic distribution of C_4 species of the dicotyledonae in relation to climate. *American Naturalist* **112**:609–623.
- Stubbendieck, J., S. L. Hatch, and C. H. Butterfield. 1992. *North American Range plants*. Fourth edition. University of Nebraska Press, Lincoln, Nebraska, USA.
- Teeri, J. A., and L. G. Stowe. 1976. Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia* **23**:1–12.
- Tieszen, L. L., M. M. Senyimba, S. K. Imbamba, and J. H. Troughton. 1979. The distribution of C_3 and C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* **37**:337–350.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* **57**:189–214.
- Tueller, P. T., and R. E. Eckert. 1987. Big sagebrush (*Artemisia tridentata*) and longleaf snowberry (*Symphoricarpos oreophyllus*) plant associations in Northeastern Nevada. *Great Basin Naturalist* **47**:117–131.

- Turner, F. B., and J. F. McBrayer. 1974. Rock Valley validation site. US/IBP Desert Biome Research Memorandum 74-2.
- Uresk, D. W. 1990. Using multivariate techniques to quantitatively estimate ecological stages in a mixed grass prairie. *Journal of Range Management* 43:282-285.
- Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:18-23.
- . 1994. Landscape to regional-scale responses of terrestrial ecosystems to global change. *Ambio* 23:67-73.
- Walker, B. H., and I. Noy Meir. 1982. Aspects of stability and resilience of savanna ecosystems. Pages 577-590 in B. J. Huntley and B. H. Walker, editors. *Ecology of tropical savannas*. Springer-Verlag, Berlin, Germany.
- Walter, H. 1971. Natural savannas. In H. Oliver and R. Boyd, editors. *Ecology of tropical and subtropical vegetation*. Oliver and Boyd, Edinburgh, Scotland.
- Werger, M. J. A., and R. P. Ellis. 1981. Photosynthetic pathway in the arid regions of South Africa. *Flora* 171:64-75.
- West, N. E. 1983. Western Intermountain sagebrush steppe. Pages 351-374 in N. E. West, editor. *Ecosystems of the world: temperate deserts and semi-deserts*. First edition. Volume 5. Elsevier, Amsterdam, The Netherlands.
- . 1985. Aboveground litter production of three temperate semidesert shrubs. *American Midland Naturalist* 113:158-169.
- Woodward, F. I. 1993. The lowland-to-upland transition—modelling plant responses to environmental change. *Ecological Applications* 3:404-408.
- Yong-Hong, L. 1989. Impact of grazing on *Aneurolepidium chinense* steppe and *Stipa grandis* steppe. *Acta Oecologica* 10:31-46.
- Yorks, T. P., N. E. West, and K. M. Capels. 1992. Vegetation differences in desert shrublands of western Utah's Pine Valley between 1933 and 1989. *Journal of Range Management* 45:569-578.
- Young, J. A., R. A. Evans, B. A. Roundy, and J. A. Brown. 1986. Dynamic landforms and plant communities in a pluvial basin. *Great Basin Naturalist* 46:1-21.

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