

Regional climatic similarities in the temperate zones of North and South America

J. M. PARUELO*† W. K. LAUENROTH*, H. E. EPSTEIN*, I. C. BURKE*, M. R. AGUIAR*† and O. E. SALA†‡ *College of Natural Resources, Colorado State University, Fort Collins, CO 80523, U.S.A., †Dpto Ecología, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, (1417) Buenos Aires, Argentina and ‡Department of Biological Sciences, Stanford University, Palo Alto, CA 94305, U.S.A.

Abstract. We performed an analysis of the climatic patterns of the temperate zones in North and South America using a global database of monthly precipitation and temperature. Three synthetic variables, identified by a principal component analysis (PCA) of the monthly data, were used: mean annual precipitation, mean annual temperature and the proportion of the precipitation falling during summer. We displayed the spatial gradient of the three variables by constructing a composite colour raster image. We used a parallelepiped classification algorithm to locate areas in both continents that are climatically similar to five North American Long Term Ecological Research sites and to two South American long-term ecological research sites. The same algorithm was used to identify areas in South America which are climatically similar to some of the major grassland and shrubland types of North America.

There is substantial overlap between the climates of North and South America. Most of the climatic patterns found in South America are well represented in North America. How-

ever, there are certain climates in North America that are not found in South America. An example is a climate with relatively low mean annual temperature and high summer precipitation. The climatic signatures of three North American LTER sites (Cedar Creek, CPER and Sevilleta) were not found in South America. The climatic signatures of two LTER sites (Konza and Jornada) had some representation in South America. Two South American research sites (Río Mayo and Las Chilcas) were well represented climatically in North America. The climates of six out of seven selected North American grassland and shrubland types were represented in South America. The northern mixed prairie type was not represented climatically in South America. Our analysis suggests that comparisons of North and South America can provide a powerful test of climatic control over vegetation.

Key words. Grasslands, shrublands, temperate zones, climatic classification, North America, South America, global change.

INTRODUCTION

Unravelling basic ecological principles, as well as solving urgent applied problems such as the evaluation of the effects of global change on ecosystems, will require a diversity of approaches including monitoring, experiments, and simulation modelling. A comparative ecosystem approach to these kinds of investigations may prove to be a very powerful way to detect and investigate how ecosystems will respond to global change. One important comparative approach will be to choose pairs or groups of similar sites on different continents. Identification of ecologically similar regions is the first step in selecting such sites to conduct monitoring, experimental or modelling comparisons of responses of ecosystems to global change. Successful examples of this approach are the comparative studies of the Mediterranean areas of Chile and California (Mooney, 1977) and of creosote bush-dominated areas of the United States and Argentina (Lowe *et al.*, 1973; Orians & Solbrig, 1977; Mares, Morello & Goldstein, 1985).

The first issue to be confronted with such an approach is

the definition of ecological similarity. We chose to use macroclimatic similarity as an indicator of ecological similarity. The basis for this is found in the continental-scale relationships between ecosystems or plant types and climatic types (Holdridge, 1947; Box, 1981; Prentice *et al.*, 1992). The advantage of using climatically defined similarity instead of an indicator based upon the distribution of ecosystems is that it is not confounded with human use. Climatically similar areas can be interpreted as having similar potentials to support ecosystems.

Several attempts have been made to classify climates at regional or continental scales. Most of them used both climatic and vegetational criteria to define bioclimatic classes (Holdridge, 1947; Box, 1981; Bailey, 1989; Yong & Feoli, 1991). Recently, Leemans & Cramer (1993) reviewed the historical approaches to classifying climate and vegetation. Multivariate techniques have often been used to classify climates (Russel & Moore, 1976; White, 1981; Denton & Barnes, 1988; White & Perri, 1989; Yong & Feoli, 1991; Briggs & Lemin, 1992). Most of these studies used cluster analysis to derive climatic classes. Two com-

mon problems associated with the use of cluster analysis are, first, the selection of the method to be used (Kalstein, Tan & Skindlov, 1987) and secondly, the definition of the number of clusters (White & Perri, 1989; Yong & Feoli, 1991). A great deal of subjectivity is associated with this part of the analyses. The continuous nature of the climatic data also make it difficult to find unambiguous clusters of sites. Due to these problems, we avoided the use of cluster analysis in the present analysis. Our approach to locating climatic similarities was based on three synthetic variables, objectively derived, and on the simultaneous display of the gradients of the three variables.

Our interest is in comparing North and South America, continents that exhibit striking similarities in the structure of their temperate zone ecosystems (Bailey, 1984, 1989). These similarities are based on similar pattern of atmospheric circulation and on the presence of important orographic barriers along the west coasts of both continents. There are a number of reasons why a comparative approach using sites in North and South America is valuable as a tool to explore the potential or actual consequences of global change. Some of the value derives from having sites with floras and faunas that have been subjected to different evolutionary histories over the past 10,000 years. Additionally, recent (past 200 years) and current land use as well as the predicted rate of climate change are different in the grassland regions of North and South America (Smika, 1992; Hall *et al.*, 1992). Using a comparative approach, we can begin to test the generality of our understanding of particular ecosystems.

Much of the monitoring, experimentation and simulation analyses in both North and South America has been focused on individual research sites. In particular, a number of long-term sites have been established through programmes such as the U.S. National Science Foundation Long-Term Ecological Research program (LTER) (Franklin, Bledsoe & Callahan, 1990). The impetus for programmes such as LTER has been that intensive, long-term data are necessarily collected at sites that represent the major ecosystem types. Our assessment is that it is important to understand the extent to which these intensively studied sites represent broader ecological regions (Burke & Lauenroth, 1993). Climatic variables provide an appropriate dataset for analysing the areal representation of such sites.

In this paper we used a monthly database of precipitation and temperature to answer the following questions.

- What are the differences and similarities in the climates of North and South America?
- How well represented are the climates of current long-term grassland and shrubland study sites in both continents?
- To what degree are the climates of major vegetation units in North America represented in South America?

METHODS

We compared the climates of the temperate zones of North and South America using the Leemans & Cramer (1991)

database. This database was constructed from actual climatic data for 2583 stations worldwide. Weather records were interpolated to a grid with a resolution of 5° of latitude and longitude. The dataset includes average monthly temperature, precipitation and cloudiness. This database has been used in a number of biogeographical and ecological studies (Solomon & Leemans, 1990; Prentice *et al.*, 1992; Leemans & Solomon, 1993; Cramer & Solomon, 1993).

Based on the amount of data available to construct the database, the quality of the data is better for North than for South America. For South America we checked the values of mean annual precipitation and of temperatures of the coldest and warmest months of the year against actual data from selected stations not included in the generation of the database (FAO, 1985). We selected weather stations that covered a broad range of temperature and precipitation. Correlation coefficients were 0.95, 0.96 and 0.95 ($n = 9$, $P < 0.01$), respectively, for mean annual precipitation and the temperatures of the coldest and warmest months of the year.

The areas covered by our analysis lie between 30° and 55° of latitude in both hemispheres, and between west longitudes 85° and 125° for North America and east longitudes 48° and 76° for South America (Fig. 1). A total of 5048 grid cells were used, 3816 for North America and 1232 for South America. For North America we did not include the area east of the 85° W meridian, where there are no substantial areas of grassland or shrubland. Monthly data of temperature and precipitation were brought into a Geographical Information System (ARC/INFO 6.1—ESRI, Redlands, CA). Months were switched for the South American sites in such a way that June corresponded to the summer solstice in both hemispheres.

To reduce the dimensions of the dataset (monthly values of precipitation and temperature, twenty-four variables) we performed a principal component analysis (PCA) (Kshirsagar, 1972; SAS, 1988) in order to extract the major variation in the minimum number of variables. The PCA of the monthly precipitation data showed that the first two axes explained 90% of the variation (73% and 17%, respectively). The eigenvector for the first axis had similar values for each of the 12 months (Table 1). The second component represented a contrast between the precipitation during summer (June, July and August) and the precipitation during winter (December, January and February) (Table 1). We interpreted the first axis as an estimate of mean annual precipitation (MAP) and the second axis as an estimate of the seasonality of precipitation. The first axis showed a correlation with MAP of 0.99 and the second axis showed a correlation of 0.76 with the proportion of the precipitation falling in summer (SEAS). The PCA analysis for monthly temperature data showed that 86% of the variance was explained by the first component (Table 1). This axis was highly correlated with Mean Annual Temperature (MAT) ($r = 0.99$). We used the information from the PCA as justification for selecting MAP, SEAS and MAT as the three variables for our comparative analyses.

To represent graphically the spatial gradients of the three variables, we assigned each variable to a band (red, green

and blue, respectively, for MAT, MAP, SEAS) and we displayed them as a composite colour raster image in ERDAS (ERDAS, Atlanta, GA). Climatic variables were rescaled to the range 0–255 for display.

Polygons of approximately $1^\circ \times 1^\circ$ were digitized around the five North America Long-Term Ecological Research (LTER) sites (Franklin *et al.*, 1990) located in grassland or shrubland areas: Cedar Creek, Konza, CPER, Jornada and Sevilleta and two long-term research sites in South America: Las Chilcas (Sala *et al.*, 1986, 1989; Oesterheld & Sala, 1990) and Río Mayo (Paruelo *et al.*, 1988; Aguiar, Soriano & Sala, 1992). The parallelepiped classification algorithm (ERDAS 7.5), based on maximum and minimum values of MAT, MAP and SEAS, was used to generate a climatic signature for each of the research site polygons. The climatic signature for each site was then projected over both continents in order to identify areas climatically similar to the selected sites.

We also digitized polygons representing seven North American vegetation types, based upon Küchler's (1964)

and Dodd's (1979) cartographic units (Table 2). The parallelepiped classification algorithm was also applied to generate a climatic signature for each of the North American vegetation units and to project these signatures over South America.

RESULTS AND DISCUSSION

Climatic patterns

The continental-scale patterns generated by our analysis highlight the large-scale similarities between North and South America, reveal considerable regional complexity in climate, and help to reinforce our knowledge of climatic patterns (Fig. 2). On both continents the grassland and shrubland areas are sandwiched between wetter areas. In North America this happens on a west–east axis, and in South America it happens on a south–west–north east axis. Both continents have an area of high precipitation (> 1500 mm MAP), moderate temperature ($\sim 10^\circ\text{C}$ MAT) and domination of winter precipitation along their west coasts

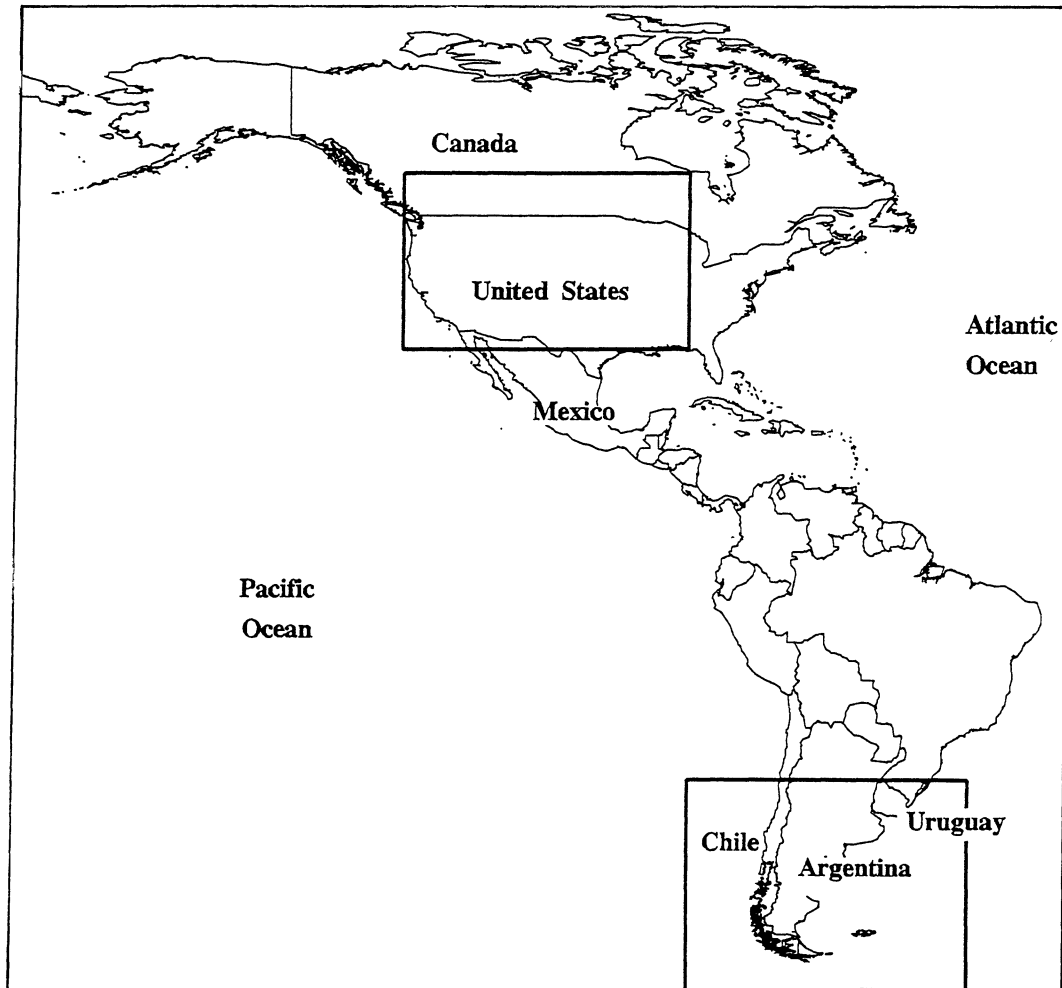


FIG. 1. Map of the Americas showing the study areas in both hemispheres. The study areas lie between the parallels of 30° and 55° for both North America and South America. For the North American region we discarded the area east of the 85°W meridian, where there are no substantial areas of grassland or shrubland.

TABLE 1. Loading factors from the PCA of the monthly precipitation data (first two components) and of the monthly temperature data (first component).

	Precipitation		Temperature
	PC1	PC2	PC1
January	0.28	− 0.36	0.28
February	0.29	− 0.33	0.28
March	0.26	− 0.23	0.29
April	0.31	0.07	0.31
May	0.30	0.23	0.19
June	0.27	0.36	0.28
July	0.27	0.36	0.26
August	0.27	0.36	0.27
September	0.30	0.23	0.30
October	0.31	− 0.03	0.31
November	0.30	− 0.27	0.30
December	0.28	− 0.36	0.28

(represented by green in Fig. 2). These are forested regions dominated by conifers in North America (Barbour, Burk & Pitts, 1980) and deciduous and evergreen trees (*Nothofagus* sp.) in South America (Cabrera, 1976); The eastern boundary in North America and the north eastern boundary in South America (represented by a complex of tan, orange and yellow) indicate high precipitation (> 1200 mm MAP), high temperature (15–20°C MAT) and no clear dominant seasonality in precipitation. These are areas of temperate deciduous forest in North America and grassland in South America (Barbour *et al.*, 1980; Soriano, 1992).

Between the two areas of high precipitation lie the grasslands and shrublands on both continents. In North America most of the grasslands are located in areas of low to moderate amounts of precipitation (300–800 mm MAP) with most precipitation concentrated during the warmest months of the year (Fig. 2). While these areas (pinkish-purple changing to purple areas (Fig. 2) in the north central United States and southern Canada) span a range of MAT from less than 5°C to greater than 20°C the majority of

them are in the region with MAT to less than 10°C. These classically continental climates are much more widespread in the temperate zone of North America than in South America.

The areas of major overlap between the two continents occur in the inter-mountain zone and desert south west of the United States and the southern and north western parts of Argentina (mottled rust colours in the western United States and southern Argentina, Fig. 2). These areas correspond to areas of relatively low precipitation (150–500 mm of MAP) and mean annual temperatures ranging from 0°C to 12°C. These areas support shrublands and shrubland–grassland mixtures and receive an important proportion of their annual precipitation in the coldest months of the year. North western Argentina and south western United States and northern Mexico (magenta colours in Fig. 2) are characterized by hot arid shrublands with strong summer seasonality in precipitation. The structure of the vegetation in these areas is similar between the two continents with a predominance of creosote bush (*Larrea* sp.) and xerophilous trees in the family Fabaceae (MacMahon & Wagner, 1985; Mares *et al.*, 1985).

The Mediterranean climates, characterized by dominant winter precipitation, were distinguished in both continents in California and Chile (rusty red colours in Fig. 2). The area in North America is larger but both support a mixture of annual grassland and sclerophilous shrubland and woodland (Mooney, 1977). On both continents these areas grade into arid shrublands towards the equator.

The relative area with a low proportion of summer precipitation (less than 15% of the rainfall falling during summer) is similar in the temperate zone of both continents (Fig. 3a). However, the relative area with a clear summer pattern of precipitation is considerably larger in North than in South America. The proportion of very dry areas (less than 200 mm) is lower in North than in South America. Most of the grassland and shrubland areas of North America correspond to the range 200–800 mm. Very wet grassland are more frequent in South America (Fig. 3b). The higher proportion of land at high latitudes and continental-

TABLE 2. Identification of Küchler (1964) cartographic units used in the analysis.

Vegetation types	Cartographic units
Sonoran desert	Creosote bush–bur sage (36) Palo verde–cactus shrub (37)
Sagebrush steppe	Sagebrush steppe (49)
Short-grass steppe	Grama–buffalo grass (58)
Northern mixed prairie	Wheatgrass–needlegrass (59) Wheatgrass–bluestem–needlegrass (60)
Southern mixed prairie	Bluestem–grama prairie (62) Mesquite–buffalo grass (76)
Tall-grass prairie	Bluestem prairie (66) Sandhills prairie (67) Blackland prairie (68)
Tall-grass savanna	Oak savanna (72) Bluestem prairie/oak–hickory forest mosaic (73) Cross timbers (75) Juniper–oak savanna (77)

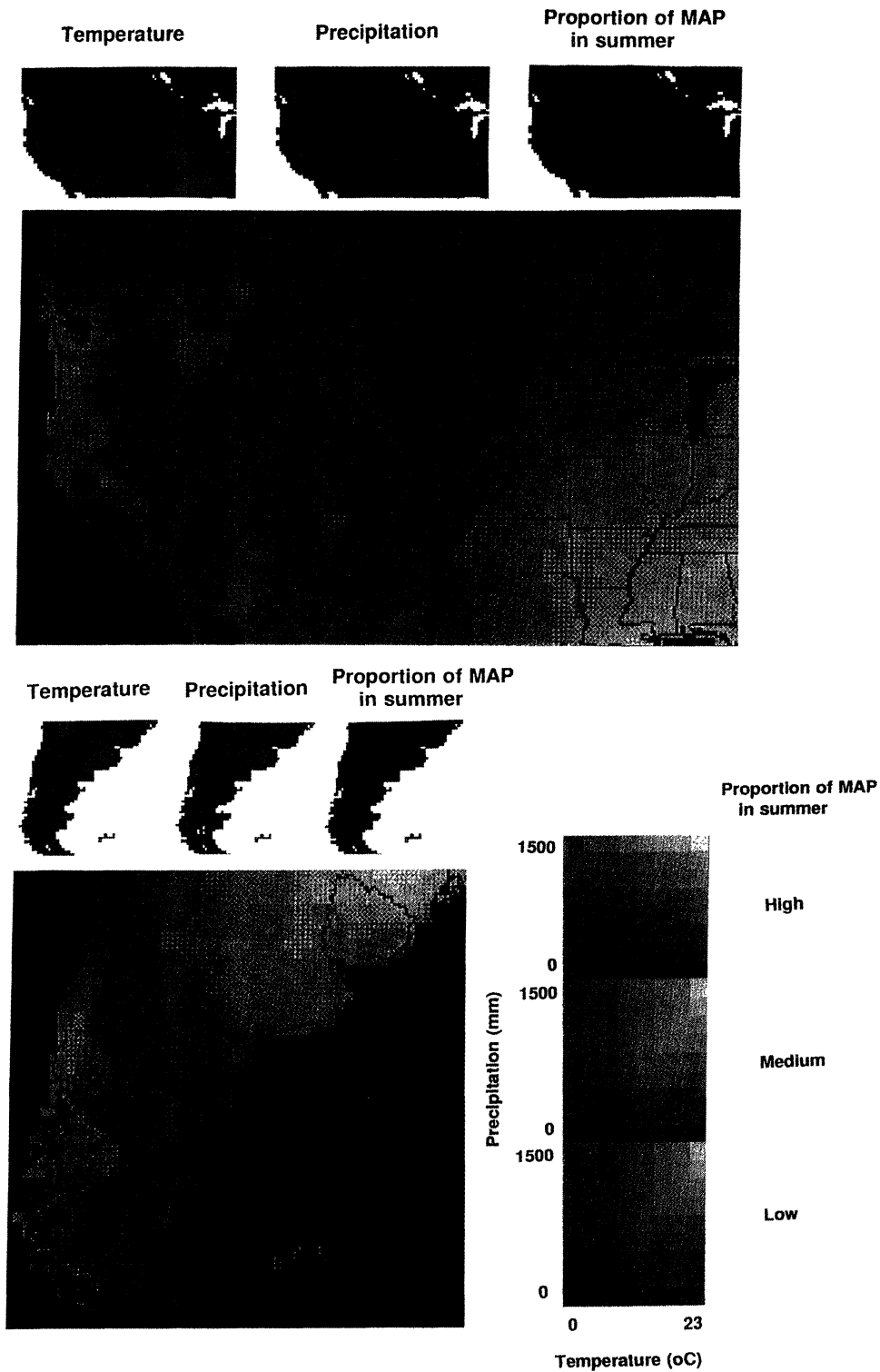


FIG. 2. Maps showing the distribution of mean annual temperature (MAT), mean annual precipitation (MAP) and seasonality (proportion of summer precipitation) (SEAS) and the climates resulting from combining these three variables in both North and South America. Each variable (MAT, MAP, SEAS) was assigned to a band (red, green, blue) and displayed as composite colour raster image (large maps). For the single variable maps (small maps) the value of each variable increases with the intensity of the colour.

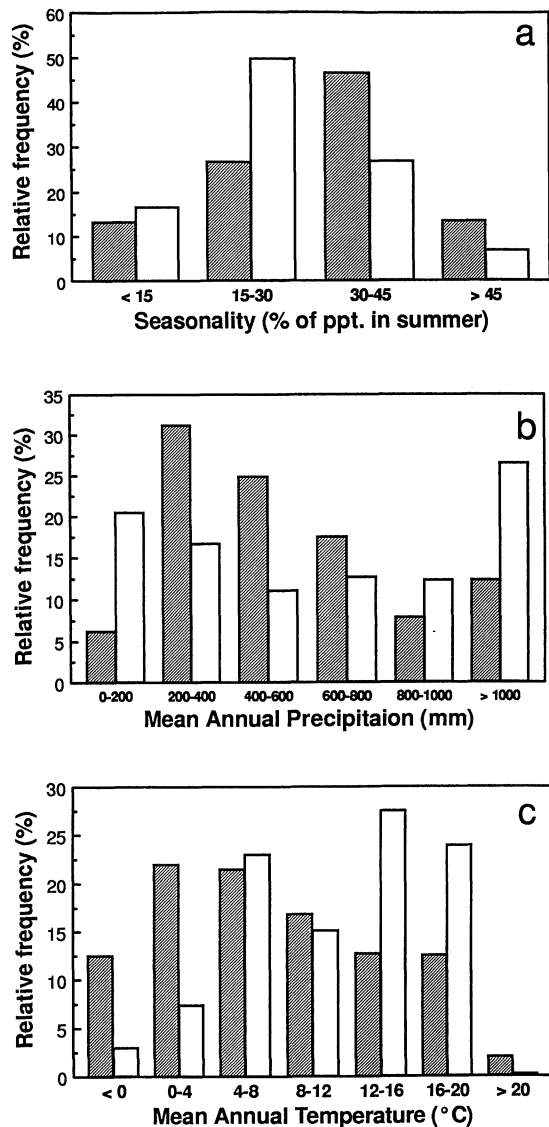


FIG. 3. Frequency distribution of the three variables studied: (a) SEAS, (b) MAP, (c) MAT, in both continents. Shaded bars: North America ($n = 3816$ grid cells), open bars: South America ($n = 1232$ grid cells).

ity is the reason for the higher relative frequency of areas with low temperatures in North America (Fig. 3c).

Analysis of site representation

Analysis of areas immediately surrounding the grassland LTER sites in the United States and projecting the result to South America indicated that these sites are poorly represented in South America but are representative of relatively large areas in North America (Fig. 4 and Table 3). Only Konza (a tall-grass prairie) and Jornada (a desert shrubland) have climatic analogues in South America. Konza is representative of a small area in the Pampas grassland region, and Jornada is representative of a small area in the Monte shrubland region. By contrast, a similar analysis of

two long-term sites in South America suggests that they are well represented in terms of North American climates. Las Chilcas is a tall-grass site in the Pampas region and is similar to Konza and some of the wetter parts of the tall-grass prairie in Kansas and Missouri. Río Mayo is a shrub steppe site in Patagonia and is very well represented in the Great Basin region.

Climatic similarities

Expanding our areal scope of similarity analysis we evaluated the degree to which climates of a selection of North American grassland and shrubland types were represented in South America (Fig. 5 and Table 4). The climate of the Sonoran desert shrublands are well represented in South America in an area also dominated by creosote bush (*Larrea* sp.), but a different species (Mares *et al.*, 1985). Sonoran desert shrublands correspond to dry zones, with a broad range of precipitation distribution patterns and high temperatures. The sagebrush steppe type which is dominated by shrubs and bunch grasses (West, 1983) is represented in the northern portion of Patagonia, an area also dominated by shrubs and bunch grasses (Soriano, 1983). These areas are relatively cold and have a distinctly low proportion of precipitation during summer (Table 4). The short-grass steppe in North America is coincident with Küchler's *Bouteloua gracilis*–*Buchloe dactyloides* type (Lauenroth & Milchunas, 1992). Similar climates are found in central Argentina in an area between the Pampas grasslands and the Monte, which is a creosote bush-dominated arid shrubland. The short-grass steppe climate is characterized by MAP around 450 mm, and a clear summer distribution pattern of the precipitation (Table 4). Areas climatically similar to the short-grass steppe in South America occur toward the warmest portion of the climatic space, where the short-grass steppe in North America begins to incorporate woody elements.

The climate associated with the northern mixed prairie (Coupland, 1992) is not present in South America. These are areas with cold temperatures, moderate amounts of precipitation and a large fraction of MAP received in the summer (Table 4). That combination of variables is not found in South America. The warmest part of the southern mixed prairie is represented in South America (Table 4). The vegetation that corresponds to this climate in South America is a woodland–grassland complex dominated by trees in the family Fabaceae, and C3 and C4 grasses (Cabrera, 1976). This vegetation unit shows a high physiognomic and floristic affinity with one of the Küchler's units included in the southern mixed grass prairie (mesquite–buffalo grass).

The climates of both of the North American tall-grass prairie types (Kucera, 1992) are very well represented in South America. These relatively humid units receive an important proportion of precipitation in summer. Both have high overlap with the tall-grass regions of Argentina and south eastern Uruguay (Soriano, 1992); however, only the warmest portion of the North American tall-grass prairies is represented in South America. An important difference in the vegetation of the two continents is that in the tall-grass

savanna types in North America trees are an important component of the vegetation, while they are not in South America. The absence of woody plants in the Pampas has been broadly discussed in the past without arriving at a clear explanation (Schmieder, 1927; Parodi, 1942; Ellemberg, 1962; Walter, 1967); the variables included in our analyses do not provide further insight. Some other climatic dimensions such as the annual thermal amplitude, inter-annual variability of the rainfall, amount of precipitation falling as snow; the evolutionary history of the region, and/or soil differences could provide some clues.

CONCLUSIONS

Several successful attempts to summarize the characteristics of the main ecosystems of the world have been made in the recent past (see the series *Ecosystems of the World* edited by D. W. Goodall). In this paper we have made connections between some of them, based on their climatic similarities.

Three synthetic variables explained most of the variation in climate for grassland and shrubland ecosystems in North and South America. These variables were mean annual temperature, mean annual precipitation and the proportion of precipitation falling during the three summer months.

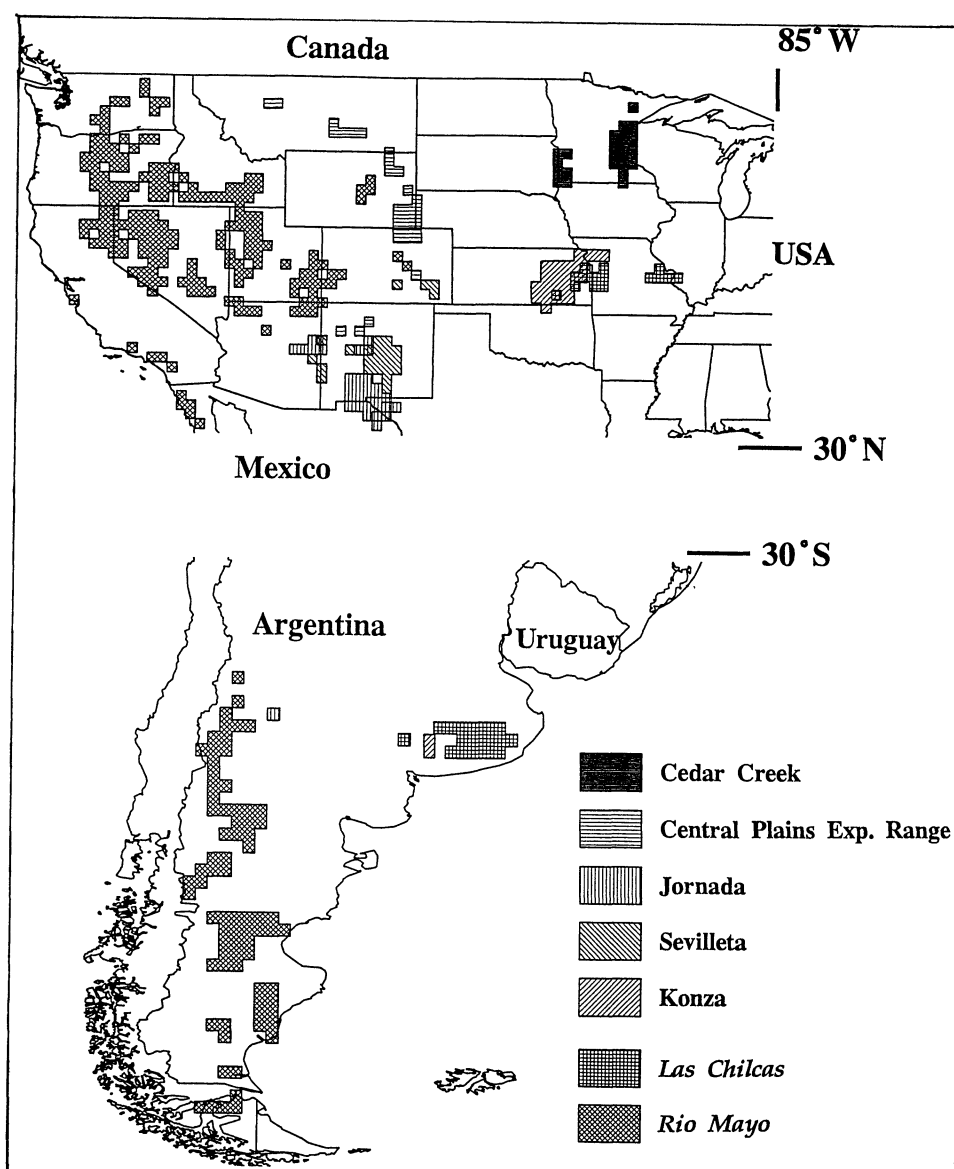


FIG. 4. Areas climatically similar to the five North American grassland sites in the Long-Term Ecological Research program (LTER) sites and to two South American long-term ecological research sites. The parallelepiped classification algorithm (ERDAS 7.5), based on maximum and minimum values of MAP, SEAS and MAT, was used to generate a climatic signature for each of the research site polygons (Table 3). The climatic signature for each site was then projected over both continents. The LTER sites included are for U.S.: Cedar Creek, MN (93.2 W, 45.4 N); CPER, CO (104.60 W, 40.82 N); Konza, KS (99.60 W, 39.10 N); Sevilleta, NM (106.68 W, 34.33 N); Jornada, NM (106.75 W, 32.62 N); and for Argentina: Las Chilcas, Buenos Aires (58.5 W, 36.5 S); Rio Mayo, Chubut (70.3 W, 45.7 S).

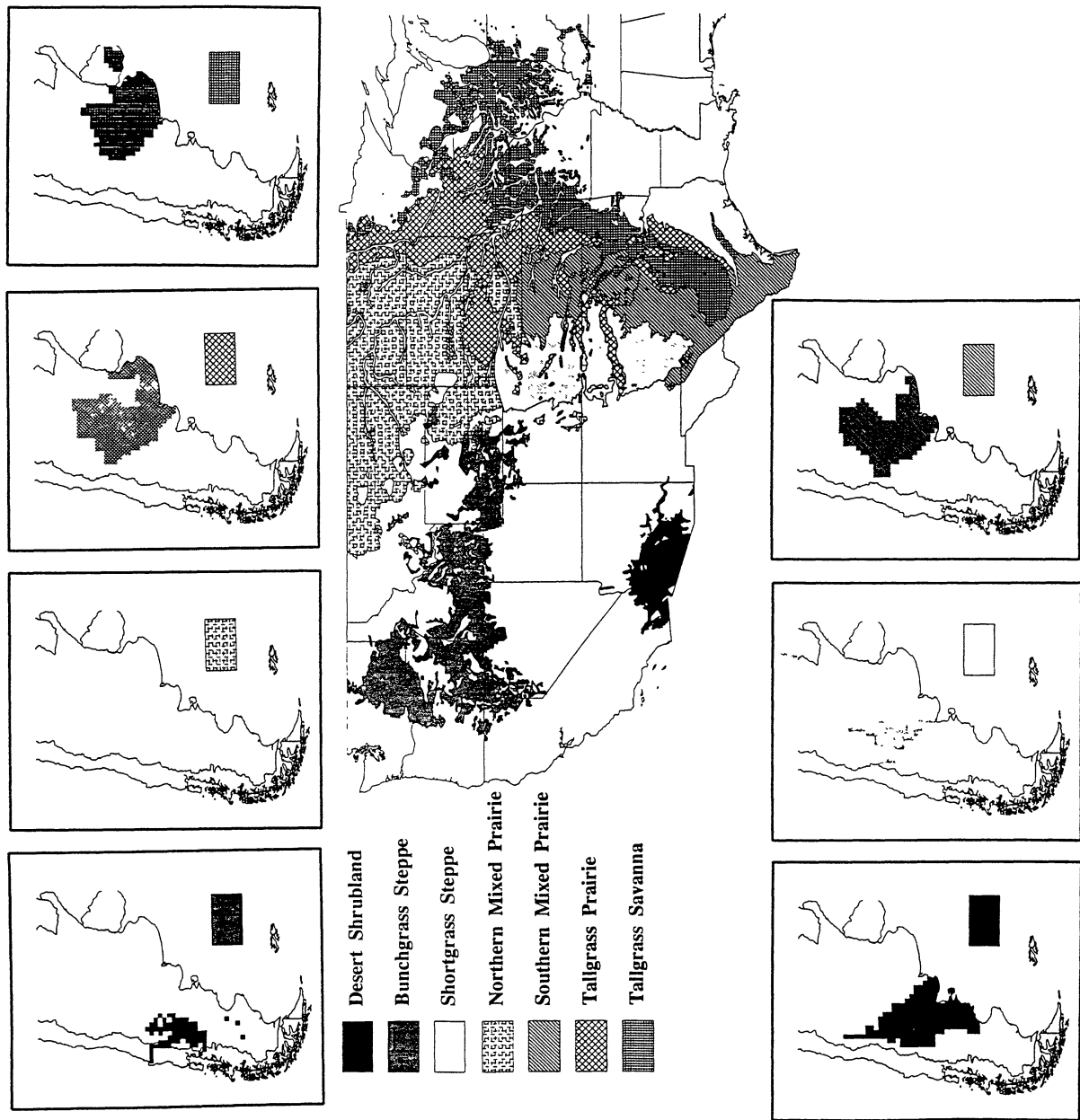


FIG. 5. Grassland and shrubland vegetation types of North America (based on Küchler, 1964 and Dodd, 1979) and areas climatically similar to these vegetation units in South America. Polygons were digitized around seven North American vegetation types. The parallelogram classification algorithm (ERDAS 7.5), based on maximum and minimum values of MAP, SEAS and MAT, was used to generate a climatic signature for each of the North American vegetation units. The climatic signature was then projected to South America.

TABLE 3. Climatic parameters for five North American LTER sites and two long-term ecological research sites in South America. Area refers to zones climatically similar to each of the sites in each hemisphere.

		North American LTER sites					South American research sites	
		Cedar Crk.	Konza	CPER	Sevilleta	Jornada	Las Chilcas	Río Mayo
MAT (°C)	Avg	5.4	12.4	8.0	10.7	16.4	13.7	8.6
	Min	4.0	11.2	7.2	9.8	9.7	13.0	6.6
	Max	6.2	13.9	9.1	12.1	18.1	14.7	10.1
	CV%	4.0	2.9	2.4	6.2	6.9	1.8	4.4
MAP (mm)	Avg	679	797	364	299	215	859	199
	Min	622	729	323	213	197	756	31
	Max	732	902	394	362	244	945	441
	CV%	6.9	6.2	5.7	13.2	12.2	4.1	55.5
SEAS	Avg	0.41	0.38	0.37	0.41	0.42	0.31	0.18
	Min	0.40	0.35	0.35	0.37	0.38	0.28	0.00
	Max	0.42	0.41	0.39	0.44	0.49	0.35	0.28
	CV%	2.2	4.5	3.8	1.8	6.2	5.1	38.9
Area (km ²)	N. America	42688	33782	51581	44466	51582	26680	332612
	S. America	—	5334	—	—	1778	30237	135179

There is substantial overlap between the climates of North and South America. Most of the climatic patterns found in South America are well represented in North America. However, there are certain climates in North America that are not found in South America. An example is a climate with relatively low mean annual temperature and high summer precipitation. The climatic signatures of three North American LTER sites (Cedar Creek, CPER and Sevilleta) were not found in South America. The climatic signatures of two LTER sites (Konza and Jornada) had some representation in South America. Two South Ameri-

can research sites (Río Mayo and Las Chilcas) were well represented climatically in North America. Northern mixed prairie vegetation types (Küchler, 1964) were not represented climatically in South America. Other Küchler vegetation types analysed had climatic signatures found in South America.

The results of this analysis will be useful in identifying climatically comparable sites in North and South America to be used in experiments on the effects of global change on terrestrial ecosystems. Additionally, the results can identify interesting differences between the two continents

TABLE 4. Selected climatic parameters for ecosystem types in North and South America. Temperature in °C, precipitation in mm/yr, and seasonality using an arbitrary scale in which 100% summer precipitation is equal to 1.

	Temperature				Precipitation				Seasonality			
	Mean	SD	Max	Min	Mean	SD	Max	Min	Mean	SD	Max	Min
Sonoran desert												
North America	19.1	2.2	22.1	9.8	196	90	478	55	0.26	0.11	0.51	0.03
South America	13.4	1.8	17.8	9.8	244	109	478	63	0.28	0.08	0.50	0.07
Sagebrush steppe												
North America	6.7	2.4	12.3	0.0	354	167	1059	165	0.13	0.05	0.29	0.02
South America	7.7	2.7	12.3	1.5	412	274	1020	165	0.13	0.05	0.25	0.04
Short-grass steppe												
North America	11.3	3.2	18.5	4.3	430	59	635	314	0.40	0.03	0.46	0.27
South America	15.0	1.7	17.8	4.4	466	104	635	314	0.36	0.06	0.45	0.27
Northern mixed prairie												
North America	6.1	2.1	11.2	1.7	389	70	635	258	0.42	0.05	0.53	0.27
South America	—	—	—	—	—	—	—	—	—	—	—	—
Southern mixed prairie												
North America	13.3	3.4	20.4	5.3	554	115	855	314	0.37	0.06	0.46	0.25
South America	15.5	1.8	19.7	9.5	637	185	855	314	0.36	0.06	0.46	0.25
Tall-grass prairie												
North America	10.1	4.3	19.4	2.7	620	121	886	400	0.40	0.07	0.52	0.20
South America	15.7	1.8	19.4	9.5	689	137	886	400	0.36	0.06	0.52	0.24
Tall-grass savanna												
North America	12.3	3.2	18.4	6.9	842	98	1047	551	0.33	0.05	0.43	0.23
South America	15.3	1.4	18.4	9.5	820	125	1047	551	0.34	0.05	0.44	0.23

that could form the basis for subsequent research. For instance, the warmest wettest portions of the region in North America support forests while climatically comparable regions in South America support grasslands. The potential of finding forests and grasslands in similar climates provides an opportunity to ask a number of interesting ecological questions, including several about responses to climate change.

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REFERENCES

- Aguiar, M.R., Soriano, A. & Sala, O.E. (1992). Competition and facilitation in the recruitment of seedlings in Patagonian steppe. *Funct. Ecol.* **6**, 66–70.
- Bailey, R.G. (1984). Delineation of ecosystem regions. *Environ. Mngmt.* **7**, 365–373.
- Bailey, R.G. (1989). Explanatory supplement to ecoregions map of the continents. *Environ. Conserv.* **16**, 307–309.
- Barbour, M.G., Burk, J.H. and Pitts, G.D. (1980). Grasslands. Benjamin/Cummings Menlo Park, CA. *Major vegetation types of North America*, pp. 518–545.
- Box, E.O. (1981). Predicting physiognomic vegetation types with climate variables. *Vegetatio*, **45**, 127–139.
- Briggs, R.D. & Lemin, R.C. (1992). Delineation of climatic regions in Maine. *Can. J. For. Res.* **22**, 801–811.
- Burke, I. & Lauenroth, W.K. (1993). What do LTER results mean? Extrapolating from site to region and from decade to century. *Ecol. Modelling*, **67**, 19–35.
- Cabrera, A.L. (1976). Regiones Fitogeograficas Argentinas. *Enciclopedia Argentina de Agricultura y Jardineria*, 2nd edn, vol. 2 (ed. by W.F. Kugler), pp. 1–85. Editorial Acme S.A.C.I., Buenos Aires.
- Coupland, R.T. (1992). Mixed prairie. *Ecosystems of the world: natural grasslands*, vol. 8A (ed. by R.T. Coupland), pp. 151–182. Elsevier, Amsterdam.
- Cramer, W.P. & Leemans, R. (1993). Assessing impacts of climate change on vegetation using climate classification systems. *Vegetation dynamics and global change* (ed. by A.M. Solomon and H.H. Shugart), p. 338. Chapman & Hall, New York.
- Cramer, W.P. & Solomon, A.M. (1993). Climatic classification and future global redistribution of agricultural land. *Clim. Res.* **3**, 97–110.
- Denton, S.R. & Barnes, B.V. (1988). An ecological climatic classification of Michigan: a quantitative approach. *For. Sci.* **34**, 119–138.
- Dodd, J.L. (1979). North American grassland map. *Perspective in grassland ecology* (ed. by R. French), p. 204. Springer Verlag, New York, NY.
- Ellemberg, H. (1962). Wald in der Pampa Argentinien? *Veroff. Geobot. Inst. ETH Zurich*, **37**, 39–56.
- FAO (1985). Agroclimatic data for Latin America and the Caribbean. FAO, Rome.
- Franklin, J.F., Bledsoe, C.S. & Callahan, J.T. (1990). Contributions of the long-term ecological research program. *Bioscience*, **40**, 509–523.
- Hall, A.J., Rebella, C.M., Ghera, C.M. & Culot, J.P. (1992). Field-crop systems of the pampas. *Ecosystems of the world: field crop ecosystems*, vol. 18 (ed. by C.J. Pearson), pp. 413–440. Elsevier, Amsterdam.
- Holdridge, L.R. (1947). Determination of world plant formations from simple climatic data. *Science*, **105**, 367–368.
- Kalstein, L.S., Tan, G. & Skindlov, J.A. (1987). An evaluation of three clustering procedures for use in synoptic climatological classification. *J. Clim. Appl. Meteorol.* **26**, 717–730.
- Kshirsagar, A.M. (1972). Multivariate analysis. Marcel Dekker, New York, NY, USA.
- Kucera, C.L. (1992). Tall-grass prairie. *Ecosystems of the world: natural grasslands*, vol. 8A (ed. by R.T. Coupland), pp. 227–268. Elsevier, Amsterdam.
- Küchler, A.W. (1964). The potential natural vegetation of the conterminous United States. *Am. Geogr. Soc.* New York NY, USA.
- Lauenroth, W.K. & Milchunas, D.G. (1992). Short-grass steppe. *Ecosystems of the world: natural grasslands*, vol. 8A (ed. by R.T. Coupland), pp. 183–226. Elsevier, Amsterdam.
- Leemans, R. & Cramer, W. (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 Analyses, Luxembourg.
- Leemans, R. & Solomon, A.M. (1993). Modelling the potential change in yield and distribution of the earth's crops under a warmed climate. *Clim. Res.* **3**, 79–96.
- Lowe, C.W., Morello, J., Goldstein, G., Gross, J. & Neumann, R. (1973). Analisis comparativo de la vegetacion de los desiertos subtropicales de Norte y Sud America (Monte-Sonora). *Ecologia*, **1**, 35–43.
- MacMahon, J.A. & Wagner, F.H. (1985). The Mojave, Sonoran and Chihuahuan deserts of North America. *Ecosystems of the world: hot deserts and arid shrublands*, vol. 12A (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 105–202. Elsevier, Amsterdam.
- Mares, M.A., Morello, J. & Goldstein, G. (1985). The Monte desert and other subtropical semi-arid biomes of Argentina, with comments on their relation to North American arid areas. *Ecosystems of the world: hot deserts and arid shrublands*, vol. 12A (ed. by M. Evenari, I. Noy-Meir and D.W. Goodall), pp. 203–238. Elsevier, Amsterdam.
- Mooney, H.A. (ed.) (1977). *Convergent evolution in Chile and California: Mediterranean climate ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Oosterheld, M. & Sala, O.E. (1990). Effects of grazing on seedling establishment: the role of seed and safe-site availability. *J. Veg. Sci.* **1**, 353–358.
- Orians, G.H. & Solbrig, O.T. (eds) (1977). *Convergent evolution in warm deserts*. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Parodi, L.R. (1942). Por que no existen bosques naturales en la llanura bonarense si los arboles crecan en ella cuando se los cultiva? *Rev. Cent. Aeron. Buenos Aires* **30**, 887–397.
- Paruelo, J.M., Aguiar, M.R. & Golluscio, R.A. (1988). Soil water availability in the Patagonian arid steppe: gravel content effect. *Arid Soil Res. Rehab.* **2**, 67–74.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992). A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* **19**, 117–134.
- Russell, J.S. & Moore, A.W. (1976). Classification of climate by pattern analysis with Australasian and Southern African data as an example. *Agric. Meteorol.* **16**, 45–70.
- Sala, O.E., Oosterheld, M., Leon, R.J.C. & Soriano, A. (1986).

- Grazing effects upon a plant community structure in subhumid grasslands of Argentina. *Vegetatio*, **67**, 27–32.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K. & Soriano, A. (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia*, **81**, 501–505.
- SAS (1988) *SAS/STAT User's guide, release 6.03 edition*. SAS Institute, Cary, North Carolina.
- Schneider, O. (1927) The pampa, a natural or culturally induced grassland? *Univ. California. Pub., Geogr.* **2**, 255–276.
- Smika, D.E. (1992) Cereal systems of the North American central great plains. *Ecosystems of the world: field crop ecosystems*, vol. 18 (ed. by C.J. Pearson), pp. 401–412. Elsevier, Amsterdam.
- Solomon, A.M. & Leemans, R. (1990) Climatic change and landscape–ecological response: issues and analysis. *Landscape–ecological impact of climatic change* (ed. by M.M. Boer and R.S. de Groot), pp. 293–316. IOS-Press, Amsterdam.
- Soriano, A. (1983) Deserts and semi-deserts of Patagonia. *Ecosystems of the world: temperate deserts and semi-deserts*, vol. 5 (ed. by N.E. West), pp. 423–460. Elsevier, Amsterdam.
- Soriano, A. (1992) Rio De Plata grasslands. *Ecosystems of the world: natural grasslands*, vol. 8A (ed. by R.T. Coupland), pp. 367–408. Elsevier, Amsterdam.
- Walter, H. (1967) *The pampa problem and its solution*, pp. 3–15. Publ. ITC, UNESCO, Centre for Integrated Surveys. Delft, The Netherlands.
- West, N.E. (1983) Overview of North American temperate deserts and semi-deserts. *Ecosystems of the world: temperate deserts and semi-deserts*, vol. 5 (ed. by N.E. West), pp. 321–330. Elsevier, Amsterdam.
- White, E.J. (1981) Classification of climate in Great Britain. *J. Environ. Mngmnt.* **13**, 241–257.
- White, E.J. & Perri, A.H. (1989) Classification of the climate of England and Wales based on agroclimatic data. *Int. J. Clim.* **9**, 271–291.
- Yong, S.C. & Feoli, E. (1991). A numerical phytoclimatic classification of China. *Int. J. Biometeorol.* **35**, 76–87.