

REGIONAL PATTERNS OF NORMALIZED DIFFERENCE VEGETATION INDEX IN NORTH AMERICAN SHRUBLANDS AND GRASSLANDS¹

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Abstract. We characterized the seasonal pattern of the Normalized Difference Vegetation Index (NDVI) of 49 grassland and shrubland sites corresponding to areas with low human impact. Each site was characterized as a vector of 21 elements, where each element corresponded to the average NDVI for one date. We used the integral of the NDVI as an estimate of the total production, and the difference between the maximum and minimum NDVI over the year as a measure of the seasonality.

Based on a Principal Component Analysis, the integral of the NDVI accounted for 63% of the variability of the SITE×DATE matrix. The difference between the maximum and minimum NDVI throughout the year accounted for 19%. Mean annual precipitation explained 67% of the variability of the integral of the NDVI curves ($P < 0.01$). The slope of the relationship between precipitation and integrated NDVI was significantly steeper for grasslands than for shrublands. The difference between the extreme values of NDVI increased with mean annual precipitation and the thermal amplitude, and decreased with mean annual temperature ($P < 0.01$).

Key words: aboveground net primary production; AVHRR/NOAA; climatic controls; global change; grasslands; multivariate analysis; Normalized Difference Vegetation Index; regional analysis; seasonality; shrublands.

INTRODUCTION

Some of the most challenging environmental problems that humankind will face during the next several decades have, as an outstanding characteristic, a global scale. Land use changes, climatic modifications, and the increase in atmospheric CO₂, are good examples of such problems. In addition to their common scale of importance, these problems are also influenced by, and in turn influence, the dynamics and composition of the atmosphere. Atmospheric processes are studied and modelled at a spatial scale of thousands of square kilometres (cells of 3–8 degrees). By contrast, ecological processes are most often studied and modelled at a spatial scale of square metres. Bridging the scale gap between ecological and atmospheric sciences is a crucial point to assess the effects of global change (Wessman 1992). The ecological knowledge generated at the plot or laboratory level may give insights about the mechanisms responsible for the changes, but the scale of these approaches has important deficiencies for describing the changes at regional scales. In this context, regional analysis of the structure and function of eco-

systems is especially relevant. The present status and the trends of the changes in the structure and function of ecosystems need to be described and monitored at regional scales to analyze the impact of the different aspects of global change upon them, and for connecting ecological to atmospheric sciences.

Two main approaches have been used to describe vegetation at regional scales. One of them describes the vegetation based on structural and floristic data (e.g., Küchler 1964). The use of these classifications often assumes a correspondence between the structure and the function of the ecosystems. The second approach is based on climatic data (Holdridge 1947, Box 1981, Bailey 1984, 1989, Nielson et al. 1992, Prentice et al. 1992). The underlying assumption of this approach, derived mainly through the logic of the environmental limitations (Box 1981), is that broad units that differ in climatic regime also have functional and structural differences.

One of the most widely used climate-based classifications is that proposed by Holdridge (1947). Holdridge defined "Life Zones" from three climatic factors: temperature, precipitation, and humidity. Emanuel et al. (1985) used this methodology to analyze the predicted changes in the distribution of ecosystems of the world under global change scenarios. In spite of their usefulness, classifications or descriptions of vegetation based on climatic data have a major shortcoming: at best they give a picture only of the potential vegetation.

A description that circumvents this shortcoming would be based on ecosystem attributes rather than on

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climatic data. McNaughton et al. (1989) pointed out the importance of annual aboveground net primary production (ANPP) as an integrative indicator of ecosystem functioning. This variable shows a significant correlation with total precipitation for ecosystems ranging from deserts to highly productive grasslands (Lauenroth 1979, Sala et al. 1988, McNaughton et al. 1993, Milchunas and Lauenroth 1993). Recent advances in the technology of remotely sensed data allow for the monitoring of the seasonal course of primary production over large areas. The function of ecosystems can be described using the Normalized Difference Vegetation Index (NDVI) derived from spectral data provided by the National Oceanic and Atmospheric Administration/Advanced Very High Resolution Radiometer (NOAA/AVHRR) satellites. The integral over the year of this index has been shown to be correlated with ANPP (Tucker and Sellers 1986, Box et al. 1989, Kennedy 1989, Prince 1990, Running 1990). Burke et al. (1991) found correlation between the integral of NDVI and primary production data simulated by the CENTURY model (Parton et al. 1987) for the central Great Plains of North America.

Soriano and Paruelo (1992) proposed the use of several attributes of the dynamics of the NDVI to define "biozones" based on ecosystem function, i.e., date of maximum NDVI peak, peak values of NDVI, shape of the NDVI curve, integral of the NDVI curve, rate of increase or decrease in NDVI over the year, date of the start and the end of the growing season, etc. These features of the seasonal NDVI curves can be used to characterize functional differences among sites. Lloyd (1990) proposed the use of NDVI to derive phenological variables in order to classify vegetation cover at continental scales. Recently, Running et al. (1994) proposed a new methodology to classify vegetation at global scales based on remotely sensed data.

Our objective was to describe the functional characteristics of North American shrublands and grasslands at a regional scale. To do this we used the seasonal course of NDVI, derived from AVHRR spectral data, as an estimator of ANPP. From this we sought answers to the following questions:

- 1) What are the main differences in NDVI among distinct types of grasslands and shrublands of North America?

- 2) Are those differences in NDVI associated with the physiognomy of the vegetation?

- 3) What are the main climatic controls of the differences in NDVI?

METHODS

Functional characterization was derived from the seasonal curves of the Normalized Difference Vegetation Index (NDVI). The NDVI was computed from spectral data of channel 1 (red, 580–680 nm) and channel 2 (infrared, 725–1100 nm) from the AVHRR/

NOAA 11 satellite: $NDVI = (\text{Channel } 2 - \text{Channel } 1) / (\text{Channel } 1 + \text{Channel } 2)$.

Most of the studies of vegetation based on NOAA/AVHRR data correspond to global scales and have been based on Global Area Coverage or Global Vegetation Index data. These products result from a subsampling of the raw data and have a spatial resolution of 4 and 15 km, respectively. The study of the relationship between structure and function at a regional scale needs more detailed data (Townshend and Justice 1988). Biweekly maximum NDVI composites (Holben 1986) of 1 km resolution corresponding to 1991 were obtained from the EROS Data Center in Sioux Falls, South Dakota, for the coterminous United States. The data set for 1991 is composed of 21 biweekly images derived from ≈ 500 Large Area Coverage images (1.1 km) of the daily orbital passes of NOAA 11. Images were geometrically registered to the Lambert Azimuthal Equal Area map projection. NDVI data obtained from the same source have been used for both local (Kremer and Running 1993) and continental scale (Loveland et al. 1991) analyses. For details about scene selection, radiometric calibration, geometric registration, and compositing see Eidenshink (1992). Image processing was performed using ERDAS 7.5 software (ERDAS Incorporated, Atlanta, Georgia).

For each of the 21 images we extracted the NDVI data for 49 areas. Each area was at least 9 km² for proper localization within the image. Study areas were selected to cover a broad range of physiognomic and climatic regimes (Fig. 1). They included most of the vegetation types of the dry domain and also several pertaining to the humid temperate domain (Bailey 1984, 1989). Selected sites corresponded to nine vegetation types according to the Küchler (1964) and Dodd (1979) classifications (Table 1). Because we were primarily interested in natural ecosystems, we located areas with low human impact (i.e., National Grasslands, National Parks, Experimental Stations, etc.) as target areas (study sites). Each study site was located on topographic maps (1:100 000) to avoid complex topographic features in the target area. From the topographic maps we also got the geographic coordinates of the study areas (Table 1). Geographic coordinates (latitude, longitude) were converted to the Lambert Azimuthal Equal Area map projection coordinates in order to overlay the study areas on the NDVI images.

We calculated the average NDVI value for the whole area of each site (ranging from 9 to 25 pixels) and for each of the 21 dates. Each study site was characterized as a vector of 21 elements, where each element corresponded to the average NDVI for a date. Spatial variability of the NDVI values within study sites was low; the coefficients of variation were lower than 7% for all the dates and sites. The 49 sites defined a matrix of 49 rows (sites) and 21 columns (dates). We analyzed the structure of this matrix using Principal Component Analysis (Kshirsagar 1972).

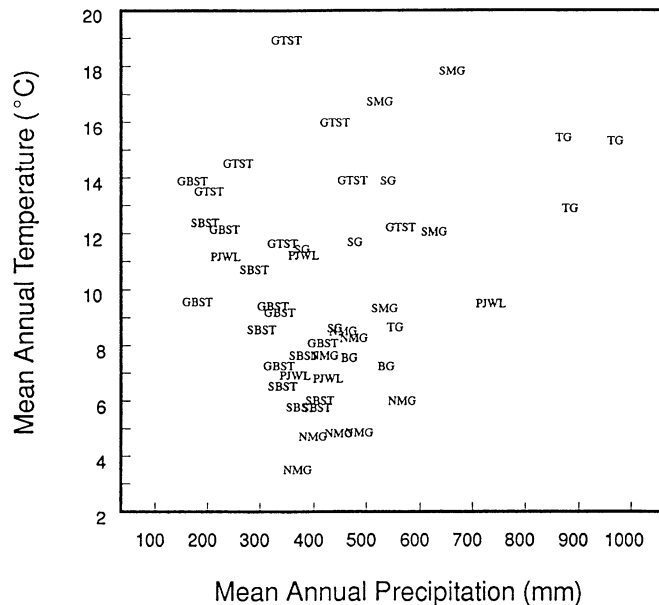
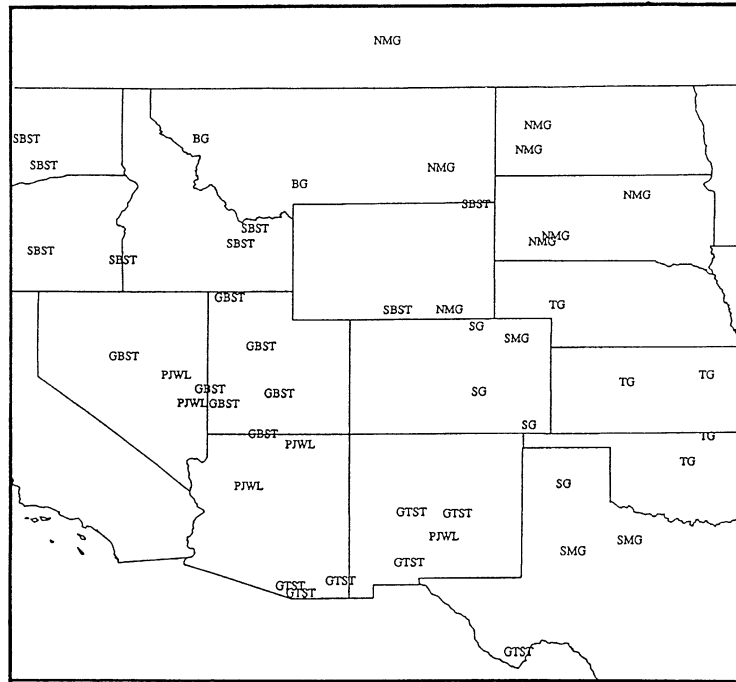


FIG. 1. Location of the 49 sites in the geographical space (upper graph), and location of the sites in the climatic space (lower graph). See Table 1 for a full description of the vegetation type names.

From the NDVI matrix of SITES×DATE we derived, for each study site, the following traits:

- Integral of the NDVI over the year.
- Difference between maximum and minimum NDVI.
- Degree of fit (r^2) of the seasonal curves of NDVI to a skewed normal model.
- Date of the maximum value of NDVI.

We used the integral of NDVI as an estimate of the total production, and the difference between the maximum and minimum NDVI as a measure of the seasonality. The coefficient of determination of the adjusted skewed normal model reflects the short-term fluctuations of productivity, and the date of maximum NDVI indicates the intra-annual distribution of the highest values of productivity.

TABLE 1. Study sites used in the NDVI analysis. St. and Vg. mean state and vegetation type (Küchler 1964, Dodd 1978), respectively. Latitude and longitude are expressed in centesimal degrees. The map column displays the name of the USGS 1:100000 sheets. The listed references are papers with a description of the corresponding site.

Study site	St.	Vg.	Long.	Lat.	Map 1:100000	References
ALE	WA	SBST	119.55	46.40	Richland	Sims et al. 1978
Bison	MT	BG	114.27	47.32	Plains	Sims et al. 1978
Bridger	MT	BG	110.78	45.78	Livingston	Sims et al. 1978
Cottonwood	SD	NMG	101.87	43.95	Kadoka	Sims et al. 1978
Dickinson	ND	NMG	102.82	46.90	Dickinson	Sims et al. 1978
Hays	KS	TG	99.38	38.87	Hays	Sims et al. 1978
Jornada	NM	GTST	106.75	32.62	White Sands	Sims et al. 1978
Osage	OK	TB	96.55	36.95	Pawhuska	Sims et al. 1978
Pantex	TX	SG	101.53	35.30	Amarillo	Sims et al. 1978
CPER	CO	SG	104.60	40.82	Eaton	Sims et al. 1978
Fort Berthold Indian Reserv.	ND	NMG	102.50	47.75	Parshall	Redmann 1975
Fort Stanton Exp. Ranch	NM	PJWL	105.55	33.48	Ruidoso	Pieper et al. 1971
Desert Experimental Ranch	UT	GBST	113.75	38.67	Wah Wah	W. Reg. Coord. Comm 1988
Texas Experimental Range	TX	SMG	99.23	33.33	Haskell	Pluhar et al. 1987
S.H. Ordway Memorial Pr.	SD	NMG	99.10	45.33	Gettysburg	Ode et al. 1980
Fort Keogh Livestock and Range Research Labs.	MT	NMG	105.88	46.30	Miles City	WRCC-40 1988
Santa Rita Exp. Ranch	AZ	GTST	110.86	31.84	Fort Huachuca	Yavitt and Smith 1983
Squaw Butte Exp. Station	OR	SBST	119.68	43.47	Harney Lake	Britton et al. 1990
Konza Prairie	KS	TG	99.60	39.10	Manhattan	Abrams and Hulbert 1987
Sevilleta	NM	GTST	106.68	34.33	Socorro	Franklin et al. 1990
Arapaho	NB	TG	101.80	41.55	Arthur	Barnes et al. 1983
Idaho National Eng. Lab.	ID	SBST	112.67	43.73	Circular Butte	Anderson and Shumar 1986
US Sheep Exp. Station	ID	SBST	112.15	44.25	Dubois	Murray 1988
Black Gap	TX	GTST	102.92	29.58	Panther Junction	Aide and Van Auken 1985
Colockun Research Unit	WA	SBST	120.17	47.30	Wenatchee	W. Reg. Coord. Comm. 1988
Appleton-Whittell Res. Ranch	AZ	GTST	110.50	31.60	Fort Huachuca	Bock et al. 1984
Matador	CAN	NMG	107.72	50.70	Swift Current	Singh et al. 1983
Snyder	TX	SMG	101.18	32.97	La Mesa	McPherson et al. 1988
Oklahoma St. Univ. Agr. Res.	OK	TG	97.23	36.05	Enid	Ewing and Engle 1988
Curlwe Valley	UT	GBST	113.08	41.87	Grouse Creek	West 1985
Portal	AZ	GTST	109.12	32.00	Chiricahua Pk.	Chew 1982
Badlands National Park	SD	NMG	102.33	43.75	Wall	Uresk 1990
Mt. Wilson	NV	PJWL	114.33	38.18	Wilson Creek	Koniak 1985
Escalante desert	UT	GBST	113.25	38.17	Wah Wah Mts.	Germano and Lawhead 1986
Glen Canyon	UT	GBST	111.87	37.10	Smoky Mts.	Rasmussen and Brotherson 1986
Alzada	MT	SBST	104.47	45.03	Alzada	MacCracken et al. 1983
Grass Valley	NV	GBST	116.75	39.82	Simpson Pks.	Young et al. 1986
Laramie	WY	NMG	105.57	41.42	Laramie	Smith et al. 1983
Springfield	CO	SG	102.73	37.37	Springfield	
E. Colorado Range Station	CO	SMG	103.17	40.38	Fort Morgan	
SSHA	WY	SBST	107.17	41.42	Bags	Burke et al. 1989
Capitol Reef Nat. Park	UT	GBST	111.30	38.52	Salina	Player and Urness 1982
Provo	UT	GBST	111.95	40.17	Provo	Brotherson & Brotherson 1981
Navajo Nat. Mon.	AZ	PJWL	110.54	36.73	Kayenta	Brotherson et al. 1981
Lowry Spring	NV	PJWL	114.90	39.16	Lowry Spring	Everett and Koniak 1981
El Paso	CO	SG	104.50	38.55	Colorado Sp.	Kinraide 1984
Reynolds	ID	SBST	116.77	43.15	Murphy	WRCC-40 1988
Coconino County	AZ	PJWL	112.35	35.27	Williams	Hessing et al. 1982
Lincoln County	NM	GTST	105.08	34.28	Fort Summer	Beavis et al. 1982
Vegetation types						
Shrublands						
SGST: Sagebrush steppe		PJWL: Pinyon-Juniper woodlands			GBST: Great Basin sagebrush steppe	
GTST: Gramma-tobosa shrubsteppe						
Grasslands						
NMG: Northern mixed-grass prairie		SG: Shortgrass steppe			BG: Bunchgrass steppe	
TG: Tallgrass prairie		SMG: Southern mixed-grass prairie				

The physiognomy of the vegetation was characterized from the Küchler (1964) and Dodd (1979) maps of the grassland and shrublands areas of USA. We obtained a qualitative representation of the structure of the vegetation based on the vegetation type of the area where each study site was located. We checked the

structural characterization (vegetation type) derived from the maps by looking at the site descriptions in published papers (see list of references in Table 1).

We analyzed the differences in the seasonal pattern of NDVI among vegetation types using Canonical Discriminant Analysis (Kshirsagar 1972). Given a clas-

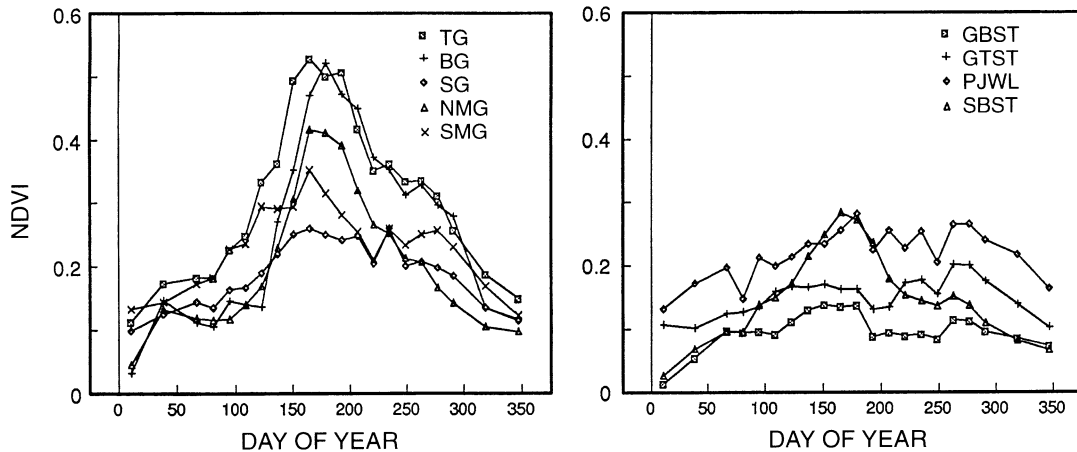


FIG. 2. Seasonal course of the NDVI for the grassland (left) and shrubland (right) vegetation types. Each curve is an average of the study sites corresponding to this type.

sification variable (vegetation types) and a set of quantitative variables (NDVI values through time), this technique derives linear combinations of the quantitative variables that summarize between-class variation. A plot of the first two axes allows for the display of the principal differences among classes. We based the comparison of the seasonal curves of NDVI among vegetation types on the squared distances between groups, derived from the pooled within-class covariance matrix (Mahalanobis distance). Comparisons among vegetation types based on the four defined traits were performed using ANOVA.

For each of the study sites we obtained the 1991 climatic data (monthly precipitation and temperature) and long-term average data for the nearest weather station to each study site, from the National Oceanographic and Atmospheric Agency (EarthInfo 1993). We analyzed the relationship between the functional attributes of the ecosystems and the climatic data using stepwise regression analysis (Kleinbaum and Kupper 1978). We included in the stepwise regression analyses mean annual precipitation, mean annual temperature, thermal amplitude, the proportion of the precipitation falling in each quarter of the year, the interactions among these variables, and their quadratic and logarithmic transformations. We performed additional analyses including mean monthly temperature and precipitation and monthly estimates of water deficit and surplus derived from the Walter (1979) climate diagrams. Statistical analyses were performed using SAS (SAS 1988).

RESULTS AND DISCUSSION

The NDVI values showed a clear seasonal pattern across the year, which was particularly evident for grasslands (Fig. 2). Principal Component Analysis showed that differences among the seasonal curves of NDVI of the study sites were associated with two main components. The first component accounted for 63%

of the total variance (Fig. 3a). Loadings of the scores on this axis were positive and similar (Table 2). This axis showed a strong correlation with the annual integral of the NDVI curve ($r = 0.99$, $P < 0.01$). The integral of the NDVI is closely related to ANPP. Support for this relationship comes from both theoretical (Tucker and Sellers 1986, Prince 1990, Running 1990) and empirical (Goward et al. 1985, Box et al. 1989, Kennedy 1989) investigations. For the region covered in this study, central North America, the integral of the NDVI shows a high correlation with ANPP ($r = 0.79$, $F = 70.3$, $df = 1, 42$, $P < 0.01$; J. M. Paruelo et al., unpublished data).

The second principal component explained 19% of the variability among NDVI curves and showed positive loadings for the coldest part of the year and negative loadings for the warmest part (Table 2). Scores for the second component were correlated with the difference between maximum and minimum NDVI values over the year ($r = 0.74$, $P < 0.01$). These results agree with those from a preliminary analysis of the NDVI dynamics for grasslands and shrublands of Patagonia in South America (Paruelo et al. 1991). Because NDVI and ANPP are strongly correlated, the percentage of the total variability related to NDVI supports McNaughton et al.'s (1989) view of ANPP as an integrative variable of ecosystem function.

The tallgrass prairie sites had the highest integral of NDVI (Fig. 4a). Northern mixed-grass prairie and shortgrass steppe sites had the lowest values among grassland sites, differing significantly only from tallgrass sites. Among shrublands, the pinyon-juniper woodlands had the highest NDVI values (Fig. 4a). Bunchgrass steppe, northern mixed-grass prairie, and tallgrass prairie sites had a significantly greater difference between maximum and minimum values of NDVI than the other units (Fig. 4b). Great Basin shrubsteppes and grama-tobosa shrubsteppes had a significantly

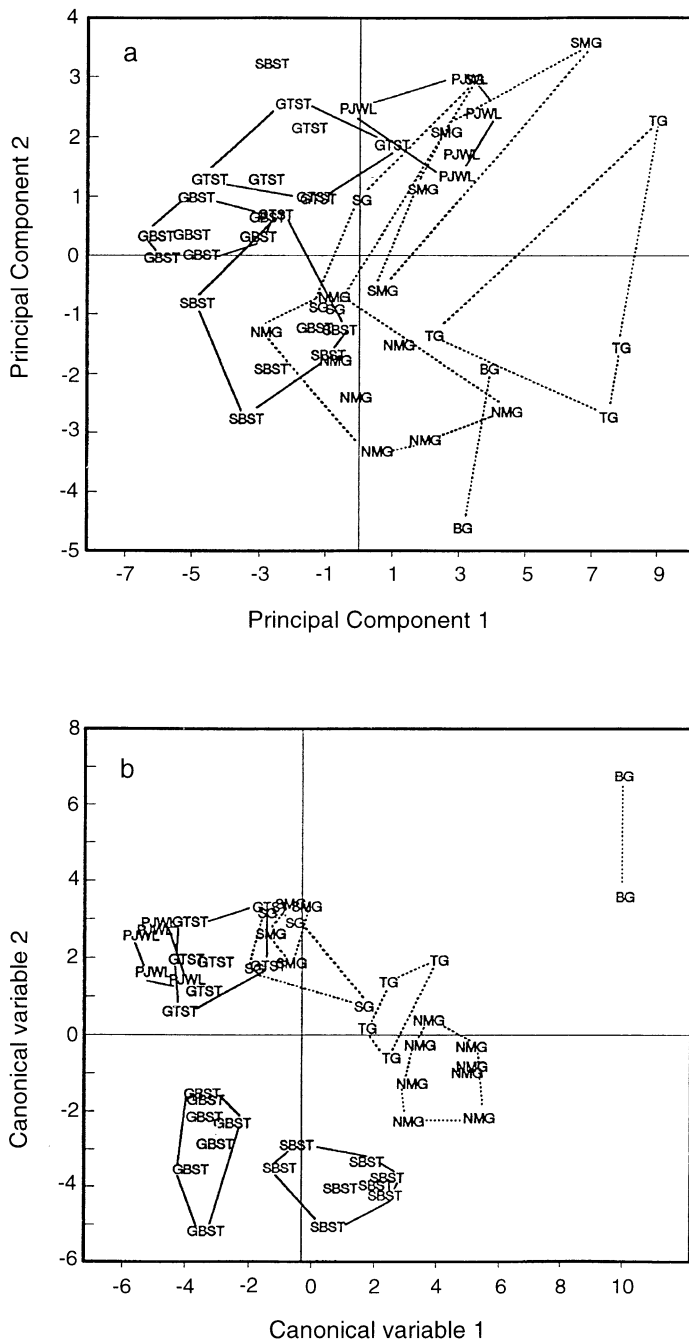


FIG. 3. (a) Plot of the first two Principal Components of the NDVI matrix of 49 sites \times 21 dates. (b) Plot of the first two canonical variables of the Canonical Discriminant Analysis. Lines connect points pertaining to the same vegetation type. For a full description of the vegetation types names see Table 1. Loading factors for the first two principal components are presented in Table 2.

smaller difference between maximum and minimum NDVI values than sagebrush steppes. Pinyon-juniper woodlands presented an intermediate pattern.

The tallgrass prairie, the southern mixed-grass prairie, and the sagebrush steppe reached their maximum NDVI values earlier (early June) than the other vegetation units (Fig. 4c). Grama-tobosa shrubsteppe differed significantly from those three units, reaching the maximum value of NDVI in late August. The other units presented an intermediate pattern. The dates of

maximum NDVI for the different vegetation types lie within the range of dates of maximum live biomass reported for IBP sites by Sims and Singh (1978). Grasslands and sagebrush steppes showed less short-term fluctuations of the NDVI than pinyon-juniper woodlands, and grama-tobosa shrubsteppe (Fig. 4d). The goodness of fit to a skew-normal model (r^2) was higher than 0.70 for grasslands and sagebrush steppes.

Northern sites (bunchgrass steppes, northern mixed-grass prairies, sagebrush steppes, and Great Basin

TABLE 2. Loadings for the first two components of the PCA of the NDVI data.

Date	PC 1	PC 2	Date	PC 1	PC 2
1	0.15	0.27	12	0.21	-0.29
2	0.22	0.04	13	0.22	-0.24
3	0.20	0.28	14	0.21	-0.24
4	0.18	0.26	15	0.23	-0.16
5	0.21	0.26	16	0.23	-0.17
6	0.21	0.23	17	0.25	-0.05
7	0.21	0.16	18	0.24	0.09
8	0.23	-0.04	19	0.23	0.10
9	0.22	-0.2	20	0.21	0.22
10	0.20	-0.29	21	0.21	0.22
11	0.20	-0.29			

shrubsteppes) showed an inverse relationship between the scores of the two axes ($r = -0.68$, $n = 23$, $P < 0.01$), meaning that seasonality and productivity increased together (Fig. 3a). The sites with the highest scores in the first axis (high productivity) presented the lowest scores in the second axis (high seasonality). In these areas high ANPP should be associated with a high peak of productivity during the relatively short growing season. The higher regularity of the pattern of NDVI displayed by northern sites (Fig. 4d) would be associated with the presence of only one NDVI peak.

For the southern sites (southern mixed-grass prairies, shortgrass steppes, grama-tobosa shrubsteppes and pinon-juniper woodlands), the relationship between the

first two PC axes was positive ($r = 0.53$, $n = 20$, $P < 0.05$). In these sites an increase in ANPP (integral of the NDVI) seemed to be related to a decrease in seasonality (difference between maximum and minimum NDVI). The more productive sites were those able to maintain high productivity during most of the year. Southern sites should be able to respond to pulses of availability of resources (mainly moisture) in the less favorable portions of the growing season because they would not be strongly limited by temperature. This response would generate a higher degree of short-term fluctuations in ANPP than in ecosystems more limited by temperature. The lower values of the coefficient of determination of the skewed model adjusted for southern rather than for northern sites supported this idea (Fig. 4d). Tallgrass prairie sites, located at intermediate latitudes, did not show any clear relationship among the scores in the PC axes.

The seasonal patterns of NDVI differed significantly among most of the physiognomic units (Fig. 3b, Table 3). Canonical Discriminant Analysis showed significant differences in the squared distances between centroids of pairs of units (Table 3 and Fig. 3b). Only the shortgrass steppe did not differ from all the other units (Fig. 3b and Table 3). Shortgrass steppe was a highly variable unit and was not significantly different from the two geographically and floristically related units: the southern mixed-grass prairie and the grama-tobosa

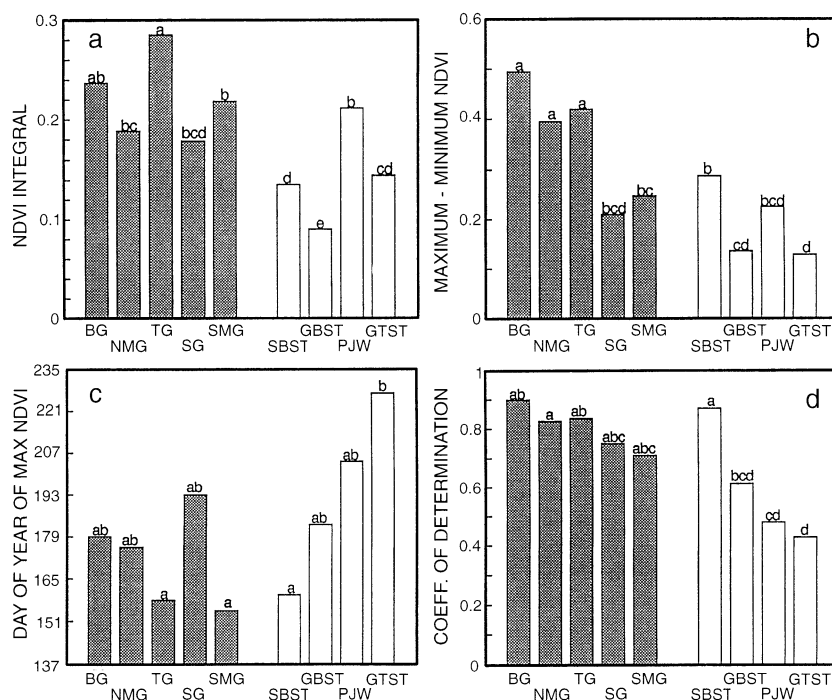


FIG. 4. Mean values for the four characteristics of the seasonal NDVI curves analyzed for the different vegetation types. (a) NDVI Integral, (b) difference between maximum and minimum NDVI, (c) date of the maximum NDVI, and (d) coefficient of determination of the fit of the seasonal curves to a skewed normal model. Different letters indicate significant differences ($P < 0.05$). For a full description of the vegetation types names see Table 1.

TABLE 3. Squared distances between the centroids of each group (vegetation type), derived from the pooled within-class covariance matrix (Mahalanobis distance) (upper right side of the matrix), and F statistics for the squared distances ($\text{ndf} = 21$, $\text{ddf} = 20$) (lower left side of the matrix). $F_{0.05} = 2.1$, $F_{0.01} = 2.88$. F values in bold are significant at 0.01, and underlined F values are significant at 0.05. See Table 1 for a full description of the vegetation type names.

	TG	BG	SG	NMG	SMG	GBST	GTST	PJWL	SBST
TG	...	166	47	41	52	88	62	91	53
BG	5.3	...	163	127	186	262	223	270	187
SG	2.3	5.2	...	44	17	38	23	47	49
NMG	<u>2.6</u>	4.8	<u>2.8</u>	...	57	69	77	117	37
SMG	<u>2.5</u>	5.9	0.9	3.7	...	59	35	53	62
GBST	5.3	9.7	2.4	6.2	3.6	...	35	49	30
GTST	5.0	8.3	1.4	6.9	2.2	3.0	...	53	67
PJWL	4.9	9.2	<u>2.5</u>	8.6	<u>2.8</u>	3.4	3.7	...	89
SBST	3.4	7.1	3.2	3.6	4.0	<u>2.7</u>	6.0	6.6	...

shrubsteppe. Shortgrass steppes showed intermediate values of the NDVI integral, seasonality, and date of the maximum NDVI to those displayed by southern mixed-grass prairies and grama-tobosa shrubsteppes.

To analyze the climatic control on the spatial variability of NDVI we used both the long-term average and the current-year data (1991). Because the relationships using both sets of data were essentially the same, we presented those that explained the highest portion of the variance (the long-term averages). Analyses performed using monthly values of temperature and precipitation, or monthly water deficit and surplus estimates, did not produce better results than the analyses based on more aggregated variables.

For the whole data set, mean annual precipitation (MAP) explained 67% of the variability of the integral of the NDVI curves ($r^2 = 0.67$, $F = 95.5$, $\text{df} = 1, 48$, $P < 0.01$). The integral of the NDVI increased linearly with MAP (Fig. 5). Paruelo et al. (1993) found the same kind of relationship between the NDVI integral and MAP for shrublands and grasslands of Patagonia.

Previous studies showed that mean annual precipitation explains a large fraction of the spatial variability of ANPP data (Lauenroth 1979, Sala et al. 1988, McNaughton et al. 1993, Milchunas and Lauenroth 1993). The proportion of the variability of the NDVI integral among sites that was explained by precipitation in the present study (67%) was similar to the proportion of the variability in ANPP that was explained by MAP in the studies cited above. This result provides support for the interpretation of the integral of seasonal curves of NDVI as an estimator of ANPP at a regional level.

The relationship between the NDVI integral and MAP was slightly different for grasslands and shrublands (Fig. 5). For grassland sites the correlation was stronger and the slope was steeper than for shrublands ($b = 0.000271$ and $b = 0.000204$, $Z = 9.47$, $P < 0.01$) (Fig. 5). Using these correlations, the ANPP (measured in NDVI units) generated for each millimetre of precipitation was 30% lower in shrubland sites than in grasslands. Milchunas and Lauenroth (1993) showed the same pattern for the relationship between ANPP and MAP for grasslands and shrublands. They found

that the slope of the ANPP vs. MAP relationship was 39% lower in shrublands than in grasslands. Webb et al. (1978) also found a lower slope for the relationship ANPP vs. actual evapotranspiration for shrublands than for grasslands.

No previous attempt has been made to quantify the relationships between the seasonality of carbon gains and climatic variables on such a large region of grasslands and shrublands. The difference between the maximum and minimum NDVI (our estimator of seasonality) increased with MAP and the thermal amplitude (AMPTEM), and decreased with mean annual temperature (MAT) (Table 4). These three variables explained 64% of the variability in the maximum–minimum difference of NDVI values ($r^2 = 0.64$, $F = 29.1$, $\text{df} = 3, 45$, $P < 0.01$).

Climatic variables explained a third of the spatial variation of the date of maximum NDVI ($r^2 = 0.34$, F

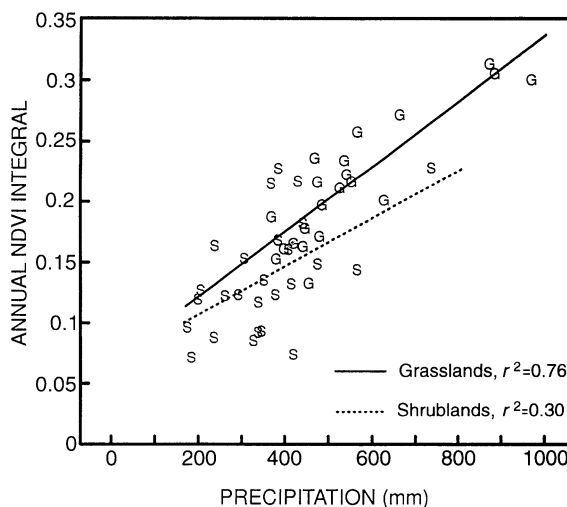


FIG. 5. Relationship between precipitation and the integral of the seasonal NDVI curves. Grassland sites are indicated with a G and shrubland sites with an S. The equations for the fitted lines are: grassland sites: $\text{INT} = 0.0640 + 0.000271 \text{ MAP}$, $F = 62.5$, $\text{df} = 1, 20$, $P < 0.001$; shrubland sites: $\text{INT} = 0.0674 + 0.000191 \text{ MAP}$, $F = 10.6$, $\text{df} = 1, 25$, $P < 0.004$.

TABLE 4. Stepwise regression analysis of the relationship between characteristics of the NDVI curves and climate. The climatic variables included in the analysis were Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT), Thermal Amplitude (AMPTEM), and the proportion of the total annual precipitation that falls in summer (JJA/MAP). Climatic data corresponded to a long-term average.*

Dependent variables	r^2	F	P	Indep. Var.	Coeff.	Fp	P
INT	0.67	95.5	0.001	MAP	$2.87 \cdot 10^{-4}$
MAXMIN	0.64	18.3	0.001	MAT	-1.4252	44.7	0.001
				MAP	0.0437	34.7	0.001
				AMPTEM	0.8594	7.8	0.008
DATEMAX	0.34	9.1	0.001	JJA/MAP	12.0789	15.2	0.001
				MAP	-0.0067	7.7	0.008
				AMPTEM	-0.1572	4.3	0.045
COEFDET	0.39	16.4	0.001	AMPTEM	0.0265	23.9	0.001
				JJA/MAP	-0.6484	9.0	0.004

* Dependent variables are: INT: integral of the seasonal curve of NDVI; MAXMIN: difference between maximum and minimum NDVI over the year; DATEMAX: day of year (Julian date) of the maximum NDVI value, and COEFDET: coefficient of determination (r^2) of the fit of the NDVI data to a skewed normal model. r^2 is the coefficient of determination of the regression model, $F = F$ -Snedecor statistics for the whole model, Fp the partial F -Snedecor statistics for each independent variable, Coeff. is the coefficient of each independent variable in the regression model, and P the probability level.

= 9.1, $df = 3, 45$, $P < 0.01$). The seasonal distribution of precipitation was the main climatic control of the date of the NDVI peak (Table 4). A high proportion of annual precipitation falling during summer resulted in a delay in the NDVI peak. Given such a seasonal distribution of precipitation, the NDVI peak tended to occur late in sites with low MAP and small AMPTEM. The coefficient of determination of the skewed normal model fitted to the seasonal curves of NDVI was high in areas with a large AMPTEM, and a low proportion of precipitation falling in summer. These two variables explained 39% of the total variability of this variable ($r^2 = 0.39$, $F = 16.4$, $df = 2, 46$, $P < 0.01$).

The characterization of ANPP at regional scales on the basis of their mean seasonal curves of NDVI may allow for the integration of highly relevant ecological information into broad-scale models of the dynamics of the atmosphere. Empirical relationships between some traits of the NDVI curves and climate variables like those presented here represent a feasible way to link atmospheric and ecological processes in an interactive manner.

The use of satellite data with high temporal and spatial cover, such as the AVHRR/NOAA-derived NDVI, can provide enough information to make formal evaluations of dynamic global vegetation models. An intensive analysis of the correspondence of different traits of the NDVI curves and functional and structural aspects of the ecosystems (ANPP, transpiration, functional-type composition, etc.) will be an important step to integrate this information in global scale models.

The spatial and temporal patterns of NDVI and the traits derived from them allow for a description of the function of the actual landcover. The relationships between climate and the functional traits derived from the NDVI data for natural areas enable us to produce maps of the potential functioning of the vegetation in the absence of intensive human modifications. These potential function maps could be compared with actual

function maps derived from the same kind of data. This opens promising possibilities for monitoring the change in land cover associated with human use at regional scales.

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