

# Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems

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## Abstract

The Chihuahuan desert of New Mexico, USA, has changed in historical times from semiarid grassland to desert shrublands dominated by *Larrea tridentata* and *Prosopis glandulosa*. Similar displacement of perennial grasslands by shrubs typifies desertification in many regions. Such structural vegetation change could alter average values of net primary productivity, as well as spatial and temporal patterns of production. We investigated patterns of aboveground plant biomass and net primary production in five ecosystem types of the Jornada Basin Long-Term Ecological Research (LTER) site. Comparisons of shrub-dominated desertified systems and remnant grass-dominated systems allowed us to test the prediction that shrublands are more heterogeneous spatially, but less variable over time, than grasslands.

We measured aboveground plant biomass and aboveground net primary productivity (ANPP) by species, three times per year for 10 years, in 15 sites of five ecosystem types (three each in *Larrea* shrubland, *Bouteloua eriopoda* grassland, *Prosopis* dune systems, *Flourensia cernua* alluvial flats, and grass-dominated dry lakes or playas). Spatial heterogeneity of biomass at the scale of our measurements was significantly greater in shrub-dominated systems than in grass-dominated vegetation. ANPP was homogeneous across space in grass-dominated systems, and in most growing seasons was significantly more patchy in shrub vegetation. Substantial interannual variability in ANPP complicates comparison of mean values across ecosystem types, but grasslands tended to support higher ANPP values than did shrub-dominated systems. There were significant interactions between ecosystem type and season.

Grasslands demonstrated higher interannual variation than did shrub systems. Desertification has apparently altered the seasonality of productivity in these systems; grasslands were dominated by summer growth, while sites dominated by *Larrea* or *Prosopis* tended to have higher spring ANPP. Production was frequently uncorrelated across sites of an ecosystem type, suggesting that factors other than season, regional climate, or dominant vegetation may be significant determinants of actual NPP.

*Keywords:* Chihuahuan desert, desertification, Jornada LTER, *Larrea tridentata*, net primary productivity, *Prosopis glandulosa*

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## Introduction

Semiarid and arid ecosystems cover a large fraction of the earth's surface – up to 30% of the globe's land area (Evenari *et al.* 1985) – and support a substantial portion of the human population (UNEP 1997). These ecosystems

provide important resources for human populations in the form of livestock forage, living area, fuel, wood, and scenic and recreational resources. Although human use has generally been extensive (pastoralism) rather than intensive (such as irrigated agriculture), human activities have influenced and altered a wide variety of ecosystem characteristics. These influences include alteration of vertebrate communities, changes in hydrologic regimes (creation of new water sources and alteration of existing

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hydrologic patterns), and introduction of new plant species (Huenneke & Noble 1996). In some semiarid regions of the world, changes in ecosystem structure and function have been so extreme that new systems resembling true deserts or arid lands have appeared. This alteration to a more arid-type system has been termed desertification (Jain 1986; Verstraete & Schwartz 1991; UNEP 1997) and is recognized as one of the important aspects of ongoing global environmental change.

One form of desertification is the conversion of semi-desert grasslands into shrub-dominated systems. Such conversion has been noted over wide areas of previous grassland, from Africa to North America. Shrub invasion and displacement of grasslands is of economic and environmental concern, both because the shrublands are capable of supporting fewer grazing animals and because open shrub-dominated systems may be vulnerable to losses of soil organic matter, nitrogen, and other resources, leading to a progressive degradation of the productive capacity of the ecosystem (Schlesinger *et al.* 1990). In the south-western region of North America, shrub encroachment into semidesert grassland has been pronounced and well-documented (e.g. Buffington & Herbel 1965; Hastings & Turner 1965; Hennessy *et al.* 1983; Gibbens *et al.* 1992; Van Auken 2000). Typically production of palatable grass forage is reduced in shrub-dominated sites; however, typical inventory techniques measure only forage production and do not quantify all primary production on a site. From a basic ecosystem function perspective, then, much historical work in the region has not confirmed whether total net primary production has actually decreased – that is, whether the ecosystem's capacity to fix carbon is actually 'degraded'.

We have previously hypothesized that desertification changes the spatial structure of the soil resources in semiarid regions (Schlesinger *et al.* 1990), rather than focusing on a decline in net primary production. In the Jornada model of desertification, the decline of grasses leads to the formation of open patches and the establishment of shrub seedlings. As shrubs grow and their canopies expand, they promote the collection and concentration of soil resources (water, organic matter, and mineral nutrients) by processes such as rainfall interception and stem-flow, trapping of wind-blown sediments, and litterfall. Meanwhile, bare intershrub areas become increasingly subject to erosion by wind and water, unfavourable light and temperature conditions, and other factors making plant growth unlikely. Hence over time, shrub-dominated ecosystems are predicted to become increasingly patchy or heterogeneous, with respect to the distribution of both living organisms and soil resources. We have tested some of these basic predictions, finding that soil resources do in fact become increasingly heterogeneous in spatial

distribution with increasing duration of shrub dominance at a site (Schlesinger *et al.* 1996; Reynolds *et al.* 1999). However, to date there have been few quantitative descriptions of the relative patchiness of biomass or of ecosystem function (particularly primary productivity) in grass- vs. shrub-dominated semiarid systems (but see Phinn *et al.* 1996).

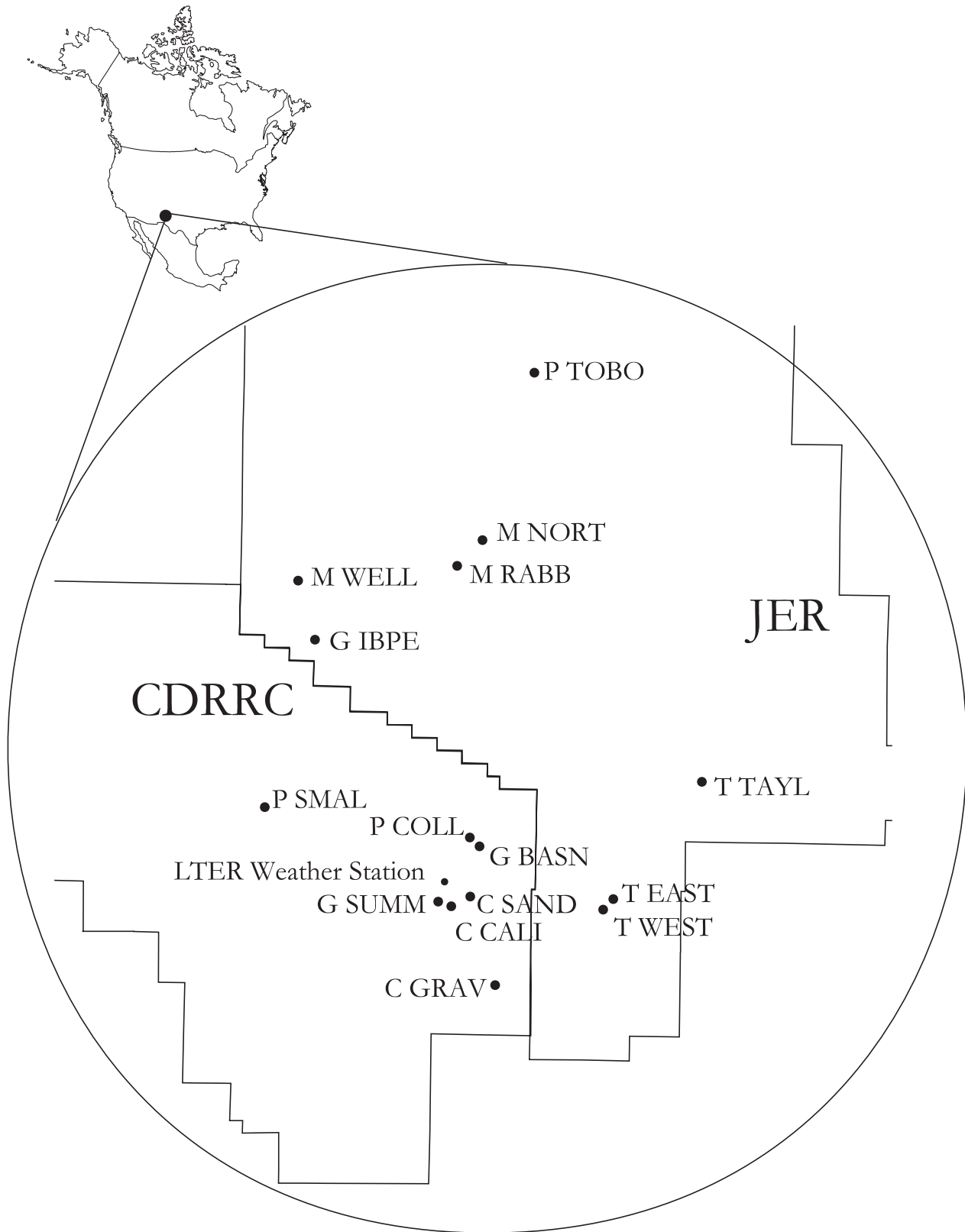
Here we report results from a long-term study of patterns of net primary productivity in grass- and shrub-dominated semiarid ecosystems of the Jornada Basin Long-Term Ecological Research (LTER) site in southern New Mexico (USA). We developed methods of evaluating patterns of aboveground biomass and plant productivity in space and time that would allow comparisons of both grass- and shrub-dominated systems (Huenneke *et al.* 2001). The objectives of our research are to understand the differences in ecosystem structure and function between semidesert grasslands and desert shrubland systems, with the Jornada model of desertification guiding our investigations of processes and feedbacks (Schlesinger *et al.* 1990). The primary objective of this paper is to compare patterns of aboveground net primary production (ANPP) in desertified shrublands with those in grass-dominated ecosystems. We are specifically interested in whether average ANPP is in fact lower in shrub-dominated systems than in grasslands, and whether spatial and temporal heterogeneity differs among ecosystem types in the same regional climate. Such comparisons of behaviour at long time scales and large spatial scales are necessary for the understanding of desertification and its implications in semiarid ecosystems worldwide.

## Materials and methods

### *Study site*

Research activities of the Jornada Basin LTER program take place on the Jornada Experimental Range, administered by the US Department of Agriculture's Agricultural Research Service (ARS), and on the Chihuahuan Desert Rangeland Research Center (formerly the College Ranch), administered by New Mexico State University. Both sites are located about 37 km north-east of Las Cruces, NM, USA (Fig. 1). Together they comprise more than 100 000 ha devoted to research.

Much of southern New Mexico has experienced the alteration of vegetation from *Bouteloua*-dominated semi-desert grassland to creosote bush, mesquite, and tarbush desert scrub during the past 100 years (Buffington & Herbel 1965; Gibbens & Beck 1988). Patterns of vegetation transitions in the context of long-term and historical environmental changes have been similar to those observed across the south-western United States (Fredrickson *et al.* 1998). The Jornada Experimental Range was established



**Fig. 1** Locator map and map of Jornada LTER site, with locations of 15 sites of productivity study and central weather station marked and identified in enlargement. JER = USDA Jornada Experimental Range; CDRRC = New Mexico State University's College of Agriculture Chihuahuan Desert Rangeland Research Center. Abbreviations for 15 sites as given in Table 1.

**Table 1** Brief descriptions of the 15 sites for productivity measurements. Site abbreviations are those used in LTER documentation and in this paper. Dominant plants are those whose biomass was consistently among the three highest species per site during spring and/or fall growing seasons. Soil type is based on the county soil survey (USDA 1980) and Gile & Grossman (1979). Year fenced is date of enclosure from livestock grazing

Site	Dominant plants	Soil type	Year fenced
<i>Creosote bush</i>			
Caliche (CALI)	<i>Larrea tridentata</i> , <i>Xanthocephalum microphalum</i> , <i>Aristida wrightii</i>	Algerita	1970s
Gravel (GRAV)	<i>Larrea tridentata</i> , <i>Prosopis glandulosa</i> , <i>Muhlenbergia porteri</i>	Casito–Terino	1970s
Sand (SAND)	<i>Larrea tridentata</i> , <i>Muhlenbergia porteri</i> , <i>Opuntia imbricata</i>	Onite–Pajarito loamy sand	1982
<i>Grasslands</i>			
Basin (BASN)	<i>Bouteloua eriopoda</i> , <i>Sporobolus cryptandrus</i> , <i>Ephedra trifurca</i>	Berino–Dona Ana sandy loam	1982
IBP (IBPE)	<i>Yucca elata</i> , <i>Bouteloua eriopoda</i> , <i>Sporobolus flexuosus</i>	Onite–Pajarito loamy sand	1969
Summerford (SUMM)	<i>Yucca elata</i> , <i>Bouteloua eriopoda</i> , <i>Ephedra trifurca</i>	Alladin gravel–sand loam	1970s
<i>Mesquite</i>			
North (NORT)	<i>Prosopis glandulosa</i> , <i>Xanthocephalum sarothrae</i> , <i>Muhlenbergia porteri</i>	Onite–Pintura loamy sand	1931
Rabbit (RABB)	<i>Prosopis glandulosa</i> , <i>Portulaca retusa</i> , <i>Salsola kali</i>	Onite–Pintura loamy sand	1931
West Well (WELL)	<i>Prosopis glandulosa</i> , <i>Xanthocephalum sarothrae</i> , <i>Muhlenbergia porteri</i>	Wink–Harrisburg sandy loam	1989
<i>Playas</i>			
College (COLL)	<i>Panicum obtusum</i> , <i>Helianthus ciliaris</i> , <i>Sida leprosa</i>	Dalby Clay	1982
Small (SMAL)	<i>Panicum obtusum</i> , <i>Cirsium ochrocentrum</i> , <i>Asclepias subverticillata</i>	[too small to be mapped]	1974
Tobosa (TOBO)	<i>Pleuraphis mutica</i> , <i>Sporobolus airoides</i> , <i>Opuntia imbricata</i>	Engholm Clay	1989
<i>Tarbush</i>			
East (EAST)	<i>Flourensia cernua</i> , <i>Muhlenbergia porteri</i> , <i>Lycium berlandieri</i>	Stellar clay loam	1989
Taylor Well (TAYL)	<i>Flourensia cernua</i> , <i>Scleropogon brevifolius</i> , <i>Muhlenbergia porteri</i>	Dona Ana–Reagan sandy loam	1989
West (WEST)	<i>Flourensia cernua</i> , <i>Scleropogon brevifolius</i> , <i>Pleuraphis mutica</i>	Stellar clay loam	1989

by the USDA in 1912 with the mission to understand the causes of this change and the consequences for land management.

We selected 15 sites for study, three in each of 5 ecosystem types (Fig. 1). These include: *Bouteloua*-dominated grasslands, *Larrea tridentata* or creosote bush shrub stands on bajada slopes, *Prosopis glandulosa* or mesquite coppice dune shrublands, *Flourensia cernua* or tarbush shrub areas on alluvial flats, and grass-dominated playas or ephemeral lakebeds. Livestock grazing has been excluded from all sites since 1989 (in some cases, much earlier; Table 1).

Soil information was based on mapping by the Dona Ana County soil survey (USDA 1980) and the Desert Soils Project (Gile & Grossman 1979; Gile *et al.* 1981). Dominant plant species, mapped soil series, and date of fencing to exclude livestock grazing are listed for the 15 sites in Table 1. The Jornada flora is well-known; the Jornada Basin LTER maintains a plant species checklist (available through <http://jornada.nmsu.edu/>), with voucher specimens in the New Mexico State University Herbarium. Nomenclature in this paper follows that of Correll & Johnston (1970), except for grasses which are named

according to Allred (1993). Those few taxa not found in Texas are named according to Kearney & Peebles (1964).

#### Sampling design and methods

Three sites of each vegetation type were selected explicitly to encompass the range of natural variation within types, rather than as randomly chosen replicates. For example, the three grasslands differ in length of time since cessation of livestock grazing, landscape position, and abundance of the dominant *Bouteloua eriopoda*. Shrub-dominated sites (creosote bush, mesquite, and tarbush) similarly exhibit a range of shrub sizes and densities within community types. Sampling effort limited the number of sites that could be studied, but variability within these ecosystem types is so great that three sites are too few for random selection to represent adequate replication. Our intention was to represent as large a range of variation as possible within the Jornada basin, and to make any test of differences among vegetation types as rigorous as possible.

The three mesquite-dominated sites are all located in areas mapped as shrub-free (grassland) in 1858 (Buffington & Herbel 1965). The three creosote-bush stands contain *Yucca elata*, suggested to reflect prior grassland, and Stein & Ludwig (1979) suggested that creosote stands in the area represented an increase of the shrub's abundance from its scattered presence in semidesert grassland. The earliest formal vegetation map available for these sites shows them as creosote bush stands by 1942 (NMSU Chihuahuan Desert Rangeland Research Center, unpublished map). Two of the tarbush stands (actually mosaics of shrub and grass patches) appeared in early maps of the Jornada Experimental Range as shrub-free, the third as tarbush (Buffington & Herbel 1965).

Each study site comprised a  $7 \times 7$  grid of 49 permanent  $1\text{-m}^2$  quadrats, separated by 10 m in each cardinal compass direction. In one site, the College Playa, the small area available for study permitted only a  $3 \times 16$  pattern or 48 quadrats. Plant biomass within these quadrats was estimated by measuring the dimensions (cover and height) of individual plants or plant parts nondestructively, and then using previously developed regressions between plant volume and aboveground biomass. The legs of a portable square frame, with an internal area of  $1\text{ m}^2$ , fit over large nails marking two diagonal corners of the quadrat. The interior of the frame was gridded with twine into sections (each 1% of the quadrat's area) to facilitate cover estimates for plants or plant parts; height was measured to the nearest centimeter. When a plant part extended into the quadrat volume from outside, or grew out of the volume from the inside, only the portion of the plant physically encompassed in the

rectangular volume above the quadrat was measured. Further details of field measurements were described by Huenneke *et al.* (2001).

During the first four years of study, reference specimens of each species encountered in the quadrats of a site were harvested from areas adjacent to the grid of quadrats at that site. In the laboratory, samples were sorted by the removal of dead material, and living biomass was dried at  $60^\circ\text{C}$  to constant mass. Harvest data were then used to construct regressions of plant dimensions vs. live aboveground biomass.

Sampling and harvests occurred three times per calendar year, to accommodate the distinctive seasonality of the Chihuahuan desert, beginning in May 1989. The winter sample occurred in February, when most species are dormant but in some (wet) years, winter annuals are present as rosettes. The spring sample was in May, after shrubs produce new leaves, and near the peak of reproduction for winter and spring annuals, in years when these are present. Fall sampling took place in September–October at the peak of biomass and reproductive activity for those shrubs, perennial grasses, and annuals associated with the dependable late-summer rains.

Harvests were made by site and by sampling date, and initial regressions for each species were calculated separately by date and site. After four years, we calculated composite regressions using the total data set for each species. Volume ( $\text{cm}^3$ ) was calculated as the product of cover for a plant part (where cover was the total area of all  $100\text{ cm}^2$  occupied) and height in cm. Linear regressions of live biomass (g) against volume were calculated for each species; each regression was tested for significant improvement due to separate consideration of sites or of harvest dates. Regressions were calculated for 154 species (plus pooled small forb seedlings, treated as a single group for each vegetation type). Only two species demonstrated significant differences among individual harvest dates (*Pleuraphis*[=*Hilaria*] *mutica* and *Panicum obtusum*, both playa grasses); these two species were harvested, and new regressions calculated, for each season in which they were green at a site. Separate seasonal regressions were required for 10 species, and site-specific regressions for 13 other species; all other species were represented adequately by a single regression covering all seasons and sites. Regressions for dominant species (those shrubs, grasses, and forbs contributing substantial biomass on any site) generally demonstrated  $R^2$  values greater than 0.75 (Huenneke *et al.* 2001).

Calculated aboveground biomass values for each species in a quadrat were summed to obtain total biomass per  $\text{m}^2$  quadrat. ANPP was measured as the positive increment of biomass for a species in a quadrat, summed for all species in a quadrat, over a time interval.

Additional details of the analysis procedure, including a discussion of the regression approach to estimating biomass, the adequacy of sample size (number of quadrats), and the power of this technique to detect differences among sites in biomass or productivity, were presented in Huenneke *et al.* (2001).

Mean and interquartile range of total biomass values were calculated for the 49 quadrats at each site. The interquartile range is the range of values between the 25th percentile and the 75th percentile (that is, the range of the middle 50% of the distribution). The interquartile (IQ) range is more robust in the face of non-normal distribution of values than standard deviation or coefficient of variation (Huber 1981; Hampel *et al.* 1986). We used the IQ range of the distribution of individual quadrat values (49 quadrats per site) as an index of spatial variation or patchiness among quadrats. A mixed model was used to analyse biomass, seasonal production, and annual production means for each site, and interquartile ranges of biomass for each site, by ecosystem type and date. This allowed us to model the correlation (covariance) structure through time of a given response variable. We tested several covariance structures using the Schwarz Bayesian criterion (Schwarz 1978). We used an autoregressive covariance structure to analyse biomass, interquartile range, and seasonal production, assuming that biomass in a site at any date was most strongly correlated to biomass in adjacent time periods. We used a compound symmetry covariance structure to analyse annual production; this is equivalent to a split-plot analysis, where observations from a given site are correlated but are assumed to be independent in time. The Mixed Procedure of SAS (Statistical Analysis System, vs. 6.12; Littell *et al.* 1996) was used to carry out these analyses. Sets of contrasts were used to test for significance of differences between shrub-dominated and grass-dominated ecosystem types (C or creosote bush, M or mesquite, and T or tarbush vs. G, grassland, and P, playa), and between upland soils and lowland, heavy clay soils (C, G, M vs. P, T). We also identified individual years and production intervals as being Wet (wetter than normal, rainfall received at the LTER central weather station 50% greater than the long-term average), Normal, or Dry (50% less than the long-term average for that interval), and examined contrasts in biomass or in aboveground productivity between wet and dry years, or in the response of different ecosystem types to wet vs. dry years.

## Results

### *Aboveground biomass*

Aboveground mean biomass varied by site and date (Fig. 2). Grassland sites supported mean biomass from

50 to as high as 800 g m<sup>-2</sup> during the growing season, with highest values usually occurring in fall. One grassland, located at the foot of Mt. Summerford on the Chihuahuan Desert Rangeland Research Center (G-SUMM), consistently supported higher aboveground biomass values than most other sites of any ecosystem type (Fig. 2); mean biomass at the other two grasslands was always less than 350 g m<sup>-2</sup> (usually <250). Perennial grasses (chiefly *Bouteloua eriopoda* and *Sporobolus* spp.), the leaf succulent *Yucca elata*, and shrubs (especially *Ephedra trifurca*) were all substantial contributors to biomass in the grassland sites. Annual grasses, and annual and perennial forbs, were represented by numerous species (at least in certain seasons), but these species contributed little to overall biomass relative to the standing crop of the dominants. Winter biomass in grasslands includes some live tissue aboveground for *B. eriopoda*, whose stolons retain some green colour internally, plus the several shrub, subshrub, and succulent species present.

Mean aboveground biomass in creosote bush sites ranged from 65 to 360 g m<sup>-2</sup>, with low values in winter and maximum values usually in spring (Fig. 2). A site on a shallow soil with caliche near the surface (C-CALI) had notably lower biomass than the other two sites on deeper soils. In all creosote bush sites in all seasons, *Larrea* contributed the largest proportion of standing biomass; but subshrubs (especially *Xanthocephalum microcephalum* and *Zinnia acerosa*) and perennial grasses (particularly *Muhlenbergia porteri*, which often grows beneath shrubs) also contributed substantial biomass in most seasons.

Mesquite dune sites had relatively high mean aboveground biomass (150–450 g m<sup>-2</sup> or more). Biomass values were roughly equal between spring and summer/fall sampling dates. At one site (M-NORT), aboveground biomass increased over several years and remained above 400 g m<sup>-2</sup> until hot dry growing seasons in 1994 and 1995 resulted in substantial decreases. From 1995 through 1998, biomass in this site remained at the lower level (Fig. 2). While *Prosopis glandulosa* was by far the most abundant species (in biomass) in all 3 mesquite sites at all sample dates, *Xanthocephalum* species and perennial grasses (especially *Muhlenbergia porteri*) were also important. In some fall seasons, annual forbs (e.g. *Salsola kali*, *Portulaca retusa*) were among the abundant species.

All tarbush sites had low and relatively unvarying mean aboveground biomass compared to the other shrub-dominated systems (Fig. 2). Mean values rarely ranged below 100 or above 200 g m<sup>-2</sup>. *Flourensia cernua* was the most abundant species, followed by perennial grasses (*Muhlenbergia porteri*, *Scleropogon brevifolia*, *Pleuraphis mutica*). Annuals, while present, never contributed substantial biomass in these sites.

Biomass in the playas demonstrated a clear and simple pattern of response to increased moisture during the

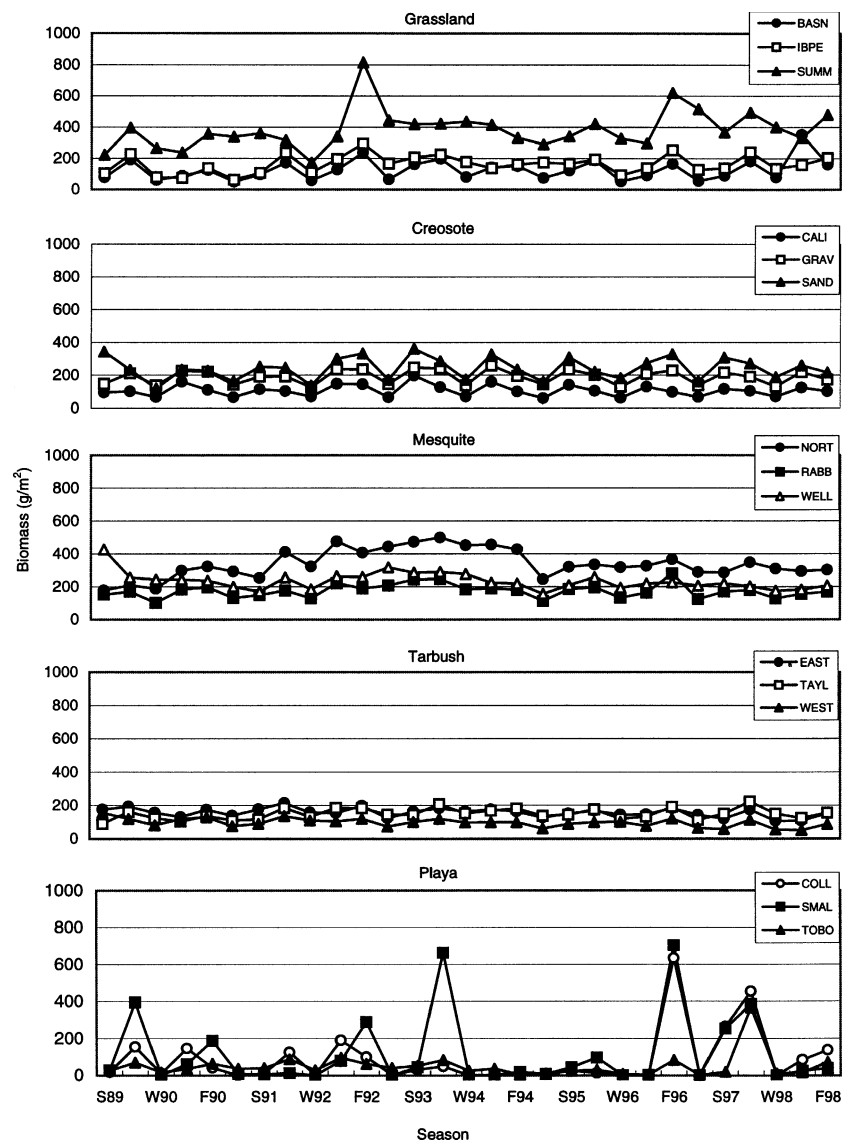


Fig. 2 Mean aboveground plant biomass values ( $\text{g m}^{-2}$ ) for 15 sites, 3 in each of 5 ecosystem types, for winter (W), spring (S), and fall (F) sampling periods from spring 1989 through fall 1998. Abbreviations for 15 sites as given in Table 1.

summer rainy periods. In winter and in dry portions of the growing season, there is virtually no aboveground green tissue among the perennial grass dominants. In most years, the two smaller playas (P-COLL and P-SMAL) experienced high soil moisture during the late summer, with high aboveground biomass in fall samples. These peaks of biomass were as great as  $400\text{--}700 \text{ g m}^{-2}$ . In 1990, an unusually wet spring led to early plant activity in P-COLL; consequently the year's high biomass was found in the spring sample rather than the fall. The largest of the playas studied, P-TOBO, did not contain standing water at any time during the study period and therefore supported relatively little aboveground biomass. When moisture was available, the dominant perennial grasses (*Panicum obtusum* at P-COLL and P-SMAL) constituted most of the playa's standing crop. Other

important species, chiefly forbs, varied among playas, among seasons, and among years.

The mixed model analysis confirmed that aboveground biomass was affected by significant interactions of ecosystem type with date or season (Table 2). Significant differences among ecosystem types at some sample dates were usually explained by the extremely low biomass values of grassy playas in dry winters; other vegetation types dominated by woody or succulent vegetation have substantial aboveground live biomass throughout the year. However, in many spring and fall seasons, the ranges of aboveground biomass overlapped substantially among ecosystem types. Standing biomass was apparently related to landscape position and/or soil type; the contrast between heavy or clay soils (Tarbush and Playa sites) and upland sites (Grassland, Mesquite, and

**Table 2** Results of mixed model analysing mean aboveground plant biomass for 15 sites, 3 in each of 5 ecosystem types, for 29 sampling dates (TIME) from spring 1989 through fall 1998. Ecosystem type (TYPE) designated as C=creosote bush, G=grassland, M=mesquite, P=playa, and T=tarbrush. Seasons designated as W=winter, S=spring, and F=late summer/fall; DF=dry fall, WF=wet fall, as categorized in the text

Source	Degrees of freedom	Type III F	<i>p</i>
Tests of fixed effects			
TYPE	4, 10	8.17	0.0034
TIME	28, 280	10.20	0.0001
TIME*TYPE	112, 280	2.55	0.0001
Contrasts:			
Shrub (C, M, T)			
vs. grass (G, P)	1, 10	2.45	0.1484
Clay (T, P) vs.			
upland (C, G, M)	1, 10	25.72	0.0005
S vs. F seasons	1, 280	57.08	0.0001
W vs. S and F	1, 280	130.08	0.0001
Dry Fall			
vs. Wet Fall	1, 280	8.28	0.0043
CMT-GP*DF-WF	1, 280	6.20	0.0134

Creosote) was highly significant. The overall contrast comparing mean biomass between shrub-dominated systems (creosote bush, mesquite, and tarbrush) and grass-dominated systems (grasslands, playas) found no significant differences (Table 2).

Interquartile (IQ) range as an index of spatial variability within sites differed substantially among vegetation types and dates, with a strong interaction (Fig. 3, Table 3). Variability was low for the grass-dominated grasslands and playas (least square means of IQ ranges from the PROC MIXED model 59.9 and 45.2, respectively), and consistently high for mesquite sites (least square mean 393). The occurrence of virtually 'empty' or bare quadrats, contrasting with high-biomass quadrats falling within shrub patches, caused the greater heterogeneity of shrub-dominated sites relative to the homogeneous grass-dominated systems. While there were significant interactions between ecosystem type and sample date, the overall contrast between shrub-dominated and grass-dominated systems was highly significant (Table 3), with higher values (or greater heterogeneity) in the shrublands. IQ ranges were lowest in winter (least square mean 142) and highest in fall (219).

#### *Aboveground net primary productivity*

Aboveground net primary production over most intervals was relatively low, as would be expected for this semiarid region. However, there were seasons where productivity

**Table 3** Results of mixed model analysing interquartile ranges of aboveground plant biomass measurements for 15 sites, 3 in each of 5 ecosystem types, for 29 sampling dates (TIME) from spring 1989 through fall 1998. Ecosystem type (TYPE) and season designations as in Table 2

Source	Degrees of freedom	Type III F	<i>p</i>
Tests of fixed effects			
TYPE	4, 10	10.87	0.0012
TIME	28, 280	8.82	0.0001
TIME*TYPE	112, 280	2.27	0.0001
Contrasts:			
Shrub (C, M, T)			
vs. grass (G, P)	1, 10	30.74	0.0002
Clay (T, P) vs.			
upland (C, G, M)	1, 10	8.90	0.0137
S vs. F seasons	1, 280	27.81	0.0001
W vs. S and F	1, 280	121.50	0.0001
Dry vs. Wet Falls	1, 280	3.48	0.0633
CMT-GP*DF-WF	1, 280	0.84	0.3592

in certain sites was high (Fig. 4); these occasional peaks were most conspicuous in the grass-dominated systems (grassland and playa). The mixed model analysing mean NPP among sites for the 28 intervals (Table 4) confirmed that there were differences among ecosystem types and among seasons or intervals, with significant interactions. An overall contrast for grass-dominated ecosystems vs. shrub-dominated was highly significant; the occasional peaks in aboveground production for the playas and at least one of the grassland sites were apparently sufficient to lead to this overall effect. However, the ranges of mean values for particular intervals often overlapped among different ecosystem types. Fall or late summer growing season productivity was significantly higher in wet falls than in dry ones, as identified in the contrasts, but the response to climatic patterns of grass-dominated systems was different from the response of shrub-dominated systems (the significant CMT-GP\*DF-WF contrast shown in Table 4). Specifically, grasslands showed greater differences between dry and wet seasons than did shrub-dominated systems.

When mean aboveground production per m<sup>2</sup> was summed for an annual period (winter, spring, and fall of a single calendar year), ANPP values generally ranged from 95 to more than 250 g m<sup>-2</sup> (least square means from PROC MIXED; also see Fig. 5). Although annual productivity values were similar for most sites for most years (with the exception of the consistently low values of productivity in tarbrush systems), some grasslands and playas had conspicuously greater productivity in some years. There was a significant interaction between ecosystem type and year, according to the PROC MIXED analysis (Table 5). An overall contrast comparing the



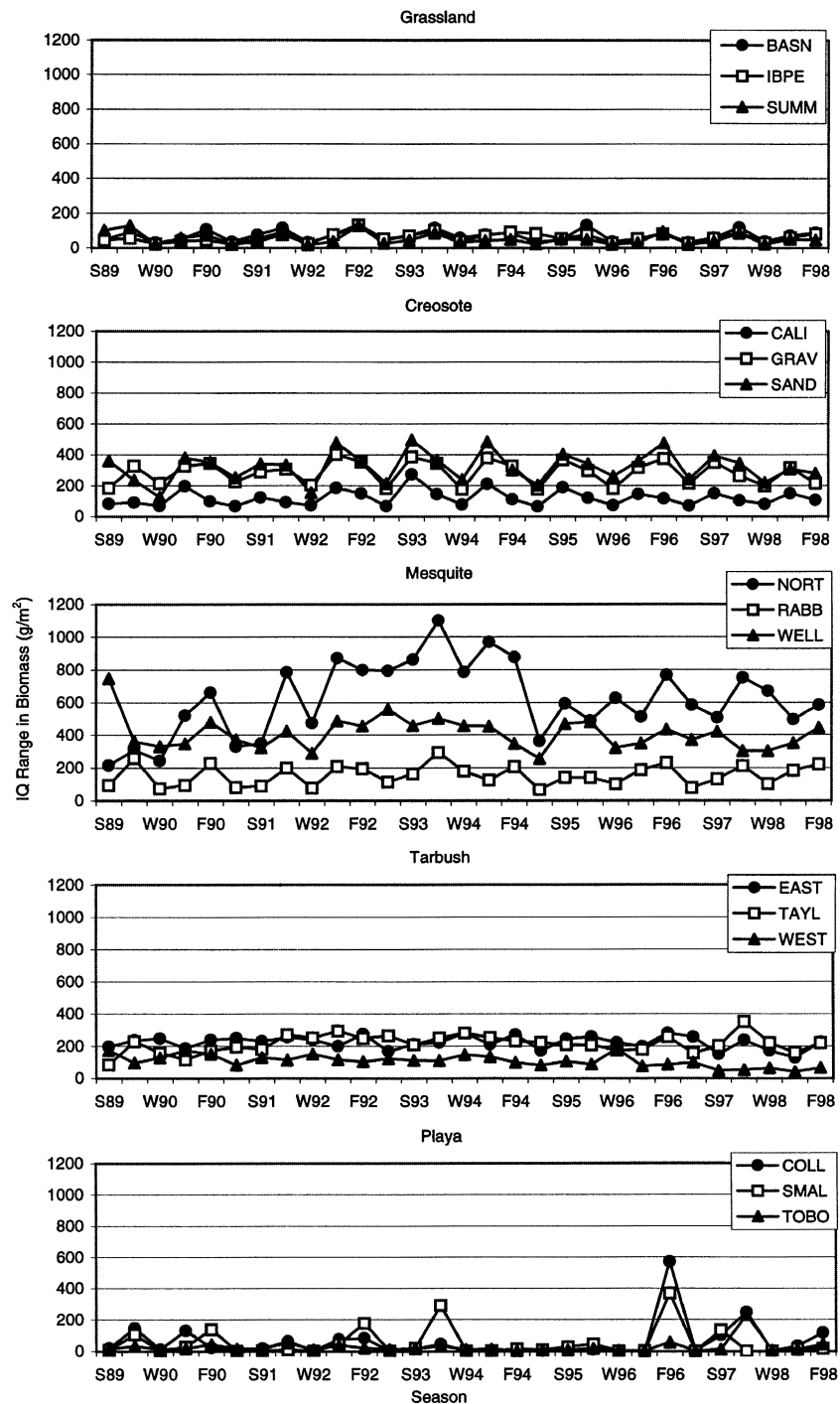


Fig. 3 Interquartile ranges of above-ground plant biomass values for 15 sites, calculated from 49 quadrats per site, for sampling periods from spring 1989 through fall 1998. Seasonal designations as in Fig. 2.

shrub-dominated systems (creosote bush, mesquite, and tarbush ecosystem types) with the grass-dominated systems (grasslands and playas) confirmed significant difference in annual production (Table 5), with shrub systems averaging  $125 \text{ g m}^{-2} \text{ year}^{-1}$  and grass-dominated systems averaging just over  $200 \text{ g m}^{-2} \text{ year}^{-1}$ .

Spatial variability in NPP per unit area is more complex than the pattern for biomass. Grasslands had consistently

low interquartile ranges (low heterogeneity) for above-ground seasonal NPP (Fig. 6). In contrast, creosote bush sites had regular peaks in patchiness corresponding in time to the peaks in average productivity (generally the spring intervals). Interestingly, mesquite systems in general displayed lower spatial variability in production than the patchy nature of aboveground biomass would suggest; the only high values of interquartile range in

productivity came during the time period that the North mesquite site was actively accumulating biomass (compare Fig. 2 with Fig. 6). Again, there were significant interactions of date with ecosystem type (PROC MIXED analysis, Table 6). An overall contrast between grass-dominated and shrub-dominated systems showed no significant difference in interquartile ranges of above-ground productivity. Overall differences between winter and the growing seasons (spring and fall) were significant, as a result of variability being extremely low during the winter interval (when virtually all quadrats have very low productivity).

#### *Temporal variation in NPP: interannual variability*

We examined the magnitude of interannual variation in NPP by calculating several indices of variation, including range, standard deviation, mean deviation from the mean, and coefficient of variation. Qualitative results were similar for all of these; only the coefficients of variation (of the 9 annual NPP values, 1990–98, for each site) are presented here. The playas demonstrated the highest interannual variability, and the tarbush sites the lowest (Table 7). Both grasslands and mesquite-dominated systems had relatively high interannual variability, while creosote bush sites and tarbush ecosystems had low coefficients of interannual variation.

The 10 years of study encompassed a range of climatic conditions (Fig. 7), including wetter than normal periods (e.g. summers of 1989, 1991; winter and spring 1992) and dry conditions during much of the 1994 and 1995 summer seasons. Wet winter/spring conditions favour growth by the C<sub>3</sub> shrubs and by a subset (winter-germinating) of the annuals. In contrast, dry conditions during summer affect those species adapted to make use of the normally dependable late summer moisture that typically provides more than half of annual precipitation (Fig. 7, line for long-term mean). While precipitation clearly influences plant production in these semiarid systems (note the significant contrasts of Dry vs. Wet falls in the mixed models analyses shown in Tables 2 and 4), preliminary attempts to correlate precipitation with production on a site-by-site basis were not satisfactory (correlations non-significant, not shown). A more mechanistic analysis of the relationship between precipitation and primary production would take into account landscape position (hence runoff and run-on), soil characteristics (rooting depth, water holding capacity), and temperature (potential evapotranspiration).

#### *Temporal variation in NPP: seasonality of production*

Because the major grasses of the Chihuahuan desert region are C<sub>4</sub> species, and because most of the shrubs

possess the C<sub>3</sub> photosynthetic pathway, we suspected that production in grasslands and in shrublands might differ in seasonal timing. That is, one might predict that in grasslands a greater proportion of total production would occur in late summer/fall, while in shrublands the greater proportion would come in the cooler temperatures of spring. Visual inspection of the seasonal NPP values for the 3 sites of each vegetation type suggests that some ecosystem types do have more predictable seasonal patterns than others (Fig. 4). We omitted playas and tarbush sites from this analysis, the former because localized run-on patterns are so obviously the driver for peaks of production, and the latter because of consistently low production values. For the other 3 types, we summarized the number of sites and years in which spring production was greater than fall production, and the number of sites and years in which fall production was greater than spring. For every creosote bush site in every year ( $N=15$ ), spring production exceeded that of fall; for mesquite, spring was greater than fall production in 11 of 15 cases; and for grasslands, spring production was greater than fall in only 4 of 15 cases. A chi-square test found significant differences in the frequency of these patterns (spring-greater vs. fall-greater) ( $\chi^2 = 21.533$ , 5 df,  $p = 0.0006$ ).

#### *Temporal variation in NPP: correlations of pattern among sites and among vegetation types*

We investigated temporal patterns of aboveground NPP, to determine whether sites with similar plant communities demonstrated similar timing and magnitude of production (Figs 4 and 5). Correlation coefficients were calculated to summarize the strength of correlation of NPP measurements during spring and fall growing seasons, for all pairwise combinations of the 15 sites ( $n=28$  intervals; Table 8). Correlation patterns among the three sites of an ecosystem type were generally significant and positive; correlations among sites of different types were only sometimes significant. Correlations of total annual ANPP were generally even weaker (values not shown). The three creosote sites were positively correlated with one another, but other sites were uncorrelated, even within an ecosystem type.

## **Discussion**

### *Effects of desertification on biomass and productivity*

Our estimates of aboveground productivity and biomass fall in the general range reported from other semidesert areas. Jornada sites are clearly more productive than true dry desert (productivities of 0–10 g m<sup>-2</sup> year<sup>-1</sup> according to Lieth 1975). Although generalizations based on literature

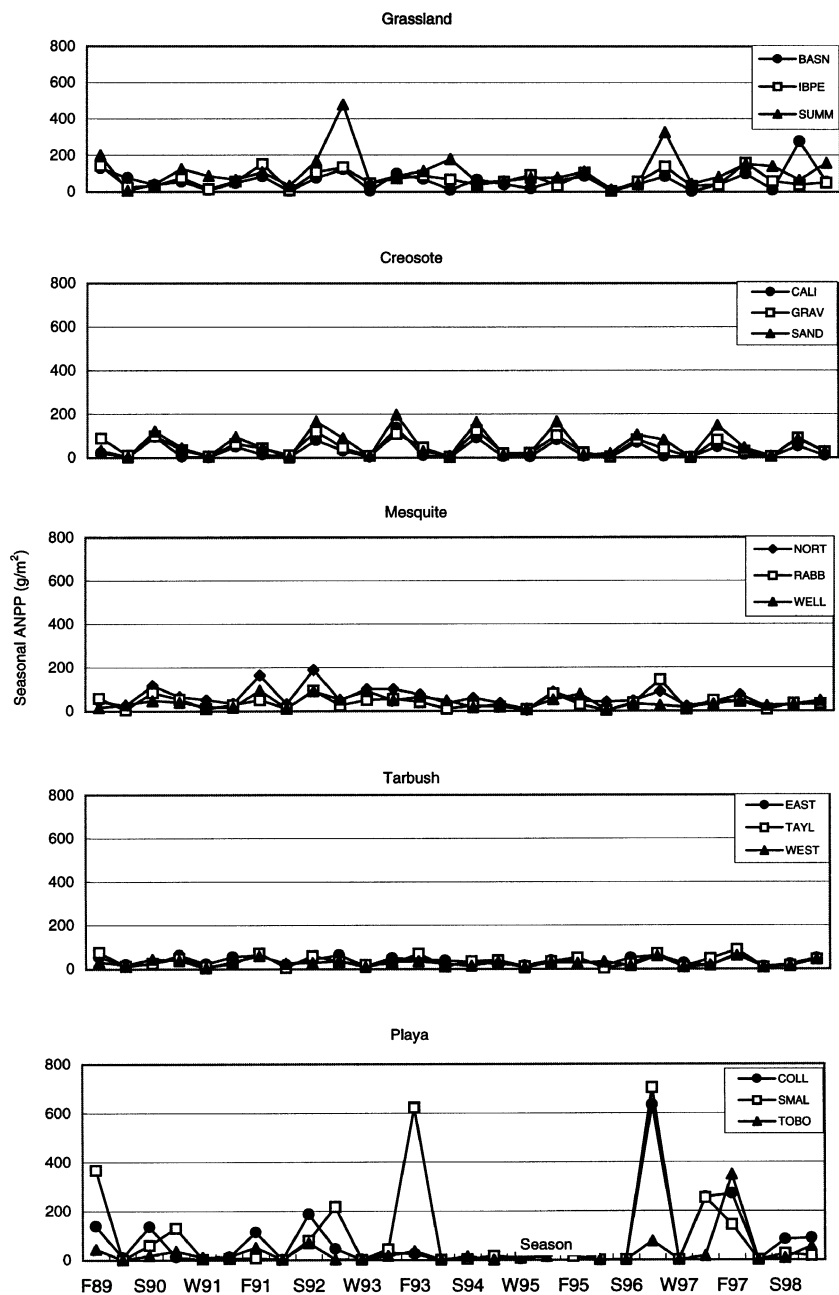


Fig. 4 Seasonal values of aboveground NPP for 15 sites, 3 per ecosystem type, from spring–fall 1989 interval to spring–fall 1998 interval. Abbreviations for 15 sites as given in Table 1; seasonal designations as in Fig. 2.

reviews imply that grasslands support higher NPP than desert scrub, our studies near the arid/semiarid ecotone suggest that the differences within a region may be rather small.

Even discounting one grassland receiving considerable runoff from an adjacent part of the landscape, the upland grasslands we studied had annual productivity values slightly higher than those in creosote bush or mesquite ecosystems (Fig. 5). Our measurements thus suggest that the displacement of grassland by desert scrub has resulted in a minor but detectable decrease in average

aboveground production. Desertification in this context is not simply a decline in productivity, defined as aboveground NPP (although certainly the productivity of palatable forage plants, and thus the economic productivity of many sites, has decreased). An additional, more substantial effect of vegetation conversion has been an increase in the spatial heterogeneity of the display of aboveground biomass, at the scale of individual plants and of bare areas large enough to initiate the sorts of erosional and physical processes that lead to soil degradation. The model of increasing heterogeneity in

**Table 4** Results of mixed model analysing mean aboveground net primary productivity for 15 sites, 3 in each of 5 ecosystem types, for 28 intervals (TIME) from spring 1989–fall 1989 through spring 1998–fall 1998. Ecosystem type (TYPE) designated as C = creosote bush, G = grassland, M = mesquite, P = playa, and T = tarbush. Seasons designated as W = winter, S = spring, and F = late summer/fall

Source	Degrees of freedom	Type III F	<i>p</i>
Tests of fixed effects			
TYPE	4, 10	8.66	0.0028
TIME	27, 270	6.51	0.0001
TYPE*TIME	108, 270	2.36	0.0001
Contrasts:			
Shrub (C, M, T)			
vs. grass (G, P)	1, 10	30.23	0.0003
Clay (T, P) vs.			
upland (C, G, M)	1, 10	1.29	0.2833
S vs. F seasons	1, 270	5.80	0.0167
W vs. S and F	1, 270	79.30	0.0001
Dry Fall vs. Wet Fall	1, 270	31.85	0.0001
CMT–GP* DF–WF	1, 270	15.39	0.0001

shrublands (Schlesinger *et al.* 1990) suggests more opportunities for loss of resources (erosion by wind or water and removal from the site) in shrublands; this in turn suggests that over a long enough period, mean aboveground productivity would further decline in those shrublands relative to average grassland values.

Considerable work has been done in a comparable tension zone between semiarid grasslands and shrublands in Argentina (e.g. Sala *et al.* 1989), where grass cover is negatively correlated (and shrub cover positively correlated) with grazing intensity. Several specific aspects of ecosystem function, including soil water balance and primary productivity, were directly affected by the relative abundance of the grass and shrub 'functional types' (Aguiar *et al.* 1996), suggesting that conversion of a site from one vegetation cover to another should be reflected in ecosystem-level properties. Indeed, Dugas *et al.* (1996) demonstrated substantial differences in radiation balance and heat fluxes between Jornada shrublands and grasslands. This argument, in addition to the preceding suggestion that bare intershrub areas should promote losses of soil resources, would support the idea that shrub-dominated systems exhibit lower net primary production than the grasslands they have replaced. On the other hand, the greater rooting volumes exploited by shrubs might counteract the loss of resources from surface soils. The comparison of three examples of each vegetation type made here is a fairly coarse test, and ranges of productivity values did overlap for the various ecosystem types, but there was a detectable and

**Table 5** Results of mixed model analysing mean aboveground annual net primary productivity for 15 sites, 3 in each of 5 ecosystem types, for 9 years (TIME) from 1990 through 1998. Ecosystem type (TYPE) designated as C = creosote bush, G = grassland, M = mesquite, P = playa, and T = tarbush

Source	Degrees of freedom	Type III F	<i>p</i>
Tests of fixed effects			
TYPE	4, 10	2.00	0.1710
TIME	8, 80	6.67	<0.001
TIME*TYPE	32, 80	6.24	<0.001
Contrasts:			
Shrub (C, M, T)			
vs. grass (G, P)	1, 10	6.57	0.0282
Clay (T, P) vs.			
upland (C, G, M)	1, 10	0.54	0.4781

significant difference in overall productivity between grasslands and the desertified shrub systems.

We note that desertification is not always expressed as woody plant incursion into grasslands, nor is the expansion of woody vegetation types always tied to increasingly arid conditions. Brown *et al.* (1997) suggest that such dramatic vegetation conversion may be a nonlinear response to changes in the seasonality, as well as the amount of precipitation. Our results should be relevant, however, to any such change in vegetation structure within the general context of a semiarid environment where the increased spatial heterogeneity of plant cover would render soil resources vulnerable to redistribution processes (Schlesinger *et al.* 1990).

#### *Spatial heterogeneity in biomass and productivity*

The distribution of aboveground biomass was more variable in shrublands than in grasslands at the scale of our sampling. Of course, smaller scale sampling would undoubtedly reveal variability in the grasslands, too; but we assume that the 1-m<sup>2</sup> scale is most relevant to the self-augmenting patterns of desertification hypothesized by Schlesinger *et al.* (1990). The greater heterogeneity of plant biomass in the shrublands suggests the potential for a greater patchiness of biological activity, especially since large plants serve such an important role in ameliorating the physical environment and structuring the presence and behaviour of other organisms. On the other hand, even the 'homogeneous' grasslands contain small patches with considerable woody biomass (e.g. clumps of succulents).

Interestingly, primary productivity appeared to be less structured spatially than biomass distribution, with little evidence to suggest any difference in the scale or

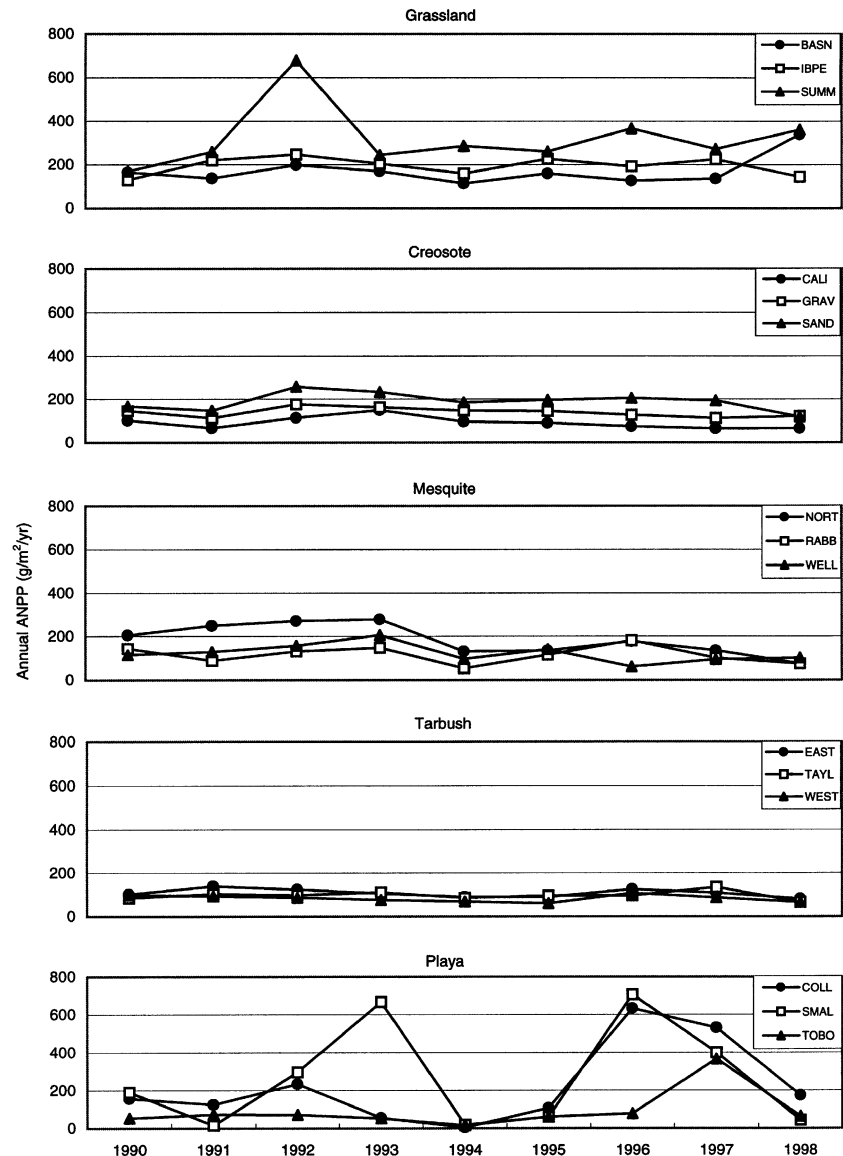


Fig. 5 Mean annual aboveground net primary production values ( $\text{g m}^{-2} \text{ year}^{-1}$ ) for 15 sites, estimated as sum of production increments from one fall sampling period to the following fall, for the complete sampling years 1990 through 1998. Abbreviations for 15 sites as given in Table 1.

patchiness of production among vegetation types (Table 6). Presumably the short-lived production of annuals and of perennial forbs in intershrub spaces reduces the contrast between shrub and intershrub quadrats.

We found few other reports that have characterized the spatial variation in productivity of grassland or shrubland systems in any comparable way. One long-term study found that unburned tall-grass prairie had higher spatial variation (as reflected in the coefficient of variation) than did burned prairie; after fire, the grassland community was more productive but more homogeneous (Briggs *et al.* 1989).

On the scale of landscapes there is considerable heterogeneity in aboveground production. In earlier studies at the Jornada, Ludwig (1986) found the highest (and least variable over time) NPP in basin swales, dominated by

*Pleuraphis*, where run-on moisture was significant – roughly  $300\text{--}600 \text{ g m}^{-2} \text{ year}^{-1}$ . Arroyos also had high NPP but slopes and alluvial fans supported the lowest annual aboveground NPP ( $50\text{--}290 \text{ g m}^{-2} \text{ year}^{-1}$ ). Ludwig (1987) used these results to point out the fallacy of assuming that production in arid lands is always quite low; his paper and work by Schlesinger & Jones (1984) in the Mojave Desert also highlight the importance of localized runoff and run-on patterns in supporting patchy areas of high productivity (Noy-Meir 1985). Our sites reflect these patterns; the highest production values were recorded for the Summerford grassland, which receives considerable run-on from the rocky slopes of Mt. Summerford. The playas also demonstrated high NPP when run-on from surrounding landscape positions was significant. Tarbush-dominated communities

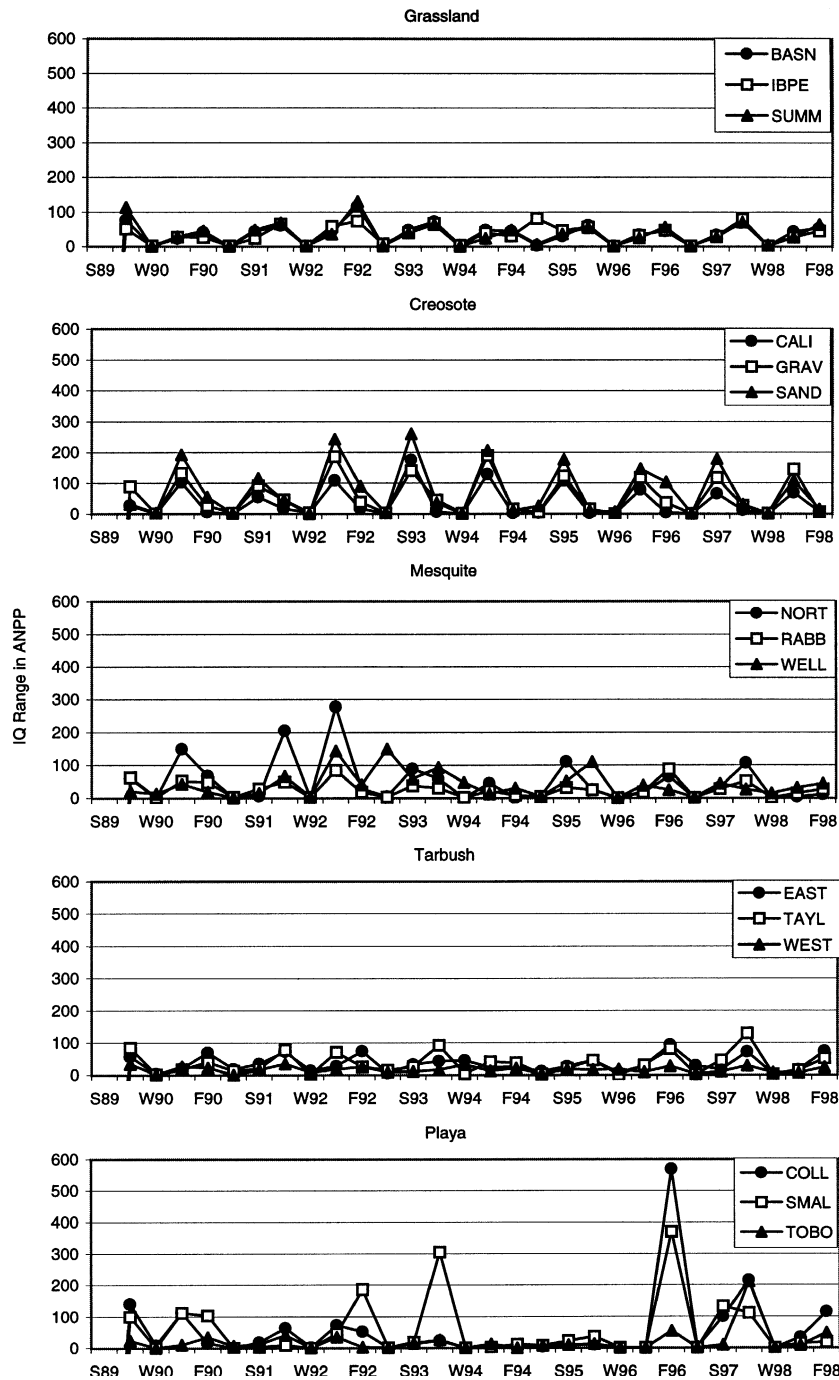


Fig. 6 Interquartile ranges of seasonal aboveground productivity values for 15 sites, calculated for 49 quadrats per site, for sampling intervals from spring–fall 1989 interval to spring–fall 1998 interval. Abbreviations for 15 sites as given in Table 1; seasonal designations as in Fig. 2.

often occur on lower slopes where run-on can be considerable; the importance of this run-on in structuring vegetation stripes or arcs of a grass–shrub–bare area mosaic has been described by Montaña (1992; also see Mauchamp *et al.* 1993) and others (e.g. Klausmeier 1999). Our tarbush sites comprise discrete patches of shrubs and grasses, but do not appear to be organized in the ‘stripes’ reported for other semiarid shrublands (e.g. Ludwig & Tongway 1995).

Variation among sites of the same ecosystem type and similar species composition may be a result of spatial variation in precipitation inputs; much of the precipitation comes in patchy summer convective storms. However, landscape position (influencing run-on or runoff) and belowground features (e.g. depth to argillic or calcic horizons) may further influence water availability and hence explain some of the intersite variation we see among locations with similar vegetation (Miller *et al.* 2001).

### Temporal variability in production

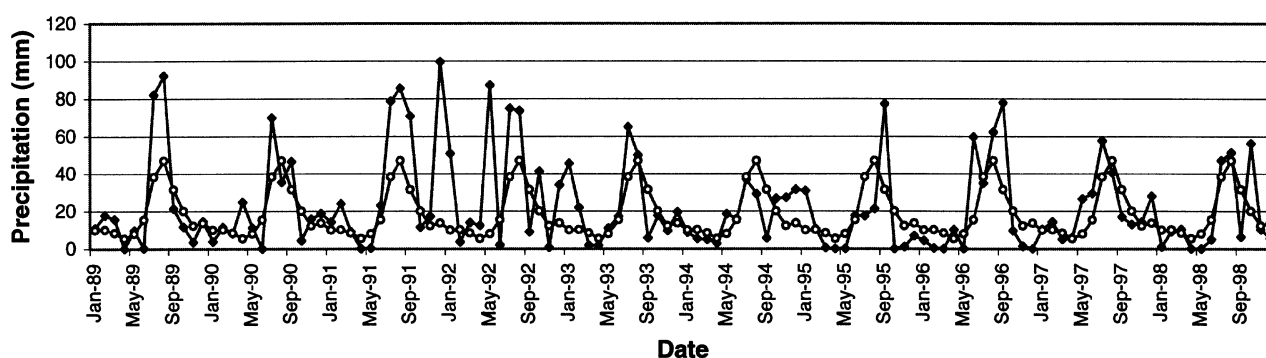
One obvious result of desertification in this region has been a dramatic change in the seasonality of plant

**Table 6** Results of mixed model analysing interquartile ranges for mean aboveground net primary productivity for 15 sites, 3 in each of 5 ecosystem types, for 28 intervals (TIME) from 1990 through 1998. Ecosystem type (TYPE) designated as C = creosote bush, G = grassland, M = mesquite, P = playa, and T = tarbush

Source	Degrees of freedom	Type III F	<i>p</i>
Tests of fixed effects			
TYPE	4, 10	5.71	0.0117
TIME	27, 270	10.04	0.0001
TYPE*TIME	108, 270	3.60	0.0001
Contrasts:			
Shrub (C, M, T)			
vs. grass (G, P)	1, 10	0.05	0.8194
Clay (T, P) vs.			
upland (C, G, M)	1, 10	2.74	0.1291
S vs. F seasons	1, 270	0.03	0.8539
W vs. S and F	1, 270	167.95	0.0001
Dry Fall vs. Wet Fall	1, 270	35.42	0.0001
CMT-GP*DF-WF	1, 270	6.57	0.0109

production. The shrublands consistently experience earlier (spring) peaks of production than do the grasslands. This phenological shift has implications for the dynamics of consumer populations, both herbivores and seed predators. There may be consequences for decomposition and soil chemistry, as well, related to both organic matter inputs and root respiration with respect to temperature and available moisture.

Interannual variations in primary productivity have been a focus of aridland studies for years, based on the generalization that water availability is both limited and unpredictable. In a review of 77 series of annual production vs. precipitation records for arid sites, Le Houérou *et al.* (1988) found that variation in production was significantly greater than variation in precipitation; that is, precipitation fails to explain completely interannual patterns of NPP. In our study, precipitation explained only a small portion of variation in production, in strong contrast with reports such as those cited in MacMahon & Wagner (1985), where nearly 80% of annual variation in production was related to precipitation inputs. Le Houérou *et al.* (1988) suggested that heavier (finer-textured) soils have higher variability in production, while sandy soils would be more consistent over time. While our playas have finer-textured soils than do the



**Fig. 7** Monthly precipitation (mm) received at the Jornada LTER weather station, January 1989–December 1998, dark line and symbols. Shown for comparison is the mean monthly precipitation (grey line and symbols), 1892 through 1987, as reported by Kunkel *et al.* (1990); note (repeated) long-term pattern of highest precipitation in late summer.

**Table 7** Coefficients of variation for annual aboveground net primary production values for 9 years of observations at 15 sites

Ecosystem type	CV for least variable site	CV for mid-range site	CV for most variable site	Mean for ecosystem type
Grassland	0.211	0.394	0.454	0.353
Playa	0.959	1.027	1.132	1.039
Creosote bush	0.161	0.224	0.309	0.231
Mesquite	0.348	0.351	0.387	0.362
Tarbush	0.178	0.194	0.200	0.191

**Table 8** Correlations of mean seasonal ANPP values, fall 1989 – fall 1998, for 15 sites. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ 

	Creosote bush				Black grama grassland				Mesquite				Grassy playa				Turbush												
	GRAV	SAND	BASN	IBPE	SUMM	NORT	RABB	WELL	COLL	SMAL	TOBO	EAST	TAYL	WEST	GRAV	SAND	BASN	IBPE	SUMM	NORT	RABB	WELL	COLL	SMAL	TOBO	EAST	TAYL	WEST	
CALI	0.898***	0.929***	0.291	-0.081	-0.103	0.416*	0.388*	0.127	0.009	-0.108	-0.069	0.139	0.011	0.032	0.898***	0.929***	0.291	-0.081	-0.103	0.416*	0.388*	0.127	0.009	-0.108	-0.069	0.139	0.011	0.032	
GRAV		0.906***	0.469*	0.116	0.011	0.461*	0.531**	0.146	0.177	0.122	0.016	0.248	0.291	0.111	0.906***	0.469*	0.116	0.116	0.011	0.461*	0.531**	0.146	0.177	0.122	0.016	0.248	0.291	0.111	
SAND			0.304	0.047	0.079	0.474*	0.540**	0.152	0.233	0.083	0.017	0.245	0.178	0.138	0.304	0.047	0.047	0.047	0.079	0.474*	0.540**	0.152	0.233	0.083	0.017	0.245	0.178	0.138	
BASN				0.388*	0.299	0.114	0.276	0.145	0.266	0.238	0.213	0.357	0.365	0.234	0.388*	0.299	0.114	0.276	0.266	0.238	0.213	0.357	0.365	0.238	0.213	0.357	0.365	0.234	
IBPE					0.673***	0.375*	0.430*	0.416*	0.513**	0.489**	0.563**	0.733***	0.793***	0.587***	0.673***	0.375*	0.430*	0.416*	0.513**	0.489**	0.563**	0.733***	0.793***	0.587***	0.563**	0.733***	0.793***	0.587***	
SUMM						0.120	0.345	0.190	0.459*	0.531	0.209	0.577**	0.421*	0.389*	0.120	0.345	0.190	0.345	0.459*	0.531	0.209	0.577**	0.421*	0.389*	0.577**	0.421*	0.389*	0.389*	
NORT							0.683***	0.725***	0.332	0.153	0.246	0.352	0.479*	0.467*	0.683***	0.725***	0.725***	0.332	0.153	0.246	0.352	0.479*	0.467*	0.352	0.479*	0.467*	0.467*	0.467*	
RABB								0.384*	0.761***	0.575**	0.274	0.441**	0.595***	0.542**	0.384*	0.761***	0.761***	0.575**	0.274	0.441**	0.575**	0.274	0.441**	0.575**	0.274	0.441**	0.595***	0.542**	
WELL									0.085	0.031	0.173	0.300	0.432*	0.291	0.085	0.031	0.173	0.300	0.432*	0.031	0.173	0.300	0.432*	0.432*	0.300	0.432*	0.291	0.291	
COLL										0.670***	0.494**	0.371	0.615***	0.568**	0.670***	0.494**	0.494**	0.670***	0.494**	0.670***	0.494**	0.371	0.615***	0.670***	0.494**	0.371	0.615***	0.568**	
SMAL											0.231	0.386*	0.622***	0.430*												0.386*	0.622***	0.430*	
TOBO																											0.507**	0.658***	0.582**
EAST																												0.689***	0.711***
TAYL																													0.704***

creosote bush and mesquite sites (supporting the generalization), the turbush systems, which also occur on heavy (high clay content) soils, actually show low interannual variation in NPP.

Others have found high interannual variation in NPP of Jornada grasslands. One study (Paulsen & Ares 1962) reported that grass production could best be explained by correlation with the preceding 15 months of rainfall (not that of a single season), and that the primary grasses of heavier soils (such as tobosa, *Pleuraphis mutica*) were far less sensitive to precipitation than was *Bouteloua eriopoda*. At least some of the local perennial grasses, however, respond vigorously to interannual differences in rainfall. Herbel & Gibbens (1996) documented increases of perennial grass cover by a factor of 10 over just two years, and they reported variation of more than 2 orders of magnitude in production measured for a species at a site over time.

## Conclusions

In conclusion, our study of aboveground net primary productivity in Jornada ecosystems demonstrates that:

- ANPP is lower, and occurs in different seasonal patterns, in desertified shrublands than in remnant grasslands;
- aboveground plant biomass is distributed in a more patchy fashion (at the square-meter scale) in shrub-dominated systems than in grass-dominated ones, but heterogeneity in NPP is not so different among ecosystem types;
- grasslands are more variable from year to year in their production than are the shrublands, with their more deeply rooted plants.

The conversion of semidesert grasslands to desert shrub systems in this region has clearly resulted in the alteration of seasonality of plant production, with likely impacts on other trophic levels. The greater spatial heterogeneity of shrublands is expressed in the abundance of relatively large intershrub patches that are bare for at least portions of the year. According to our model of desertification processes, these bare areas afford the opportunity for increased loss and redistribution of soil resources. However, the presumed acceleration of transport processes does not yet appear to have resulted in a substantial decrease in site productivity over the last century of shrub invasion.

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## References

- Aguiar MR, Paruelo JM, Sala OE, Lauenroth WK (1996) Ecosystem responses to changes in plant functional type composition: An example from the Patagonian steppe. *Journal of Vegetation Science*, **7**, 381–390.
- Allred KW (1993) *A Field Guide to the Grasses of New Mexico*. Department of Agricultural Communications, New Mexico State University, Las Cruces, NM.
- Briggs JM, Seastedt TR, Gibson DJ (1989) Comparative analysis of temporal and spatial variability in above-ground production in a deciduous forest and prairie. *Holarctic Ecology*, **12**, 130–136.
- Brown JH, Valone TJ, Curtin CG (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 9729–9733.
- Buffington LC, Herbel CH (1965) Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs*, **35**, 139–164.
- Correll DS, Johnston MC (1970) *Manual of the Vascular Plants of Texas*. Texas Research Foundation, Renner, TX.
- Dugas WA, Hicks RA, Gibbens RP (1996) Structure and function of C<sub>3</sub> and C<sub>4</sub> Chihuahuan Desert plant communities: Energy balance components. *Journal of Arid Environments*, **34**, 63–79.
- Evenari M, Noy-Meir I, Goodall DW (eds) (1985) Hot Deserts and Shrublands, A. *Ecosystems of the World*, Vol. **12A**. Elsevier, Amsterdam.
- Fredrickson E, Havstad KM, Estell R, Hyder P (1998) Perspectives on desertification: south-western United States. *Journal of Arid Environments*, **39**, 191–207.
- Gibbens RP, Beck RF (1988) Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. *Journal of Range Management*, **41**, 186–192.
- Gibbens RP, Beck RF, McNeely RP, Herbel CH (1992) Recent rates of mesquite establishment in the northern Chihuahuan Desert. *Journal of Range Management*, **45**, 585–588.
- Gile LH, Grossman RB (1979) The Desert Project Soil Monograph. Document no. PB80-135304, National Technical Information Service, Springfield, VA.
- Gile LH, Hawley IW, Grossman RB (1981) Soils and geomorphology in the basin and range area of southern New Mexico – guidebook to the Desert Project. Memoir 39, New Mexico Bureau of Mines and Mineral Resources, Santa Fe, NM.
- Hampel FR, Ronchetti EM, Rousseeuw PJ, Stahl WA (1986) *Robust Statistics: the approach based on influence functions*. Wiley, New York.
- Hastings JR, Turner RM (1965) *The Changing Mile*. University of Arizona Press, Tucson, AZ.
- Hennessy JT, Gibbens RP, Tromble JM, Cardenas M (1983) Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *Journal of Range Management*, **36**, 370–374.
- Herbel CH, Gibbens RP (1996) *Post-drought vegetation dynamics on arid rangelands in southern New Mexico*. Agricultural Experiment Station Bulletin 776, New Mexico State University, Las Cruces, NM.
- Huber PJ (1981) *Robust Statistics*. Wiley, New York.
- Hueneke LF, Clason D, Muldavin E (2001) Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments*, **47**, 257–270.
- Hueneke LF, Noble I (1996) Ecosystem function of biodiversity in arid ecosystems. In: *Functional Roles of Biodiversity: a Global Perspective* (eds Mooney HA, Cushman JH, Medina E, Sala OE, Schulze E-D), pp. 99–128. J. Wiley & Sons, Chichester.
- Jain JK (ed.) (1986) *Combating desertification in developing countries*. Scientific Publishers, Jodhpur, India.
- Kearney TH, Peebles RH (1964) *Arizona Flora*. University of California Press, Berkeley, CA.
- Klausmeier CA (1999) Regular and irregular patterns in semiarid vegetation. *Science*, **284**, 1826–1828.
- Kunkel KE, Malm NR, Earl RA (1990) Climate guide, Las Cruces, 1851–1987. Research Report 623, New Mexico State University Agricultural Experiment Station, Las Cruces, NM.
- Le Houérou HN, Bingham RL, Skerbek W (1988) Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments*, **15**, 1–18.
- Lieth H (1975) Primary production of the major vegetation units of the world. In: *Primary Productivity of the Biosphere* (eds Lieth H, Whittaker RH), pp. 203–215. Ecological Studies 14, Springer-Verlag, New York.
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) *SAS® System for Mixed Models*. SAS Institute Inc., Cary, NC. 633pp.
- Ludwig JA (1986) Primary production variability in desert ecosystems. In: *Pattern and Process in Desert Ecosystems* (ed. Whitford WG), pp. 5–17. University of New Mexico Press, Albuquerque, NM.
- Ludwig JA (1987) Primary productivity in arid lands: myths and realities. *Journal of Arid Environments*, **13**, 1–7.
- Ludwig JA, Tongway DJ (1995) Spatial organization of landscapes and its function in semiarid woodlands, Australia. *Landscape Ecology*, **10**, 51–63.
- MacMahon JA, Wagner FH (1985) The Mojave, Sonoran and Chihuahuan Deserts of North America. pp 105–202 in Evenari *et al.* op. cit.
- Mauchamp A, Montaña C, Lepart J, Rambal S (1993) Ecotone dependent recruitment of a desert shrub, *Flourensia cernua*, in vegetation stripes. *Oikos*, **68**, 107–116.
- Miller D, Archer SR, Zitzer SF, Longnecker MT (2001) Annual rainfall, topographic heterogeneity and growth of an arid land tree (*Prosopis glandulosa*). *Journal of Arid Environments*, **48**, 23–33.

- Montaña C (1992) The colonization of bare areas in two-phase mosaics of an arid ecotone. *Journal of Ecology*, **80**, 315–327.
- Noy-Meir I (1985) Desert ecosystem structure and function. pp. 93–103. In: *Evenari et al. op. cit.*
- Paulsen HA, Ares FN (1962) Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the southwest. USDA Technical Bulletin 1270.
- Phinn S, Franklin J, Hope A, Stow D, Huenneke L (1996) Biomass distribution mapping using airborne digital video imagery and spatial statistics in a semiarid environment. *Journal of Environmental Management*, **47**, 139–164.
- Reynolds JF, Virginia RA, Kemp PR, DeSoyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecological Monographs*, **69**, 69–106.
- Sala OE, Golluscio RA, Lauenroth WK, Soriano A (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia*, **81**, 501–505.
- Schlesinger WH, Jones CS (1984) The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. *Botanical Gazette*, **145**, 116–124.
- Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, **77**, 364–375.
- Schlesinger W, Reynolds J, Cunningham G *et al.* (1990) Biological feedbacks in global desertification. *Science*, **247**, 1043–1048.
- Schwarz G (1978) Estimating the dimension of a model. *Annals of Statistics*, **6**, 461–464.
- Stein RA, Ludwig JA (1979) Vegetation and soil patterns on a Chihuahuan Desert bajada. *American Midland Naturalist*, **101**, 28–37.
- United Nations Environment Programme (UNEP) (1997) *World Atlas of Desertification*, 2nd edn. Edward Arnold, London, and Wiley, New York.
- USDA Soil Conservation Service (1980) Soil Survey of Doña Ana County, New Mexico. USDA SCS, in cooperation with US Department of Interior and NM Agricultural Experiment Station.
- Van Auken OW (2000) Shrub invasions of North American semi-arid grasslands. *Annual Review of Ecology and Systematics*, **31**, 197–215.
- Verstraete MM, Schwartz SA (1991) Desertification and global change. *Vegetatio*, **91**, 3–13.