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Patterns of Net Primary Production in Chihuahuan Desert Ecosystems

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The Jornada Basin of southern New Mexico has long been an important location for the study of productivity in desert ecosystems. Researchers have studied the magnitude and sustainability of plant production since the founding of the USDA Jornada Experimental Range (JER) in 1912. The consistent administration and research focus of the JER and of the Chihuahuan Desert Rangeland Research Center (CDRRC) have facilitated a number of long-term studies of vegetation dynamics and productivity. These long-term data sets are especially critical for understanding arid ecosystems, where interannual and decadal scale variation in climate is great and plant performance is strongly constrained by the physical environment. Long-term data, including the net primary productivity (NPP) data that are the focus of this chapter, are also essential for understanding the progression or rather, degradation of ecosystem structure that has been called desertification.

Through the years a variety of approaches have been used to evaluate plant production in the Jornada Basin. These approaches span the range from applied or management-oriented techniques, focused primarily on assessing patterns of palatable forage production, to more basic empirical studies based on dimension analysis or similar measurements of plant growth, to estimates based on photosynthetic measurements, to remote sensing and modeling approaches. NPP was a particular focus of the work

performed during the International Biological Programme or IBP (1970s) and is still a

major emphasis in the Long-Term Ecological Research (LTER) era. Thus, the Jornada

provides a unique opportunity to compare the strengths and weaknesses of different

approaches applied to a complex system.

Ecosystem science has provided a set of general hypotheses about the factors

regulating NPP in arid and semiarid ecosystems (reviewed by Noy-Meir 1973; Hadley

and Szarek 1981; Ludwig 1986, 1987). These premises include the following:

1. Plant productivity is low relative to that of other ecosystems (Lieth 1975).

2. NPP is regulated primarily by localized water availability and hence should be
   correlated closely with precipitation (Le Houerou 1984; Le Houerou et al. 1988).
   This premise is related to Noy-Meir's (1973) definition of deserts as "water-
   controlled ecosystems with infrequent, discrete, and largely unpredictable water
   inputs." Water and energy flows are considered to be coincident because plant
   production cannot take place without water expenditure through transpiration.

3. A pulse-reserve pattern (Noy-Meir 1973) characterizes the behavior of populations
   (including producer populations) in deserts, such that the episodic availability of
   resources in excess of some threshold (such as the "pulse" of precipitation)
   stimulates growth and the production of a large reserve (e.g., of photosynthetic
   tissues, propagules, and organic matter).

4. Deserts, especially shrubland systems, are dominated by long-lived, stress-tolerant
   plants with slow growth and low population turnover. Low aboveground

productivity and high biomass accumulation ratios, at least in woody plants, should reflect this low rate of turnover.

5. Soil texture has been proposed as an important determinant of aboveground NPP in arid and semiarid systems, with coarse sandy soils having greater infiltration of water to depth, lower rates of evaporative loss from the surface, and therefore greater water availability and NPP than fine-textured soils in the same climatic regime. This has been termed the inverse-texture hypothesis (Noy-Meir 1973; Sala et al. 1988), because the reverse is predicted to occur in more humid regions where water-holding capacity is presumed to be more important than infiltration in determining soil moisture availability.

6. Abiotic constraints and the physiological tolerances of organisms, rather than biological interactions among organisms, dictate productivity levels. In other words, deserts represent areas where plants are stress tolerators, rather than competitors or ruderals.

The history of vegetation conversion in the region and the compelling need to understand desertification processes and their implications for system productivity and stability suggest additional questions that can and should be addressed. Our objective in this chapter is to review the history of NPP studies in the Jornada Basin, examining the degree to which studies there have given insight into these general hypotheses and examining the following specific questions:

1. Is NPP lower in shrublands (desertified) than in grasslands?

2. Is there evidence that NPP has declined over time at Jornada sites with
progressive loss of soil resources or degradation?

3. Is NPP related to the diversity or composition of the plant community in
averages or temporal patterns; that is, do biological factors such as species or
growth form differences play a role?

4. Is NPP in this arid environment constrained most strongly by current and local
precipitation? Do shrublands differ from grasslands in temporal variability
and response to current precipitation?

5. Do biomass accumulation ratios reflect the slow growth and low turnover
predicted for woody desert species?

6. Are Jornada empirical data consistent with the inverse-texture hypothesis; that
is, are there consistent differences in productivity between fine- and coarse-
textured soils that support the idea of greater control of water availability by
surface properties and processes (infiltration and evaporation) than by water-
holding capacity of the profile?

The chapter concludes by identifying those areas in which future research should
be focused to make the greatest advances in our understanding of ecosystem function.

History of NPP Work at the Jornada

Over the past century, a number of important studies in the Jornada Basin have
contributed to our understanding of NPP in arid environments. Early work on the JER
focused on observations of forage productivity and the basic patterns of growth of the
primary forage (perennial grass) species (Nelson 1934; Canfield 1939). After dry periods

in the 1930s and particularly after the onset of the 1950s drought, scientific work

centered on attempts to understand forage production and its response to drought on

different soil types. The chief long-term data set on plant production from the Jornada

was a study maintained from 1957 to 1988, summarized by Herbel and Gibbens (1996).

Forage (perennial grass) production was assessed by clipping at sites located on 12

different soils; production or yield was obtained in annual sampling during October or

November of each year. Rain gauges provided measures of monthly precipitation at most

sites. Sampling of most of these transects was maintained and extended from 1978

through 1998 using clipping approaches to estimate production of all species (not just

forage grasses) (Gibbens unpublished data).

In the 1970s, ecosystem studies were carried out at two Jornada Basin sites (one

creosotebush [*Larrea tridentata*] shrubland and one black grama [*Bouteloua eriopoda*]

grassland) under the auspices of the IBP. An IBP report (Pieper et al. 1983) described

plant biomass and productivity at the IBP grassland and drew comparisons with study

sites at Fort Stanton, New Mexico (a more mesic site with blue grama), and Santa Rita,

Arizona. Three years of data were contrasted, one noted as being "dry." Standing crop in

both grazed and ungrazed areas contained about 50% warm season grasses, but black

grama was less common and less important in the grazed locations. Summer forbs were

noted as an important component of summer/fall biomass. The general values of NPP

observed were typical of published values for semiarid grasslands and desert scrub

elsewhere, 80 g C/m^2/yr (or roughly 160 g/m^2/yr plant dry weight). Pieper et al. (1983)

reported that aboveground NPP (ANPP) was usually higher in ungrazed than grazed

locations at the IBP grassland. Values were on the order of 100–200 g/m^2 per year,

excluding any estimate for yucca and mesquite (*Prosopis glandulosa*) (described as too

variable and too poorly sampled). Warm season grasses were the most important

component, but warm season forbs and shrubs also contributed significantly to total

ANPP during these IBP studies.

During the initial phase of the Jornada LTER program, productivity studies were

concentrated along transects from the base of Mount Summerford to the playa near the

CDRRC headquarters. Permanent quadrats and line intercept transects located every 30 m

along 3-km transects were used to assess plant composition and biomass. Annual

fertilization of one of the two transects was carried out to investigate the degree to which

nitrogen availability limited production and composition in this semiarid system.

Reviews by Ludwig (1986) summarized the observations coming from this and other

LTER I work. He emphasized high variability over both space and time, documenting

localized spots of extremely high productivity and considerable variation among years.

Measures of aboveground production varied from 2–15× among years (table 11-1).

Table 11-1. Ranges of values for annual aboveground net primary production for various
ecosystems at the Jornada, from Ludwig (1987).

	Lowest annual value (g/m^2/yr)	Highest annual value (g/m^2/yr)
Bajada alluvial fans	53	292
Bajada small arroyos	37	318
Bajada large arroyos	30	456
Basin slopes	48	179
Basin swales	292	592
Basin playa	52	258

Another Ludwig study, near Carlsbad, New Mexico, reported equally variable results for a creosotebush stand (243–416 g/m^2/yr) and a mesquite-invaded grassland (23–82 g/m^2/yr) over just two years. Ludwig's (1986) review of data from other deserts documented 3–10-fold increases in ANPP between dry and wet years. One of the major conclusions from the Jornada IBP work on desert shrublands (Ludwig 1987) was that localized production (in small parts of the landscape) can be extremely high, as table 11-1 suggests.

In the second phase of the Jornada LTER program, a network of 15 sites was established to facilitate formal comparisons of plant composition, biomass, and ANPP in five major vegetation types (three sites in each): black grama grassland, grass-dominated playas, creosotebush shrublands, mesquite dune systems, and tarbush (*Flourensia cernua*) shrublands. This LTER program has monitored ANPP using consistent methods since spring 1989; these measurements provide a core set of observations for comparison of ecosystem function and structure among Jornada plant communities. Each site contains a grid of 49 1-m^2 permanent quadrats arranged at 10-m intervals in a 7×7 square. Sampling occurs three times per year: February, to capture winter annuals; May, timed to measure shrub leafout and to reflect a late-season sample of the spring bloom of annuals; and September–October, representing the peak biomass for the greatest number of annuals and other fall-flowering species. Plants or plant parts within the rectangular volume above each quadrat are measured nondestructively; plant dimensions are used to estimate living biomass per species per quadrat based on regressions developed during the first few years of sampling from adjacent harvested samples.

Huenneke et al. (2001, 2002) summarized methods and reported spatial and temporal patterns of ANPP over the first decade of this study. Further details of sampling and analysis, including an assessment of the adequacy of sample size, are given by Huenneke et al. (2001). The resulting data are consistent in intensity and methodology across ecosystem types, as well as over time. The method also allows more complete characterization of community productivity, spatially explicit description of pattern, and greater temporal resolution of aboveground productivity than is typically provided by rangeland yield estimates. This study demonstrated the impact of the patchiness of arid vegetation and variability in composition on the adequacy of sampling. Comprehensive sampling of all vascular plants within 49 square-meter quadrats was only marginally adequate for describing community attributes (e.g., aboveground biomass) in the most heterogeneous of systems. Given this demonstration, we are reluctant to draw strong conclusions when comparing our estimates of production with those from other studies where sample sizes are markedly smaller.

Fourteen years of results (figure11-1; Huenneke et al. 2002 with additional unpublished data more recently available) showed that grasslands exhibit the greatest variation in production values over time; at least some grasslands (and grass-dominated playas) in some seasons are capable of achieving high rates of ANPP, but these peaks do not appear consistently, nor are those peaks restricted necessarily to summer rather than spring. In contrast, creosotebush-dominated sites demonstrate extremely regular scrublands were less markedly seasonal than creosotebush systems, and demonstrated considerable variability among the three sites. Tarbush-dominated systems were

remarkably invariant in aboveground biomass and in ANPP over time despite a
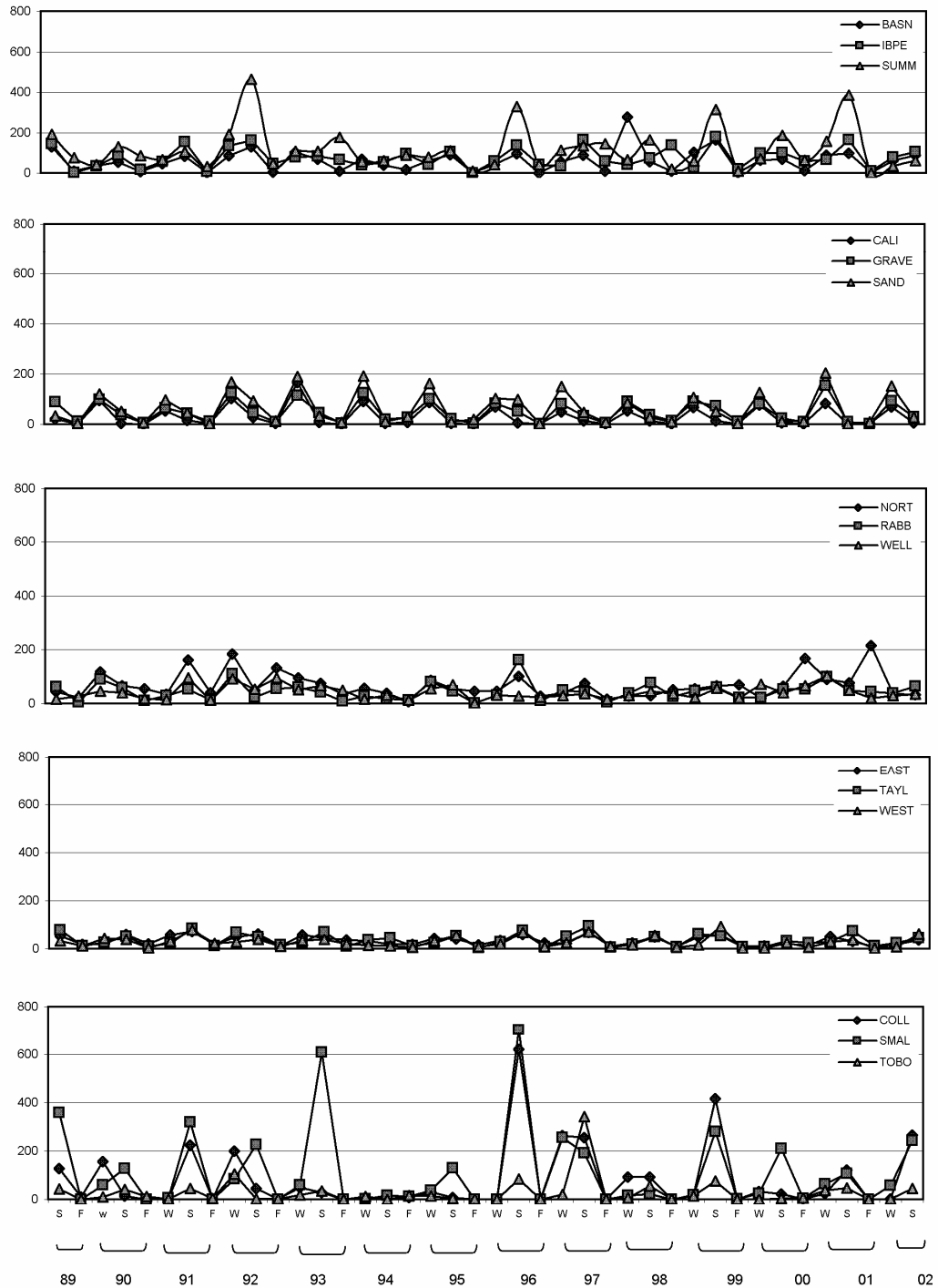
substantial grass component.

Fig. 11-1. Annual aboveground net primary production (ANPP; g/m^2) by season for 15 sites in 5 ecosystem types in the Jornada Basin. Figure reproduced from Huenneke et al. (2002) with additional unpublished data more recently available.

A primary focus for the NPP study was spatial heterogeneity; the Jornada

desertification hypothesis (Schlesinger et al. 1990; see also chapter 1) predicts that shrub-

dominated systems are patchier in structure than the more homogenous grasslands and

that patchiness is exacerbated by self-reinforcing patterns of increased biotic function

within shrub patches compared to decreased biotic function in interplant spaces. At the

scale of our monitoring, aboveground biomass was patchier in shrub-dominated systems

than in the grasslands. In most growing seasons, ANPP followed the same pattern (i.e.,

greater spatial heterogeneity in shrublands; Huenneke et al. 2002).

Variation in mean ANPP is considerable even within structurally similar sites in a

single year, such that it is difficult to assess differences among ecosystem types. In any

one season, ANPP values may have very similar ranges across all ecosystem types.

However, during the 13-year (1990–2002) record, black grama grasslands were capable

of supporting higher rates of production than shrub-dominated systems (Huenneke et al.

2002 with additional unpublished data more recently available). One of the next major

challenges for the Jornada Basin LTER program is to better understand the drivers of

variation in productivity among sites: What landscape-scale factors explain differences

among the three sites sampled within each of the five ecosystem types? Based on

differences in geomorphological setting or history, redistribution of water (e.g., from

runoff to run-in[a] relationships) and soil differences merit exploration to understand this

variability.

Whether comparing different studies from the Jornada or attempting to compare rates of production at the Jornada to those measured at other locations, one quickly encounters difficulties. Most typically, studies present biomass and/or productivity of only the perennial grasses, the primary forage for livestock (e.g., Paulsen and Ares 1962; Valentine 1970; various studies summarized in Herbel and Gibbens 1996). It is clear, however, both from LTER studies (Huenneke et al. 2002; see also chapter 10) and from other work that woody plants, succulents, and other nonforage species can contribute substantial percentages of ANPP even in grasslands (e.g., Lane et al. 1998). In much of the arid and semiarid rangeland literature, reported production values greatly underestimate actual total values (and ecological potential). This makes direct comparison among studies difficult and has perhaps exacerbated the view that conversion to woody plant dominance represents extreme degradation. Our data (Huenneke et al. 2002) confirm that differences between grassland and shrubland productivity, though detectable over the long term, are not enormous when one considers the entire plant community. Another major difficulty, of course, is the great range of methods applied, from visual estimates to clipping to nondestructive dimension analysis. This history of diverse approaches greatly limits the power of comparison, whether among or between Jornada studies and those reported from other sites.

Applications of Jornada NPP Results to Hypotheses

Production Is Constrained by Water and Nutrient Availability

At least since the 1970s, the predominant model for arid ecosystems has posited that dryland ecosystems respond primarily to water with pulse response of both vegetative

and reproductive growth to large precipitation events or episodes of water availability

(e.g., Beatley 1974; Hadley and Szarek 1981). However, Jornada work during the IBP

and early LTER periods tested the idea that primary productivity might be at least

partially constrained by nitrogen (Ettershank et al. 1978). Ludwig (1987) reviewed

fertilization results from that and other works, finding evidence of significant nitrogen

limitation. In reality, water and nitrogen undoubtedly interact. Gutierrez and Whitford

(1987a, b; Gutierrez et al. 1988) observed strong interactions between water and nitrogen

amendments for annuals in the early LTER transect work. Herbel (1963) found a strong

effect of nitrogen when water was available for *Hilaria* (=*Pleuromorpha*) *mutica*. For the

herbaceous component at least, nitrogen availability appears to be an important constraint

on primary production (chapter 6).

Temporal Variation in NPP: Correlation with Precipitation Patterns

The influence of water availability on production is typically investigated by examining

the correlation of production with precipitation inputs. Herbel (1963) documented a

positive correlation between growth in one important Jornada perennial grass

(*Pleuromorpha mutica*) with a substantial lag effect (higher production in the year after

water availability had been high, or the converse, drought in one year reducing response

of the grass to next year's moisture). The year lag contrasted with studies of blue grama

(*Bouteloua gracilis*) by Sala and Lauenroth (1982), who found that even very small rain

events can stimulate short-term positive response. Preliminary inspections of correlations

between more recent LTER data from the ANPP sites and precipitation records from

those sites revealed very few positive correlations between rainfall and production at any

one site with or without lag times. Local precipitation inputs may be a poor proxy for water availability due to the importance of runoff and run-in patterns in redistributing water. The aggregation of growth responses by species differing dramatically in life history, physiology, and growth form also probably obscures any simple correlation.

Noy-Meir (1985) suggested that efficiency ratios such as the slope of the relationship between NPP and rainfall or the slope dP/dr are best for comparing NPP among desert systems. Le Houerou et al. (1988) reviewed production studies from numerous semiarid ecosystems to estimate the efficiency with which precipitation is converted into plant production. The conclusion was that each mm of rain produces on average 4 kg/ha/yr (0.4 g/m^2). For Jornada Basin upland grasslands, the LTER productivity data are about 248 g/m^2 from a long-term average annual precipitation of 245 mm, or about twice the productivity predicted by Le Houerou et al. (1988).

There has also been substantial attention paid in the literature to the relationship between the variability in production and the variability in precipitation. Knapp and Smith (2001) analyzed long-term productivity data from 11 different LTER sites with particular attention to temporal variability in ANPP and the relationship to variation in precipitation inputs. Mean values for both ANPP and precipitation at the Jornada Basin were among the lowest among the 11 sites, and variability in precipitation was relatively high, as might be expected. However, the sites with the greatest interannual variation in precipitation did not, in fact, have the highest variability in ANPP. Jornada ecosystems (and the other LTER sites in their analysis that are dominated by grasses) showed the highest pulses of production in response to relative maxima in precipitation (maximum

precipitation–mean/mean) (Knapp and Smith 2001, fig. 2B). Jornada ecosystems appear to have asymmetric responses to climate with greater pulses of ANPP in relatively wet years compared to the declines in production in relatively dry years (Knapp and Smith 2001; Huenneke et al. 2002). Pulses in ANPP may then cascade into pulses of consumer activity and/or reproduction, again with varying lag times depending on life histories (Ostfield and Keesing 2000; see also chapter 12).

One factor contributing to the poor fit of local ANPP values to climate data is the high degree of spatial variability in precipitation (chapter 3). Because a large proportion of the annual precipitation is delivered in the form of localized convective storms, rainfall inputs are extremely patchy, and no single location's rainfall record (e.g., the central LTER weather station) is an accurate measure of the precipitation received at any of the dispersed 15 ANPP (chapter 3) study sites. Most (13 of the 15) sites had simple collecting gauges at or near the production plots for much of the study period, so we were able to obtain crude local estimates of rainfall. Regressions of seasonal NPP values against local precipitation amounts for individual sites were nearly always insignificant. Various lag times have been proposed (or determined based on regression from individual species growth data) for different components of the vegetation; that is, growth appears to respond to precipitation received in a prior season or a prior year rather than the current season. Even when we incorporated different lag times into our regressions, the fit for total production values remained extremely poor. We suspect that different species have very different patterns of response to precipitation, and therefore no simple relationship

exists between precipitation received in any one interval and total community

aboveground production.

Finally, one additional source of variability likely serves to obscure the

precipitation–ANPP relationship: landscape location and spatial context for a site. Local

precipitation may not be the primary determinant of soil moisture availability; runoff and

run-in can be substantial in certain topographic positions, and surface soil characteristics,

animal disturbance, and other factors may constrain or enhance infiltration (chapter 5).

Thus we expect that spatially explicit models may be required to explain variation among

sites in NPP not adequately explained by local precipitation (chapter 18).

NPP Reduction in Shrublands versus Grasslands: Desertification as Degradation

Our study of 15 sites affords the first real opportunity to examine this question carefully,

because it delves into patterns of productivity over many seasons and in multiple

locations for each ecosystem type. Hence, we are able to assess differences among

ecosystems relative to the tremendous spatial and temporal variation. For any given

season, productivity rates in shrub-dominated systems may equal those in grasslands

(Huenneke et al. 2002). Tarbush-dominated systems, however, are consistently low in

productivity (despite a significant grass component). Grasslands demonstrate occasional

higher peaks of production than those seen in any season in a creosotebush or mesquite

system. Thus, although long-term means may not differ substantially, grasslands are at

least capable of higher production. The Summerford grassland is unusual in supporting

extremely high production rates in several years; the most likely explanation is its

location at the base of Mount Summerford where runoff from the mountain is consistent

and perhaps aspect or shelter from prevailing winds contributes to favorable site water balance.

Two provisos are necessary when discussing the higher ANPP values sustained in grassland relative to shrub-dominated systems. First, our current shrublands represent a mix of recently desertified former grassland sites and sites long occupied by shrubs. These diverse settings are being compared with sites that have resisted shrub invasion and the loss of grasses; sites that may be unusual in some respect (Gibbens et al. 2005; see also chapter 10). One should not rashly presume that comparing today's shrublands with today's grasslands is a comparison of equivalent sites differing only in the nature of the current vegetation.

Second, the tremendous range of variation (spatial and temporal) in ANPP values renders most comparisons with published values from arid ecosystems meaningless. Most studies fail to document the adequacy of sample numbers to capture a representative range of spatial variation (Huenneke et al. 2001). Similarly, most published studies are of relatively short duration and so do not portray production over long enough time periods to represent the range of variation possible at a given site. Without such assessment of the range of variation, attempts to compare the relative magnitude of production across locations are futile.

NPP in Relation to Soil Texture

The long-term data set described by Herbel and Gibbens (1996) furnishes an excellent opportunity to address the inverse texture hypothesis—the prediction that coarse, sandy soils will exhibit greater infiltration rates and therefore greater moisture availability and

productivity than sites with clay-dominated soil textures. In fact, the Jornada Basin data

show a clear and consistent pattern of coarser-textured soils supporting lower perennial

grass yields than finer textured soils. Maximum, minimum, and average values of grass

production all demonstrated the same pattern (table 11-2).

Table 11-2. Aboveground net primary production (kg/ha) of perennial grasses in relation to soil texture: a test of the inverse-texture hypothesis, which predicts that ANPP will be greater on coarser textured soils in arid and semi-arid ecosystems. Data from Herbel and Gibbens (1996).

Soil texture, soil [1]	Peak Yield	Mean Yield	Minimum Yield
Clay, A	1805	648	133
Clay loam, G	3718	1259	14
Clay loam, G	4061	2433	569
Silt loam, D	3017	785	61
Loam, B	6547	2126	20
Loamy sand, P	1031	401	7
Sand, O	918	188	9
Sand, O	453	207	11
Sand, T	800	354	38
Sand, T	1037	335	27

[1] See Table 4-1, this volume for description of A, G, D, B, P, O, and T soil map unit designations.

ANPP appears to be greatest in sites on loamy soils, and the sandy or coarser soils

do not generate ANPP values as high as (much less greater than) those from finer

textured soils. Similar rejection of the hypothesis is supported by the LTER data:

Mesquite and creosotebush sites have coarser soils than do grasslands but certainly do not

have higher average productivity (Huenneke et al. 2002). Average ANPP (across three

sites of each community type) for 13 years (1990–2002) for the clay-textured playa sites,

the clay loam–textured tarbush sites, the loam-textured upland grassland sites, the gravel

and sand–textured creosotebush sites, and the sand-textured mesquite sites were 205, 97,

248, 144, and 156 g/m^2, respectively (table 11-3).

Table 11-3. Mean biomass (g/m^2), mean annual aboveground production (ANNP, g/m^2), and biomass accumulation ratios or mean residence time of aboveground plant biomass (the Ratio of Biomass to ANNP) for the 5 main community types in the Jornada Basin. Mean biomass was calculated as the average (across three sites of each ecosystem type) of the annual peak aboveground biomass for 14 years (1989-2002). ANNP was calculated as the average (across three sites of each community type) of the 12-month aboveground production for 13 years (1990-2002) (Huenneke at al. 2002 with additional unpublished data).

Community Type	Mean Biomass	Mean ANPP	Ratio
Creosotebush	222	144	1.5
Upland grassland	319	248	1.3
Mesquite	277	156	1.8
Lowland playa	192	205	0.9
Tarbush	159	97	1.6

The highest ANPP values anywhere are on the heavy soils of playas and the

loamy grassland soils. (However, it is true that ANPP is consistently low on the fine-

textured soils of tarbush sites.) Results from Jornada productivity studies are generally

not consistent with the inverse-texture hypothesis. The implication is that surface

processes of water infiltration and evaporation from bare soil surface are not the primary

factors driving ANPP. Instead, perhaps the water-holding capacity of profile and the

relative topographic position determining a sites runoff/run-in balance are more important

as functional characteristics.

NPP in Relation to Diversity and Structure of Plant Community

The Jornada Basin long-term data sets represent good opportunities to study diversity–

ecosystem function relationships with both observational and manipulative approaches.

Chihuahuan Desert communities are less complex structurally than most forest types, though more challenging than more mesic grassland or herbaceous communities. The communities encompass a relatively wide range of richness values, from extremely simple mesquite sites to diverse grasslands. Our data are providing opportunities for others to test hypotheses about the shape of the productivity–species richness relationship. Fertilization-induced increases in productivity in the first years of the Jornada LTER program were accompanied by modest decreases in species richness (Gough et al. 2000).

In the long-term LTER study of the 15 ANPP sites, the low degree of evenness is striking across virtually all ecosystem types. The single most dominant species in each site contributes largest proportion of ANPP, and only a small number (one or two) of subdominants add any substantive proportion to total community production (chapter 10). There has been no change in the identity of those dominants at any site over 12 years of study. Our pattern of the single dominant (either a shrub or a perennial grass, depending on the ecosystem type) contributing most of the biomass and production contrasts with the suggestion of Hadley and Szarek (1981) of a general pattern of annuals contributing about half the annual NPP in hot desert systems. Certainly annuals can constitute high numbers and high surface cover in some sites in some seasons, but the larger perennial plants with long-lasting aboveground structures dominate ecosystem function in the sense of ANPP in the Jornada Basin. Chew and Chew (1965) estimated that 70% of the production of a creosotebush community near Portal, Arizona, was contributed by the dominant shrub, a somewhat smaller percentage of the total than at the Jornada.

We observe no compensatory behavior among species (in terms of contributing to productivity) between dry and wet years; rather, there are additive effects of species richness in grassland with across-the-board increases for all species in favorable years. Nor is there any simple correlation of richness with ANPP, either within a season or over the length of the study.

An ongoing LTER experiment addresses the diversity–function relationship through plant removals that have reduced species and functional group richness. In 1995 we initiated a long-term plant diversity experiment in which groups of species have been removed from a mixed creosotebush-mesquite shrub site. In the short term, this experiment tests the hypothesis that growth and resource use of one species group (e.g., perennial grasses) are constrained by interactions (such as competition for soil water) with other species groups (e.g., shrubs). However, in the first five years of this removal experiment, we observed no strong positive responses, suggesting that the removal of any one species group in fact releases any other group from water limitation.

NPP Reduction Observed within a Site or Community over Time: Desertification as Degradation

Even with the long history of study at the Jornada, there has been little consistency of method over any reasonable time period, so we have had no direct way of comparing results or providing a true long-term perspective of basin-wide changes in ANPP. Year-to-year (and also decadal scale) variation is so great that it is not immediately possible to say that within a given site there has been significant degradation or loss of productive capacity. Given that shrublands have ranges of production largely overlapping with the

range of values of grasslands (except for peaks), it seems that primary change has been

alteration in the identity of the producers and a loss in the capacity to respond to

favorable years, rather than an overall directional decrease in production rates.

Biomass Turnover and the Dynamic Nature of Semiarid Plant Communities

We calculated the biomass accumulation ratio for each of the five ecosystem types as an

indicator of the mean residence time of aboveground plant biomass (table 11-3). The

biomass accumulation ratio or mean peak biomass divided by annual productivity

(Whittaker 1975) is 0.9 for the playas, which contain only short-lived herbaceous

vegetation whose aboveground portions are replaced completely in each wet season.

Surprisingly, even the mesquite sites, so strongly dominated by the woody shrub

component, had a biomass accumulation ratio of only 1.8 (suggesting complete turnover

of aboveground biomass on average within two years). One mesquite site (M-NORT)

showed a multiyear directional trend in biomass accumulation with aboveground biomass

increasing during the 1990–94 period. The magnitude of the increase was substantial.

However, the 1994–95 dry conditions coincided with a sharp decline in biomass to

former levels, and in the subsequent years there has been no directional change, merely

fluctuation in NPP that is typical of the other sites being studied.

Belowground Productivity

There have been few formal studies of belowground plant biomass and productivity in

Jornada ecosystems, although there has been considerable descriptive work.

Belowground biomass (and allocation belowground or root:shoot ratio) is generally

assumed to be high in arid and semiarid systems. However, Chew and Chew (1965)

found that creosotebush near Portal had a rather low proportion of root biomass. Ludwig

(1977) presented data for eight species of woody plants at the Jornada showing root:shoot

ratios of mean 0.9; he described these as generalized (not specialized) root systems. On

the other hand, Gibbens and Lenz (2001) have documented very extensive root systems

for a number of Jornada plants, demonstrating impressive proliferation in specific soil

volumes and suggesting highly plastic and responsive allocation. Brisson and Reynolds

(1994) similarly described patterns of root distribution in creosotebush at the Jornada that

suggested intricate and plastic relationships among neighboring individuals.

Pieper et al. (1983) found root:shoot ratios greater than 1 (1.4–2) for vegetation

sampled in the long-term forage production study with higher values in grazed than in

ungrazed communities. Grasses constitute much of this belowground biomass. In

absolute terms, belowground biomass was less in grazed areas (due largely to the

difference in species composition with fewer grasses and thus fewer shallow fibrous

roots).

In the productivity study carried out across the 15 LTER sites, we were not able to

study the belowground portions of these ecosystems and so cannot extrapolate from our

measurements of aboveground biomass and productivity to total values. Ludwig (1977)

reviewed a number of studies and concluded that the often stated generalization that

desert shrubs have high root:shoot ratios is too simplistic; values for creosotebush at the

Jornada, for example, varied from 0.23 to 2.7. Mean values for eight Jornada species

averaged 0.925. If we apply this ratio to our average aboveground biomass values (table

11-3), we would estimate that total plant biomass (above- and belowground) ranges from about 300 g/m^2 in the tarbush ecosystem type to more than 500 g/m^2 in the grassland and mesquite ecosystems.

Remaining Challenges

Our challenge at the Jornada LTER is to better understand the sources of variation in NPP—the most basic measure of ecosystem function. To what degree is variation a simple reflection of variable site characteristics or local precipitation? Spatially explicit models may be necessary to understand local variation: topographic position, fluxes of materials, or organisms from one landscape position to another, and so on (chapter 18).

Are remote sensing methodologies suitable for monitoring NPP on the spatial and temporal scales appropriate for these landscapes? There is little evidence suggesting that remotely sensed data are adequate for assessing plant biomass and ANPP in this arid region (poor correlations). Variety of indices have been tried and different indices fit different ecosystems best.

Which mechanisms of nutrient losses are of a magnitude sufficient to cause degradation of productive capacity within a site? Mesquite sites are areas of greatest sand and dust generation; however, net flux may be different due to landscape position relative to prevailing winds, characteristics of vegetation structure (roughness) that would trap dust or waterborne sediments, for example. Thus both eolian and hydrologic fluxes are crucial to study at landscape as well as any localized scale (chapter 9).

Conclusions

What have we learned from the Jornada Basin about NPP in arid ecosystems? First, these ecosystems are more complex in time than a simple pulse-reserve model would suggest: There are no simple relationships between precipitation input and system function (not even threshold relationships). Instead, the varying life span and multiple modes of response (from vegetative growth to belowground storage to seedling recruitment) may contribute to the potential for complex multiyear dynamics. More significant as an immediate problem is the tremendous spatial variation in rates of aboveground production within ecosystems of a given type. This variation makes it difficult to extrapolate from point-based measurements to larger, management-relevant scales. We have found it necessary and desirable to move beyond local determinants (such as soil features and local precipitation) to spatially explicit parameters that reflect a site's landscape location in order to better understand temporal and spatial patterns of production (chapter 18).

A significant contribution of LTER studies of plant production is that total community composition includes significant contributions from species other than perennial grasses. Hence, traditional estimates of ANPP (based on forage alone or on clipping of grasses) are far lower than our more dynamic and comprehensive estimates. In the short term, this makes it frustrating or impossible to compare our estimates with those from previous work or other sites; in the long run, this more comprehensive view provides a sounder basis for applications, such as remediation efforts, or for understanding organic matter or carbon dynamics and sequestration.