ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem

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Abstract Aboveground net primary production (ANPP) dynamics are a key element in the understanding of ecosystem processes. For semiarid environments, the pulse-reserve framework links ANPP to variable and unpredictable precipitation events contingent on surficial hydrology, soil moisture dynamics, biodiversity structure, trophic dynamics, and landscape context. Consequently, ANPP may be decoupled periodically from processes such as decomposition and may be subjected to complex feedbacks and thresholds at broader scales. As currently formulated, the pulse-reserve framework may not encompass the breadth of ANPP response to seasonal patterns of precipitation and heat inputs. Accordingly, we examined a 6-year (1999–2004), seasonal record of ANPP with respect to precipitation, soil moisture dynamics, and functional groups in a black grama (*Bouteloua eriopoda*) grassland and a creosotebush (*Larrea tridentata*) shrubland in the northern Chihuahuan Desert. Annual ANPP was similar in the grassland ($51.1 \ g/m^2$) and shrubland ($59.2 \ g/m^2$) and positively correlated with annual precipitation. ANPP differed among communities with respect to life forms and functional groups and responses to abiotic drivers. In keeping with the pulse-reserve model, ANPP in black grama grassland was dominated by warm-season C_4 grasses and subshrubs that

responded to large, transient summer storms and associated soil moisture in the upper 30 cm. In contrast, ANPP in creosotebush shrubland occasionally responded to summer moisture, but the predominant pattern was slower, non-pulsed growth of cool-season C_3 shrubs during spring, in response to winter soil moisture accumulation and the breaking of cold dormancy. Overall, production in this Chihuahuan Desert ecosystem reflected a mix of warm-temperate arid land pulse dynamics during the summer monsoon and non-pulsed dynamics in spring driven by winter soil moisture accumulation similar to that of cool-temperate regions.

Introduction

Net primary production is a fundamental integrating process in all ecosystems (McNaughton et al. 1989). Thus, understanding temporal patterns and controls of production has significant implications for decomposition and site fertility, carbon storage, and the composition and dynamics of producer and consumer communities (Chase et al. 2000; Tilman et al. 2001; Parton et al. 1995, 2007). At regional to global scales, aboveground net primary production (ANPP) is highly correlated with annual precipitation (Webb et al. 1978). This is particularly the case across North American grasslands where variation in precipitation explains more than 90% of variation in ANPP (Sala et al. 1988). At a local or site scale, however, annual precipitation often explains considerably less of the interannual variation in ANPP (Knapp and Smith 2001; Huxman et al. 2004; Adler and

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Levine 2007; Swemmer et al. 2007). Locally, temporal variation in ANPP within sites is controlled by a variety of interacting factors including resource heterogeneity, seasonality, plant functional types, disturbance, and the seasonal and spatial variability of precipitation events (Seastedt and Knapp 1993; Briggs and Knapp 1995; Gosz et al. 1995; Reynolds et al. 2004; Huxman et al. 2004; Knapp et al. 2006). Consequently, understanding patterns and controls of ANPP within a site over time requires long-term data that integrate multiple abiotic drivers and biotic responses.

The dynamics of ANPP in semiarid and arid environments have been described in a pulse-reserve framework in which biologically significant rainfall events trigger pulses of growth that lead to reserves of net primary production (Noy-Meir 1973). Under this framework, the vagaries of precipitation events in time, space, and amount generate highly variable patterns and dynamics in arid land ecosystems. The original pulse-reserve paradigm was recently modified to account for residual soil moisture dynamics, plant functional types (Ogle and Reynolds 2004; Reynolds et al. 2004), hydrological transport, landscape feedbacks (Loik et al. 2004; Tongway and Ludwig 1997; Ludwig et al. 2005), and hierarchically structured trophic dynamics (Schwinning and Sala 2004). One outcome of pulse-reserve dynamics in arid ecosystems may be the potential for ANPP to be decoupled in time from processes such as decomposition (McClain et al. 2003; Austin et al. 2004; Austin and Vivanco 2006).

While the pulse-reserve framework has proven to be a useful description of arid land structure and dynamics, there may be seasonal climatic patterns in some arid regions where the pulse-reserve paradigm may not apply. For example, in arid regions with cold wet winters, soil moisture storage is an ongoing, cumulative process at a time of little or no production. Growth that occurs in spring likely responds to the breaking of cold dormancy rather than pulse precipitation events under the traditional framework. Thus, the degree to which the revised pulse-reserve paradigm (Reynolds et al. 2004; Ogle and Reynolds 2004) explains patterns of ANPP in different arid land ecosystems remains to be determined empirically. Accordingly, we used a 6-year record of ANPP in two northern Chihuahuan Desert plant communities (black grama grassland and creosotebush shrubland) to determine the degree to which seasonal and interannual patterns of ANPP were linked to variable and discrete precipitation events, soil moisture dynamics, and other climatic factors. We focused our analyses on both ANPP responses among plant communities and within functional groups (e.g., C_3/C_4 grasses, forbs, and shrubs). We then placed our results into a regional grassland context and here present a pulse-reserve model that incorporates seasonal precipitation dynamics and feedbacks.

Materials and methods

Study site

Our study was conducted as part of the Sevilleta Long-Term Ecological Research Project located in the Sevilleta National Wildlife Refuge about 80 km south of Albuquerque, New Mexico, USA (latitude 34°20′20″, longitude 106°43′30″). The refuge lies in an ecotone between desert shrublands and grasslands of the Colorado Plateau and Great Basin (dominated by *Atriplex canescens* and *Oryzopsis hymenoides*), Chihuahuan Desert scrub and Desert grasslands (dominated by *Larrea tridentata* and *Bouteloua eriopoda*, respectively), and the semi-arid shortgrass steppe (dominated by *Bouteloua gracilis*) (Gosz 1993; Muldavin 2002). Livestock grazing has been excluded from the refuge since 1973 following a century of more or less continuous use. Native herbivores such as pronghorn, rabbits, and rodents occur at low densities at the site while arthropods such as grasshoppers can be locally abundant. Sampling sites were located in *Larrea*-dominated shrublands and *B. eriopoda* grasslands at the southern end of McKenzie Flats, a gently sloping plain rising from north to south to about 1,616 m on the eastern side of the refuge. Soils were sandy loams with approximately 60% sand with silt content ranging from 18 to 22%. In addition, a petrocalcic layer occurs starting around 15–50 cm below the soil surface (Kieft et al. 1998; Buxbaum and Vanderbilt 2007).

The long-term (1989–2006) mean annual precipitation (MAP) at the study site was 256 mm and is distinctively bimodal with 53% coming primarily in the form of convective thunderstorms during the summer monsoon (July–September) and 47% falling as a mixture of snow and rain during winter. The average annual precipitation from 1999 to 2004 was 224 mm. Drought conditions prevailed from winter of 2002 through summer of 2003, during which time precipitation was 55% of the long-term mean. Temperatures were typical of a mid-elevation, continental climate with cold winters (minimum of −15.5°C) and warm to hot summers (maximum of 43.0°C). The average annual daily temperature from 1999 to 2004 was 14.4°C, with a winter average of 7.2°C and a summer average of 21.6°C.

Sampling design and data collection

In 1999, two sites were established approximately 0.5 km apart, one in a creosotebush (*L. tridentata*)-dominated shrubland and another in a black grama (*B. eriopoda*)-dominated grassland. An automated meteorological station located between the sites measured precipitation (event-scale via tipping bucket), air and soil temperature, and soil moisture content (0–30 cm time domain reflectometry probe) at 1-min intervals. At each site five circular,

200-m-diameter trapping webs approximately 0.3 km apart were established to measure both ANPP and rodent abundance (Parmenter et al. 2003). Four 1-m^2 permanent quadrats were located in the internal corners of a 5×5-m subplot in each cardinal direction around the perimeter of each trapping web yielding 16 quadrats per web and 80 ANPP quadrats per site.

Vascular plant standing biomass was estimated by species using a volumetric method (Huenneke et al. 2001). Biomass estimates were conducted 3 times each year—in winter (February), spring (May), and fall (September) between 1999 and 2004. Volumes in cubic centimeters were measured using height, width, and length of individual branch systems for shrubs and individual bunches or patches for grasses. For species with thin, essentially linear growth form only height was measured. The cover and height of all separate vegetative units for each species that fell within the 1-m^2 quadrat (regardless of where they were rooted) were measured.

Total standing biomass was estimated using a two-step approach (Huenneke et al. 2001). First, in areas adjacent to the permanent ANPP sampling plots we harvested up to 15 samples per species representing the range of volumes measured on the permanent quadrats. Each sample was sorted to remove all soil, root material, and dead plant material (all green and "tawny" material judged to be the current year's growth was kept, but gray detached or attached litter was removed). Remaining live material was then oven-dried to constant weight at 55°C. Datasets are available at http://sev.lternet.edu (SEV001, 129, 157, and 182).

Net primary production calculations

Linear regressions with intercepts through the origin were developed for current season dry biomass against volume for each species using SAS GLM (SAS Institute 1989). These regressions were then applied to individual volume units measured for each species on a quadrat and summed over the quadrat, with all species then summed to give total biomass per quadrat. Of the 532 regressions computed 457 (85%) had r^2-values that exceeded 0.80 and this included all the dominants (e.g., *Larrea* ranged from 0.82 to 0.99; *B. eriopoda*, from 0.83 to 0.98; see Electronic supplementary material S1). Those species with weaker regressions were typically sporadic in occurrence and were represented by few individuals with low biomass. For most species, regressions from harvests over 1–2 years for a given season were sufficient (e.g., annual forbs and grasses, subshrubs) and harvesting discontinued. For other species, particularly the dominants, the ratio of live biomass to dead varied widely across years and seasons, and harvesting and sorting were maintained across the study period. The exceptions were that harvests were not conducted in 2001 and some data

were lost for winter and spring of 2003. For those missing values, regressions from other years and seasons with similar precipitation were used. The biomass estimates of the two main dominants using this volumetric method compared well with independent direct harvest samples at nearby sites (within 10%).

ANPP (g/m^2) was calculated seasonally. The winter collection (February) was taken as the baseline zero point for growth for that year. Spring production (May) was then calculated as the difference in biomass from February to May, and summer/fall production as the difference in biomass from May to September. The inter-seasonal calculations were done by species on a quadrat-by-quadrat basis. Negative differences were taken as zero. Total yearly ANPP on a quadrat basis is then the sum of spring and summer production values. Total standing biomass, seasonal, and yearly ANPP were averaged across the 16 quadrats for each web (see Electronic supplementary material S2 for summary data). Web ANPP values ($n = 5$) were then used in a repeated measures ANOVA to evaluate differences among sites, seasons, and years using the ANOVA procedure in SAS (SAS Institute 1989). Linear regressions were used to evaluate the relationships between ANPP and (1) total seasonal precipitation (winter–spring, October–May; summer, June–September), (2) average spring (March–May) and summer (June–September) percent soil water content, and (3) total season growing degrees days between samples (10°C base).

Regional analysis

To provide a regional context for production at the Sevilleta, the relationship between MAP and mean annual ANPP among a set of grassland and shrubland sites (see Electronic supplementary material S3 for data sources) was evaluated using simple linear regression [SAS GLM (SAS Institute 1989)]. Together these datasets represented a range of production values along a precipitation gradient from 226 mm in southern New Mexico to 835 mm in northeastern Kansas, USA.

Results

General patterns of ANPP

Averaging across years, annual ANPP was not significantly different between creosotebush shrubland and black grama grassland (59.2 and 51.2 g/m^2, respectively), but the distribution of production among growth forms and functional groups differed between ecosystem types (Fig. 1). In the black grama grassland, graminoids accounted for 78.4% of the annual ANPP with *B. eriopoda*, a C$_4$ warm-season grass, comprising the majority of the production (31.8 g/m^2

per year). Tall shrubs were rare, but smaller subshrubs (*Ephedra torreyana*, *Hoffmannseggia glauca*, *Sphaeralcea wrightii*, *Gutierrezia sarothrae*) and succulents (*Opuntia phaeacantha*) were common and accounted for 13.3% of annual ANPP (Fig. 1a).

In contrast, the shrubland was dominated by the tall C_3 shrub, *L. tridentata*, which accounted for 76.3% (45.2 g/m^2 per year) of the annual ANPP. At 14.8%, the relative abundance of subshrubs and succulents was similar to that of the grassland, but species composition differed with *Chaetoppappa ericoides*, *Thymophylla acerosa*, and *Opuntia macrocentra* as the most common species along with *G. sarothrae*. Grass production in the shrubland site accounted for only 8% (4.2 g/m^2) and included species that were uncommon in the grassland such as *Dasyochloa pulchella* and *Muhlenbergia porteri*. Production of other C_3 species
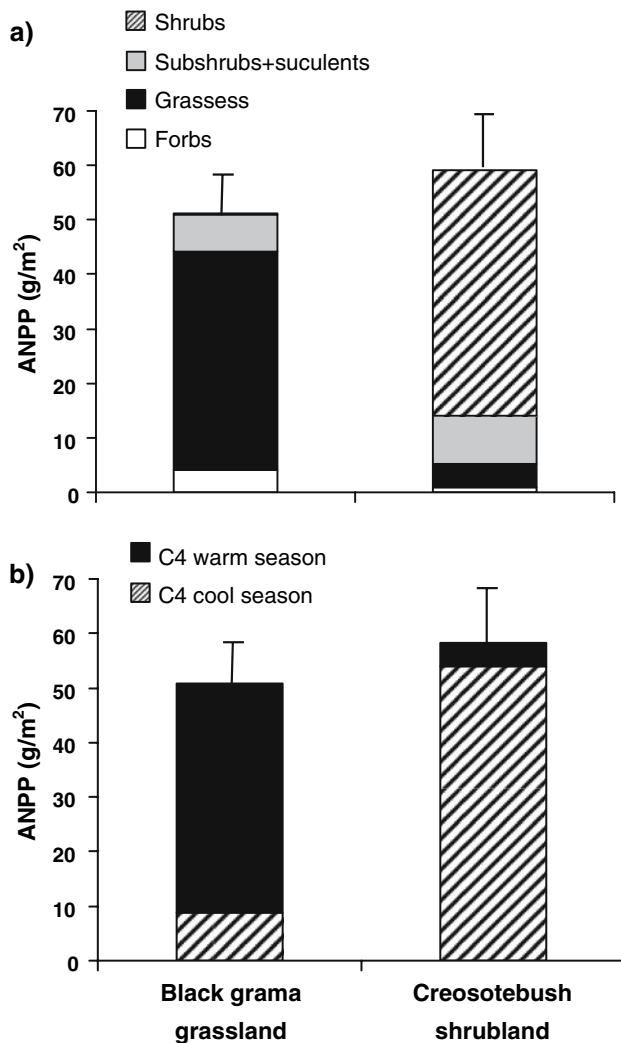
was similar among sites, but C_4 production in creosotebush shrubland was half that of the grassland and was driven primarily by C_4 grasses (Fig. 1b).

On a regional basis, our estimates of annual ANPP for both the grassland and shrubland fall at the lower end of the productivity/MAP relationship along with those from desert sites in the Jornada Basin (Fig. 2). The highest values (mean of 417.9 g/m^2) are from tallgrass prairie where MAP is also high. The ANPP values from the Colorado shortgrass steppe in some cases approach those for both the Sevilleta and Jornada Basin sites, but, on average, they are higher (mean 93.7 g/m^2), as is MAP (351 mm). The distribution of values from the transect studies also generally follows the trend of increasing ANPP with increasing moisture from west (shortgrass steppe) to east (tallgrass prairie).

Annual and interannual dynamics of ANPP

There was significant temporal variability in annual ANPP within sites ($P < 0.001$), and patterns differed between shrubland and grassland (Fig. 3; see Electronic supplementary material S2 for additional summary statistics). In 2000, for example, grassland production was significantly lower ($P < 0.01$) than that of shrubland. Grassland ANPP tended to track annual precipitation, with low production during the lower rainfall years of 2000 and 2003. In contrast, ANPP in creosotebush shrubland increased through 2002 before declining with the severe drought of 2003, followed by a rapid recovery in 2004. These patterns primarily reflect the responses of the two dominants in each system. Much of the yearly variation in ANPP of *B. eriopoda* and subordinate species in the grassland was attributed to annual precipitation (Fig. 4a). In contrast, the relationship was strongest among non-dominants or species other than *Larrea* in shrubland (Fig. 4b).
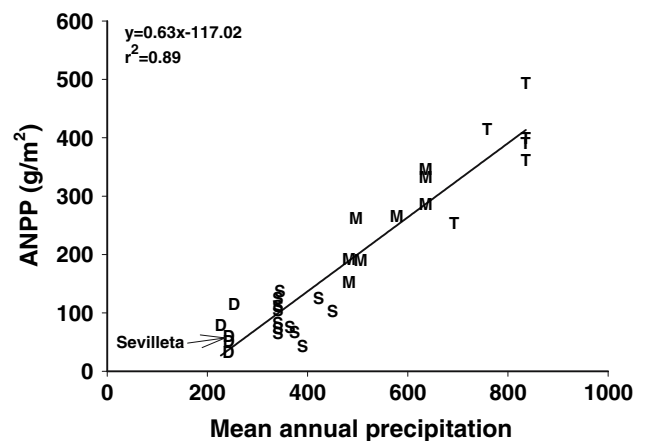

Fig. 1 **a** Comparison of mean ($\pm$ SE) aboveground annual net primary production (ANPP) between black grama (*Bouteloua eriopoda*) grasslands and creosotebush (*Larrea tridentata*) shrublands with respect to **a** life form composition and **b** photosynthetic pathway ($n = 30$)

Fig. 2 Regional comparison of annual ANPP and long-term mean annual precipitation (MAP). *D* Desert grassland, *S* shortgrass steppe, *M* mixedgrass prairie, *T* tallgrass prairie
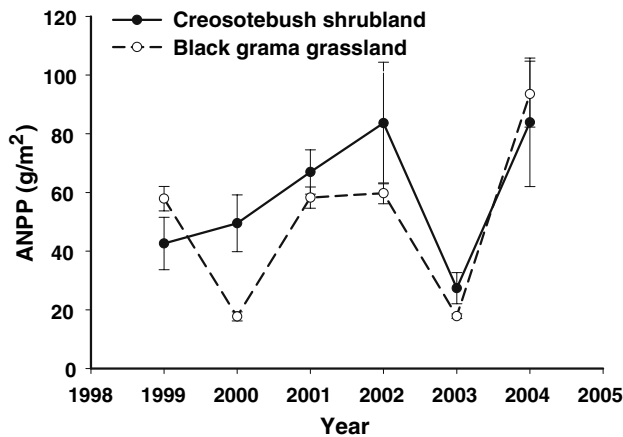
Fig. 3 Mean (± SE) annual ANPP in a creosotebush (*L. tridentata*) shrubland and black grama (*B. eriopoda*) grassland over the 6-year period 1999–2004 on the Sevilleta National Wildlife Refuge in central New Mexico, USA (*n* = 5)
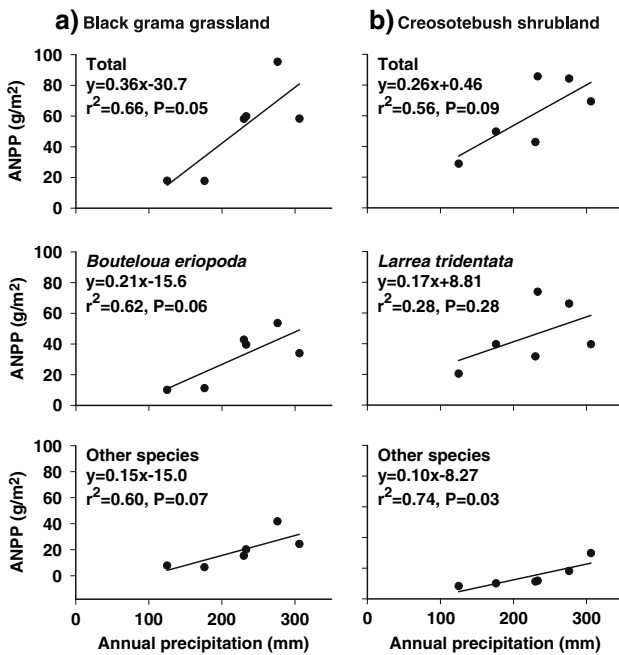

Fig. 4a, b Relationship between annual ANPP and annual precipitation (1999–2004). **a** Black grama grasslands. **b** Creosotebush shrublands

Fig. 5 Relationship between winter/spring (October–May) and summer/fall (June–September) ANPP and seasonal precipitation and percent soil moisture content. *Top panel* Grassland: total production, *B. eriopoda*, and non-dominants. *Middle panel* Creosotebush: total production, *L. tridentata*, and non-dominants. *Bottom panel* Seasonal precipitation and soil water content in the top 30 cm

Annual patterns of ANPP often masked important seasonal differences between the two systems. Grassland production peaked in the summer/fall, with only weak responses in the spring (Fig. 5). Summer soil moisture in the upper 30 cm was a stronger predictor of total summer/fall ANPP, *B. eriopoda* production and that of other C_4 species than was rainfall (Fig. 6a). With the exception of spring production among C_3 species (Fig. 6b), winter precipitation had little effect on grassland ANPP. Timing and amount of summer precipitation also affected grassland summer/fall ANPP (Fig. 7a). For example, there were 20
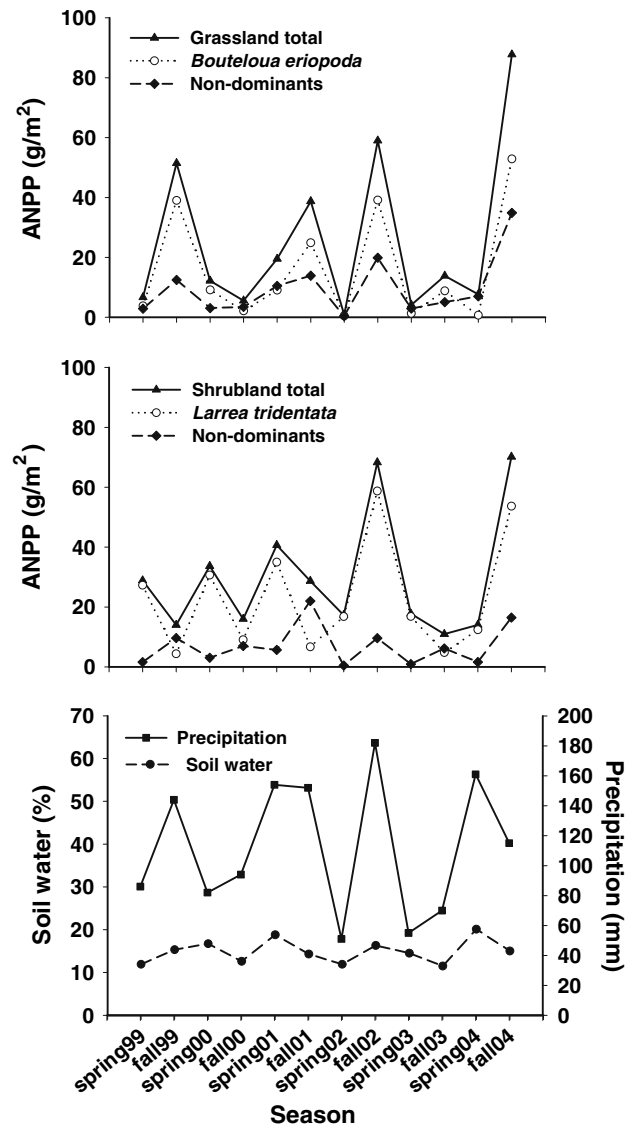
summer storm events in 2000, 18 of which were less than 15 mm and two only 23 mm. Overall, summer precipitation was only 12% below normal, but soil moisture remained low throughout the season, and summer/fall ANPP was 90% below average at 4.5 g/m². In contrast, in 2001 there were also many (17) small (<15 mm) storm events, but one 49.1-mm storm event brought seasonal precipitation from 17% below to 21% above normal and generated a large spike in soil moisture. Summer/fall ANPP was over 8 times that of 2000 at 38.5 g/m². In addition, the 3 largest production years were associated with the early onset of the summer monsoon in July (1999, 2002, and 2004).
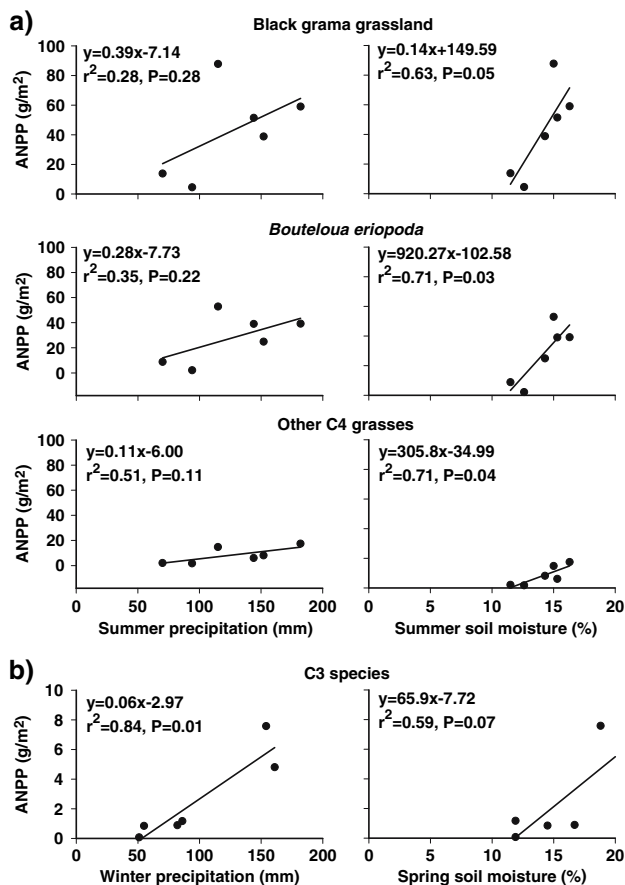
Fig. 6 **a** The relationship between total ANPP, production of *B. eriopoda*, and other C_4 grasses, and summer precipitation and summer soil moisture content at 30 cm in black grama grasslands between 1999 and 2004. **b** The relationship between spring ANPP of C_3 species and winter precipitation and spring soil moisture content in black grama grassland

ANPP in shrubland was more variable seasonally (Fig. 5). *Larrea* and C_3 subshrubs (*Gutierrezia, Chaetopappa*, and *Thymophylla*) responded to winter/spring precipitation, and, for the subshrubs, spring soil moisture content as well (Fig. 8). Otherwise, soil moisture content was only significant for C_4 species (Fig. 8). While the overall amount of winter precipitation affected shrubland production, the timing of storm events was less important (Fig. 7b). For example, in 1999 and 2000, winter precipitation was nearly equal (86 and 82 mm), but in 1999, the majority of moisture came in two early winter storms plus a series of smaller events (18) throughout the winter. In contrast, in 2000, there were 12 small events, but the majority of moisture came in a single late-spring event. Despite these differences, spring ANPP in shrubland differed little between years (28.9 and 33.7 g/m²). In addition, large shrubland production responses can also occur in summer, e.g., in summer/fall 2002 in response to large late-summer storms and below-normal seasonal temperatures.

Spring ANPP in C_3-dominated shrubland was positively related to spring growing degree days ($r^2 = 0.67$, $F = 8.27$, $P = 0.045$), but summer and total ANPP were not correlated with spring or summer growing degree days. In C_4-dominated grassland neither seasonal nor total ANPP were correlated with spring or summer growing degree days.

Discussion

### ANPP estimates in a regional context

The ANPP estimates presented here are significantly lower than previously reported for this site, particularly with respect to black grama grasslands (e.g., 51.2 versus 184.5 g/m² per year in Knapp and Smith 2001). The tight linear relationship between ANPP and MAP found here provides strong indirect support for the accuracy of our revised, allometrically based estimates of ANPP, and confirms the strong regional scale coupling between ANPP and annual precipitation (Webb et al. 1978; Sala et al. 1988). Our estimates are potentially conservative because the timing of measurements may miss peak seasonal biomass, i.e., spring harvests in some years may miss late-spring growth pulses and fall harvests may occur after peak biomass. Spring underestimates are captured in the subsequent fall measurements, and losses in late summer due to senescence are relatively small. In some years, losses due to arthropod herbivory may be significant. Regardless, the values reported here are in line with several analyses of annual ANPP of mid-continent grassland and shrubland ecosystems (Fig. 2) in the context of gradients of MAP (Sims and Singh 1978; Sala et al. 1988; Lauenroth and Sala 1992; Lane et al. 1998; Paruelo et al. 1999; Barrett et al. 2002; McCulley et al. 2005).

A seasonal ANPP dynamics framework

What the regional relationship does not reflect is the role of seasonality and the temporal scale at which precipitation events regulate ANPP in arid land ecosystems. We have summarized seasonal ANPP response in a framework that links seasonal precipitation regimes driven by multiple global climate phenomena, soil moisture, and functional group composition (Fig. 9). This framework builds upon the pulse-reserve paradigm (Noy-Meir 1973) but is partitioned seasonally to reflect the different winter and summer precipitation and temperature regimes. Our framework incorporates the soil water and functional group components (Reynolds et al. 2004) while noting that triggers of production pulses (sensu Noy-Meir 1973; Ludwig et al. 2005) are important, yet they may differ seasonally.

Specifically, in summer, ANPP reflects typical pulse-reserve phenomena. Amount and intensity of precipitation

Fig. 7 Examples of inter-annual variation in precipitation and soil moisture, and ANPP on a seasonal basis: **a** winter/spring 1999 and 2000 where seasonal ANPP equals 28.9 and 33.7 g/m^2, respectively, and **b** summer/fall 2000 and 2001 where seasonal ANPP equals 4.5 and 38.5 g/m^2, respectively. Storm events show summed contiguous days of precipitation. Soil moisture is the average daily percent moisture content at 30 cm (begun in mid-February 1999)
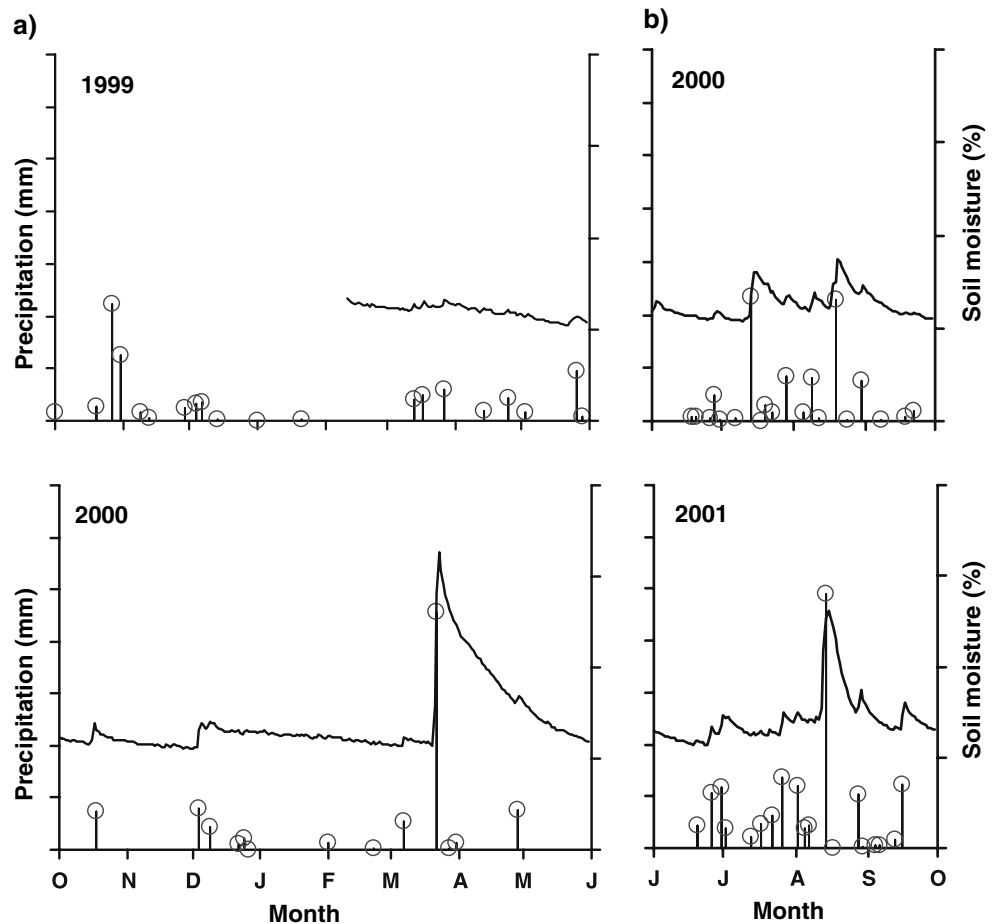
is highly variable and largely driven in our region by the North American Monsoon (Gutzler 2000). Hence, soil moisture is also highly dynamic in the summer (Gosz et al. 1995; Pennington and Collins 2007), particularly in the upper 30 cm of soil. This structures a summer functional group that relies on short-term supplies of shallow soil moisture under warm conditions (C$_4$ grasses, forbs and shallow-rooted subshrubs, and CAM succulents). Given large, episodic rain events that provide sufficient transient soil moisture, pulses of ANPP are stimulated. In addition, following Ogle and Reynolds (2004), feedback effects between soil moisture and summer precipitation occur such that as upper soils approach water-holding capacity precipitation events become less effective in triggering individual growth pulses. Although warm-season species dominate the summer ANPP response, C$_3$ shrubs such as *Larrea* can also respond to summer precipitation (see Reynolds et al. 1999), particularly in late fall (e.g., fall 2002), but such responses are smaller than production by the summer functional group.

In contrast, the winter pathway is different and not fully described by the pulse-reserve model. In winter, climate dynamics are driven in part by the El Niño–Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) that

generate low-intensity storms over several days' duration (Molles and Dahm 1990; Gutzler et al. 2002). Although the ENSO and PDO are by definition pulsed on interannual and decadal scales, in any given year there is less of a "pulse" effect in winter when soil moisture accumulates compared to summer when soil moisture is rapidly lost via evapotranspiration (Bhark and Small 2003; Kurc and Small 2004). While winter precipitation is still somewhat variable, moisture stored over the course of the winter is available for growth when cold dormancy is broken. This favors a spring functional group of deep-rooted C$_3$ shrubs such as *Larrea*, along with C$_3$ grasses, forbs, and subshrubs that take advantage of the stored moisture before rising temperatures and drying soils suppress C$_3$ photosynthesis (Kurc and Small 2004). This pattern also occurs in *Larrea* shrublands in the Jornada Basin 350 km south of our study site (Huenneke et al. 2002). Schwinning and Sala (2004) referred to this phenomenon in their hierarchical framework as "higher order pulse events" of accumulated seasonal precipitation. Yet, if heat is taken into account, the winter pathway is more analogous to a temperate ecosystem response to the arrival of spring rather than a pulse precipitation phenomenon unique to semiarid or arid ecosystems. This is reflected in the significant response of
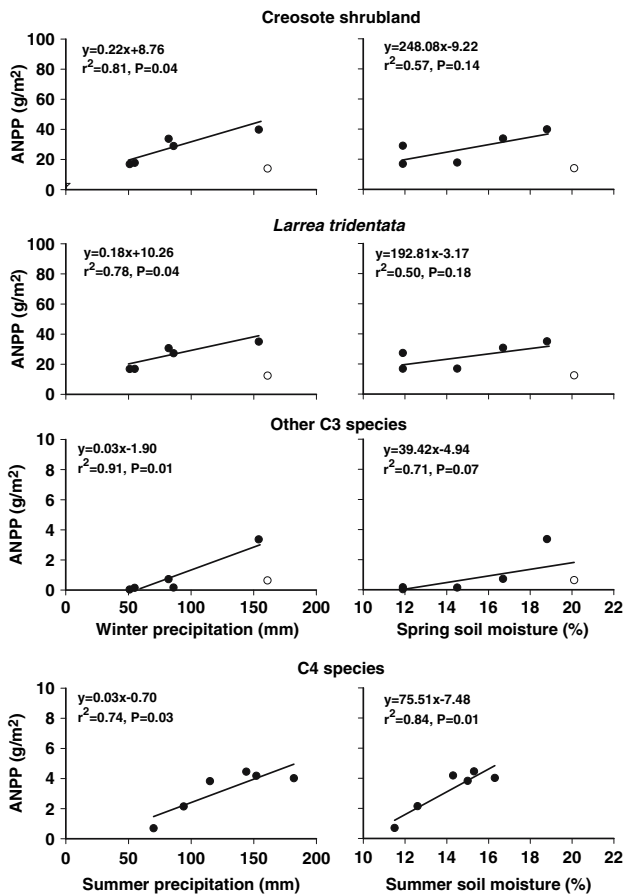
Fig. 8 Relationship between ANPP, production of *L. tridentata*, other C_3 species, and winter precipitation and spring soil moisture content at 30 cm in creosotebush shrublands between 1999 and 2004 (*open symbol* shows 2004 outlier). Relationship between summer ANPP of C_4 species and summer precipitation and soil moisture content in creosote shrublands

the C_3-dominated ecosystem to growing degree days in spring that is not evident in the summer that is in contrast to the C_4-dominated grassland where available moisture during the summer monsoon is the main driver of ANPP. That is, while spring growth can be interpreted as an annual, thermally driven "pulse" event in C_3-dominated shrubland, it essentially reflects a cool-temperate component of what is otherwise a warm-temperate arid ecosystem.

Although soil moisture availability is a key driver of production, there may also be lags and thresholds that can decouple ANPP and soil moisture inputs. For example, Oesterheld et al. (2001) detected a relationship between previous-year precipitation and current-year production in shortgrass steppe, and Reynolds et al. (2004) and Ogle and Reynolds (2004) suggested that threshold responses to antecedent soil moisture conditions may exist. We were unable to detect a lag response in our short time series, but the response by *B. eriopoda* to a few large precipitation events (>25 mm) versus a series of small ones may reflect a soil moisture threshold for growth. Thus while there may be a physiological response among grasses to small rainfall events (e.g., Sala and Lauenroth 1982), this may not necessarily translate into a significant pulse of ANPP.

Water availability interacts with soil nutrient pools to affect production pulses. For example, Seastedt and Knapp (1993) hypothesized that "luxury uptake" of nutrients in tallgrass prairie following drought leads to an above-normal production pulse. Indeed, two out of three highest production dates in mesic tallgrass prairie followed drought periods (Briggs and Knapp 1995). Reynolds et al. (1999) found compensatory growth in *Larrea* and *Prosopis glandulosa* stands at the end of experimentally applied
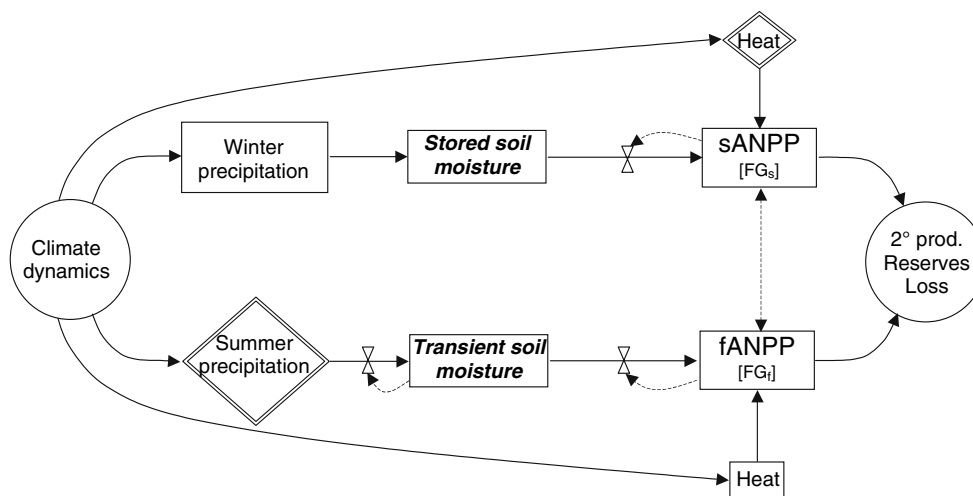

Fig. 9 A conceptual framework showing abiotic drivers and triggers of seasonal ANPP in a semiarid ecosystem with a bimodal distribution of moisture, a warm growing season, and a cold dormancy period. Summer/fall production (*fANPP*) is mostly by the C_4 functional group (FG_f) where growth is triggered by inputs of variable and transient soil

moisture generated from sufficiently large summer rainfall events. Spring production (*sANPP*) is by a C_3 shrub functional group (FG_s) whose response is triggered by heat in spring that breaks winter dormancy and generates growth from stored winter soil moisture. *Dashed lines* represent pertinent interactions and feedbacks

summer drought. At our sites on the Sevilleta, White et al. (2004) demonstrated a significant negative correlation between drought severity and potentially mineralizable nitrogen such that the most extended droughts corresponded to the greatest potential soil fertility. Hence, the large 2004 response in our black grama grassland (and possibly creosotebush shrublands) may have resulted from a large pool of available nitrogen that accumulated during the prior 18-month drought period. In addition, ANPP increased significantly on plots fertilized with nitrogen during years of normal and above-average precipitation at our study site indicating that ANPP in this arid land ecosystem is also nitrogen limited (S. C. Collins, unpublished data). In our study, spring moisture in 2004 generated a production pulse beyond what would have been predicted from precipitation alone, again indicating that ANPP in this arid land ecosystems is co-limited by nitrogen availability.

Other biotic and abiotic drivers such as fire, landscape structure, and soil structure can affect ANPP in arid land ecosystems. Fires affect soil erosion (Ravi et al. 2006, 2007), carbon storage, and nutrient redistribution (White et al. 2006), which add considerable complexity to spatial and temporal heterogeneity in arid land ANPP dynamics. In addition, landscape heterogeneity affects the distribution of water and nutrients, and hence the large-scale pattern, amount, and variation of ANPP in arid and semiarid ecosystems (Knapp et al. 1993; Briggs and Knapp 1995; Ludwig et al. 2005; Huenneke et al. 2002). Soil texture affects plant functional type composition and distribution (Peters et al. 2006) which then affects ANPP response. Thus, although annual precipitation and ANPP are highly correlated at continental scales, local interactions and feedbacks between biotic and abiotic variables reduce the local relationship between ANPP and annual precipitation.

In conclusion, ANPP in this arid land system is exceedingly low and highly contingent on a combination of seasonal moisture dynamics and temperature controls in the context of other abiotic drivers such as soil nutrient pools, landscape structure, and fire. These factors are reflected in the diverse functional group structure of the vegetation that is responding to both cool-temperate and warm-semiarid conditions that generate high seasonal and annual variability in grassland and shrubland ANPP. Indeed, these results extend beyond arid ecosystems in that within- and between-season precipitation patterns may have significant effects in more mesic grassland systems, as well (Knapp et al. 2006; Swemmer et al. 2007). This complexity goes beyond that explained by the pulse-reserve paradigm, in general, and calls for a broader framework that explicitly incorporates seasonal dynamics over multiple temporal scales and their feedback effects on processes in grassland ecosystems.

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