Linking precipitation and C_3–C_4 plant production to resource dynamics in higher-trophic-level consumers

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Abstract. In many ecosystems, seasonal shifts in temperature and precipitation induce pulses of primary productivity that vary in phenology, abundance, and nutritional quality. Variation in these resource pulses could strongly influence community composition and ecosystem function, because these pervasive bottom-up forces play a primary role in determining the biomass, life cycles, and interactions of organisms across trophic levels. The focus of this research is to understand how consumers across trophic levels alter resource use and assimilation over seasonal and interannual timescales in response to climatically driven changes in pulses of primary productivity. We measured the carbon isotope ratios ($\delta^{13}C$) of plant, arthropod, and lizard tissues in the northern Chihuahuan Desert to quantify the relative importance of primary production from plants using C_3 and C_4 photosynthesis for consumers. Summer monsoonal rains on the Sevilleta Long Term Ecological Research (LTER) site in New Mexico support a pulse of C_4 plant production that has tissue $\delta^{13}C$ values distinct from C_3 plants. During a year when precipitation patterns were relatively normal, $\delta^{13}C$ measurements showed that consumers used and assimilated significantly more C_4-derived carbon over the course of a summer, tracking the seasonal increase in abundance of C_4 plants. In the following spring, after a failure in winter precipitation and the associated failure of spring C_3 plant growth, consumers showed elevated assimilation of C_4-derived carbon relative to a normal rainfall regime. These findings provide insight into how climate, pulsed resources, and temporal trophic dynamics may interact to shape semiarid grasslands such as the Chihuahuan Desert in the present and future.

Key words: C_3 plants; C_4 plants; carbon; Chihuahuan Desert, New Mexico, USA; food web; lizard; plant photosynthetic type; precipitation; primary production; pulse; resource; stable isotope.

Introduction

A perennial challenge in ecology is to understand how consumers interact with resources to structure food webs and the consequences of these interactions for ecosystem function (Elton 1927, Lindeman 1942, Chase et al. 2000, Bukovinszky et al. 2008). In many ecosystems seasonal shifts in temperature and precipitation induce pulses of primary productivity that vary in phenology, abundance, and nutritional quality (Coviella and Trumble 1999, Yang et al. 2008). Because resources derived from these pulses play a primary role in fueling the life cycles and population dynamics of organisms across trophic levels, variation in the timing and quality of such pulses can influence consumer productivity, trophic interactions, and the structure of communities (Chase et al. 2000, Ritchie 2000, Boyer et al. 2003). How consumers across trophic levels alter their use and assimilation of resources in response to climatically driven pulses of primary production, however, remains an open question.

The focus of this research is to understand how consumers across trophic levels alter resource use and assimilation over seasonal and interannual timescales in response to climatically driven changes in primary productivity. In most arid ecosystems, precipitation is the primary factor limiting productivity and the timing and magnitude of precipitation events determines plant phenology, diversity, and abundance (Schwinning and Sala 2004). On the Sevilleta Long Term Ecological Research (LTER) site in the Chihuahuan Desert of New Mexico, primary productivity is divided into two seasonally distinct pulses, which are tightly coupled to winter and monsoonal precipitation inputs (Muldavin et al. 2008). Primary production during the spring is tied to winter precipitation and is almost exclusively composed of growth by annual and perennial plants that use the C_3 photosynthetic pathway. In contrast, summer monsoonal rains and warmer summer temperatures result in primary production that is dominated by perennial C_4 grasses (Ode et al. 1980, Muldavin et al. 2008). Essential to this study is the observation that distinctive photosynthetic biochemistry of these plant types produces differences in the carbon isotope ratios ($\delta^{13}C$) of C_3

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(−25.0‰ to −28.6‰ Vienna Pee Dee Belemnite [VPDB]) and C$_4$ (−12.8‰ to −14.8‰ VPDB; Appendix A) plant tissues, which can be used to trace nutrient transfer from producers into consumers (Ehleringer et al. 1997).

In this investigation we use the differences between C$_3$ and C$_4$ δ^{13}C values to examine the relative importance of these nutrient sources for consumers both seasonally and annually. The use of stable isotopes to trace the flow of resources through food webs provides a quantitative picture of the relative contributions that resources make to the nutrient and energy budgets of individuals (Fry et al. 1978, Wolf and Martinez del Rio 2003). To date, only a limited number of studies have investigated the importance of C$_3$ and C$_4$ plants as dietary sources for consumers such as grasshoppers (Fry et al. 1978) and ungulates (Ambrose and DeNiro 1986, Cerling et al. 1993). Even fewer studies have examined the transfer of nutrients from C$_3$ and C$_4$ plants into higher trophic levels (Petelle et al. 1979, Magnusson et al. 1999, 2001). Although there is no consensus, research to date suggests that C$_3$ and C$_4$ plants vary greatly in their importance across consumer taxa at individual, population, and community levels.

The relative paucity of research exploring the importance of C$_3$ and C$_4$ plants to consumers is surprising because, although C$_4$ plants represent less than 2% of higher plant species (Ehleringer et al. 2002) they are estimated to account for ~18% of global vegetative cover and ~22% of total global primary production (Ehleringer et al. 1997, Still et al. 2003). Research on the nutritional ecology of arthropods also indicates that C$_4$ plants are less nutritious than C$_3$ plants because they contain less nitrogen and more fiber and are tougher to process and digest (Barbehenn et al. 2004a, b). These differences in food quality have been found to impact the ability of herbivorous insects to accumulate energy, which greatly affect their growth, fecundity, and survival rates (Awmack and Leather 2002, Barbehenn et al. 2004b, Raubenheimer and Simpson 2004). These studies suggest that shifts in the relative productivity and nutritional quality of C$_3$ and C$_4$ plants that will likely result from forecasted changes in precipitation, atmospheric CO$_2$ concentration, and nitrogen deposition (Collatz et al. 1998, Coviella and Trumble 1999, Ehleringer et al. 2002, IPCC 2007) could affect the total energy and nutrients available to higher trophic levels.

As a first step toward understanding these resource dynamics, we examine how seasonal and annual variation in precipitation affects the assimilation of C$_3$ and C$_4$ carbon across a food web. In this study, we use the lizard community, a taxonomically diverse group of insectivores, to examine the relative importance of C$_3$ and C$_4$ plants across trophic levels. As suggested by Post (2002), we use these higher-trophic-level consumers to present an integrative picture of resource use in lower-level consumers and to describe the relative contributions of C$_3$ and C$_4$ plants to the productivity of this food web. Our goals are to: (1) quantify seasonal changes in the proportion of carbon derived from C$_3$ and C$_4$ plants assimilated by the lizard community, (2) quantify year-to-year changes in C$_3$ and C$_4$ carbon input in response to changes in precipitation, and (3) explore the implications of these results for our understanding of the effects of climate change on resource pulse utilization, trophic interactions, and the function of ecosystems.

METHODS

Study site

This research was conducted on the Sevilleta LTER site located 100 km south of Albuquerque, New Mexico, an ecotonal landscape of Chihuahuan desert shrub and grasslands (Muldavin et al. 2008). Data were collected from a 0.9 × 0.5 km strip of land that encompassed a flat bajada and a shallow rocky canyon of mixed desert shrub and grassland dominated by the creosote bush (*Larrea tridentata*) and black grama grass (*Bouteloua eriopoda*).

Weather and plant measurements

We used precipitation and net primary production (NPP) data collected by the Sevilleta LTER site. Climate data were recorded hourly by a meteorological station located 1 km from the study site. Aboveground net primary productivity was measured three times each year during winter (February), spring (May), and fall (September) at shrub–grassland sites within 2 km of our study site. All NPP data and methodology are available in the Sevilleta archival data set SEV156 (Muldavin 2006).

Tissue collection and sample preparation for stable isotope analysis

From May to October of 2005 and 2006 we collected plant, lizard, and arthropod tissues for carbon stable isotope analysis. During mid-summer of 2005, we randomly collected leaf and stem samples from the 38 most abundant species of plants; these species produce >90% of the annual biomass on our study site (see Appendix A). Approximately 3.5 mg of plant material was then loaded into precleaned tin capsules for isotope analysis.

All animal research was conducted with the approval of the institutional animal care and use committee (University of New Mexico, Institutional Animal Care and Use Committee [UNM-IACUC] number 05MCC004). Lizards were captured by hand using noose poles and by drift fence and pitfall trap arrays (Enge 2001) randomly scattered over a 0.5-km^2 area. Each lizard was toe-clipped for permanent identification and snout–vent length (SVL), body mass (in grams), and sex were recorded. For stable isotope analysis, we obtained a 50-μL blood sample from each lizard, and only sampled individuals once in a two-week period. We acquired a total of 367 blood samples from 11 lizard species. Blood samples were obtained by slipping a micro-capillary tube (Fisherbrand heparinized 50-μL

capillary tubes; Fisher, Pittsburgh, Pennsylvania, USA) ventral and posterior to the eyeball to puncture the retro-orbital sinus. Before and after this procedure a local anesthesia (0.5% tetracaine hydrochloride ophthalmic solution; Akorn, Lake Forest, Illinois, USA) was applied to the eye. Blood samples were stored on ice and centrifuged within 24 h to separate plasma and red blood cells. For isotope analysis 15 μL of plasma were pipetted into a tin capsule, air dried, and then folded.

Arthropods were captured once every two weeks from May through October of each year in pitfall traps, as well as by hand and sweep netting. Individuals were frozen, lyophilized, and ground into a fine powder, and 0.5-mg samples were loaded into tin capsules for isotope analysis.

Stable isotope analysis

Carbon isotope ratios of samples were measured on a continuous flow isotope ratio mass spectrometer (Thermo-Finnigan IRMS Delta Plus; Thermo-Finnigan, Waltham, Massachusetts, USA) with samples combusted in a Costech ECS 4010 Elemental Analyzer (Costech Analytical Technologies, Valencia, California, USA) in the University of New Mexico Earth and Planetary Sciences Mass Spectrometry laboratory. The precision of these analyses was ±0.1‰ SD for $\delta^{13}C$. A laboratory standard calibrated against international standards (valine $\delta^{13}C$ −26.3‰ VPDB) was included on each run in order to make corrections to raw values. Stable isotope ratios are expressed using standard delta notation (δ) in parts per thousand (‰) as: $\delta X = (R_{smpl}/R_{stnd} − 1) \times 1000$, where R_{smpl} and R_{stnd} are the molar ratios of $^{13}C/^{12}C$ of a sample and standard, respectively.

Estimation of C_3 and C_4 carbon incorporation into arthropods and lizards

We used $\delta^{13}C$ values of consumer tissues and a two-end-point mixing model to estimate the proportion of a consumer's assimilated carbon that was derived from each plant photosynthetic type (Martinez del Rio and Wolf 2005):

$$\delta^{13}C_{tissue} = p(\delta^{13}C_{C_4}) + (1 − p)(\delta^{13}C_{C_3}) + \Delta.$$

In this model p is the fraction of dietary C_4 plant material incorporated into a sampled tissue. We chose to analyze the isotope composition of whole bodies for arthropods because this best reflects the diet of lizards. For lizards we chose plasma because it has a rapid ^{13}C turnover rate with an interspecific retention time ranging from 25 to 44 days (Warne et al., in press). In the above model Δ is a discrimination factor, which is defined as the difference in isotope values between an animal's tissues and food when feeding on an isotopically pure diet (DeNiro and Epstein 1978). For our mixing-model estimates we used discrimination ($\Delta^{13}C$) values resulting from a diet switch study for two species of lizards (Sceloporus undulatus and Crotaphytus collaris) fed a

diet of C_4-raised crickets (Warne et al., in press). We found the plasma of these lizards had a mean $\Delta^{13}C = −0.2‰ ± 0.4‰$ VPDB, while crickets fed a C_4-based dog food had a $\Delta^{13}C = −0.9‰ ± 0.4‰$. Reviews of stable isotope ecology have reported $\Delta^{13}C$ values for arthropods ranging from $−0.5‰ ± 0.3‰$ (Spence and Rosenheim 2005) to $0.3‰ ± 0.1‰$ (McCutchan et al. 2003). Although variation in our assumed $\Delta^{13}C$ values would affect proportional estimates of the C_3 or C_4 resources consumed, the observed trends would not change.

Data analysis

To compare the seasonal isotope values of consumers between a spring C_3-dominated and a summer C_4-dominated ecosystem we present the $\delta^{13}C$ (mean ± SE) of each consumer species during the pre-monsoon (May, June, and early-mid-July) and monsoonal periods for each year of this study. We defined the monsoon period as beginning with the first day of recorded monsoon rains in July (monsoon 2005 = 25 July to 15 October; monsoon 2006 = 6 July to 15 October). The effects of seasonal and interannual primary production patterns on consumer resource assimilation ($\delta^{13}C$) were determined by two-way ANOVA using the PROC MIXED procedure (Littell et al. 2006) in SAS (SAS Institute 1999). To examine these effects in the lizard community as a whole, lizard species were treated as random effects in the PROC MIXED model. In order to determine the significance of seasonal and year effects, post hoc analyses were conducted using Tukey-Kramer's hsd test (Sokal and Rohlf 1995). Prior to analysis the data were tested for homogeneity of variance and confirmed to meet the assumptions of ANOVA.

RESULTS

Seasonal and annual shifts in precipitation and plant productivity

The long-term mean annual precipitation for 1991–2006 across the LTER was 273 ± 74 mm (mean ± SD) with ~50% of this precipitation produced by convective thunderstorms during the summer monsoon (July–September 1991–2006 = 140 ± 50 mm) and ~50% falling as snow and rain during the winter and spring (October to June 1991–2006 = 133 ± 59 mm). During 2005 winter precipitation of 215 mm resulted in spring net plant productivity (NPP) of 31.9 ± 4.0 g/m² for C_3 plants and C_4 NPP of 1.8 ± 9.2 g/m² (Fig. 1). Summer monsoonal rainfall of 143 mm induced C_4-dominated NPP of 51.1 ± 8.7 g/m² and C_3 NPP of 16.3 ± 1.7 g/m² (Fig. 1).

While 2005 was a year of relatively "normal" rainfall, 2006 set state and regional records with the driest winter for the Sevilleta LTER at 48 mm of precipitation and the wettest summer monsoon, which produced 240 mm of rainfall (Fig. 1). The failure of winter rains in 2006 led to spring NPP that was one-sixth of that reported for 2005, with C_3 NPP of 4.9 ± 0.4 g/m² and spring C_4 NPP of 0.3 ± 0.1 g/m² (Fig. 1). The heavy monsoon rains in
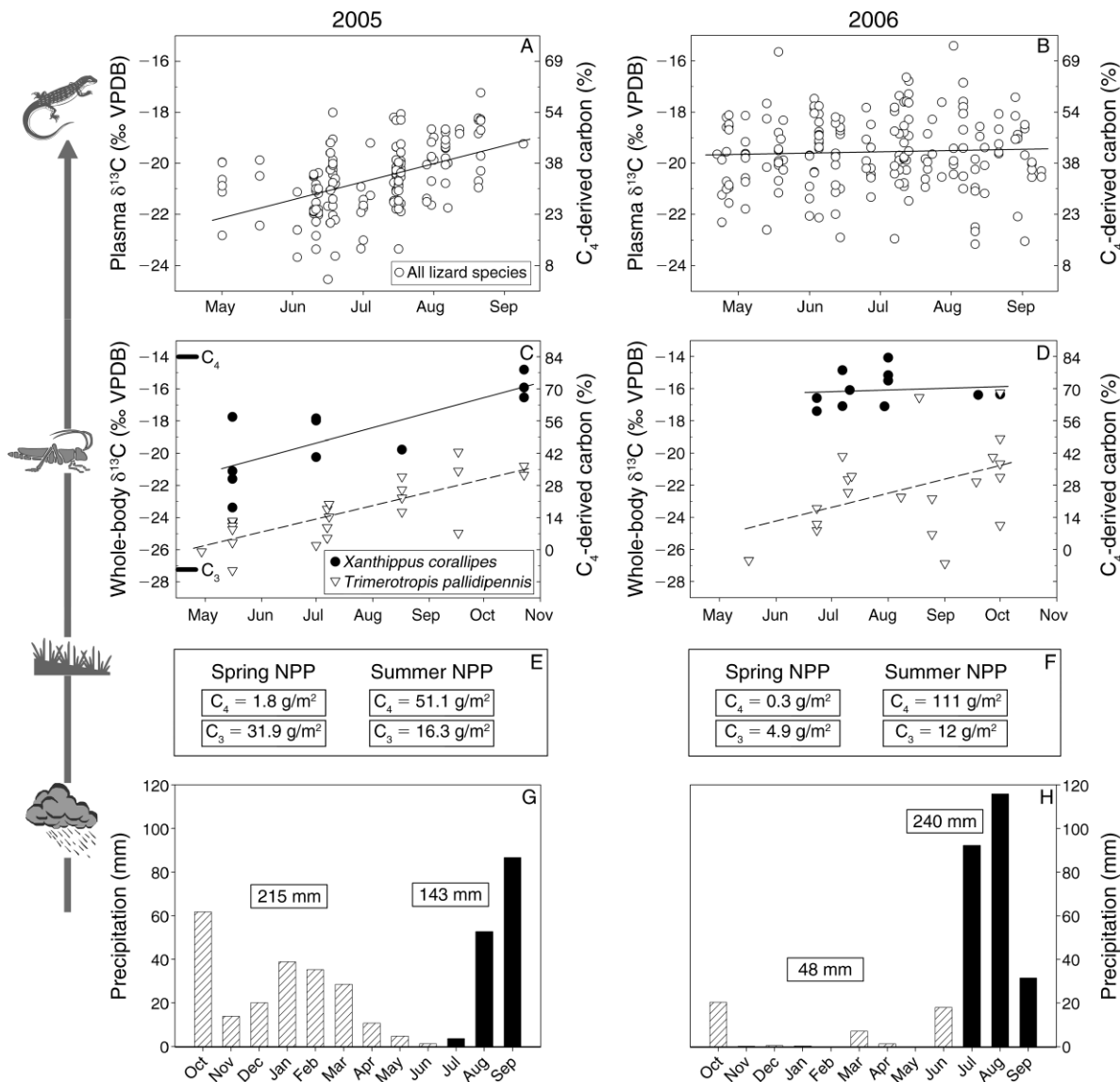
Fig. 1. (A–D) Carbon isotope data ($\delta^{13}C$) for grasshoppers and lizards, (E, F) net primary production, and (G, H) precipitation at the Sevilleta Long Term Ecological Research (LTER) site, northern Chihuahuan Desert, New Mexico, USA, in 2005 and 2006. Carbon isotope data (left y-axes) show shifting seasonal use of C_3 and C_4 plants by the grasshoppers *Trimerotropis pallidipennis* and *Xanthippus corallipes* (C, D); the right y-axes show mixing-model estimates of C_4 carbon assimilation. Bars on the left axis of panel (C) are mean $\delta^{13}C$ values of C_3 plants (−27.3‰ Vienna Pee Dee Belemnite [VPDB] standard; 24 species) and C_4 plants (−14.3‰ VPDB; 14 species). The $\delta^{13}C$ data for the lizard community of 11 species show seasonal shifts in 2005 (panel A), but not in 2006 (panel B). Fitted lines in the consumer plots are ordinary least-squares regressions. Annual precipitation is separated into winter (October–June; hatched bars) and monsoon precipitation (July–September; black bars). Values in boxes are total precipitation for winter and for monsoon seasons.

2006 resulted in a doubling of summer C_4 NPP with 111 ± 9.5 g/m² compared to the previous year, while C_3 NPP was 12 ± 1.7 g/m², comparable to 2005 (Fig. 1).

Shifts in consumer resource assimilation

Arthropods showed clear seasonal shifts in their assimilation of resources derived from C_3 plant productivity in the spring to C_4 resources in the summer (Fig. 1). A shift toward more positive $\delta^{13}C$ values in consumer tissues is termed "enrichment" and reflects a relative increase in the amount of ^{13}C between samples. Enrichment in the $\delta^{13}C$ of consumer tissues reflects a shift toward more assimilated C_4 plant material because these plants have more positive $\delta^{13}C$ values (−14.3‰ ± 0.05‰ [mean ± SE], range = −12.8‰ to −14.8‰ VPDB) relative to C_3 plants (−27.3‰ ± 0.04‰, range = −25.0‰ to −28.6‰ VPDB; Appendix A). A guild analysis of herbivorous arthropods showed that season had a

TABLE 1. Carbon isotope values (mean ± SE, Vienna Pee Dee Belemnite [VPDB] standard, with sample sizes in parentheses) for whole-body tissues of arthropods and plasma of lizards.

	2005 $\delta^{13}C$ (‰)		2006 $\delta^{13}C$ (‰)	
Consumer	Pre-monsoon	Monsoon	Pre-monsoon	Monsoon
Grasshoppers				
Psoloessa texana	−15.7 ± 0.5 (5)	−15.3 ± 0.2 (2)	−14.9 ± 0.6 (2)	−14.2 ± 0.3 (2)
Trimerotropis pallidipennis	−24.8 ± 0.3 (13)	−21.5 ± 0.6 (11)	−24.8 ± 0.7 (4)	−22.2 ± 0.6 (19)
Xanthippus corallipes	−20.0 ± 0.8 (7)	−16.8 ± 1.1 (4)	−17.0 ± 0.4 (2)	−15.8 ± 0.4 (8)
Tenebrionid beetles				
Eleodes spp.	−22.0 ± 0.4 (14)	−22.2 ± 0.2 (15)	−21.7 ± 0.4 (12)	−21.3 ± 0.6 (9)
Cricket				
Ceuthophilus pallidus	−18.6 ± 0.9 (5)	−18.5 ± 0.4 (5)	−19.5 ± 0.6 (7)	−18.9 ± 0.3 (15)
Ant and wasp				
Aphaenogaster cockerelli	−19.8 ± 0.1 (9)	−18.4 ± 0.1 (4)	−20.3 ± 0.6 (3)	−18.2 ± 0.3 (9)
Dasymutilla spp.	−24.1 ± 0.9 (3)	−18.0 ± 1.9 (5)	−22.9 ± 0.5 (3)	−19.8 ± 1.0 (3)
Spider				
Hogna carolinensis	−19.6 ± 0.6 (5)	−17.2 ± 0.6 (6)	−18.4 ± 1.2 (3)	−16.6 ± 0.9 (5)
Scorpion				
Vaejovis coahuilae	−19.3 ± 0.8 (4)	−18.7 ± 0.4 (4)	−20.0 ± 0.5 (3)	−18.5 ± 0.4 (5)
Lizards				
Aspidoscelis inornata	−20.8 ± 0.6 (9)	−17.9 ± 0.3 (3)	−18.3 ± 0.2 (21)	−18.1 ± 0.3 (9)
Aspidoscelis neomexicana	−20.7 ± 0.2 (15)	−19.4 ± 0.2 (10)	−18.4 ± 0.2 (6)	−19.8 ± 0.1 (4)
Aspidoscelis tesselata	−20.9 ± 0.3 (11)	−20.6 ± 0.6 (3)	−20.1 ± 0.4 (5)	−20.7 ± 0.4 (6)
Crotaphytus collaris	−20.9 ± 0.2 (17)	−20.8 ± 0.5 (3)	−20.0 ± 0.3 (15)	−20.0 ± 0.2 (14)
Gambelia wislizenii	−21.0 ± 0.01 (2)	−18.9 ± 0.3 (5)	−18.9 ± 0.5 (3)	
Holbrookia maculata	−20.6 ± 0.3 (6)	−18.7 ± 0.3 (6)	−18.6 ± 0.3 (4)	−17.3 ± 0.5 (6)
Phrynosoma modestum	−20.9 ± 0.1 (4)	−19.2 ± 0.3 (4)	−20.4 ± 0.4 (9)	−19.2 ± 0.6 (5)
Sceloporus magister	−21.5 ± 0.3 (5)	−18.7 (1)	−21.3 (1)	−20.3 ± 0.7 (2)
Sceloporus undulatus	−21.5 ± 0.3 (13)	−19.5 ± 0.4 (11)	−20.4 ± 0.3 (17)	−19.6 ± 0.2 (18)
Urosaurus ornatus	−23.5 ± 0.09 (4)	−21.1 ± 0.4 (3)	−21.8 ± 0.6 (5)	−22.5 ± 0.4 (4)
Uta stansburiana	−22.0 ± 0.04 (2)	−21.0 ± 0.3 (3)	−19.9 ± 0.2 (13)	−19.0 ± 0.4 (12)
Lizard mean	−21.1 ± 0.1 (86)	−19.6 ± 0.2 (52)	−19.7 ± 0.1 (99)	−19.4 ± 0.2 (80)

Notes: Each year is split into pre-monsoon (May to mid-July) and monsoon seasons (mid-July to mid-October). The study was conducted at the Sevilleta Long Term Ecological Research (LTER) site, in the northern Chihuahuan Desert, New Mexico, USA.

significant effect on $\delta^{13}C$ of the generalist grasshoppers *Trimerotropis pallidipennis* (two-way ANOVA, $F_{1,43} = 14.67$, $P < 0.001$) and *Xanthippus corallipes* ($F_{1,18} = 9.24$, $P < 0.005$). For both generalist species during 2005, summer $\delta^{13}C$ values were significantly enriched over those found in spring by 3.3‰ ± 0.9‰ VPDB (Tukey-Kramer hsd test, $P = 0.002$) and 3.3‰ ± 1.1‰ ($P = 0.03$), respectively. These seasonal shifts in tissue $\delta^{13}C$ values translate into a >30% increase in the proportional consumption of C_4 plant biomass over the summer by both grasshoppers (Fig. 1). There was not a year effect or season × year interaction on these species' tissue $\delta^{13}C$, and neither exhibited significant seasonal enrichment during 2006 (Tukey test, $P > 0.05$). In contrast to these generalist consumers, neither season nor year affected the $\delta^{13}C$ of the grasshopper *Psoloessa texana*. This grasshopper exhibited specialization on C_4 biomass as shown by unchanging $\delta^{13}C$ values in 2005 (−15.5‰ ± 0.4‰ VPDB, $n = 7$; Table 1) and 2006 (−14.6‰ ± 0.7‰ VPDB, $n = 4$) that were consistently near C_4 $\delta^{13}C$ values.

A trophic analysis of the arthropods showed that seasonal and interannual variation in C_3 and C_4 productivity also had no effect (see Appendix B for ANOVA results) on the detritivorous cricket *Ceuthophilus pallidus* or the darkling beetles (family Tenebrionidae). Both detritivores had tissue $\delta^{13}C$ values that were consistently intermediate to those of C_3 or C_4 plants across seasons and years (−18.9‰ ± 0.2‰ VPDB, $n = 32$; −21.9‰ ± 0.2‰ VPDB, $n = 51$, respectively; Table 1). Higher-trophic-level arthropods, in contrast, showed a significant effect of season on tissue $\delta^{13}C$ of the omnivorous ant *Aphaenogaster cockerelli* (two-way ANOVA, $F_{1,21} = 11.16$, $P = 0.003$), the parasitic and nectivorous velvet ant *Dasymutilla* spp. ($F_{1,10} = 8.0$, $P = 0.02$), and the predaceous spider *Hogna carolinensis* ($F_{1,15} = 5.71$, $P = 0.03$). There was no significant year effect or season × year interaction on these species' tissue $\delta^{13}C$ values.

Shifts in lizard resource assimilation

The 11 lizard species sampled in this study represent almost the entire community of lizards (14 spp.) in our study site. We found a significant effect of season on plasma $\delta^{13}C$ of the lizard community (two-way fixed and random-effect ANOVA, $F_{1,304} = 60.22$, $P < 0.0001$). During 2005, mean summer $\delta^{13}C$ plasma values for the lizard community were significantly enriched by 1.5‰ ±

0.2‰ VPDB over those observed in the spring (Tukey test, $P < 0.001$). This represents a 15% increase (ordinary least squares [OLS] regression, $r^2 = 0.3$, $P < 0.001$; Fig. 1A) from spring to summer in the assimilation of carbon derived from C$_4$ sources.

In addition, there was a significant year effect (two-way fixed and random-effect ANOVA, $F_{1, 304} = 67.73$, $P < 0.0001$) and season × year interaction ($F_{1, 304} = 18.58$, $P < 0.0001$) on tissue δ^{13}C values of the lizard community. Following the failure of C$_3$ production during the spring of 2006, the lizard community did not exhibit a significant spring-to-summer δ^{13}C enrichment (Tukey test, $P > 0.05$), which is in stark contrast to 2005 (Fig. 1A, B). These interannual differences were driven by significant differences between the spring periods (Tukey test, $P < 0.0001$); the lizard community in 2006 had δ^{13}C values that were elevated by 1.3‰ ± 0.2‰ VPDB over those of spring 2005 (Fig. 1). Lizards also showed greater variability in their δ^{13}C values in 2006 (residuals, SD = 1.5; Fig. 1B), compared to 2005 (residuals, SD = 1.1; Fig. 1A).

Lizard species and families varied in the direction and rates of seasonal and interannual δ^{13}C enrichment (Fig. 2). For the sake of clarity we do not present here the detailed ANOVA results for each of the 11 lizard species analyzed in this study; for two-way ANOVA results of individual lizard species please see Appendix B. Season had a significant positive effect on the tissue δ^{13}C of five of the six lizard species from the family *Phrynosomatidae* (*Holbrookia maculata*, *Urosaurus ornatus*, *Sceloporus undulatus*, *S. magister*, and *Phrynosoma modestum*), excluding *Uta stansburiana*. During 2005, these species showed a mean 17% increase (range = 8–20%; Fig. 2A) in spring-to-summer C$_4$ carbon assimilation. There was also a year effect on the plasma δ^{13}C of *H. maculata*, *Urosaurus ornatus*, *S. undulatus*, and *Uta stansburiana*. During 2006 this group showed a smaller mean seasonal increase in C$_4$ assimilation of 6% (range = 0–10%; Fig. 2B). There was not, however, a strong season × year interaction on these lizards' δ^{13}C. Among the three lizard species of the family *Teiidae* there were significant season and year effects, as well as season × year interaction on the plasma δ^{13}C values of the two smaller species, *Aspidoscelis inornata* and *A. neomexicana*. During 2005, *A. inornata*, the smallest (mass ≈ 4 g) showed a 27% increase in the assimilation of C$_4$-derived carbon resources and *A. neomexicana* (mass ≈ 7 g) showed an 11% increase (Fig. 2A). There was no significant season or year effect on the plasma δ^{13}C of the largest *Teiidae* species *A. tesselata* (mass ≈ 23 g). The collared lizard (*Crotaphytus collaris*, family *Crotaphytidae*), a large sit-and-wait predator, also showed no seasonal or annual shifts in tissue δ^{13}C values in either year.

DISCUSSION

The extremes in precipitation and primary production experienced by the Sevilleta ecosystem during this study provide a unique opportunity to examine the potential effects of climate change on resource use and trophic interactions in food webs. During 2005 winter precipitation levels were "normal" and spring primary production was dominated by plants using C$_3$ photosynthesis (94% of total spring NPP). Starting with the pulse of monsoon rains in July, new primary production, in contrast, was largely composed of C$_4$ plants (76% of total summer NPP). The second year of this study, 2006, was a year of extremes in which winter precipitation failed and the summer monsoon was the wettest in the instrumental record. In a "normal" year like 2005, the total productivity of C$_4$ plants accounts for ~50% of annual NPP (ANPP). During the extremes of 2006, in contrast, C$_4$ production constituted 87% of ANPP. Two factors contributed to this effect, a large reduction in C$_3$ ANPP (one-third of the previous year) and a two-fold increase in C$_4$ production during the monsoon period.

Commensurate with these patterns consumers across trophic levels showed variation in seasonal and interannual patterns of resource use and assimilation. Using lizards to integrate carbon flow through the food web, we found that under a "normal" precipitation regime (e.g., 2005) the lizard community exhibited a seasonal increase in their assimilation of C$_4$-derived carbon from a mean of 27% (12–35%) in the spring to 42% (31–55%) in the summer. During the spring of 2006, in contrast, the failure of winter rains resulted in an elevated incorporation of C$_4$-derived resources by the food web; C$_4$ plants accounted for 40% (25–51%) of the carbon assimilated by the lizard community, compared to only 27% (11–34%) in the previous spring. Surprisingly, the intense monsoon and doubling of summer C$_4$ production in 2006 did not produce an increase in the proportion of C$_4$ resources moving through the food web. Although C$_4$ biomass was the bulk of new production during 2006 (87% of ANPP), C$_3$ carbon still accounted for 60% of the energy flowing through the food web. This food web is thus largely fueled by C$_3$-derived resources even when C$_3$ production is minimal and C$_4$ biomass is abundant.

This is an important observation because C$_3$ plants are higher in nutritional quality than C$_4$ plants and are normally abundant during the spring. The fact that many consumer reproductive cycles are timed to this peak period of nutrient availability in a seasonally shifting resource landscape (Coviella and Trumble 1999, Awmack and Leather 2002, Durant et al. 2005, 2007) begs several questions. How would the repeated failure of monsoonal or winter rains, and the associated reductions in C$_3$ and C$_4$ production, cascade through the food web to affect community structure and ecosystem function? Could the functional ecology of consumers (e.g., body size, feeding guild, or trophic level) mediate the impacts of climate change and altered patterns of primary production? Does the resource pulse from the monsoon act as a reserve, or resource buffer,
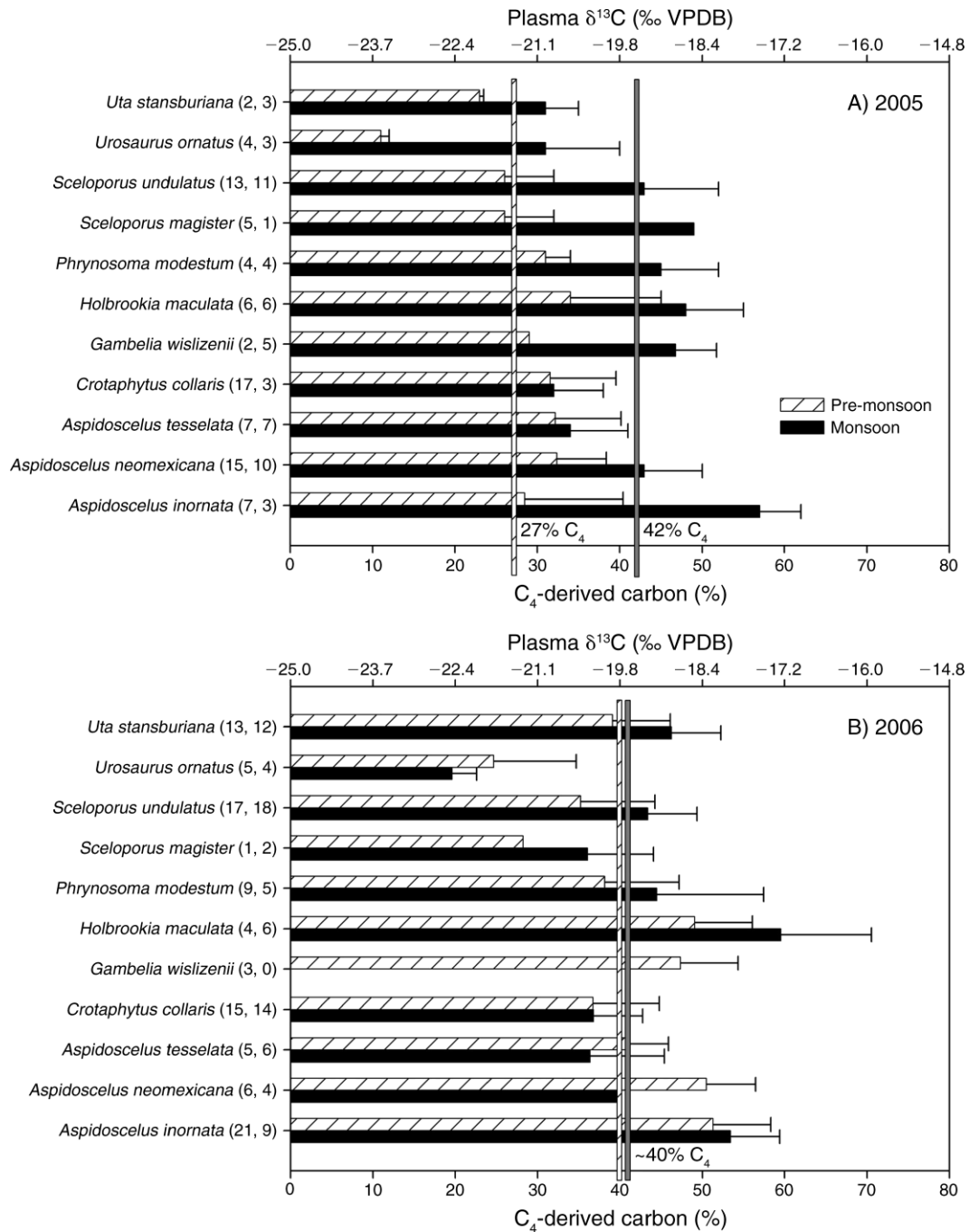
FIG. 2.   Pre-monsoon (hatched bars) and monsoon (black bars) carbon incorporation patterns for each species of the Sevilleta Long Term Ecological Research (LTER) site lizard community are shown for (A) 2005 and (B) 2006. Values in parentheses are numbers of individuals sampled during the pre-monsoon season and the monsoon season, respectively. Carbon isotope values ($\delta^{13}C$ Vienna Pee Dee Belemnite [VPDB] standard) are displayed along the top axis, with mixing-model estimates along the bottom axis. Horizontal bars show $\delta^{13}C$ mean (+SE) for each species per season. Vertical bars correspond to the mean percentage of C_4 use by the lizard community during the spring (hatched) and monsoon (solid) seasons.

that can fuel parts of the food web during seasonal droughts?

These questions, which we address in the following discussion, take on a fresh urgency when recent predictions for climate change in the American South-

west are taken into account. A recent report found a broad consensus among climate models that shows the southwest will become more arid and prone to drought conditions (Seager et al. 2007). Although climatologists are only now considering how climate change will

specifically affect seasonal winter and monsoonal precipitation patterns, it is also clear that a warming climate will increase the frequency and intensity of extreme events like those experienced during this study (Sheppard et al. 2002, Lenart et al. 2007, Allan and Soden 2008).

Cascading effects of climate change on trophic structure and ecosystem function

The climate extremes and droughts predicted for the American Southwest, and arid regions in general (reviewed in Lenart et al. 2007), could dramatically alter the trophic structure and function of this Chihuahuan Desert ecosystem (see also Chase et al. 2000, Ritchie 2000, Boyer et al. 2003). If the winter drought of 2006, for example, was prolonged over multiple years with little to no spring C_3 production, then consumers that are more dependent upon a C_3-derived food chain could be more heavily impacted than C_4-dependent animals. These effects may be both direct and indirect; for herbivorous arthropods, the lower nutrient content and reduced digestibility of C_4 plants has been shown to result in smaller adult body sizes, as well as lower growth rates, survival, and fecundity (Awmack and Leather 2002, Barbehenn et al. 2004a, Raubenheimer and Simpson 2004). Taken in aggregate, increased C_4 use by the bulk of the arthropod community could have cascading negative effects on upper trophic levels. Resource availability could be reduced (by reduced arthropod abundance, size, and nutritional quality) during a season in which large quantities of resources are being directed into growth and reproduction. This could result in delays or reduced investment in reproduction or the greater use of stored resources (Zera and Harshman 2001). A prolonged seasonal drought could thus alter the presence and influence of predators such as lizards (Spiller and Schoener 2008). Ultimately this could affect the structure and function of the Sevilleta ecosystem.

Several factors would drive this ecosystem-level change. Predator and prey interactions can influence herbivory patterns on plants, which in turn can determine the quantity and quality of plant litter that is returned to the soil and plant nutrient cycle (reviewed in Schmitz 2008). Recent work suggests that such variation in plant litter may alter decomposition rates (reviewed in Throop and Archer 2009). Belovsky and Slade (2000) found that increased numbers of grasshoppers in a semiarid grassland similar to the Sevilleta did increase decomposition rates and subsequent soil nitrogen availability and primary production. They found that grasshoppers increased the rates of decomposition and primary production because they have high population densities with rapid turnover rates that selectively consume plants with high nitrogen content. If, however, prolonged seasonal droughts reduced the abundance of grasshoppers, the dominant herbivore on the Sevilleta, then we would expect a slowed nutrient cycle; this is to say we would expect a reduction in soil nutrient availability and subsequent primary production (Belovsky and Slade 2000, Schmitz 2008). Coupled with drought-induced desertification, a slowed nutrient cycle would also contribute to increased woody encroachment of Chihuahuan Desert grasslands (Archer and Smeins 1991, Rapport and Whitford 1999).

Such precipitation-driven alterations to ecosystem structure could be further mediated, however, by changes in atmospheric CO_2 concentration and nitrogen deposition. While increased nitrogen deposition could increase plant growth and quality (Throop and Lerdau 2004), elevated atmospheric CO_2 concentration will decrease the nutrient density of C_3 plants but not C_4 plants (Barbehenn et al. 2004a). Recent studies indicate that herbivores will likely shift the plants or plant photosynthetic type they consume in response to nitrogen and CO_2-induced alterations to nutrient availability (Cleland et al. 2006, Peters et al. 2006). These interactions will likely influence the community composition of plants and herbivores alike, as environmental conditions change in the future (Smith et al. 2000, Peters et al. 2006). Indeed, Cerling et al. (1997) reported a global expansion of C_4 grasslands 6–8 million years before present (myr bp) when low atmospheric CO_2 levels were hypothesized to have given C_4 grasses a competitive advantage over C_3 grasses in tropical regions (Ehleringer et al. 1997). This expansion of C_4 grasslands also coincided with changes in the abundances of mammalian grazers (Ehleringer et al. 2002).

Consumer-mediated effects of climate change on trophic structure

Isotope data from this study as well as recently published research for grasshoppers on the Sevilleta LTER suggest that such a cascading scenario in Chihuahuan grasslands would be mediated by consumer feeding guild (e.g., specialist or generalist consumer of C_3 or C_4 plants). The species-rich Sevilleta grasshopper community has a spectrum of generalist to specialist consumers of C_3 and C_4 plants (Engel et al. 2009). If C_3 production was dramatically reduced for multiple years, then presumably C_3 specialists would be forced to marginal habitat or disappear from the system. In contrast, our isotope data suggest that generalist grasshoppers such as *Xanthippus corallipes* and *Trimerotropis pallidipennis* are more able to capitalize on new production from both C_3 and C_4 plants. This may provide more flexibility in the face of climate change and a failure of either C_3 or C_4 production (see also Cleland et al. 2006). Ritchie (2000), however, showed that the population dynamics of generalist herbivores, in contrast to grass specialists, are more strongly affected by variation in plant nitrogen content. These contradictory effects of more dietary flexibility but increased sensitivity to nutrient density pose an interesting line of inquiry for future research regarding how insects of differing

feeding guilds will respond to climate change (see Peters et al. 2006).

As with arthropods, lizard responses to the cascading effects of a prolonged winter drought could also be mediated by functional traits such as body size and foraging ecology. The only other isotope study of multiple lizard species, conducted in a Brazilian savanna community, showed that body size scaled positively with the proportion of carbon that these lizards derived from C_3 or C_4 sources (Magnusson et al. 2001). The authors were unable to elucidate the factors driving these allometric trends, but argued that lizards of differing sizes function as separate "ecological species" (sensu Polis 1984). Although we did not find similar allometric trends, we did observe variation among lizard species that was suggestive of a body size effect on resource assimilation. The differences in carbon assimilation between the small-bodied *Uta stansburiana* and *Urosaurus ornatus* vs. the larger lizards in the family *Phyrnosomatidae*, for example, suggest that different-sized lizards may be tied to arthropod taxa of given sizes (see also Anderson and Karasov 1988) and/or degree of specialization on C_3 or C_4 resources. These smaller-bodied lizards had $\delta^{13}C$ values that showed them to be more dependent on a C_3-derived food chain, and with a prolonged winter drought they could thus be more impacted than C_4-dependent lizards.

Standing C_3–C_4 biomass as resource buffers

Another factor that could mediate consumer interactions with a changing environment is the persistence of C_3 and C_4 biomass. Over the long term our data suggest that differences in the persistence of C_3 and C_4 biomass in the environment could have delayed effects on consumer life cycles and trophic dynamics. Although definitive data are lacking, several studies suggest that biomass from C_4 plants may decompose at slower rates than C_3 plants due to higher concentrations of non-digestible structural carbon such as lignin (Ross et al. 2002, Vanderbilt et al. 2008, Throop and Archer 2009). Indeed the increased assimilation of C_4 biomass by the food web during the spring of 2006 suggests that in the presence of no new growth, the standing-dead C_4 biomass from the previous summer monsoon was either more available or preferable to standing C_3 biomass. Standing biomass could thus act as an interannual resource buffer, which can fuel parts of the food web during seasonal droughts. The effects of this buffering were seen in the detritivores *Ceuthophilus pallidus* and *Eleodes* spp., which were apparently unaffected by the seasonal and annual variability in C_3 and C_4 production. These detritivores showed no seasonal or annual shifts in carbon sourcing and had $\delta^{13}C$ values that were intermediate to C_3 and C_4 plants.

For higher trophic levels, however, standing biomass would likely be of limited value as a resource buffer. Although grasshoppers show a degree of omnivory (O'Neill et al. 1997) they are generally restricted to diets of living plant biomass by morphological, physiological, and nutrient constraints (Mattson 1980). In response to drought, grasshoppers may thus include a degree of standing C_4 biomass, but would also be compelled by nitrogen constraints to include either novel living plant tissues or even animal tissues. Because we focused on the lizard community to integrate the food-web dynamics of lower trophic levels, the elevated C_4 incorporation in lizards during the spring of 2006 may also have reflected shifts in their own foraging behavior. They may have consumed different arthropod species in 2006 compared to those they consumed in the previous year. Presumably, these different arthropods would have derived their resources from standing C_4 biomass. Alternatively, if their fat stores had $\delta^{13}C$ values close to C_4 plants, then their elevated plasma $\delta^{13}C$ values in the spring of 2006 could also have reflected some reliance upon endogenous fat stores derived from C_4 sources to fuel survival and reproduction (Zera and Harshman 2001; R. W. Warne, C. A. Gilman, D. A. Garcia, and B. O. Wolf, *unpublished manuscript*). This is a feasible hypothesis because lizards develop fat stores in the summer and fall when C_4 plants dominate the Sevilleta ecosystem. The importance of standing C_4 biomass as an interannual resource buffer to consumers across trophic levels is thus an open question that deserves further investigation.

An important point regarding standing C_4 biomass is also highlighted by the extreme monsoon period of 2006, which induced a doubling of summer C_4 production. If, as suggested by our isotope data, the majority of this biomass was not consumed, then vast quantities of C_4 detritus would have been subsequently funneled into the detritivore food web in 2007 (Belovsky and Slade 2000, Wardle et al. 2002). If C_4 biomass decomposes at a slower rate than C_3 biomass because of higher concentrations of lignin (Ross et al. 2002, Vanderbilt et al. 2008, Throop and Archer 2009), this increase in C_4 abundance could then further alter the soil nutrient cycle. Furthermore, the predicted increase in the frequency and intensity of extreme monsoons will also increase soil nutrient loss (Austin et al. 2004, Lenart et al. 2007, Allan and Soden 2008). These coupled processes will alter the availability of soil nutrients and accelerate desertification and woody encroachment in Chihuahuan grasslands (Rapport and Whitford 1999). Our results thus suggest that forecasted changes in precipitation, atmospheric CO_2 concentration, and nitrogen deposition (IPCC 2007) could drive shifts in consumer resource use in response to changes in C_3 and C_4 plant productivity and nutritional quality. Ultimately, climate-driven differences in C_3 and C_4 primary production, their relative persistence in the environment, and commensurate trophic interactions could have profound and long-term effects on the structure and function of semiarid grasslands such as the Chihuahuan Desert.

Literature Cited

Allan, R., and B. Soden. 2008. Atmospheric warming and the amplification of precipitation extremes. Science 321:1481.

Ambrose, S., and M. DeNiro. 1986. The isotopic ecology of East African mammals. Oecologia 69:395–406.

Anderson, R. A., and W. H. Karasov. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. Ecological Monographs 58:79–110.

Archer, S., and F. Smeins. 1991. Ecosystem-level processes. Pages 109–139 *in* R. K. Heitschmidt and J. W. Stuth, editors. Grazing management: an ecological perspective. Timber Press, Portland, Oregon, USA.

Austin, A., L. Yahdjian, J. Stark, J. Belnap, A. Porporato, U. Norton, D. Ravetta, and S. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–235.

Awmack, C., and S. Leather. 2002. Host plant quality and fecundity in herbivorous insects. Annual Review of Entomology 47:817–844.

Barbehenn, R. V., D. N. Karowe, and Z. Chen. 2004a. Performance of a generalist grasshopper on a C$_3$ and a C$_4$ grass: compensation for the effects of elevated CO$_2$ on plant nutritional quality. Oecologia 140:96–103.

Barbehenn, R. V., D. N. Karowe, and A. Spickard. 2004b. Effects of elevated atmospheric CO$_2$ on the nutritional ecology of C$_3$ and C$_4$ grass-feeding caterpillars. Oecologia 140:86–95.

Belovsky, G., and J. Slade. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. Proceedings of the National Academy of Sciences (USA) 97:14412–14417.

Boyer, A., R. Swearingen, M. Blaha, C. Fortson, S. Gremillion, K. Osborn, and M. Moran. 2003. Seasonal variation in top-down and bottom-up processes in a grassland arthropod community. Oecologia 136:309–316.

Bukovinszky, T., F. van Veen, Y. Jongema, and M. Dicke. 2008. Direct and indirect effects of resource quality on food web structure. Science 319:804.

Cerling, T., J. Harris, B. MacFadden, M. Leakey, J. Quade, V. Eisenmann, and J. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389:153–158.

Cerling, T., Y. Wang, and J. Quade. 1993. Expansion of C$_4$ ecosystems as an indicator of global ecological change in the late Miocene. Nature 361:344–345.

Chase, J., M. Leibold, A. Downing, and J. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81:2485–2497.

Cleland, E., H. Peters, H. Mooney, and C. Field. 2006. Gastropod herbivory in response to elevated CO$_2$ and N addition impacts plant community composition. Ecology 87:686–694.

Collatz, G. J., J. A. Berry, and J. S. Clark. 1998. Effects of climate and atmospheric CO$_2$ on the global distribution of C$_4$ grasses: present, past, and future. Oecologia 114:441–454.

Coviella, C. E., and J. T. Trumble. 1999. Effects of elevated atmospheric carbon dioxide on insect–plant interactions. Conservation Biology 13:700–712.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506.

Durant, J., D. Hjermann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli, and N. Stenseth. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecology Letters 8:952–958.

Durant, J., D. Hjermann, G. Ottersen, and N. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271.

Ehleringer, J., T. Cerling, and M. Dearing. 2002. Atmospheric CO$_2$ as a global change driver influencing plant–animal interactions. Integrative and Comparative Biology 42:424–430.

Ehleringer, J. R., T. E. Cerling, and B. R. Helliker. 1997. C$_4$ photosynthesis, atmospheric CO$_2$ and climate. Oecologia 112:285–299.

Elton, C. 1927. Animal ecology. Macmillan, New York, New York, USA.

Enge, K. M. 2001. The pitfalls of pitfall traps. Journal of Herpetology 35:467–478.

Engel, S., H. Lease, N. McDowell, A. Corbett, and B. Wolf. 2009. The use of tunable diode laser absorption spectroscopy for rapid measurements of the ^{13}C of animal breath for physiological and ecological studies. Rapid Communications in Mass Spectrometry 23:1281–1286.

Fry, B., A. Joern, and P. L. Parker. 1978. Grasshopper food web analysis: use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. Ecology 59:498–506.

IPCC [Intergovernmental Panel on Climate Change]. 2007. Climate change 2007: the physical science basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Lenart, M., G. Garfin, B. Colby, T. Swetnam, B. Morehouse, S. Doster, and H. Hartmann. 2007. Global warming in the Southwest: projections, observations and impacts. The Climate Assessment Project for the Southwest (CLIMAS), University of Arizona, Tucson, Arizona, USA.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–417.

Littell, R., G. Milliken, W. Stroup, R. Wolfinger, and S. Oliver. 2006. SAS for mixed models. Second edition. SAS Institute, Cary, North Carolina, USA.

Magnusson, W. E., M. C. de Araujo, R. Cintra, A. P. Lima, L. A. Martinelli, T. M. Sanaiotti, H. L. Vasconcelos, and R. L. Victoria. 1999. Contributions of C$_3$ and C$_4$ plants to higher trophic levels in an Amazonian savanna. Oecologia 119:91–96.

Magnusson, W. E., A. P. Lima, A. S. Faria, R. L. Victoria, and L. A. Martinelli. 2001. Size and carbon acquisition in lizards from Amazonian savanna: evidence from isotope analysis. Ecology 82:1772–1780.

Martinez del Rio, C., and B. O. Wolf. 2005. Mass balance models for animal isotopic ecology. Pages 141–174 *in* J. M. Starck and T. Wang, editors. Physiological and ecological adaptations to feeding in vertebrates. Science Publishers, Enfield, New Hampshire, USA.

Mattson, W., Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

McCutchan, J. H., W. M. Lewis, C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390.

Muldavin, E. H. 2006. ANPP quadrat sampling data for

Sevilleta LTER Burn NPP Study. ⟨http://sev.lternet.edu/project_details.php?id=SEV156⟩

Muldavin, E. H., D. I. Moore, S. L. Collins, K. R. Wetherill, and D. C. Lightfoot. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. Oecologia 155:123–132.

Ode, D. J., L. L. Tieszen, and J. C. Lerman. 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. Ecology 61:1304–1311.

O'Neill, K., S. Woods, and D. Streett. 1997. Grasshopper foraging on feces: observational and rubidium-labeling studies. Environmental Entomology 26:1224–1231.

Petelle, M., B. Haines, and E. Haines. 1979. Insect food preferences analysed using $^{13}C/^{12}C$ ratios. Oecologia 38:159–166.

Peters, H., E. Cleland, H. Mooney, and C. Field. 2006. Herbivore control of annual grassland composition in current and future environments. Ecology Letters 9:86–94.

Polis, G. 1984. Age structure component of niche width and intraspecific resource partitioning: Can age groups function as ecological species? American Naturalist 123:541–564.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Rapport, D., and W. Whitford. 1999. How ecosystems respond to stress. BioScience 49:193–203.

Raubenheimer, D., and S. J. Simpson. 2004. Organismal stoichiometry: quantifying non-independence among food components. Ecology 85:1203–1216.

Ritchie, M. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. Ecology 81:1601–1612.

Ross, D., K. Tate, P. Newton, and H. Clark. 2002. Decomposability of C_3 and C_4 grass litter sampled under different concentrations of atmospheric CO_2. Plant and Soil 240:275–286.

SAS Institute. 1999. SAS/STAT user's guide. Version 8. SAS Institute, Cary, North Carolina, USA.

Schmitz, O. 2008. Herbivory from individuals to ecosystems. Annual Review of Ecology, Evolution, and Systematics 39:133–152.

Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. Huang, N. Harnik, A. Leetmaa, and N. Lau. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181.

Sheppard, P., A. Comrie, G. Packin, K. Angersbach, and M. Hughes. 2002. The climate of the US Southwest. Climate Research 21:219–238.

Smith, S., T. Huxman, S. Zitzer, T. Charlet, D. Housman, J. Coleman, L. Fenstermaker, J. Seemann, and R. Nowak. 2000. Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. Nature 408:79–82.

Sokal, R., and F. Rohlf. 1995. Biometry. Third edition. W. H. Freeman, New York, New York, USA.

Spence, K. O., and J. A. Rosenheim. 2005. Isotopic enrichment in herbivorous insects: a comparative field-based study of variation. Oecologia 146:89–97.

Spiller, D., and T. Schoener. 2008. Climatic control of trophic interaction strength: the effect of lizards on spiders. Oecologia 154:763–771.

Still, C. J., J. A. Berry, G. J. Collatz, and R. S. DeFries. 2003. Global distribution of C_3 and C_4 vegetation: carbon cycle implications. Global Biogeochemical Cycles 17:1–14.

Throop, H., and S. Archer. 2009. Resolving the dryland decomposition conundrum: some new perspectives on potential drivers. Progress in Botany 70:171–194.

Throop, H., and M. Lerdau. 2004. Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. Ecosystems 7:109–133.

Vanderbilt, K. L., C. S. White, O. Hopkins, and J. A. Craig. 2008. Aboveground decomposition in arid environments. Journal of Arid Environments 72:696–709.

Wardle, D., K. Bonner, and G. Barker. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. Functional Ecology 16:585–595.

Warne, R. W., C. A. Gilman, and B. O. Wolf. In press. Tissue carbon incorporation rates in lizards: implications for ecological studies using stable isotopes in ectotherms. Physiological Biochemical Zoology.

Wolf, B. O., and C. Martinez del Rio. 2003. How important are columnar cacti as sources of water and nutrients for desert consumers? A review. Isotopes in Environmental and Health Studies 39:53–67.

Yang, L., J. Bastow, K. Spence, and A. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Zera, A., and L. Harshman. 2001. The physiology of life history trade-offs in animals. Annual Review of Ecology and Systematics 32:95–126.

APPENDIX A

Whole-plant $\delta^{15}N$ and $\delta^{13}C$ values for the 38 most abundant species of C_3 and C_4 plants at the Sevilleta Long Term Ecological Research site (*Ecological Archives* E091-113-A1).

APPENDIX B

ANOVA results for the effects of season and annual primary production patterns on resource assimilation ($\delta^{13}C$) in lizards and arthropods (*Ecological Archives* E091-113-A2).