

Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie

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Abstract

Global climate change is expected to result in a greater frequency of extreme weather, which can cause lag effects on aboveground net primary production (ANPP). However, our understanding of lag effects is limited. To explore lag effects following extreme weather, we applied four treatments (control, doubled precipitation, 4 °C warming, and warming plus doubled precipitation) for 1 year in a randomized block design and monitored changes in ecosystem processes for 3 years in an old-field tallgrass prairie in central Oklahoma. Biomass was estimated twice in the pretreatment year, and three times during the treatment and posttreatment years. Total plant biomass was increased by warming in spring of the treatment year and by doubled precipitation in summer. However, double precipitation suppressed fall production. During the following spring, biomass production was significantly suppressed in the formerly warmed plots 2 months after treatments ceased. Nine months after the end of treatments, fall production remained suppressed in double precipitation and warming plus double precipitation treatments. Also, the formerly warmed plots still had a significantly greater proportion of C₄ plants, while the warmed plus double precipitation plots retained a high proportion of C₃ plants. The lag effects of warming on biomass did not match the temporal patterns of soil nitrogen availability determined by plant root simulator probes, but coincided with warming-induced decreases in available soil moisture in the deepest layers of soil which recovered to the pretreatment pattern approximately 10 months after the treatments ceased. Analyzing the data with an ecosystem model showed that the lagged temporal patterns of effects of warming and precipitation on biomass can be fully explained by warming-induced differences in soil moisture. Thus, both the experimental results and modeling analysis indicate that water availability regulates lag effects of warming on biomass production.

Keywords: ANPP, biomass, climate change, global warming, lagged effects, precipitation, soil drying, soil moisture, soil water, warming

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Introduction

Scientists currently have abundant evidence of ongoing climate change and its effects on many ecosystems from polar glaciers and tundra to tropical marine

habitats (Walther *et al.*, 2002; Parmesan & Yohe, 2003). Average global temperatures have increased 0.74 °C in the last century and are predicted to increase 1.1–6.4 °C further by the end of this century (IPCC, 2007). Additionally, global climate change is predicted to increase the frequency of extreme weather events, including the frequency of unusually warm, wet, or dry years (Easterling *et al.*, 2000; IPCC, 2007). These anomalous years may have effects on ecosystems that could carry over

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into following years. In studies of the relationship of climate with aboveground net primary productivity (ANPP) in grasslands, it is not uncommon to find ANPP affected for 1 to several years following a particularly wet or dry year – a lag effect (Wiegand *et al.*, 2004). At the global scale, climate effects on plant growth are likely responsible for a reported 2 years lag between patterns of interannual variability in temperature and atmospheric CO₂ concentration (Braswell *et al.*, 1997).

Lagged effects have been documented in grasslands in South Africa, Europe, Patagonia, and 15 different sites across North America. The effect of unusually wet or dry periods on biomass can last for less than a year up to 7 years, with 1 year being the most commonly reported lag time (Cable, 1975; Webb *et al.*, 1978; Smoliak, 1986; Gibbens & Beck, 1988; Lauenroth & Sala, 1992; Dunnett *et al.*, 1998; O'Connor *et al.*, 2001). Wet years that increase ANPP in grasslands can be followed by 1 or more years when biomass is higher than expected by rainfall or temperature in those years (Hansen *et al.*, 1982; Snyman & Fouché, 1991; Oesterheld *et al.*, 2001). Likewise, one dry year can lead to reductions in ANPP in following years, compared with predictions based on climate–ANPP relationships alone. Carry-over effects from a high-biomass year, whether due to temperature or rainfall or both, can buffer the system from the effects of a drought, and conversely, a poor year previous to a drought can amplify its effects (Goward & Prince, 1995; Oesterheld *et al.*, 2001; Wiegand *et al.*, 2004). The intensity of drought may determine the length of the lag period (Yahdjian & Sala, 2006) and the lag can be longer for grasslands in good condition compared with those in poor conditions (Wiegand *et al.*, 2004).

Although lags are usually reactions to dry or wet years, the mechanisms creating the lagged effects of climate on ANPP have not been well studied. Lagged effects are variously attributed to stored soil water (Oesterheld *et al.*, 2001; Wiegand *et al.*, 2004), carbohydrate storage in perennials (Dunnett *et al.*, 1998; Anderson & Inyoue, 2001), the number of available meristems (Benson *et al.*, 2004; Dalgleish & Hartnett, 2006), and/or a change in the amount of nutrients available due to a change in the amount of litter available for decomposition (Schimel & Parton, 1986). Higher plant-level carbon uptake, whether due to temperature or rainfall, in addition to contributing to current growth and reproduction, can be allotted to increased storage or to an increased number of buds, tillers, and branches with meristems that will initiate growth in the following year (Goward & Prince, 1995; Herben *et al.*, 1995; Osterheld *et al.*, 2001; Dalgleish & Hartnett, 2006). Plant size, density, and recruitment may also increase, having

the same carry-over effect as numbers of meristems (Gibbens & Beck, 1988; Lauenroth *et al.*, 1994; Goward & Prince, 1995; Anderson & Inyoue, 2001; Yahdjian & Sala, 2006). Increased biomass production in deciduous species results in greater litter mass, most of which will decompose during the following year. If rate of decomposition keeps pace with the increased litter mass, increased mineralization of nutrients can augment growth (Schimel & Parton, 1986). Several authors have proposed that specific species may contribute to ANPP lags if they have greater shoot longevity (Noble, 1977) or if variation in rooting depth and distribution allow some plants to access stored soil water from an earlier wet year (Dunnett *et al.*, 1998; Snyman, 2000; Jobbágy & Sala, 2000; Wiegand *et al.*, 2004). According to Dodd & Lauenroth (1997), soil texture will help determine ANPP lags by affecting the availability of stored soil water. Interactions among populations, communities, and ecosystems processes have also been proposed to be part of the causal mechanisms of lags in ANPP (Webb *et al.*, 1978).

Though these various mechanisms have been proposed for ANPP lags, none have been rigorously tested to identify key mechanisms underlying lag effects. Identification of key mechanisms could be useful to improve models predicting ANPP, for example, in resolving differences between spatial and temporal models (Jobbágy & Sala, 2000; Osterheld *et al.*, 2001; Wiegand *et al.*, 2004). The objective of this study was to explore lagged effects of interannual climate variation on aboveground plant biomass production by quantifying responses of key ecosystem variables to variation in temperature and precipitation. To do this, we exposed half of our experimental plots in an Oklahoma tallgrass prairie to 1 year of elevated temperatures and half to 1 year of double precipitation in a fully factorial design and followed them through a pretreatment year, the treatment year, and a posttreatment year. We analyzed temporal patterns of aboveground biomass, soil moisture, and available N over the seasons and among years to gain insight into immediate and lagged effects of temperature and precipitation. To help determine how much soil moisture and soil available N explained the observed results, we parameterized a terrestrial ecosystem (TECO) model with the experimental data and then explored mechanisms of lag effects on terrestrial carbon cycling processes.

Specifically, our questions were (1) Does an extreme weather year cause lagged responses in biomass? (2) Do the lagged patterns in biomass relate to patterns of soil temperature, available soil N, or soil moisture? (3) Will feeding the experimental data on available soil N and soil moisture into the TECO model reproduce any lagged effects seen in the biomass data?

Methods

Study site

The experiment was conducted at the Kessler Farm Field Laboratory (KFFL) ($34^{\circ}58'54''N$, $97^{\circ}31'W$) in McClain County, Oklahoma, approximately 25 miles southwest of the University of Oklahoma, Norman, on the Central Redbed Plains of Oklahoma (Tarr *et al.*, 1980). The site is an old field tallgrass prairie, abandoned from agriculture 30 years ago and lightly grazed until 2002 when large herbivores were excluded. The site is dominated by perennial plants, the C₄ grasses *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Panicum virgatum*, the C₃ forb *Ambrosia psilostachya*, and the C₃ annual grass *Bromus japonicus*. The C₄ plants at this site consist almost entirely of perennial grasses. In spring, the dominant C₃ plants were winter annual forbs and *B. japonicus*, an annual grass. In summer, C₃ plant composition was largely of perennial forbs.

Mean annual temperature at the site is 16.3 °C, with monthly air temperature ranging from 3.3 °C in January to 28.1 °C in July. The mean annual precipitation (MAP) is 967 mm (averaged from 1948 to 1999, Oklahoma Climatological Survey). Precipitation is usually highest in May and June (240 mm), followed by September and October (192 mm), and lowest in January and February (82 mm), and July and August (125 mm). The soil is a silt loam with 36% sand, 55% silt, and 10% clay in the top 15 cm (A. Subedar & Y. Luo, unpublished data). The proportion of clay increases with depth. The soils are part of the Nash–Lucien complex, typically having high fertility (42.2 kg ha⁻¹ total N, 85.6 kg ha⁻¹ P), neutral pH (7.05), high available water capacity, and a deep moderately penetrable root zone (USDA, 1979).

Experimental design

The experiment utilized a randomized block design with two levels of warming (ambient and +4 °C) and two levels of precipitation (ambient and doubled). Twenty 3 m × 2 m plots were placed 1.5 m apart in two rows 3 m apart. Every other plot had two 165 cm × 15 cm radiant infrared heaters suspended above it at a height of 1.4 m (Kalglo electronics Inc., Bethlehem, PA, USA). Previous experimentation determined that, at this height, two heaters, each with a radiation output of 100 W m⁻² would warm the soil surface approximately 4 °C (Wan *et al.*, 2002). Rigorous testing has shown that the infrared radiation from the heater does not generate any visible light affecting photosynthesis (Kimball, 2005). The remaining 10 plots each had two 'dummy' heaters, the same size and shape

as the infrared heaters, constructed of metal flashing, suspended over the plots at the same height and position as in the warmed plots.

Five of the warmed plots and five of the unwarmed plots had attached 'water catchments,' an angled sheet of corrugated plastic of the same size as the plots. During a rainfall, these catchments directed precipitation onto the plots via three 12.5 mm diameter PVC pipes that distributed the water evenly over the plots. All the plots were fitted with the PVC pipes whether or not they were attached to water catchments. With this design, extra precipitation was only supplied to the doubled precipitation treatment plots during natural rain.

Heaters, dummy heaters, water catchments, and PVC pipes were in place and functional for 1 year, from February 20, 2003 to February 20, 2004 (the treatment year). Soil temperature in the middle of each plot was monitored hourly with automated thermocouples (Campbell Science Equipment, Logan, UT, USA) placed at 15 cm above the ground and at depths of 7.5, 22.5, 45, 75, and 105 cm. Soil water content (volumetric) was logged at the same frequency using segmented TDR probes (time domain reflectometry; ESI Equipment, Victoria, BC, Canada). Soil water content was measured over five depth intervals, 0–15, 15–30, 30–60, 60–90, and 90–120 cm. For most of the study period, half of the TDR probes were functioning properly.

Estimation of aboveground biomass production

Aboveground biomass was estimated three times a year. In summer (peak biomass, late August) and in fall (early November), biomass was measured directly by clipping half of the plots at 10 cm at each observation time. The same half plot was clipped at the same time each year. Clipping each year reduced any effect that number of meristems could have on ensuing biomass by removing all the meristems above 10 cm. In spring (late April), the indirect point-frame method was used (McNaughton, 1979; Frank & McNaughton, 1990; McNaughton *et al.*, 1996), counting green (live plant) and brown (standing litter) hits on each of 10 pins in a frame placed facing each of four directions in two diagonal quarters of each plot. Pin hits in the plots were correlated by a linear function to pin hits in calibration plots clipped at 10 cm. Spring biomass is largely composed of C₃ species and fall biomass largely composed of C₄ species. Because we clipped each year, total summer biomass represents annual productivity. Summer and fall biomass was dried for 3 days in 65 °C ovens and weighed. Dried biomass retained its color and most of its shape so that it could be hand sorted into litter, C₄ plants, and C₃ plants, and then weighed.

Soil nutrient probes

We used plant root simulator probes (PRSTM) to monitor soil nutrients during this experiment. The PRS probes consist of anion or cation exchange membranes imbedded in plastic stakes (Western Ag Innovations Inc., Saskatoon, Canada). The probes were installed for a period of 1 month four times per year. At the end of the month, the PRS probes were removed and extracted for NH₄⁺ and NO₃⁻. After washing off the soil from the PRS probes, they were sent to Western Ag Innovations for extraction. At Western Ag, the probes were extracted with 17.5 mL of 0.5 M HCl for 1 h in a zip lock bag, and the extractant was analyzed for NH₄⁺ and NO₃⁻ using a Technicon Autoanalyzer. The values were reported in units of $\mu\text{mol N } 10\text{ cm}^{-2}$ of membrane surface.

Calculations and statistical analysis

The effects of warming and double precipitation on temperature and soil moisture were analyzed separately using repeated measures ANOVA with year and warming or double precipitation as main effects and day of year as the repeated factor using the PROC MIXED procedure of SAS 8.01 (SAS Institute, Cary, NC, USA).

The species present in each plot during spring, summer, and fall, as well as vegetation structure, were sufficiently different from season to season to warrant separate statistical analyses on the three seasons' observations. The effects of warming and double precipitation on biomass were analyzed using a repeated measures ANOVA with warming and double precipitation designated as main effects, block as a random effect, and year as the repeated factor using the PROC MIXED procedure of SAS 8.01 (SAS Institute). For analysis of significant differences in spring and fall biomass, only green biomass was used as it represented the most recent growth, most likely to be affected by treatments and recent condition. Spring growth has a larger proportion of C₃ species, and fall growth more C₄. For summer, total biomass was analyzed because, as plots were clipped each year, it is an estimate of ANPP. As variability between plots in pretreatment summer and fall biomass was large, for summer and fall, the values used in the ANOVA were standardized by their difference from the mean in 2002. Standardization involved subtracting the 2002 summer and fall biomass of each plot from the summer and fall 2002 biomass averages, then adjusting the 2003 and 2004 summer and fall biomass of each plot by those values. As no pretreatment data were available for spring biomass, the log-transformed green plot biomass values were used in the ANOVA. When the ANOVA indicated significant effects or interactions, the pdiff option of the lsmeans statement was used to test for significant differences between particular pairs of

treatments. All means used in figures are least-squares means.

For analysis of the two functional groups in summer and fall, green C₃ and C₄ biomass was calculated as a proportion of the total green biomass. As the two values are proportional to each other, only one of them, C₄, was analyzed in an ANOVA using the same model as for biomass above, after being arcsine-square root transformed. Nitrogen data from the PRS probes were analyzed using an ANOVA by sampling date using the PROC MIXED procedure of SAS. Differences between particular treatments within a given sampling date were determined using the pdiff option in the lsmeans statement of the PROC MIXED.

Simulation of lag effects with the TECO model

A process-based ecosystem model (TECO, Weng & Luo, 2008) was used to explore whether soil moisture alone could reproduce the pattern of biomass, and to examine how lagged effects could be reproduced. The TECO model was designed to examine ecosystem carbon cycling processes in response to multifactor global change. It evolved from a terrestrial carbon sequestration model (Luo & Reynolds, 1999; Weng & Luo, 2008) which has been extensively applied to modeling responses of the Duke Forest to CO₂ enrichment (Luo *et al.*, 2001, 2003; Xu *et al.*, 2006). The model contains four major components: a canopy photosynthesis module, a soil water dynamic module, a plant growth module, and a soil carbon transfer submodule (Weng & Luo, 2008). The multilayer process-based canopy module calculates radiation transmission based on Beer's law. For each layer, foliage is divided in sunlit and shaded leaf area. Leaf photosynthesis is estimated based on Farquhar *et al.* (1980) and stomatal conductance based on Ball *et al.* (1987). The plant growth module and carbon transfer module take into consideration plant growth, plant respiration, and carbon transfers among the carbon pools of plant soil. Allocation of assimilates over the plant components depends on growth rate of leaves, stems, and roots, and varies with phenology. The soil water dynamic module simulates soil moisture dynamics, which are determined by precipitation, evapotranspiration, and runoff.

The climate data used to drive the model are from a MESONET station of Washington, Oklahoma located on KFFL. We first calibrated the TECO model against the measured soil moisture and total biomass treatment means from 2002 and 2003 at the site. Then, the model was run to get simulated aboveground biomass by forcing the soil moisture equal to the measured soil moisture from the plots in the four treatments every 24 h.

Results

Aboveground biomass and production

Warming significantly affected spring biomass, while the $2 \times$ precipitation treatments had greater effects on summer and fall biomass (Fig. 1 and Table 1).

Warming stimulated biomass production in the spring of the treatment year but depressed biomass the following spring. In spring 2003, after treatments had been applied for 2 months, warmed and warming plus double precipitation plots had nearly twice the

biomass of the control and double precipitation plots, averaging $45.25 \pm 17.66 \text{ g m}^{-2}$ in the control and double precipitation plots and $84.24 \pm 17.66 \text{ g m}^{-2}$ in the warmed and warmed plus double precipitation plots (Fig. 1a). The following spring (2004) had the opposite pattern; warming suppressed biomass production (a year \times warming interaction, Table 1 and Fig. 1a). Although there is no pretreatment spring data, these results are undoubtedly due to the treatments because the spring pattern is so different from the summer and fall 2002 patterns of biomass. In summer 2002, plots assigned to control had the highest biomass (Fig. 1b,

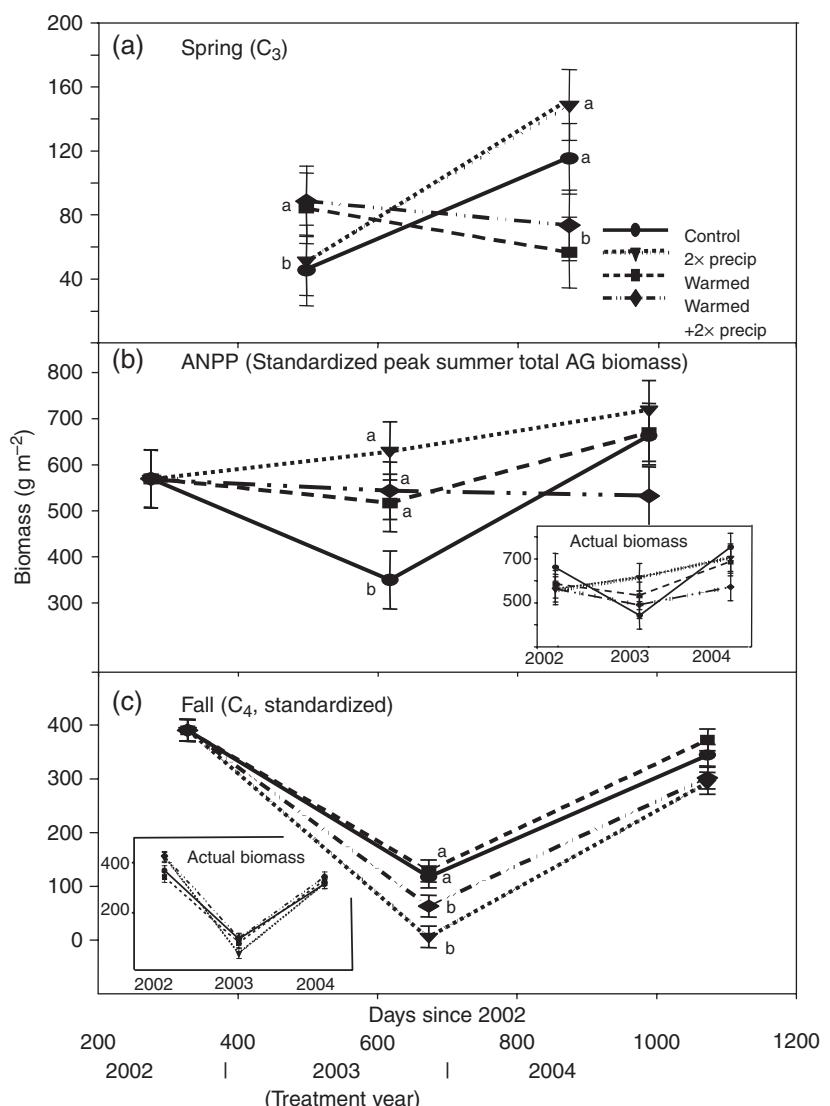


Fig. 1 Aboveground net primary productivity (ANPP) and spring and fall production. Green aboveground (AG) biomass is given for spring and fall; total AG biomass for summer. As the plots were clipped every year, the summer biomass represents annual ANPP. Spring vegetation is dominated by C_3 species, fall by C_4 . Summer and fall data were standardized to bring all plots to the average during the pretreatment year. Insets represent actual biomass for summer and fall. Similar letters indicate treatments that are not significantly different within a season and year ($P < 0.05$). Lines between data points were added for the purpose of clarity only and do not indicate that the changes over time were strictly linear.

Table 1 Results of a repeated-measures ANOVA on standardized values of aboveground green biomass for spring and fall, and standardized total biomass for summer

Effect	Spring		Summer		Fall	
	F	P>F	F	P>F	F	P>F
	(C ₃)		(ANPP)		(C ₄)	
Year	0.78	0.385	6.73	0.003	18.73	<0.001
2 × precipitation	0.88	0.356	1.97	0.168	8.91	0.005
Warming	0.35	0.556	0.00	0.961	0.15	0.700
Year × precipitation	0.09	0.760	2.25	0.118	7.60	0.002
Year × warming	20.8	0.0001	0.52	0.601	0.13	0.881
Precipitation × warming	0.06	0.803	3.71	0.060	0.11	0.744
Year × precipitation × warming	0.01	0.935	1.69	0.196	0.14	0.868

Year was designated a repeated factor. Significant effects and interactions are highlighted in italics.

inset); in fall 2002, plots assigned to the doubled precipitation and warmed plus doubled precipitation treatments had the greatest biomass (Fig. 1c, inset), yet in spring 2003, control and double precipitation plots had the least biomass (Fig. 1a).

Peak summer biomass, or ANPP, was significantly stimulated by double precipitation (Table 1 and Fig. 1b) during the treatment year only. Warming also had a large but nonsignificant stimulating effect on green summer biomass (Table 1 and Fig. 1b) during the treatment year.

In fall, double precipitation significantly reduced production in 2003, and still had a slightly depressive effect in 2004, but there was no effect of warming (Table 1 and Fig. 1c).

Aboveground biomass differed significantly between years in summer and fall, but not in spring (Table 1) and generally corresponded to differences in seasonal rainfall across the three years. Highest spring biomass occurred in 2004, while 2002 had the greatest summer and fall biomass (Fig. 1). Lowest summer and fall biomass was in the dry year of 2003 (Fig. 1).

Functional groups as proportion of green biomass

Warming promoted the production of C₄ plants in the fall only (Table 2, Fig. 2). During the summer, warmed plots had a smaller proportion of C₄ biomass and more C₃ biomass than other plots in all the three years, indicating a pre-existing condition (Table 2, Fig. 2). Among summers, 2004 had a greater proportion of C₃ plant biomass than previous years for all the treatments.

In fall, the effects of year, warming, and the three-way interaction of year × precipitation × warming were statistically significant (Table 2). In fall 2002, the proportion of C₃ biomass was quite low, but increased in 2003 and 2004 (Fig. 2). In fall 2003, during the treatment year, the warmed and warmed plus double precipitation plots

Table 2 Results of a repeated-measures ANOVA on the proportion of green biomass consisting of C₄ species

Effect	Summer		Fall	
	F	P>F	F	P>F
Year	5.69	0.006	7.75	0.001
2 × precipitation	4.48	0.040	0.13	0.725
Warming	6.62	0.014	4.46	0.041
Year × 2 × precipitation	0.70	0.503	1.85	0.171
Year × warming	0.53	0.594	1.32	0.279
2 × precipitation × warming	0.87	0.357	1.10	0.758
Year × 2 × precipitation × warming	0.35	0.707	3.68	0.034

Year was designated as the repeated factor. Significant effects and interactions are highlighted in italics.

had for the first time a higher proportion of C₄ plants and a lower proportion of C₃ plants than the other treatments. For the formerly warmed plots, this effect carried over into fall 2004 (Fig. 2), 9 months after treatments were discontinued. The former warmed plots continued to have a much higher proportion of C₄ and lower proportion of C₃ in fall 2004 than other treatments (Fig. 2). Control, 2 × precipitation, and warming plus 2 × precipitation all had high proportions of C₃ plants in the fall of 2004 (Fig. 2).

Temperature and soil moisture

Relative to the temperature in control plots, the air temperature at 15 cm decreased by 0.4 °C in the double precipitation plots, increased by 4.2 °C in the warmed plots, and by 4.8 °C in the warming plus doubled precipitation treatment during the treatment period. The warming effect of the heaters was greater during the summer months and less in the winter months, presumably due to a canopy effect that reduced heat

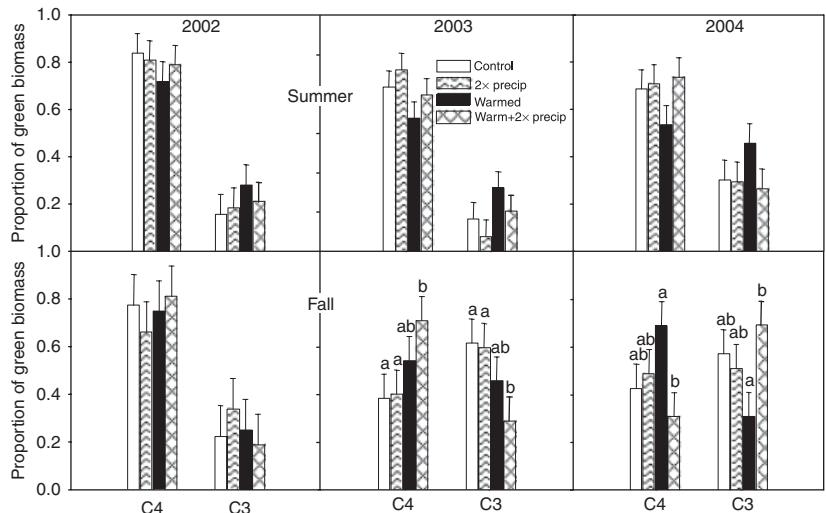


Fig. 2 C_3 and C_4 biomass as a proportion of the total green biomass for summer and fall over 3 years. Top panel is summer data; lower panel is fall. Similar letters indicate treatments that are not significantly different within a season and year ($P < 0.05$).

convection from the soil surface during the summer. Soil temperature in warmed and warmed plus doubled precipitation plots was higher than that measured in control and doubled precipitation plots at all soil depths during the treatment year. After the heaters were turned off, temperature of air and soil down to 15 cm immediately returned to the level of the control in all plots (Fig. 3). There was a slight lag in temperature recovery in the deeper soil layers of warmed plots with the deepest layer showing the slowest recovery time of 3 weeks (arrows in Fig. 3, bottom right).

Total annual precipitation at the site during the observation period was 824, 622, and 965 mm for the years 2002, 2003 and 2004, respectively (Oklahoma Climatological Survey). Throughout the study period, increases in soil moisture corresponded to recent rains (Fig. 4). Although treatments were assigned to plots arbitrarily, soil moisture differed significantly between plots before the treatments began, such that the plots assigned to the doubled precipitation treatment had lower soil moisture in the uppermost layer than the other plots (Fig. 4b). All the plots displayed increasing average soil moisture with depth, even during the treatment year (Fig. 4).

Soils in the 0–15 and 15–30 cm depths immediately began to dry when heaters were turned on (Fig. 4b and c). However, soil moisture did not begin to show differences between treatments until it rained on March 12, 2003 (Fig. 4b and c). Afterward, control and doubled precipitation plots generally had similar levels of soil moisture in the top two layers, while the warming plus doubled precipitation treatment had less, and warming plots had the least (Fig. 4d–f). Exceptions were during rainfalls, when all the plots had similar high levels of soil moisture in the upper most layer, and during the

extremely dry period in the fall of 2003 when warming plus doubled precipitation plots had soil moisture levels similar to those measured in the warming plots in the 15–30 cm layer (Fig. 4c). Over the treatment year, soil water content in the surface 15 cm averaged $19.9 \pm 0.9\%$ in the control ($n = 5$), 21.3% in the double precipitation treatment ($n = 1$ functioning TDR), $14.4 \pm 0.4\%$ in the warming treatment ($n = 2$), and $16.4 \pm 0.4\%$ in the warming and doubled precipitation treatment ($n = 3$). In the deepest three soil layers, doubled precipitation plots had the highest soil moisture, followed by control plots, then warming plus doubled precipitation plots, and finally, warming plots (Fig. 4d–f). One exception occurred during the fall drought of 2003, when soil water content of control and warming plus doubled precipitation plots were similar in the 90–120 cm layer (Fig. 4f).

Following the end of treatments on February 20, 2004, soil moisture in the surface layer (0–15 cm) of warmed plots did not recover to the level of the control plots for over 3 weeks, when it rained heavily on March 17, 2004 (Fig. 4b and c). The recovery period in deeper soil layer was progressively longer, and, at the 90–120 cm layer, soil moisture in warmed plots did recover for over 10 months (Fig. 4f). Shortly, after treatments ended on February 20, 2004, warming plus double precipitation plots regained their pretreatment year position of having higher soil water content than other plots in the uppermost soil layer (Fig. 4).

Soil nitrogen availability

Soil mineral N as measured by the PRS probes is shown in Fig. 5. During the summer of the treatment year,

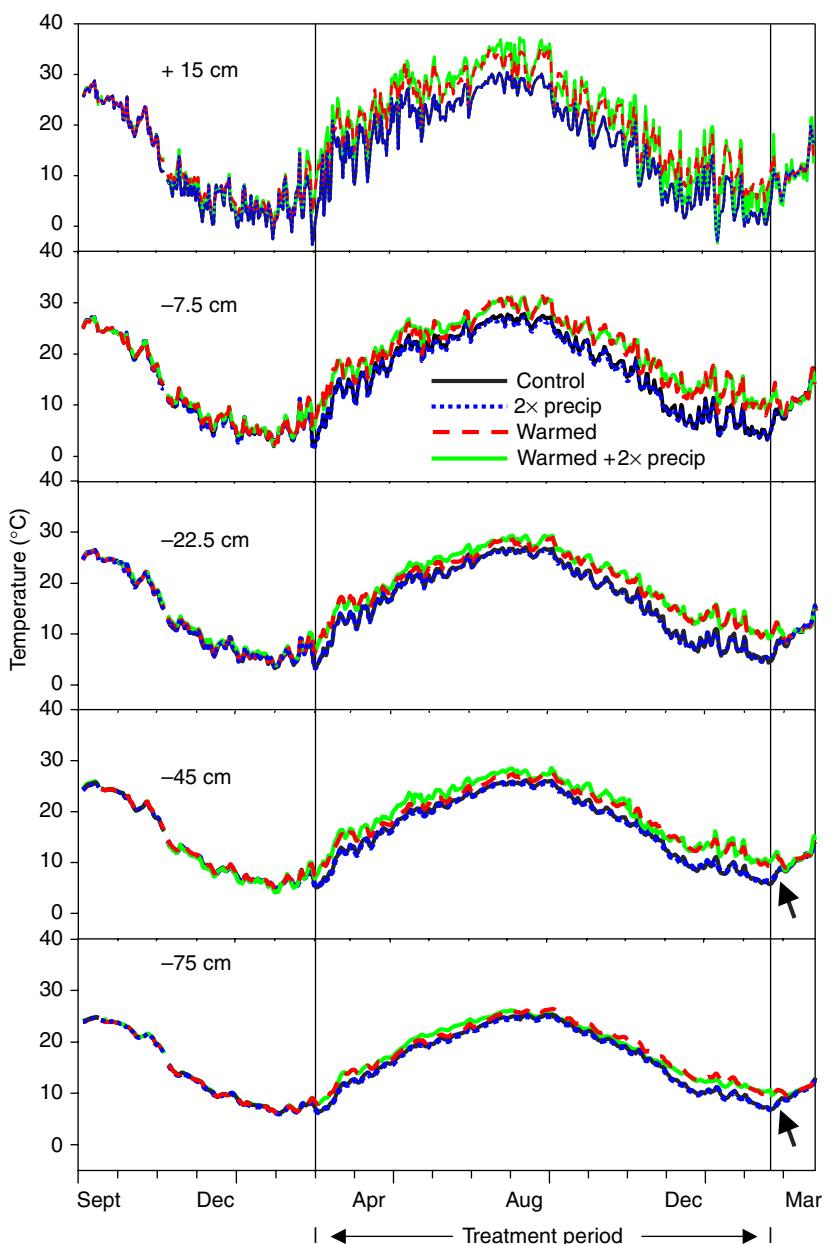


Fig. 3 Daily average temperature at 15 cm above the soil surface and at four depths below the surface. Dark vertical bars indicate the treatment period, from February 20, 2003 to February 20, 2004.

mineral N levels in the warming treatment were greater than the other treatments, but this dropped to insignificance in the fall sampling. In the winter of 2004, however, the warming treatment once again showed greater mineral N than the other treatments. These patterns do not positively correlate with those in biomass, where the greatest response was in the 2 × precipitation treatment, with the warming treatment being no different from any of the other treatments. Indeed, in the fall of the treatment year (2003), biomass in the warming treatment was significantly lower than some of the other treatments. Perhaps lower N uptake

because of water limitations in the warming treatment is the reason that soil N availability was greater in the warming treatment in the following winter of 2004. The PRS probes are generally sensitive to plant uptake, reflecting greater nutrient availability when uptake rates are low and lesser N availability when uptake is high (Hangs *et al.*, 2004).

TECO model simulation

When the measured soil moisture at the 15–30 cm level was used to force the TECO model and the N-miner-

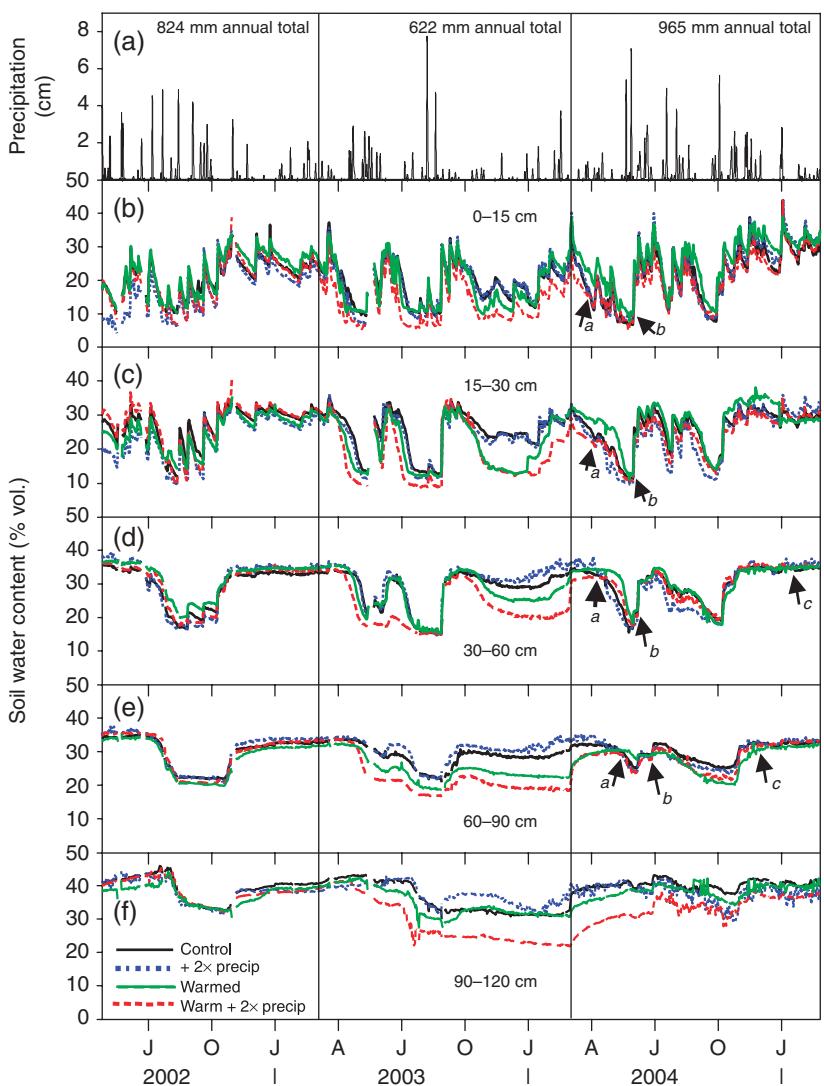


Fig. 4 Daily rainfall and soil moisture at five different depths for the study period: (a) daily rainfall (Oklahoma Mesonet). (b–f) daily soil moisture at five different depths. The dark vertical lines represent the treatment period. Arrow a indicates the point in 2004 when soil moisture in the warmed treatment recovered to the level of the control in each soil layer. Arrow b indicates the point at which all four treatments were approximately equal, and arrow c indicates the point at which the patterns of the level of soil moisture in plots assigned to the different treatments returned to that of the pretreatment year.

alization subprocesses were turned off, the overall simulation results approximately reproduced the pattern of total observed biomass from each treatment, including the spring 2004 lag (Fig. 6). The model did, however, delay fall senescence time compared with observations. For the spring of 2003 and 2004, the simulation correctly predicted the rank order of treatments, although the modeled biomass values for warmed plots are slightly larger than the observed values in 2003 and in 2004. The best corresponding values for the observed spring 2004 data in the simulation are 9 weeks later than measured (arrow a in Fig. 6). Rank order of treatments in summer does not fit the simulation, although the model did reproduce the low

biomass of the former warmed plus double precipitation plots in July of 2004 (arrow b in Fig. 6), again with a date shift. The model successfully accounts for lag effects seen in 2004 by considering only soil moisture.

Discussion

Temperature and precipitation as predictors of biomass and ANPP

ANPP is typically positively related to both precipitation and temperature in grasslands and other ecosys-

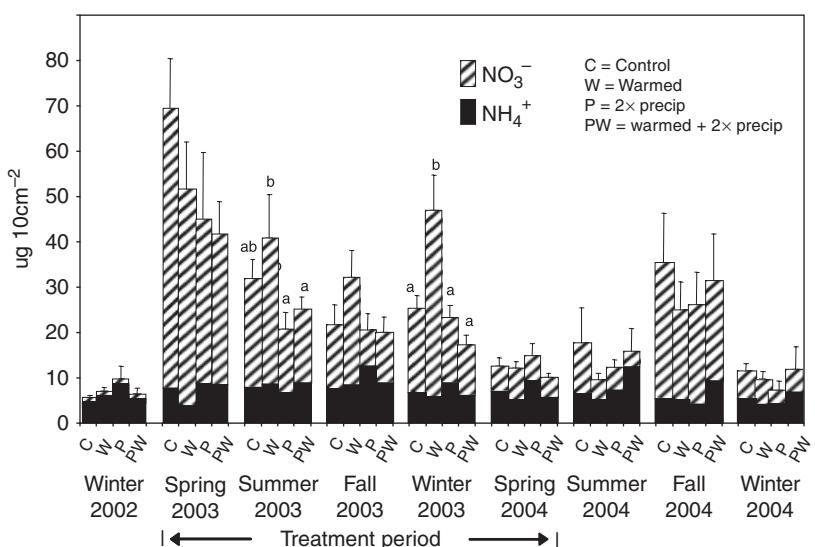


Fig. 5 Available soil N measured as NO_3^- and NH_4^+ . Similar letters indicate treatments that are not significantly different within a season and year ($P < 0.05$).

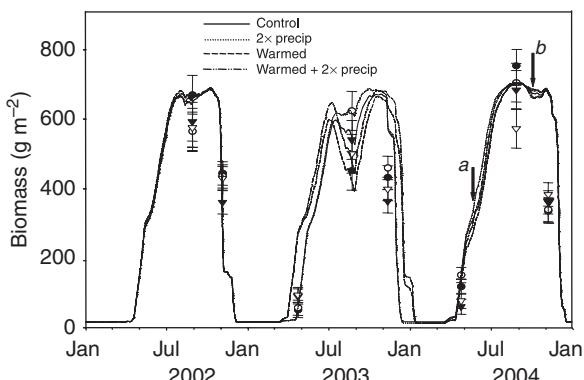


Fig. 6 Results of terrestrial ecosystem model simulation (curves). Symbols are total observed biomass: ●, control; ○, double precipitation; ▼, warmed; ▽, both warmed and double precipitation. Arrows a and b indicate times in the spring and summer of 2004, respectively, when simulated relative biomass of the four treatments matches the observed ranks of total biomass measured in the experiment.

tems world-wide (Sneva & Hyder, 1962; Noy-Meir, 1973; Lauenroth, 1979; Le Houérou *et al.*, 1988; McNaughton *et al.*, 1989; Paruelo *et al.*, 1999; Knapp & Smith, 2001). However, the relationship between precipitation and ANPP is usually tighter than that between temperature and ANPP (Sala *et al.*, 1992), probably because warming almost always lowers soil moisture (Rustad *et al.*, 2001; Wan *et al.*, 2002; but see Zavaleta *et al.*, 2003). This would explain the results of the current study, in which warming increased biomass during the first spring, but decreased biomass when soil moisture was limiting the following spring. Corre-

spondingly, double precipitation increased biomass during a droughty summer. Such results are in line with other studies demonstrating an interaction between warming and drought in their effect on biomass, such as that of Peñuelas *et al.* (2004) who, at four shrubland sites, found that warming increased biomass in northern areas but had no effect in dry southern areas. A more curious result of this experiment is the decreased fall production in the double precipitation plots during the treatment year (Fig. 1c). This is likely due to the significantly greater proportion of C₃ plants in these plots during the fall (Fig. 2). At this site, most C₃ species are winter annual, active only during the spring and in the fall after the rains begin. However, in 2003, the autumn was quite dry, lacking the typical October rains (Fig. 4a).

Two studies in particular point to the central role of precipitation in determining ANPP. Sala *et al.* (1988) found that precipitation was sufficient to explain regional variation in ANPP ($r^2 = 0.90$) but that temperature also needed to be taken into account when examining sites over time. Additionally, Epstein *et al.* (1997) found that relationships between temperature and ANPP in the Great Plains disappeared when MAP was held constant. Temperature had a greater affect on biomass at lower levels of precipitation, under 80 cm yr⁻¹.

Using soil moisture as an index (rather than precipitation) could integrate both precipitation and the drying effects of warm temperatures. Though not designed to predict ANPP, the TECO model, which incorporates soil moisture, was adequately able to reproduce the patterns of biomass over time seen in this experiment. If ANPP were related to soil water potential, rather than to

precipitation or soil moisture, perhaps an even tighter relationship could be found, as soil water potential would include effects of soil texture, as well as temperature and precipitation. To account for and reproduce lag effects, perhaps future modeling studies may examine more of the various proposed mechanisms of lag effects, as well as precipitation, temperature, species composition, and soil texture (Epstein *et al.*, 1997). The work of Knapp *et al.* (2002) suggests that variation in soil moisture should also be included in such models. They found that variation in ANPP is more closely related to variation in soil moisture than to mean soil water content. When soil moisture varies dramatically within a year, ANPP is decreased, indicating that interruptions in water supply can be more important than the total annual moisture. Previous year's climate or biomass also needs to be taken into account in models because of the effects of numbers of individuals and meristems on biomass (Lauenroth *et al.*, 1994; Goward & Prince, 1995; Anderson & Inouye, 2001; Osterheld *et al.*, 2001; Yahdjian & Sala, 2006). Wiegand *et al.* (2004) used a 'memory index' combining the effects of the current and previous year's climate in their model for predicting ANPP. They found that temperature and 'memory' can dampen lag effects.

Lagged effects of warming and precipitation on plant biomass

We observed lag effects of 2 months on spring production and 9 months on fall production and the proportion of C₄ species. The drop in green biomass in the doubled precipitation plots compared with other treatments in the fall of the treatment year (Fig. 1c) seems anomalous, but could possibly be explained by an increased proportion of C₃ species in those plots. In this ecosystem, C₃ species grow most in the relatively cooler temperature of spring, while C₄ species come to dominate during the warm summer and fall. In fact, fall C₄ production is highly correlated to total fall green biomass ($r^2 = 0.89$; R. A. Sherry, unpublished data).

The drying effect of temperature on soil moisture adequately explained the patterns and differences in biomass between treatments during the treatment period, and 2 months later in the spring of 2004. Increased mineral availability due to increased decomposition was unlikely to have contributed to these biomass differences during the treatment year, because the patterns of available soil N did not correlate with the patterns of biomass. The warming treatment had greater available N than all the other three treatments during the treatment year, while in terms of biomass, the warming and the warming plus 2 × precipitation treatment were comparable throughout the treatment year.

Lower N uptake because of water limitation in the warming treatment could explain the greater soil N availability in the warming treatment during the treatment year. The lack of a role of available N in contributing to our results was also supported by the TECO model simulation. The influence of factors such as meristem limitation and differences in recruitment on aboveground biomass were not addressed in this study, but is likely to be involved in the greater fall biomass of warmed plots, both during the treatment year, and the following fall.

Responses of functional groups

During the fall of the treatment year (2003), warmed and warmed plus 2 × precipitation plots had a significantly higher proportion of their biomass represented by warm season (C₄) grasses than the control and 2 × precipitation treatment. This is not surprising because of the increased water-use efficiency (WUE) of C₄ grasses and their greater photosynthetic efficiency at higher temperatures (Sage & Monson, 1999). Another warming experiment in the same area has also demonstrated a shift to more C₄ grasses with warming (Wan *et al.*, 2005). In the fall of the posttreatment year (2004), the former control, double precipitation, and warming plus double precipitation plots still had a low proportion of C₄ plants, while the formerly warmed plots had recovered to their former levels of C₄ plants (Fig. 4). The large proportion of C₃ in the formerly warmed plus 2 × precipitation in the fall of 2004 plots may be explained by the high soil moisture of these plots during the posttreatment year (Fig. 2), indicating that plants in this ecosystem are capable of fairly rapid responses to heat and moisture levels.

Heat and drought do not always increase C₄ species relative to C₃ species. Alward *et al.* (1999) reported a decrease in the dominant C₄ grass and increases in C₃ species with increasing minimum temperatures in the Colorado steppe. Epstein *et al.* (1998) found C₃ species to have a negative relationship to MAP. Lauenroth *et al.* (1978) and Knapp *et al.* (2001) found that warm season grasses increased with increased water. Some of these differences can be explained if C₃ shrubs, a large component of the vegetation at some of the above sites, and C₃ forbs (common at our site) have different responses to warming and precipitation. However, as differences in response to temperature and water have been found within one functional group or lifeform (Chapin & Shaver, 1985; Llorens *et al.*, 2004; Peñuelas *et al.*, 2004; Sebastiá, 2007), some of these inconsistencies may be due to species-specific responses.

Species composition can also interact with precipitation, temperature, and soil texture in determining

ANPP. Sebastiá (2007) saw that a shift from grasses to forbs caused increased biomass with decreased water availability in a subalpine grassland. Coleman & Bazzaz (1992) found that total final biomass of a C₃ species was greater than that of a C₄ species grown under the same increased temperature conditions, even though early growth of the C₃ species was slowed. In our study, production was decreased in fall 2004 in double precipitation plots, presumably because fall growth is largely in C₄ species at our site and the double precipitation plots were enriched in C₃ species (Fig. 2). When Epstein *et al.* (1998) examined their data at the species level, mean annual temperature, rather than precipitation, was the more important variable determining production in 55% of the species they studied. Differential species responses to changes in precipitation and temperature are likely to coincide with demographic changes. Williams *et al.* (2007) found that warming could differentially affect growth, seed production, seedling emergence, and establishment in different species. At their field experiment in Tasmania, they found that warming had greater negative effects on demographic parameters of the two forb species they examined than on the C₃ and C₄ grass species.

Conclusion

In addition to actual ANPP data from grasslands and other terrestrial ecosystems, lag effects are predicted in models of ANPP, and are seen in satellite normalized difference vegetation index and atmospheric CO₂ data. Our data experimentally corroborates these observations of lag effects while demonstrating one mechanism – a lag in soil moisture recharge. This correlation does not necessarily preclude the simultaneous action of other mechanisms, such as meristem limitation (Benson *et al.*, 2004; Dalgleish & Hartnett, 2006). Although other contributing mechanisms for lag effects are not entirely excluded, experimental and TECO model simulation results indicate that soil moisture alone can adequately account for large portions of observed lags in primary productivity in this study and rules out a large role for available N.

Our warming and doubled precipitation experiment demonstrated that warming increased plant productivity in spring if soil moisture was adequate. During summer and fall, or under spring drought, soil moisture became the major determinant of plant biomass. Our study showed that a deficit in soil moisture due to warming continued to affect spring plant productivity at least 2 months after treatments were stopped. For proportion of C₃ and C₄ functional groups, the lag was up to 9 months, even though these functional groups also demonstrated that they could respond quickly to

greater soil moisture. In the 0–15 cm layer of soil, soil moisture in warmed plots took 3 weeks to return the levels of control plots after treatments ended. For the lowest level of soil examined, the lag in soil moisture recharge over 10 months. This lag in soil moisture recharge and biomass production can partly explain the lags seen in atmospheric CO₂ concentration following anomalous years, as well as production lags seen in other studies of ANPP.

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