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ARTICLE

Warmer and wetter climate promotes net primary production in C_4 grassland with additional enhancement by hay harvesting

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Abstract

Grassland ecosystems provide essential services to society. To maintain ecosystem functions and services of grasslands under changing environments, it is critical to understand how grasslands respond and feedback to climate change. Here, we present results from a long-term (16 years) warming and clipping (to mimic hay harvesting or grazing) experiment conducted in a grassland ecosystem dominated by C_4 grasses in the Great Plains, USA. We analyzed responses of net primary production (NPP), aboveground NPP (ANPP), and belowground NPP (BNPP) to the expanded ranges of climate conditions observed in the experiment. NPP, ANPP, and BNPP all responded to the climatic variables nonlinearly, with higher degrees of nonlinearity for BNPP than that for ANPP. BNPP peaked at the optimum air temperature of 17.5–18.5°C while ANPP peaked at the optimum air temperature of 18.5–20.0°C. The optimum air temperatures for both ANPP and BNPP were higher than mean annual temperature (16.3°C) at the site. The optimum precipitation for BNPP was intermediate levels (775–1250 mm) while ANPP was maximized in wetter conditions (1250–1605 mm) compared with BNPP. Clipping significantly reduced ANPP and shifted the optimum conditions for BNPP to warmer and wetter conditions. In summary, C_4-grass dominant ecosystems have the potential to increase NPP in future warmer and wetter conditions, and clipping may amplify this positive effect in this grassland ecosystem.

KEYWORDS
climate change, clipping, grassland, hay harvesting, net primary production, warming experiment

INTRODUCTION

Net primary production (NPP) is a carbon (C) flux that links terrestrial ecosystems with the atmosphere and thus it is a major process that can trigger ecosystem C cycle feedbacks to climate change (Field et al., 2007; Luo, 2007). As many models have widely projected increasing temperature trends along with altered precipitation regimes in future, it is vital to understand how NPP responds to changes in temperature and precipitation and feedbacks to climate change (Franklin et al., 2016; IPCC, 2013a; Sala et al., 2017). Yet, predicting responses of NPP to climate change is still challenging due to the nonlinearity and the complex interactions between climatic factors (Huston, 1997; Yachi & Loreau, 1999).

The roles of temperature and precipitation in regulating ecosystem production varied across ecosystems as well as different components of NPP, that is, aboveground NPP (ANPP) and belowground NPP (BNPP) (Field et al., 2007; Luo, 2007; Mooney & Gulmon, 1979). For example, warming stimulated ANPP in colder ecosystems (Rustad et al., 2001), but reduced ANPP in warmer ecosystems (Lin et al., 2010). Similarly, above-average temperature was beneficial to sagebrush productions in colder areas but detrimental in hotter areas (Kleinhesselink & Adler, 2018). Warmer climate enhanced foliage biomass while root biomass was inhibited by warmer climate in forests (Lilley et al., 2001). In grass-legume ecosystems, BNPP was also found to have a negative relationship with temperature (Lilley et al., 2001; Reich et al., 2014).

In addition to temperature, changes in precipitation can also have significant impacts on ecosystem production. BNPP increased from drought to wetter treatments in a mixed-grass prairie (Byrne et al., 2013). Similarly, BNPP in a tallgrass prairie had a positive relationship with increased precipitation (Xu et al., 2012). In a synthesis study, Wu et al. (2011) concluded that increases in precipitation stimulated ANPP and BNPP. In contrast, other studies reported no effects of increased precipitation on ecosystem production (Kleinhesselink & Adler, 2018; Rustad et al., 2001). Temperature and precipitation could also interactively affect ecosystem production, but the interactive effects were generally smaller than the single effect of temperature or precipitation (Wu et al., 2011). Importantly, studies on interactive effects of temperature and precipitation are still inadequate to fully understand when and where climate change would stimulate or depress ecosystem production.

Due to the existence of nonlinear responses of ecosystem production to temperature and precipitation, identifying optimum climatic conditions for ecosystem production is critical to assess whether climate change will increase or decrease ecosystem production. Numerous studies have observed nonlinear responses of ecosystem production (i.e., NPP, ANPP, and BNPP) to temperature and precipitation (Knapp et al., 2016; Luo et al., 2017; Schlenker & Roberts, 2009; Zhu et al., 2016). Fox example, according to Zhu et al. (2016), ecosystem production generally exhibited saturated or symmetrical responses to changing climatic conditions. Wilcox et al. (2017) also found that the sensitivity of BNPP to altered precipitation declined with mean annual precipitation. With increasing frequency of climate extremes (IPCC, 2013a, 2013b), it is important to understand whether nonlinear responses of ecosystem production to temperature and precipitation are likely to become more common.

Moreover, land-use management, such as hay harvesting and grazing, can not only directly influence plant production but also have indirect effects on plant production through its interactions with climate variables (Canadell & Schulze, 2014; Gao et al., 2008). As hay harvesting or grazing physically removes aboveground parts of plants, it usually leads to higher temperature and lower soil moisture by changing light availability (Collins et al., 1998; Wan et al., 2002). Alternatively, clipping may help conserve soil moisture by reducing transpiration of leaves (Frank et al., 2018). Clipping decreased ANPP but increased carbon allocation to belowground production (Gao et al., 2011; Shi et al., 2016; Xu et al., 2012). Furthermore, clipping was found to modify precipitation effects on ANPP and BNPP in a tallgrass prairie, depending on levels of precipitation: negative and positive precipitation effects under normal and lower precipitation conditions, respectively (Xu et al., 2013). Therefore, the regulations of clipping on the responses of ecosystem production to climate change need to be further examined.

In this study, we examined how ecosystem production (i.e., NPP, ANPP, and BNPP) of a grassland dominated by C_4 plants responded to climate condition (i.e., temperature and precipitation) and how the responses were modified by land management practice in a long-term (16 years) warming and clipping experiment in the Great Plains, USA. We tested three hypotheses: (1) ecosystem production (i.e., NPP, ANPP, and BNPP) nonlinearly responds to temperature and precipitation; (2) interactions between temperature and precipitation positively affect ecosystem production; and (3) clipping reduces ecosystem production in higher levels of climatic conditions (i.e., warmer and wetter conditions). We further projected NPP, ANPP, and BNPP in a temperature-precipitation space to determine the optimum climate conditions for ecosystem production using the relationship between climate variables and ecosystem production.

MATERIALS AND METHODS

Descriptions of the long-term experiment

The long-term experimental site was located in the Kessler Atmospheric and Ecological Field Station in central Oklahoma in the Great Plains, USA (34°58′31.8″N, 97°31′19.6″W), which had remained uncultivated and ungrazed for 40 years before the experiment began in 1999. The site was mostly dominated by C_4 grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and few C_3 forbs (*Ambrosia psilostachya*, *Solidago nemoralis*, and *Solidago rigida*). During the experimental period from 1999 to 2015, mean annual temperature for this site was 16.0°C, ranging from 15.3 to 20.0°C. Mean annual precipitation of the study period was 837 mm, ranging from 515 to 1605 mm. The driest year (2005) and wettest year (2015) were classified by the Standardized Precipitation Evapotranspiration Index (SPEI), with SPEI being <-2 and >2, respectively (Jung et al., 2019).

In 1999, 12 square plots of 2 m in length were established. Each plot was subdivided into four equal-sized subplots (1 m × 1 m). The experimental design was a nested design with warming as the main factor and clipping as a nested treatment with six replicates. To treat the plots for continuous warming year-round, we suspended infrared (IR) heaters (Kalglo Electronics, Bethlehem, PA, USA) 1.5 m above the ground with a radiation output of 100 W/m^2. The control plots with ambient temperature had dummy heaters to ensure a similar shading effect. There was a buffer area of 3 m between the warmed and control plots to avoid heating the control plots. Plants in two diagonal subplots were clipped at a height of 10 cm above the ground once a year in peak biomass season, usually in July or August to mimic hay harvesting. The other two subplots remained unclipped. After clipping the plants, the materials were removed from the plots, used for measurements of ANPP, and not returned back to the plots.

IR warming can cause dry-down of shallow soil layers, especially during those periods with less rainfall as artifact effects (Kimball et al., 2018; Sherwood & Fu, 2014). However, our measurements showed that soil moisture content in the warmed plots was not significantly lower than that in the control plots in most of the time (except winter time) (Jung et al., 2019; Wan et al., 2002). Therefore, this warming method simulated the environmental conditions under future climate warming (1.4–5.8°C in the 21st century) (IPCC, 2013a; Wan et al., 2002). On average, daily mean air temperature was increased by 1.4°C in our warming experiment (Jung et al., 2019).

Measurements of climatic data

Air temperature was measured by sheltered thermocouples at a height of 25 cm above the ground in the center of each control and warming plots. Detailed information on the air temperature measurements has been described previously (Luo et al., 2009). Missing data of temperature due to mechanical issues of the data logger or the probes were estimated through regressions between available data and reference air temperatures from the Washington station of Oklahoma Mesonet, which was located 200 m away from the study site ($R^2 > 0.98$ and $p < 0.01$) (Brock et al., 1995; McPherson et al., 2007). The annual precipitation data during the study period from 2000 to 2015 were obtained from the Mesonet station.

The radiative energy emitted by the IR heating system will be converted to thermal energy when the radiation hits any objects, such as leaves and soil surface. Therefore, the air temperature measured at 25 cm above the ground within a canopy, which was approximately 1 m tall, over the growing season potentially reflected aerodynamic mixing of heat dissipated from the leaves, soil surface, and ambient air. In general, the measured air temperature in this study could closely represent leaf temperature because boundary layer conductance was high for the narrow grass leaves and wind speed was high in this Great Plains area (Brock et al., 1995; Gates et al., 1965; McPherson et al., 2007; Sinolair, 1970; Vogel, 2009). Thus, as a grass-dominant ecosystem with high wind speed, air temperature in this ecosystem was a suitable metric for assessments of temperature effects on plant production.

Plant production measurements

NPP and its components, ANPP and BNPP, were measured at peak plant biomass each year. For ANPP, we weighed oven-dried (65°C for 72 h) clipped plant biomass as described earlier for the clipping treatment. Plant biomass, that is, ANPP, in unclipped plots was estimated indirectly with a pin-contact method (Frank & McNaughton, 1990). Detailed procedure for estimating aboveground biomass in unclipped plots was described previously in Sherry et al. (2008). Briefly, we counted total hits of C_3 and C_4 plants in both unclipped and clipped plots in peak biomass season, including four directions that the pin frame faced. Then we established correlations between total hits and biomass of both C_3 and C_4 plants in the clipped plots, using a regression method. These correlations were applied to the unclipped plots to estimate the biomass in unclipped plots. The coefficients of the regressions ranged from 0.51 in August of 2002 to 0.84 in August of 2003 (Luo et al., 2009). BNPP was estimated with the root ingrowth-core method (Gao et al., 2008). We took soil samples sequentially from the following three depths: 0–15, 15–30, and 30–45 cm, with soil cores of 4.05 cm in diameter in both unclipped and clipped subplots within each plot in the fall of each year. The sequential soil cores were taken from the same spot in each subplot to estimate annual root growth, that is, BNPP. We backfilled the holes using soils in similar layers from adjacent area; that is, we took soils from shallow (0–30 cm) and deep (30–90 cm) layers and sieved soils to remove roots before putting into the holes. Root samples were gently washed, oven-dried at 70°C for 48 h, and weighed to calculate BNPP. For this analysis, root biomass from the entire depth of 0–45 cm was used. No root samples were taken in 2000–2004 and root samples were not processed in 2011, so data of BNPP and NPP were missing for these years.

Data analysis

We used the linear-mixed effect model in this study. This model has been applied to the Jasper Ridge Global Change Experiment and its assumptions (i.e., linear and nonlinear terms as main effects and interactive term as interactive effect) have been described in detail (Zhu et al., 2016). In this study, we used two environmental variables, annual mean air temperature (T) and annual precipitation (P), as the continuous variables and clipping treatment (C) as the categorical variable to represent whether or not a plot was clipped.

To conduct the analysis, we first tested time-dependent effects, that is, the progressive effect, of treatments (i.e., warming, clipping, and interaction of warming and clipping) using standard analysis of variance (ANOVA). Despite significant treatment effects in some years, coefficients of ANOVA did not show significant temporal trends (i.e., $p > 0.05$ for the linear regressions between years and significant coefficients of ANOVA) (Appendix S1: Figure S1).

To test how the ecosystem production responded to the environmental factors, in the linear mixed-effects model, the main and interactive environmental factors were set as fixed effects and the plots were set as random effects (Bates et al., 2015). Linear functions for T, P, and C, as well as quadratic functions for T^2 and P^2 were used. Since there were only two environmental factors, temperature–precipitation interaction ($T{:}P$) was used to test their interactive effect. Ecosystem production, that is, NPP, ANPP, and BNPP, was log-transformed to satisfy normality before any statistical analysis. To ensure the environmental variables were statistically comparable, T and P were standardized by subtracting mean and divided by standard deviation (SD). Because of the log-scaled ecosystem production and standardized environmental variables, the estimated climate effects were interpreted as proportional changes in plant production (d log y, where d was the proportional change and y was NPP, ANPP, or BNPP) with respect to the change of a SD in environmental parameters (dx, where x was a SD of T or P), $d \log y/dx = (dy/y)/dx$. The estimated clipping effects were interpreted as changes in log plant production with respect to the clipping treatment (C). The estimated coefficients for environmental factors (T and P) and clipping treatment (C) were summarized in Table 1.

The nonlinear model with a quadratic function was selected since it fit our data better than the linear model according to Akaike information criterion (AIC). AIC is an index of the goodness of fit of a model, including a penalty for overfitting. We used a model having lower AIC value. Although delta AIC (difference between nonlinear and linear models) of ANPP was relatively smaller (i.e., 3.0) than delta AIC of NPP (i.e., 44.9) and BNPP (i.e., 56.3), nonlinear model for ANPP was the best model and substantially different from the linear model since delta AIC of ANPP was larger than 2 (Burnham & Anderson, 2004). The selected models explained 29% (NPP), 31% (ANPP), and 29% (BNPP) of the observed variations. AIC values of linear and nonlinear models for NPP, ANPP, and BNPP were shown in Appendix S1: Table S1.

The nonlinear model, which was selected as the best one, was then used to predict the plant production in the response surfaces. We calculated expected plant production using the environmental variables for each treatment. Continuous temperature and precipitation used for

TABLE 1 Model coefficients (means and 95% confidence intervals)

Coefficient	NPP	ANPP	BNPP
T^2	−0.039 (−0.075, −0.003)	0.005 (−0.029, 0.039)	−0.107 (−0.176, −0.039)
P^2	−0.131 (−0.166, −0.095)	−0.036 (−0.062, −0.009)	−0.274 (−0.342, −0.207)
T	0.118 (0.065, 0.171)	0.096 (0.044, 0.148)	0.092 (−0.01, 0.194)
P	0.148 (0.088, 0.208)	0.153 (0.095, 0.211)	0.111 (−0.004, 0.225)
C	−0.003 (−0.075, 0.069)	−0.167 (−0.237, −0.098)	0.056 (−0.082, 0.193)
T:P	0.034 (−0.03, 0.098)	0.06 (0.002, 0.119)	−0.035 (−0.157, 0.088)
T:C	−0.011 (−0.085, 0.063)	−0.009 (−0.081, 0.062)	0.037 (−0.104, 0.178)
P:C	−0.01 (−0.082, 0.062)	0.063 (−0.006, 0.133)	−0.043 (−0.18, 0.094)
T:P:C	0.07 (−0.018, 0.159)	−0.046 (−0.125, 0.033)	0.193 (0.025, 0.362)

Note: Model structure: Plant production (net primary production [NPP], aboveground NPP [ANPP], or belowground NPP [BNPP]) ~ $T^2 + P^2 + T + P + C + T{:}P + T{:}C + P{:}C + T{:}P{:}C + (1|\text{Plot})$. T: Temperature; P: Precipitation; C: Clipping; T:P: Temperature–precipitation interaction; T:C: Temperature–clipping interaction; P:C: Precipitation–clipping interaction; T:P:C: Temperature–precipitation–clipping interaction.

the predictions were 15.2–20.1°C and 485–1650 mm, respectively. Categorical factors for clipping treatment were 0 for unclipped control and 1 for clipped treatment. We then visualized the prediction results by temperature and precipitation under unclipped or clipped conditions.

To evaluate model performance, we did in-sample predictions to compare the modeled plant production with the observed plant production. Overall, the model predicted plant production well ($r_{\mathrm{NPP}} = 0.65$, $r_{\mathrm{ANPP}} = 0.55$, and $r_{\mathrm{BNPP}} = 0.58$; Appendix S1: Figure S1a). Modeled and observed NPP, ANPP, and BNPP were close to the 1:1 reference line.

To test model assumptions of normality, residual diagnostics regarding progressive (year-dependent) effects were performed. If progressive year effects were present, the residual (i.e., unexplained component of observed data) would be correlated with year. However, the residuals in diagnostics did not show such correlations (Appendix S1: Figure S2b). The histogram in Appendix S1: Figure S2c validated the assumption of normality of the model residuals. All analyses were performed with the packages "lme4" (Bates et al., 2015) and "ggplot2" (Wickham, 2009) in R (version 3.3.1) (R Core Team, 2016).

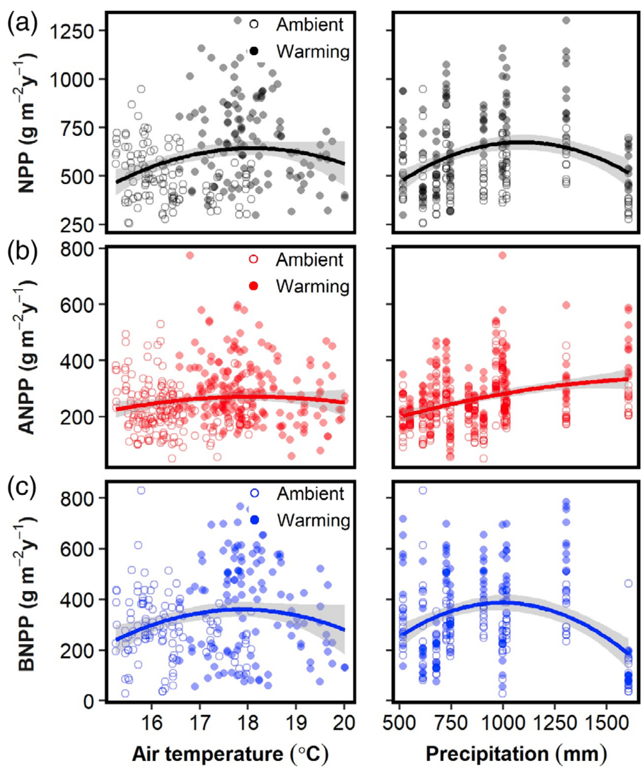

FIGURE 1 Nonlinear responses of plant production to air temperature and precipitation. Hollow and filled circles indicate ambient and warming treatment, respectively. Black, red, and blue colors represent net primary production (NPP) (a), aboveground NPP (ANPP) (b), and belowground NPP (BNPP) (c), respectively. Gray shading shows 95% confidence interval

RESULTS

Nonlinear responses of plant production to temperature and precipitation

In the study period, annual air temperature ranged from 15.3 to 20.0°C with a threefold difference in annual precipitation (505–1605 mm) (Figure 1). The ranges of precipitation in this study fell beyond from 10th to 90th percentiles over the past 120 years of historical precipitation (Jung et al., 2019). Both relationships between NPP and BNPP and climatic variables, that is, air temperature and precipitation, showed unimodal shapes (hump-shape) (Figure 1). Negative warming effects on BNPP were larger than ANPP, resulting in decreases in NPP with higher

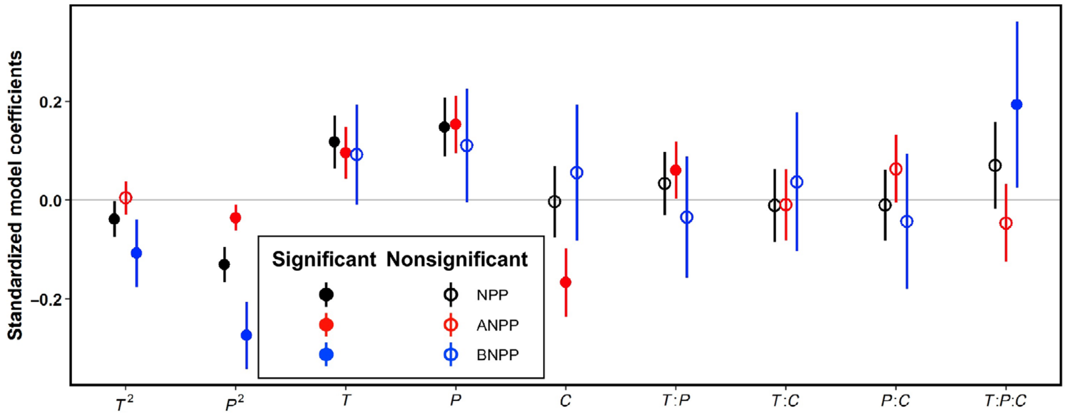

FIGURE 2 Standardized model coefficients. Circles indicate model's coefficients within 95% confidence interval. Sample sizes of net primary production (NPP), aboveground NPP (ANPP), and belowground NPP (BNPP) are 240, 384, and 240, respectively. *T*: Temperature; *P*: Precipitation; *C*: Clipping; *T*:*P*: Temperature–precipitation interaction; *T*:*C*: Temperature–clipping interaction; *P*:*C*: Precipitation–clipping interaction; *T*:*P*:*C*: Temperature–precipitation–clipping interaction

temperature (Figure 1). For example, warming caused hump-shaped responses of NPP and BNPP, both of which peaked at the intermediate temperature range (17.5–18.5°C) that was slightly higher than the long-term averaged temperature (17.2°C). However, ANPP did not exhibit a clear hump-shaped relationship in comparison to NPP and BNPP. Similar to the responses of plant production to air temperature, clear hump-shaped relationships of NPP and BNPP with precipitation were observed, having the peak production at the intermediate level of precipitation (900–1100 mm; Figure 1), which was slightly higher than long-term averaged precipitation (873 mm). ANPP also exhibited a nonlinear response to precipitation but followed a saturating rather than hump-shaped pattern (Figure 1).

Coefficients for the linear mixed effect model

Except for ANPP response to temperature, the standardized quadratic coefficients (T^2 and P^2) in the linear mixed effect model for fitting the relationship between plant production and temperature or precipitation were all significantly negative (Table 1 and Figure 2). That is, the response curves of plant production to climatic factors had concave down hump-shapes (Figure 1). The only exception to this pattern was the relationship between ANPP and precipitation, which showed a saturated pattern at the high level of precipitation and could be explained by the slightly significantly negative standardized quadratic coefficient (Figures 1 and 2).

The coefficients for the linear terms of temperature (T) and precipitation (P) in the mixed effect model were all positive, indicating increases in plant production linearly with temperature and precipitation, peaking at higher values of temperature and precipitation with exception of BNPP. Clipping (C) significantly decreased ANPP while it had no significant effects on either NPP or BNPP. The temperature-precipitation interaction was significantly positive for ANPP, suggesting that the interaction between temperature and precipitation would be an additional positive effect on ANPP since the single effects of temperature and precipitation were both positive. In addition, interactive effect among temperature, precipitation and clipping (T:P:C) on BNPP was significantly positive, meaning that the positive effects were intensified when temperature, precipitation, and clipping effects were combined.

Response of plant production to temperature and precipitation in response surfaces

Modeled plant production and its respective contour lines were codetermined by the main effects of temperature, precipitation, and clipping and their interactive effects. Within observed climate ranges, the response surfaces of NPP, ANPP, and BNPP generally showed a rising ridge pattern under unclipped and clipped conditions, that is, a simple maximum pattern, with exception of BNPP under unclipped condition (Figure 3). Temperature had a stronger effect on NPP and ANPP at higher precipitation levels, that is, between the long-term average (873 mm, horizontal gray dashed line in Figure 3) and the maximum precipitation (1650 mm). The maximum NPP and

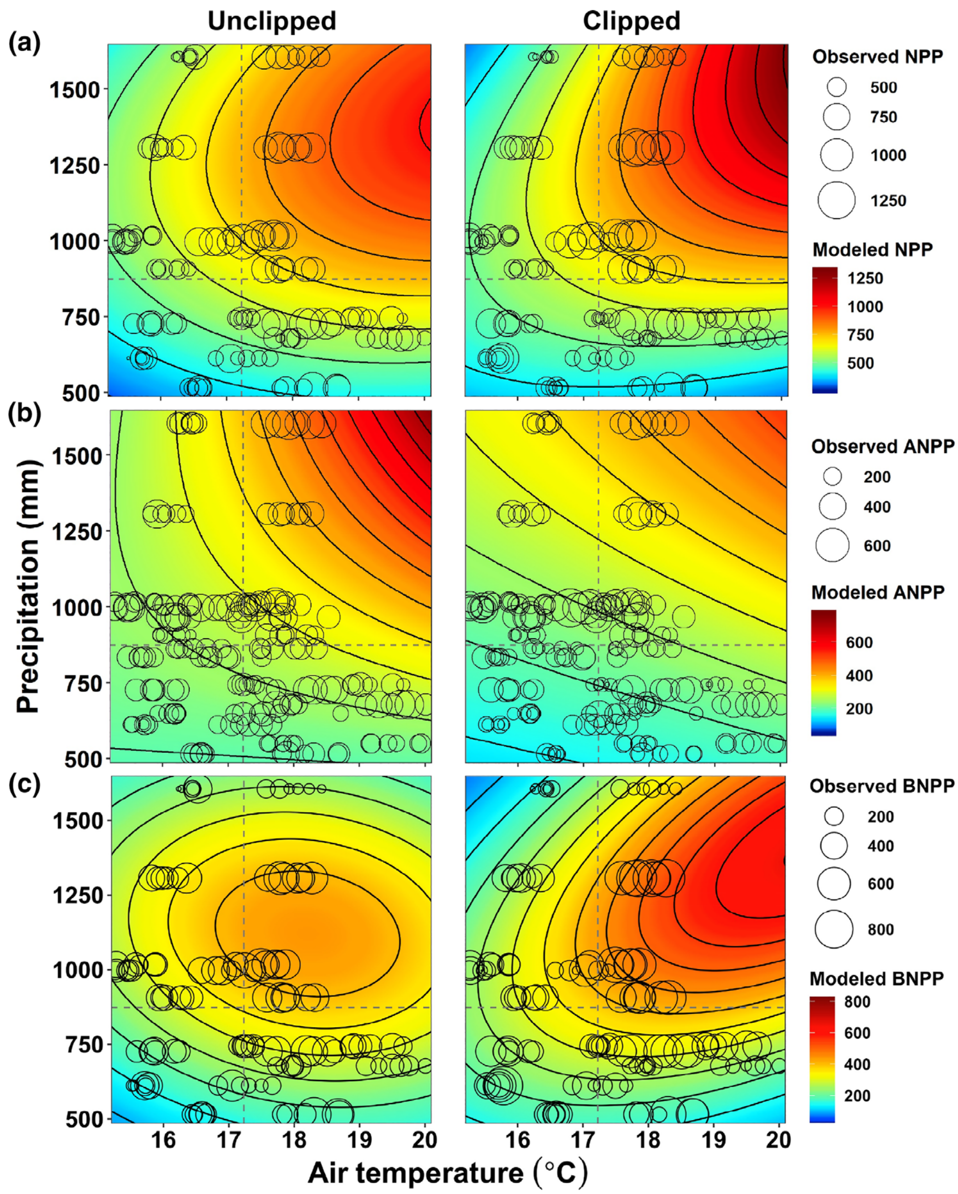

FIGURE 3 Predicted and observed net primary production (NPP) (a), aboveground NPP (ANPP) (b), and belowground NPP (BNPP) (c). The *x*- and *y*-axes are continuous air temperature (15.2–20.1°C) and annual precipitation (485–1650 mm), respectively. Gradient colors with contour lines indicate modeled results. Bubbles represent observed data collected from each plot. Vertical and horizontal gray dash lines indicate long-term average of temperature (17.2°C) and annual precipitation (873 mm), respectively

ANPP both occurred at high levels of temperature and precipitation (Figure 3a,b). In contrast, within the precipitation range between the long-term average (horizontal gray dashed line in Figure 3c) and 1490 mm, temperature increases strongly stimulated BNPP (Figure 3c). BNPP under the unclipped condition first increased with increase in temperature when precipitation was at relatively low level but started to decline with increased temperature when precipitation exceeded 1490 mm. Alternatively, BNPP can be decreased when precipitation level was drier conditions (i.e., lower than long-term average), but stimulated by decreases in precipitation from 1650 to 1490 mm. Together, BNPP reached its maximum values at intermediate level of precipitation (1000–1250 mm) and relatively high temperature (Figure 3c). Overall, clipping decreased ANPP in the response surface, but the clipping treatment shifted the optimum environmental conditions for NPP and BNPP to higher levels of temperature and precipitation.

DISCUSSION

By analyzing NPP, ANPP, and BNPP from a long-term warming and clipping experiment of 16 years, we tested three hypotheses regarding (1) nonlinear responses of ecosystem production to climatic variables, (2) interactive effects of climatic variables on ecosystem production, and (3) clipping impacts on the interaction of climate variables in regulating ecosystem production. Firstly, we found nonlinear relationships between ecosystem production and climatic variables (i.e., temperature and precipitation), except for the relationship between ANPP and temperature. Secondly, we detected a positive interactive effect of temperature and precipitation on ANPP. Lastly, clipping only amplified the interactive effect of temperature and precipitation on BNPP. Projections of NPP, ANPP, and BNPP based on those relationships revealed that warmer and wetter conditions were the optimum conditions for NPP and ANPP while BNPP reached peak values under warmer temperature but intermediate precipitation conditions. In addition, clipping shifted peak NPP and BNPP to higher temperature and precipitation levels while ANPP was significantly reduced under clipping.

Warmer and wetter climate conditions stimulate plant production

Previous studies have demonstrated that response curves of ecosystem production against climate gradients were nonlinear, that is, symmetrical and asymmetrical responses of NPP to temperature or precipitation (Knapp et al., 2017; Luo et al., 2017; Wilcox et al., 2017; Zhu et al., 2016). Consistently, our results exhibited nonlinear responses—plant production increased with climatic variables until it reached a peak at optimal condition, and then slightly decreased or saturated under higher levels of climatic conditions possibly due to life-history constraints (Hsu et al., 2012; Zhu et al., 2016). Similar patterns were reported previously in a C_3-dominated grassland in California (Zhu et al., 2016) and they found long-term average climate condition was the optimum condition for NPP, showing concave down responses to temperature and precipitation. When temperature was high and soil was moist, plants naturally tended to minimize heat stress by cooling their leaves through increased transpiration and thus more water loss (Crawford et al., 2012), which might exert a negative effect for plant production. In addition, growth suppression under high precipitation might also be attributed to more frequent cloudy days (thus less radiation for photosynthesis) and nutrient leaching (Reichstein et al., 2013; Wang et al., 2020; Zhu et al., 2016). Contrary to our results, ANPP of semiarid ecosystems showed a positive asymmetry response to precipitation: the magnitude of stimulation under extreme wet conditions was greater than the magnitude in decrease under extreme dry conditions (Felton et al., 2019). The contrasting results might be caused by different plant community compositions and ecoregion as Felton et al. (2019) have observed varied sensitivities of plant production to climate among different plant functional types in a semiarid area, that is, higher positive asymmetry of forbs than C_4 grasses.

Interestingly, while single factor of temperature or precipitation played a negative role in their higher levels in our observations (Figure 1) as well as previous studies (Schlenker & Roberts, 2009; Zhu et al., 2016), in our study site NPP would peak at warmer and wetter conditions due to combined effects of temperature and precipitation as well as their interaction (Figure 3). The negative effect of temperature or precipitation on NPP in their higher levels eliminated when the single-factor effects of temperature and precipitation were combined (Figure 3), as reflected in the response space without interaction effects (e.g., absence of T:P and T:P:C in the model; Appendix S1: Figure S3). Both empirical and modeling studies across different ecosystems (e.g., tropical, temperate, and boreal forests and grasslands) suggested that the single positive effects of temperature or precipitation on NPP would be intensified when warming was combined with additional precipitation inputs (Luo et al., 2008; Schuur, 2003; Wu et al., 2011). Since our study site was dominated by C_4 grasses, this ecosystem was expected to have higher optimum temperature and water use efficiency (Way et al., 2014; Yamori et al., 2014). While warm years were usually not wet at this site during the study period (Appendix S1: Figure S4), warmer and wetter conditions would favor production of C_4 plant species (Lundgren & Christin, 2016). In addition, more rainfall during warm months could benefit C_4 grasses (Knapp et al., 2020). As anomalies of temperature and precipitation in the Great Plains kept increasing over time (Kunkel et al., 2013), our results imply that this grassland ecosystem has a potential to increase NPP under the possible warmer and wetter climate (Allan & Soden, 2008; Greve et al., 2014; Wentz et al., 2007).

Contrasting responses of ANPP and BNPP to climatic variables

Response surfaces of ANPP and BNPP exhibited different patterns in this study as a result of their different responses to temperature and precipitation. Temperature had a significantly positive effect on ANPP and marginally positive effect on BNPP (i.e., positive coefficients of T in Figure 2). These results were consistent with previous studies documenting positive temperature effects on NPP, ANPP, and BNPP within a single ecosystem (Litton & Giardina, 2008; Reich et al., 2014; Xu et al., 2012; Xu et al., 2013) as well as across different ecosystems based on a meta-analysis (Wu et al., 2011). In fact, an earlier analysis from the same experiment as the present study concluded that increased temperature exerted positive impacts on ANPP and BNPP due to high rain use efficiency in this ecosystem (Xu et al., 2012). In contrast, in a C_3-grass dominant ecosystem, negative temperature effects on NPP, ANPP, and BNPP were detected (Zhu et al., 2016), which was distinct from the present study in a C_4-grass dominant ecosystem. It has been well understood that the optimum temperature for photosynthesis of C_4 species was generally higher than that for C_3 species (Yamori et al., 2014). Although ANPP and BNPP had similar positive responses to temperature, BNPP had a greater degree of nonlinearity than ANPP (more negative coefficient of T^2 in BNPP than ANPP in Figure 2), which might be due to higher temperature sensitivity of BNPP than ANPP (Gibson, 2009; Xu et al., 2013).

Increased precipitation enhanced ANPP before saturating at the high level of precipitation in this study (Figure 1 and significant positive and negative coefficients of P and P^2 for ANPP, respectively, in Figure 2), which was partly consistent with previous studies (Hsu et al., 2012; Huxman et al., 2004; Sala et al., 2012; Ye et al., 2017). Similarly, BNPP showed marginally significant positive response to precipitation (coefficient of P for BNPP in Figure 2) but presented greater nonlinearity than ANPP (Figure 1 and more negative coefficient of P^2 for BNPP than ANPP in Figure 2). Due to the limited number of studies about BNPP response to a wide range of precipitation, fully comparing our results with previous findings is difficult, but previous water addition treatments were found to stimulate BNPP (Wilcox et al., 2015; Xu et al., 2013). A recent synthesis demonstrated that extremely wet conditions triggered negative responses of BNPP to precipitation while ANPP kept increasing with wetter conditions (Wilcox et al., 2017), which supported our nonlinear response of BNNP to precipitation and an increasing pattern of ANPP under high precipitation despite slightly nonlinear responses. The decline of BNPP under an extremely wet condition would be attributed to decrease in root lifespan due to water logging of soil (Kozlowski, 1997).

Given these various responses of ANPP and BNPP to climate variables, different optimal conditions for ANPP and BNPP were predicted in the response surfaces. As for ANPP, the warmer and wetter conditions were optimal conditions, which was in line with previous studies: A positive warming effect on ANPP could be intensified by additional precipitation (Dukes et al., 2005; Wu et al., 2011). This effect of precipitation on ANPP was clear within intermediate–high temperature while a nonlinear effect of precipitation on BNPP was identified in the same temperature range. The nonlinear effects of precipitation on BNPP were exhibited under both drier and wetter conditions, which has been observed from previous studies (Kozlowski, 1997; Xu et al., 2013).

The regulatory role of clipping on the climate change effects

Clipping-mediated reduction in ANPP found in this study was consistent with previous studies (Carlyle et al., 2014; Shi et al., 2016). Grazing-mediated reductions in ANPP were linked to soil nutrient loss in other ecosystems (Giese et al., 2013; Liu et al., 2015); this was a potential cause of the observed reduction in ANPP in clipped plots even though we did not measure it in this study. In addition, there were less organic material inputs by removing plants (Luo et al., 2009). While clipping reduced ANPP in the overall response space, ANPP was still maximized in the warmer and wetter condition, same as under the unclipped condition (Figure 3b), indicating that clipping would not change the directions of the effects of temperature and precipitation and their interaction on ANPP. Previous studies illustrated that clipping increased temperature but decreased soil moisture by reducing shading, leading to negative effects on plant production under normal precipitation condition, but positive effects on plant production under the limited precipitation condition due to less water demands by removing plants (Li et al., 2011; Xu et al., 2012, 2013). Yet, our analysis did not detect such patterns of clipping effects. The combination of warming and clipping might have exacerbated not only soil nutrient loss via soil erosion (Xue et al., 2011), but also soil water loss, especially under water addition experiments (Zhou et al., 2006). This might explain clipping-mediated suppression of ANPP under warming via nutrient loss and stress of temperature and soil moisture (Xue et al., 2011).

On the other hand, clipping significantly altered the response surface of BNPP from simple maximum to rising ridge pattern due to its interactions with climatic variables. Clipping enhanced warming effects on BNPP, especially under higher precipitation levels due to increased rain use efficiency (Xu et al., 2012). Furthermore, BNPP was increased by warming and clipping treatments (Xu et al., 2012, 2013, 2014), which supported our results, that is, higher BNPP under clipped warmer and wetter conditions. These increases led to the pattern of stimulated NPP under warmer and wetter conditions.

Our results from a long-term experimental study suggested that warmer and wetter climate conditions, one of the climate scenarios predicted for the future in this region, could further enhance NPP in this C_4-grass dominant ecosystem. Plant production in this ecosystem responded nonlinearly to temperature or precipitation individually, with slightly negative effects under warmer or wetter conditions. However, the overall positive effects of temperature or precipitation and their interaction would offset the negative effects at high temperature and high level of precipitation. Importantly, clipping stimulated BNPP under warmer and wetter conditions but decreased ANPP with no shift in the optimum condition. Another factor that might contribute to the changes in plant production was a gradual increase in atmospheric CO_2 concentration from 369 ppm in 2000 to 401 ppm in 2015 (Keeling et al., 2005). Especially under warmer and wetter conditions, rising CO_2 concentration has been reported to enhance production of C_4 plants (Augustine et al., 2018) and suppress production of C_3 plants (Zhu et al., 2016). However, forage quality in grassland ecosystems may decrease as a result of increased production, which is a challenge to sustain high livestock yields (Augustine et al., 2018). Future research should include field experiments manipulating both temperature and precipitation as well as elevated CO_2 in order to explore not only effects of climate change on plant production under warmer and wetter conditions beyond what we have observed in this study on plant production to confirm our results, but also the potential interactive effects between climate change and rising atmospheric CO_2 concentration. Overall, our 16-year experiment highlights that possible future climate in this region, that is, high temperature and high precipitation, would favor the increase of NPP, and clipping may amplify this positive effect in this grassland ecosystem.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Chang Gyo Jung and Yiqi Luo contributed equally to this work. Yiqi Luo designed the experiments. Chang Gyo Jung, Xia Xu, Zheng Shi, Shuli Niu, Jianyang Xia, Rebecca Sherry, and Lifen Jiang collected the data. Chang Gyo Jung, Lifen Jiang, Kai Zhu, Enqing Hou, and Yiqi Luo performed data analyses. All authors discussed the results and wrote the manuscript.

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