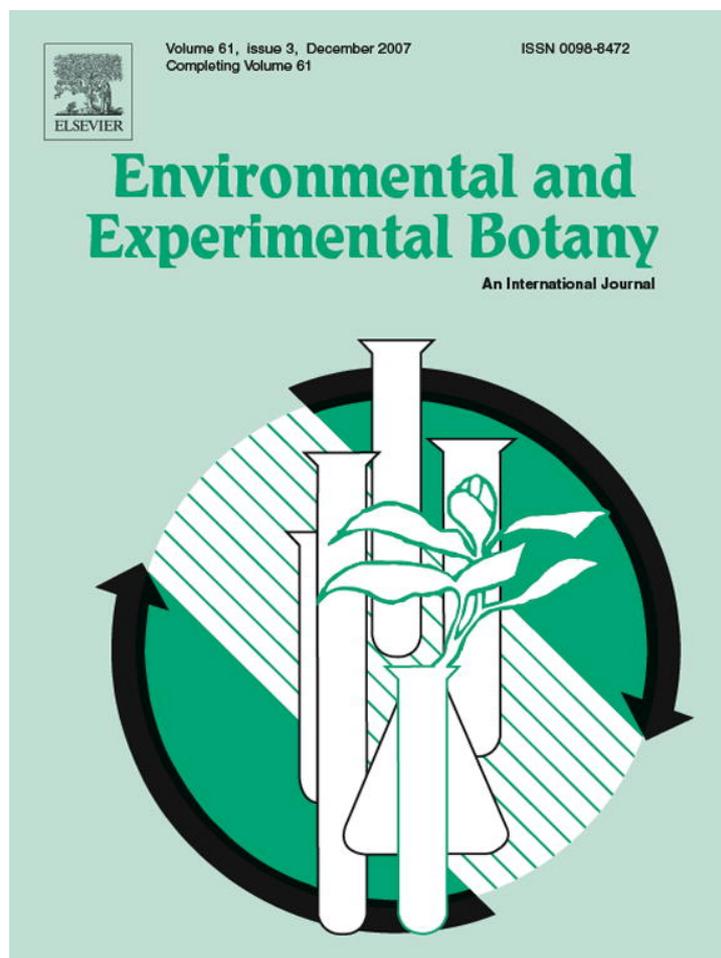


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Temperature response of C₄ species big bluestem (*Andropogon gerardii*) is modified by growing carbon dioxide concentration

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Abstract

Climate change factors interact to modify plant growth and development. The objective of this study was to evaluate the response to temperature of big bluestem (*Andropogon gerardii* Vitman) development, growth, reproduction and biomass partitioning under low and high carbon dioxide concentrations ([CO₂]) grown in controlled environmental conditions. Ten sunlit soil–plant–atmosphere–research (SPAR) chambers were used to study the effects of two [CO₂] of low (360 μL L⁻¹) and high (720 μL L⁻¹), and five different day/night temperatures of 20/12, 25/17, 30/22, 35/27 and 40/32 °C. Big bluestem cv. Bonelli seeds were sown in pure, fine sand, in 11 rows at equal spacing and after emergence were thinned to 10 plants per row. At maturity, individual plants were harvested and divided into leaves, stems, panicles and roots. Biomass decreased either above or below the optimum temperature of 30/22 °C. The effect of high [CO₂] on biomass accumulation (12–30% increase) was visible at less than optimum temperature (30/22 °C) and absent at two high temperatures. With increase in temperature, irrespective of the [CO₂], biomass partitioned to leaves increased (35%) where as that to stems decreased (33%). Panicle weight was 6–7% of biomass at 25/17 °C and fell to 1.6% at 40/32 °C. The biomass partitioned to roots, across the temperatures, was constant for plants grown at low [CO₂] but decreased by 7% for those grown at high [CO₂]. The decrease in panicle/seed production at two high temperatures (>30/22 °C) might reduce this species population and dominance in tallgrass prairies. The temperature response functions at different [CO₂] will be useful to improve the predictive capabilities of dynamic global vegetation models in simulating dynamics of rangelands, where big bluestem is the dominant species.

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Keywords: Big bluestem; Biomass; Development; Growth rates; Partitioning; Seed number

1. Introduction

Greenhouse gases continue to increase in the atmosphere with carbon dioxide concentration ([CO₂]) expected to double by the end of the century (IPCC, 2001). The increase in [CO₂] since industrialization has resulted in 0.6 °C increase of the Earth's mean temperature (Hansen and Sato, 2004). Projections indicate that the Earth's mean temperature would increase anywhere from 1.5 to 11 °C by the turn of the century (Stainforth et al., 2005). These changes in climate would alter the responses to [CO₂] and temperature of rangelands that occupy 47% of the Earth's land area and in turn the global carbon budget. It is essential to understand the response of dominant species to environmental factors in a given rangeland as the community properties are strongly influenced by the characteristics of the

dominant species (Grime, 1998; Levine, 1999). Several studies have quantified growth, development, and biomass production and partitioning of grasses in response to high [CO₂], but the effect of high [CO₂] on the temperature response of major plant species, particularly C₄ species is less explored.

Grass species with the C₄ photosynthetic cycle have capacity for higher dry matter accumulation due to higher photosynthetic rates and greater light utilization efficiency and longer growth duration (Ludlow, 1985). Big bluestem (*Andropogon gerardii* Vitman), a C₄ species, is one of the dominant grasses in the tallgrass prairie, comprising up to 80% of the biomass on favorable sites (Weaver, 1954). Big bluestem is native to grasslands of Canada, Mexico and United States (Weaver and Fitzpatrick, 1934; Risser et al., 1980). It has been widely studied for the effects of high [CO₂] on photosynthesis, morphology, physiology, growth, development and biomass (Owensby et al., 1993; Knapp et al., 1994, 1999; Chen et al., 1994; Kiniry et al., 1999; Adam et al., 2000). Photosynthesis and biomass of big bluestem were increased under high [CO₂] conditions (Owensby et al.,

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1993; Knapp et al., 1999; Adam et al., 2000). Leaf longevity of this species was also increased on exposure to high [CO₂] (Knapp et al., 1999). However, studies have not been conducted to determine the effects of the projected temperature increase along with changes projected for [CO₂] on biomass production, partitioning and reproduction of big bluestem. Studies with crop plants show a severe reduction in fruit set or seed set under supra-optimal temperature conditions (Reddy and Hodges, 2000).

The latitude and climate influence the global distribution of grass taxa (Hartley, 1958; Hartley and Slater, 1960). When all other climatic conditions are equal, C₄ plants tend to be favored over C₃ plants in warm, humid climates; conversely, C₃ plants tend to be favored over C₄ plants in cooler climates (Collatz et al., 1998; Ehleringer et al., 1997). As a result, the projected changes in climate may have profound influence on the mix of species in a given environment. The crossover day time growing season mean temperature for C₃/C₄ species under current climatic conditions is about 22 °C (Ehleringer et al., 1997). Thus, increase in temperature would move the current C₄/C₃ boundaries northward (Collatz et al., 1998). In a review of C₄ species, Porter (1993) found a 22% increase in growth by doubling atmospheric [CO₂] conditions. A 4 °C increase in temperature increased biomass of both C₃ and C₄ weed species by 19% (Hunt et al., 1996). In a later comparison of C₃ and C₄ grass species responses to high [CO₂], Wand et al. (1999) concluded that high [CO₂] increased total biomass of C₄ species by 33% due to an increase in leaf area; the species also had 25% higher carbon assimilation rate. Information about how high [CO₂] influences reproductive fitness of individual species in single and multiple species stands is not available (Bazzaz and McConaughay, 1992), and is essential to understand the population dynamics of ecosystems in future climates.

Understanding environmental effects on seed production and quality of the native grasses is essential as seeds are a valuable resource for restoration of ecosystems, commercial cultivation of pastures and man-directed germplasm improvement programs (Vogel et al., 1989). Furthermore, the current dynamic global vegetation models (DGVMs) do not simulate seed dispersal and production of the various component plant species (Cramer et al., 2001). The establishment of individual plants of each functional type in the DGVMs is either uniform as in HYBRID (Friend et al., 1997) or determined by the effect of climate on a given functional type as in IBIS (Foley et al., 1996) and SDGVM (Woodward et al., 2001). An understanding of the reproductive responses of native grasses to climate change factors such as [CO₂] and temperature would help in improving the predictive capabilities of the DGVMs.

Big bluestem has been studied extensively for growth and physiological responses to environmental stresses such as high [CO₂], soil temperature (DeLucia et al., 1992) and drought (Knapp, 1984, 1985). Little is understood about the growth and development of this species under projected higher temperatures. Much less is known about the interactive effects of high [CO₂] and higher temperatures on big bluestem, projected to occur simultaneously in the future climates. Studies in crop plants have shown that [CO₂] × temperature interaction may be detrimental to some plant species and some may remain in

vegetative phase at high temperature (Bhattacharya and Geyer, 1993) and increase in growth [CO₂] and temperature is known to shift positively the optimum for photosynthesis. Therefore, we hypothesize that under well-watered conditions higher biomass production would be favored by high growth temperature under high [CO₂] compared to that under low [CO₂] resulting in a positive shift of optimum growth temperature and big bluestem would remain vegetative under high temperature conditions irrespective of [CO₂]. To test our hypothesis, an experiment was conducted to evaluate the response to temperature (20/12 to 40/32 °C) of development, growth, reproduction, biomass and partitioning of big bluestem under low and high [CO₂] grown in naturally sunlit, controlled environment growth chambers.

2. Materials and methods

2.1. Soil–plant–atmosphere-research (SPAR) facility

The naturally sunlit, controlled-environment growth chambers used for this study are known as SPAR units. Briefly, each SPAR unit consists of a steel soil bin (1.0 m tall by 2.0 m long by 0.5 m wide), and a Plexiglas chamber (2.5 m tall by 2.0 m long by 1.5 m wide) to accommodate above ground parts. The Plexiglas transmits 96.6 ± 0.5% of incoming photosynthetically active radiation (PAR, wavelength 400–700 nm) (Zhao et al., 2003). Each SPAR unit consists of a heating and a cooling system and an environment monitoring and control system. The SPAR facility has the capability to control temperature precisely at predetermined set points for plant growth studies under near ambient levels of PAR. Details of operation and control of SPAR chambers have been described by Reddy et al. (1992, 2001).

2.2. Plant culture

Seeds of big bluestem (*A. gerardii* Vitman) cv. Bonilla (Sustained Horizons, Lake Norden, South Dakota, USA) were sown in 11 equally spaced rows (across the 2 m long soil bin) in the SPAR units on 18 May 2004. The rooting medium used to fill the SPAR soil bins was pure, fine sand. Emergence was observed 5 days later. At 7 days after emergence (DAE), plants were thinned to 10 plants per row, thus retaining 110 plants per SPAR unit. A computer-controlled timing device supplied half-strength Hoagland's nutrient solution (Hewitt, 1952) three times a day (0800, 1200 and 1600 h) to each chamber through a drip irrigation system to ensure favorable nutrient and water conditions. To simulate border plants, variable-density black shade cloths along the border of plants were adjusted regularly to match plant heights in order to simulate natural shading in the presence of other plants.

2.3. Treatments

The [CO₂] was at 360 ± 10 μL L⁻¹ and temperature was 30/22 °C until emergence in all SPAR units. At first true leaf stage (10 DAE) [CO₂] and temperature treatments were imposed simultaneously. The [CO₂] in five SPAR units was set to 720 μL L⁻¹ (high) while the other five remained at 360 μL L⁻¹

Table 1

Average of measured day, night and mean temperature during the experimental period, and average [CO₂] from a typical day during the experimental period in each treatment

Treatments		[CO ₂] ($\mu\text{L L}^{-1}$)	Temperature ($^{\circ}\text{C}$)		
[CO ₂] ($\mu\text{L L}^{-1}$)	Temperature ($^{\circ}\text{C}$)		Day	Night	Mean
720	20/12	724.5 \pm 1.64	21.0 \pm 0.11	12.7 \pm 0.10	17.4 \pm 0.11
	25/17	716.4 \pm 0.54	25.6 \pm 0.08	17.5 \pm 0.11	22.1 \pm 0.09
	30/22	711.3 \pm 0.87	29.8 \pm 0.06	21.8 \pm 0.13	26.3 \pm 0.08
	35/27	721.2 \pm 0.57	34.2 \pm 0.05	26.4 \pm 0.16	30.8 \pm 0.09
	40/32	723.2 \pm 0.82	38.5 \pm 0.08	30.5 \pm 0.19	35.0 \pm 0.11
360	20/12	364.1 \pm 0.98	20.5 \pm 0.07	12.5 \pm 0.08	17.0 \pm 0.08
	25/17	364.7 \pm 0.68	24.8 \pm 0.04	17.1 \pm 0.10	21.5 \pm 0.06
	30/22	362.3 \pm 1.13	29.7 \pm 0.03	21.9 \pm 0.13	26.3 \pm 0.08
	35/27	364.0 \pm 0.49	34.2 \pm 0.06	26.3 \pm 0.16	30.8 \pm 0.09
	40/32	363.2 \pm 0.82	39.6 \pm 0.03	31.5 \pm 0.19	36.1 \pm 0.11

(low). Five SPAR units at a given [CO₂] received five different day/night temperature treatments of 20/12, 25/17, 30/22, 35/27 and 40/32 $^{\circ}\text{C}$, with day temperature from sunrise to 1 h after sunset. The [CO₂] was monitored and controlled every 10 s and integrated over 900-s intervals throughout the day. No [CO₂] control was possible during the night time. Air temperature in each SPAR unit was monitored and adjusted every 10 s throughout the day and night, and maintained within $\pm 0.5^{\circ}\text{C}$ of treatment set points. The recorded average temperature and [CO₂] in each of the SPAR units are presented in Table 1.

2.4. Measurements

Plant height, tiller number and main stem leaf number were recorded at weekly intervals from 10 to 94 DAE. Time to first and 50% panicle emergence were recorded for all plants in each treatment. Final tiller number, number of panicle bearing tillers, panicle bearing nodes and panicles per plant were recorded at final harvest (125 DAE). At harvest, all plants were cut at the base close to the soil and each plant was separated into leaves, stems and panicles. Roots at 25 cm interval (0–25, 25–50, 50–75 and 75–100 cm) depth were obtained by washing the soil dug from the soil bin over a fine screen. Panicles and seeds were dried under shade, while all other plant components were oven dried at 70 $^{\circ}\text{C}$ for 3 days and the dry weights were recorded.

2.5. Statistical analysis

A uniformity test of the SPAR units conducted in a previous study by determining sorghum growth parameters under controlled environments indicated no statistical differences among SPAR units (Reddy, personal communication, 2000), hence, individual plants harvested from a given SPAR unit were used as replicates in the statistical analysis and to derive the standard errors. A two-way ANOVA was carried out to determine the interactive effects of [CO₂] and temperature using PROC GLM in SAS (SAS Institute, 1997). Rates of stem elongation, node and tiller addition were calculated by linear regression using PROC REG in SAS (SAS Institute, 1997). Temperature response

functions at two levels of [CO₂] were compared for differences using PROC GLM in SAS (SAS Institute, 1997). The average temperatures recorded during the treatment period in each of the SPAR units were used in fitting response functions. The standard errors of each mean were calculated and presented in the figures. Cardinal temperatures (T_{\min} , T_{opt} and T_{\max}) for growth, development and biomass components were calculated from the response functions to study the effects of [CO₂] treatments. Mathematically, the T_{\min} , T_{opt} and T_{\max} values were determined by the low temperature intercept on the x -axis, the optimum derived by the first derivative set to zero and solved, and the T_{\max} intercept on the x -axis, respectively, of each quadratic response function.

3. Results

3.1. Growth and developmental rates

The interaction between [CO₂] and temperature was not significant ($P > 0.05$) for plant height and tiller number per plant but was significant ($P = 0.02$) for main tiller leaf number per plant. Plant height was more sensitive to temperature than [CO₂]. Averaged over temperature treatments, plant height did not differ between [CO₂] treatments (Fig. 1). Among temperature treatments, plants were tallest (160 cm) when grown at 25/17 and 30/22 $^{\circ}\text{C}$ and shortest (18 cm) when grown at 40/32 $^{\circ}\text{C}$ (Fig. 1). Main tiller leaf number was lower at high [CO₂] by 6% compared to that at low [CO₂] and increased with increase in temperature. Stem elongation rate (Fig. 2), derived from the linear phase of increase in plant height over time was lower at high [CO₂] compared to the rates observed at low [CO₂] except at the lower temperature tested. Stem elongation rates declined sharply at the two higher temperatures (-38% at 35/27 $^{\circ}\text{C}$ and -87% at 40/32 $^{\circ}\text{C}$) as compared to optimum at 30/22 $^{\circ}\text{C}$. Leaf addition rates increased with increase in temperature in both [CO₂] (Fig. 2). Tiller number per plant increased by 27% with a doubling of the [CO₂], and the tiller number also increased with an increase in temperature (Fig. 3).

The days after emergence to 50% panicle initiation were not modified by the [CO₂]. However, temperature treatments

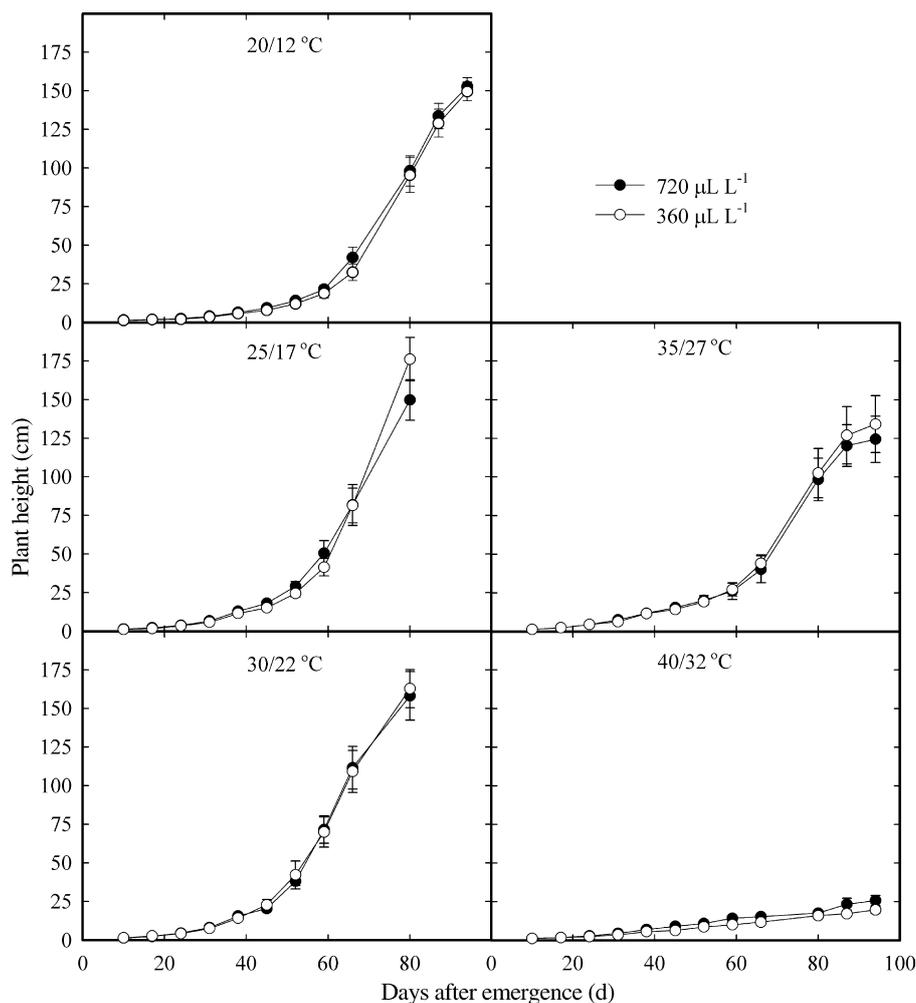


Fig. 1. Temporal trends in plants height as influenced by temperature and $[CO_2]$ on big bluestem. Error bars represent the standard error of the means ($n = 110$).

delayed time to panicle initiation on either side of the optimum of 30/22 °C. To reach 50% panicle initiation, big bluestem plants grown at 20/12, 25/17, 30/22, 35/27 and 40/32 °C took 97, 86, 77, 87, and 99 days, respectively, at high $[CO_2]$ and 96, 85, 78, 90, and 99 days, respectively, at low $[CO_2]$.

3.2. Reproductive parameters

Reproductive parameters in response to temperature followed similar trends under both $[CO_2]$ treatments. No significant ($P > 0.05$) interaction was detected between $[CO_2]$ and temperature for panicle bearing tillers, panicle bearing nodes, panicles per plant and seed number per panicle. High $[CO_2]$ reduced panicle bearing tillers and panicle bearing nodes per plant significantly ($P < 0.05$) when compared to those at low $[CO_2]$ (Fig. 3). The responses to temperature of the reproductive parameters followed quadratic trends with defined optima, above or below which decreases were recorded (Fig. 3). Seed number per panicle also followed a quadratic trend in response to temperature, with no significant difference between $[CO_2]$ treatments (Fig. 4). Plants grown at 20/12 and 40/32 °C produced similar number of panicles, but the panicles at 40/32 °C did not set seed at either $[CO_2]$.

3.3. Biomass and components

High $[CO_2]$ increased per plant leaf dry weight significantly ($P < 0.0001$) over low $[CO_2]$ (Fig. 5). Leaf weight at high $[CO_2]$ was 24% higher than that at low $[CO_2]$. No significant difference was observed between $[CO_2]$ treatments for stem weight, panicle dry weights or total dry weight of above-ground parts. In contrast, temperature treatments led to significant differences in leaf, stem and panicle dry weights (Fig. 5). Leaf dry weight increased with increase in temperature; in contrast, stem and panicle dry weights were reduced by temperatures on either side of the optima (Fig. 5). Similar to stem weight, root dry weight decreased numerically with increase in temperature. Root weight was numerically higher in the high $[CO_2]$ treatment at temperatures lower than the optimum of 30/22 °C (Fig. 5). High $[CO_2]$ -grown plants had higher total biomass than low $[CO_2]$ -grown plants, but the difference was not statistically significant (Fig. 6).

3.4. Partitioning

The partitioning of dry matter between leaves, stems, panicles and roots across $[CO_2]$ treatments and in response to tempera-

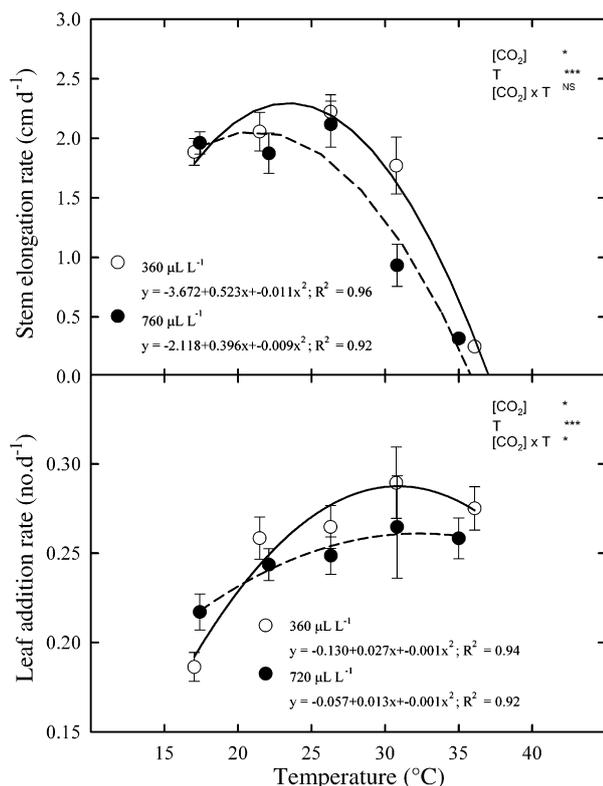


Fig. 2. The effect of [CO₂] and temperature treatments on stem elongation and leaf addition rates of big bluestem. Temporal trends in plant height and main tiller leaf number, between 10 and 97 days after emergence, were used to derive the rates. The average temperatures recorded for each temperature treatment at a given [CO₂] during the treatment period (emergence to harvest) were used to fit the response functions. Regression analysis using PROC GLM in SAS (SAS Institute, 1997) showed the quadratic model was significant ($P < 0.05$) in describing temperature response, but the difference between [CO₂] was not significant ($P > 0.05$). Standard errors of the means are shown. Significance levels for [CO₂], T and [CO₂] × T are shown: *** $P < 0.001$; * $P < 0.05$; NS, non-significant ($P > 0.05$).

ture is shown in Fig. 6. Partitioning of biomass towards leaf and stem tissues (Fig. 7) followed opposite trends. Averaged over the [CO₂] levels, increase in temperature increased partitioning to leaves from 15 to 50%, while partitioning to stems was reduced from 48 to 20%. Partitioning to panicles was not much affected from 20/12 to 35/27 °C, and ranged from 4 to 7%, but was reduced to 2% at 40/32 °C. The [CO₂] treatments modified the partitioning to roots. Partitioning to roots was constant across the temperature treatments at low [CO₂], but at high [CO₂] a 7% decrease in root partitioning was observed with increase in temperature from 25/17 to 40/32 °C.

3.5. Growth and developmental responses to temperature

The quadratic regression equations were solved to derive the cardinal temperatures for each of the processes and to understand if [CO₂] treatments modified plant response to temperature. The temperature response functions of several growth parameters at high [CO₂] moved to cooler temperatures on average compared to values derived at low [CO₂] (Figs. 2–5). The T_{min} values identified for stem elongation, leaf addition and tiller per plant

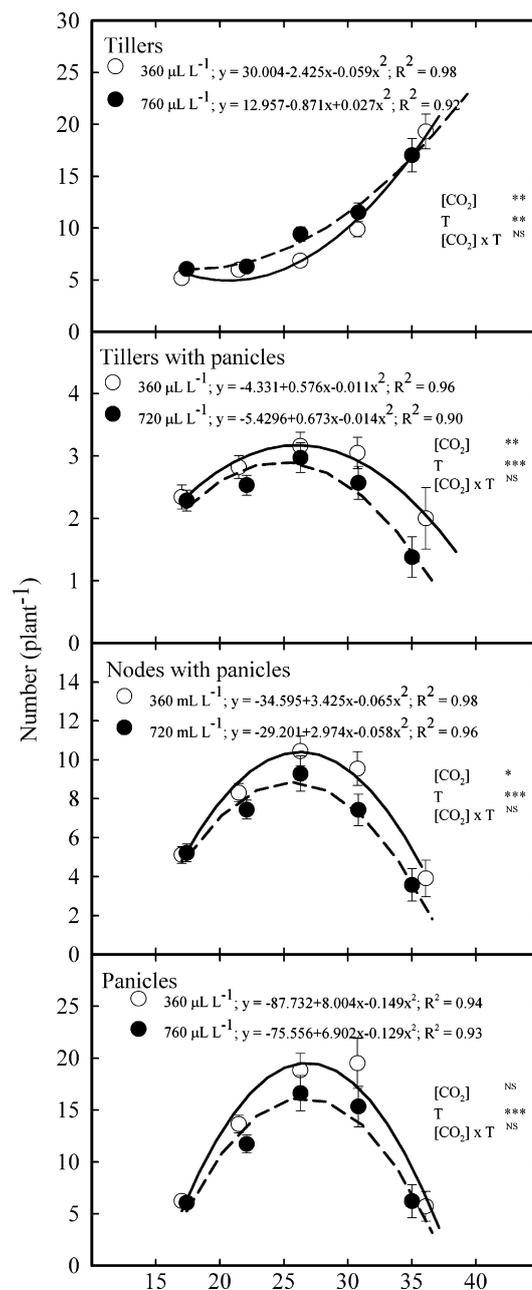


Fig. 3. The [CO₂] and temperature effects on tiller number, panicle bearing tillers, panicle bearing nodes and panicle number per plant measured at final harvest (125 days after emergence) of big bluestem. The average temperatures recorded for each temperature treatment at a given [CO₂] during the treatment period (emergence to harvest) were used to fit the response functions. Regression analysis using PROC GLM in SAS (SAS Institute, 1997) showed the quadratic model was significant ($P < 0.05$) in describing temperature response, but the difference between [CO₂] was not significant ($P > 0.05$). Standard errors of the means are shown as vertical bars. Significance levels for [CO₂], T and [CO₂] × T are shown: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, non-significant ($P > 0.05$).

may not be reliable estimates as we lack enough points towards the lower temperature range (Table 2). The T_{max} at high [CO₂] compared to low [CO₂] was reduced from 0.5 to 3.5 °C for stem elongation and tillers, panicles and stem weight per plant, while it was increased by 0.5–3.4 °C for panicle and total biomass weight and seed number per plant. The T_{opt} decreased for many

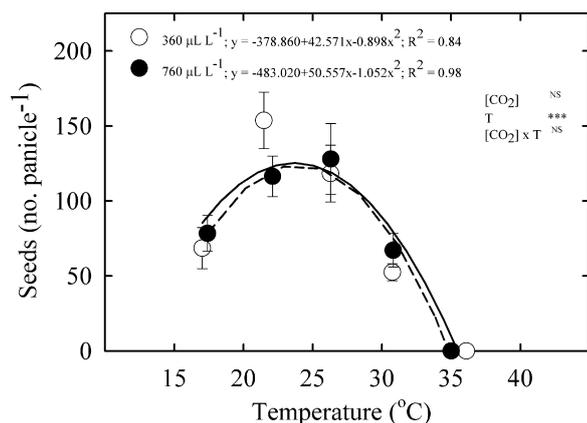


Fig. 4. Response to temperature of seed number per panicle ($n = 10$; 10 panicles from each treatment were counted for filled and unfilled spikelets) of big bluestem at low ($360 \mu\text{L L}^{-1}$) and high ($720 \mu\text{L L}^{-1}$) $[\text{CO}_2]$. Regression analysis using PROC GLM in SAS (SAS Institute, 1997) showed the quadratic model was significant ($P < 0.05$) in describing temperature response, but the difference between $[\text{CO}_2]$ was not significant ($P > 0.05$). Standard errors of the means are shown as vertical bars. Significance levels for $[\text{CO}_2]$, T and $[\text{CO}_2] \times T$ are shown: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, non-significant ($P > 0.05$).

of big bluestem growth and development parameters under high $[\text{CO}_2]$ (Table 2). The optima for growth rates of stem elongation and leaf addition decreased by 2 and 2.4°C , respectively. The T_{opt} for tiller number per plant decreased from 20.7°C at low

$[\text{CO}_2]$ to 16.0°C at high $[\text{CO}_2]$. The T_{opt} for stem, root and total dry weight were lower at high $[\text{CO}_2]$ by 1.6, 2.5 and 1.4°C , respectively, compared to those at low $[\text{CO}_2]$. The temperature optima for reproductive parameters were also modified under high $[\text{CO}_2]$ (Table 2). The T_{opt} for days to 50% panicle initiation was 29.5°C at low $[\text{CO}_2]$, while it was reduced to 26.3°C at high $[\text{CO}_2]$. At high $[\text{CO}_2]$, the T_{opt} for panicle bearing tillers and panicle bearing nodes were reduced by 1.3 and 0.7°C . The T_{opt} for panicles per plant did not change. In contrast, the T_{opt} for panicle weight was increased 1°C , whereas for seed number the increase in T_{opt} was only 0.2°C at high $[\text{CO}_2]$ compared to those at low $[\text{CO}_2]$.

4. Discussion

The effects of $[\text{CO}_2]$ and temperature are expected to co-occur both in the present and future climates. The present study, under controlled environment, sunlit, well irrigated and fertilized conditions, provides ample evidence for the stronger effect of temperature than $[\text{CO}_2]$ in regulating growth and development of big bluestem. Overall, growth and developmental processes recorded a lower optimum temperature under high $[\text{CO}_2]$ than under low $[\text{CO}_2]$. Big bluestem has been widely studied to determine the effects of current and projected future $[\text{CO}_2]$ on growth (Knapp et al., 1994; Owensby et al., 1993; Bremer et al., 1996).

Table 2
Calculated cardinal temperatures of various growth and development parameters of big bluestem (*Andropogon gerardii* Vitman) grown at a range of temperatures and atmospheric $[\text{CO}_2]$

Parameter	$[\text{CO}_2]$ ($\mu\text{L L}^{-1}$)	Cardinal temperatures ($^\circ\text{C}$)		
		T_{min}	T_{opt}	T_{max}
Stem elongation (cm d^{-1})	360	8.6	23.0	37.3
	720	6.3	21.0	35.8
Leaf addition (leaves d^{-1})	360	5.2	33.9	62.6
	720	-4.3	31.5	67.3
Tillers (plant^{-1})	360	-10.0	20.7	51.3
	720	-11.1	16.0	43.1
Panicles (plant^{-1})	360	15.4	26.8	38.3
	720	15.4	26.6	37.8
50% Panicle initiation (days)	360	2.6	30.0	57.4
	720	5.6	26.7	47.7
Leaf Weight (g plant^{-1}) [†]	360	-7.88 (I) ^a	0.68 (S) ^a	Linear fit
	720	-3.75 (I)	0.43 (S)	
Stem weight (g plant^{-1})	360	8.8	24.4	40.1
	720	8.3	22.8	37.3
Panicle weight (g plant^{-1})	360	12.5	26.9	41.4
	720	11.0	27.9	44.8
Root weight (g plant^{-1})	360	11.6	27.3	43.0
	720	2.3	22.8	43.4
Total biomass (g plant^{-1})	360	10.0	27.1	44.2
	720	4.9	25.7	46.6
Seed number (plant^{-1})	360	11.1	23.3	35.4
	720	11.1	23.5	35.9

^a Response to temperature for leaf weight was linear, I and S in parentheses indicate intercept and slope of the linear fit.

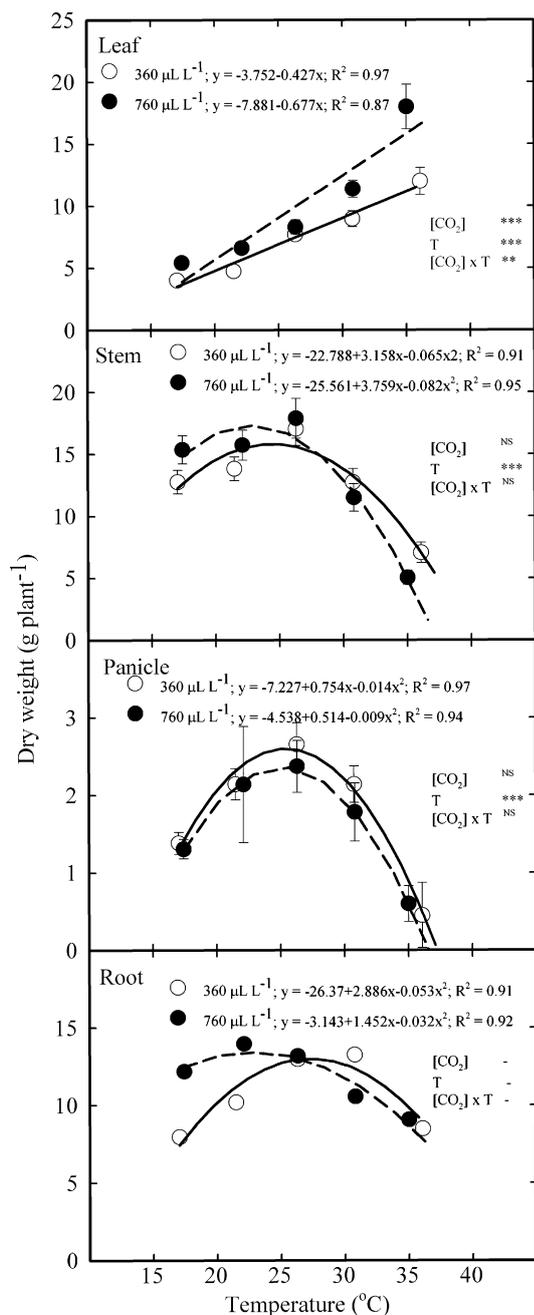


Fig. 5. Effects of $[\text{CO}_2]$ and temperature on biomass components measured at final harvest (125 days after emergence) of big bluestem. Plants were separated into leaves (leaf and sheath), culms (of all tillers), panicles (of all tillers) and roots (per plant was derived by dividing the total root weight of each SPAR unit by number of plants). Standard errors of the means are shown as vertical bars; root weight values have no error bars as no statistical analysis was possible. Significance levels for $[\text{CO}_2]$, T and $[\text{CO}_2] \times T$ are shown: *** $P < 0.001$; ** $P < 0.01$; NS, non-significant ($P > 0.05$); (-) not analyzed.

In the present study, a significant interaction between $[\text{CO}_2]$ and temperature was detected for only the main tiller leaf number and leaf weight per plant. Similarly, in a study with *Bouteloua gracilis* (blue grama), a C_4 species, Read and Morgan (1996) observed that only leaf dry weight was enhanced at high $[\text{CO}_2]$. In our study, plants grown at low temperature had more leaves in the high $[\text{CO}_2]$, while at optimum and above optimum tempera-

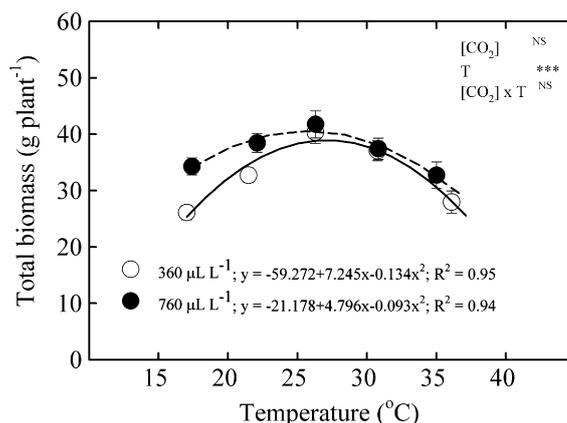


Fig. 6. Biomass of big bluestem at 125 days after emergence grown at two $[\text{CO}_2]$ and five different temperatures. The average temperatures recorded for each temperature treatment at a given $[\text{CO}_2]$ during the treatment period (emergence to harvest) were used to fit the response functions. Regression analysis using PROC GLM in SAS (SAS Institute, 1997) showed the quadratic model was significant ($P < 0.05$) in describing temperature response, but the difference between $[\text{CO}_2]$ was not significant ($P > 0.05$). Standard errors of the means are shown. Significance levels for $[\text{CO}_2]$, T and $[\text{CO}_2] \times T$ are shown: *** $P < 0.001$; NS, non-significant ($P > 0.05$).

tures more leaves were observed in the low $[\text{CO}_2]$ treatment. The greater increase in tiller number per plant at high $[\text{CO}_2]$ resulted in a final increase in per plant leaf weight, even though a slight but significant decrease in leaf number was observed. The decrease in leaf addition at high temperatures under high $[\text{CO}_2]$ conditions could be due to an increase in meristem and leaf temperature above the treatment temperature due to a decrease in stomatal conductance. In a recent study with two native Australian C_4 species (*Astrelba lappacea* and *Bothriochloa bladhii*) under greenhouse conditions, midday leaf temperature was higher than the treatment temperature by 0.4–0.5 °C when $[\text{CO}_2]$ increased from 350 to 700 $\mu\text{L L}^{-1}$ and higher by 0.8–1.0 °C when $[\text{CO}_2]$ increased from 350 to 1200 $\mu\text{L L}^{-1}$ (Siebke et al., 2002).

The absence of a significant growth response to high $[\text{CO}_2]$ observed in this study, particularly at optimum temperatures is similar to several earlier studies with big bluestem. Carbon dioxide acts as a resource and also regulates water use (Morse and Bazzaz, 1994). In big bluestem, the effect of high $[\text{CO}_2]$ on growth and biomass is due to the water-use regulator role of $[\text{CO}_2]$. For instance, Owensby et al. (1993) observed high $[\text{CO}_2]$ does not enhance growth of big bluestem under well-watered conditions; however, biomass and leaf area, averaged over several clippings, increased under water deficit conditions due to increased water-use efficiency through reduced stomatal conductance and lower transpiration rates, compared to plants grown at low $[\text{CO}_2]$. The lack of increase in biomass under well-watered conditions is due to the weak direct response of C_4 photosynthesis to $[\text{CO}_2]$ and water-use efficiency has little role in irrigated environment (Wilsey et al., 1994). The ratio of assimilation at 700–350 $\mu\text{L L}^{-1}$ $[\text{CO}_2]$ was 1.02 in big bluestem (Polley et al., 1992), providing evidence for the lack of increase in biomass under high $[\text{CO}_2]$ conditions in the present study. This small response of photosynthesis and biomass accumulation to high $[\text{CO}_2]$ under well-watered conditions is not unique

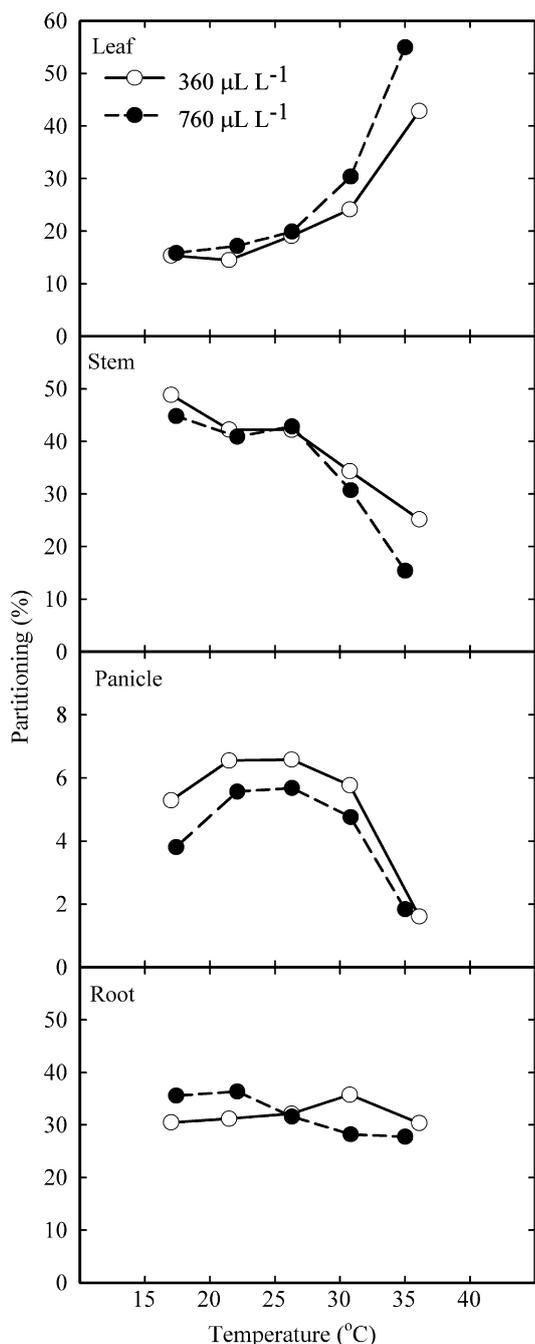


Fig. 7. Biomass partitioning to leaves, culms, panicles and roots of big bluestem grown for 125 days after emergence at two $[CO_2]$ and five different temperatures.

to big bluestem; similar observations were made by Read and Morgan (1996) in another C_4 species, *B. gracilis* (blue grama).

The C_4 monocots are principal components of relatively undisturbed natural ecosystems such as prairies, tropical grasslands and savannas. Production of grasslands is predicted to change under projected climatic scenarios (Coughenour and Chen, 1997). Big bluestem is the principal component of tall grass prairies in the United States. Any change in the potential growth and development of the dominant species may severely affect the carbon assimilation and in turn alter the global carbon cycle. Temperature plays a major role in regulating the CO_2

balance of plants as it affects both assimilation and respiration (Morison and Lawlor, 1999). The response to temperature suggests that big bluestem performs best near optimum growth temperatures of 30/22 °C. However, increase in temperature enhanced the vegetative parameters such as tiller number and leaf weight across the tested temperature range in this study. The increase in vegetative growth is crucial to the spread of the species or its movement across the temperature crossover boundary of C_3 - C_4 species; as it is predicted to move northward (Ehleringer et al., 1997). Silletti and Knapp (2002) concluded that big bluestem cover was limited by the decreasing summer temperature and was not associated with precipitation variables. This can be attributed to the observed decrease in tiller and leaf number per plant in our study. However, in the current study a decrease in seed number per panicle was recorded with decrease/increase in temperature on either side of the optimum of 23.4 °C which is 2.6 °C lower than the T_{opt} for biomass. The response of panicle number and seed number to temperature was independent of $[CO_2]$. This suggests that the processes (pollen production, germination, tube growth) leading to fertilization and seed set are mainly sensitive to temperature and that little relationship exists between vegetative and reproductive heat tolerance (Kakani et al., 2002, 2005; Salem et al., 2007). This decrease in seed number would severely hamper the species survival and spread in a given location based on current and projected temperatures.

Mean temperature of 26 °C was found optimal for most of the vegetative and reproductive components studied, except for leaf weight that followed a linear trend with temperature. The optimum temperature for root growth was 22.8 °C at high $[CO_2]$, much lower than at low $[CO_2]$ of 27.3 °C. The present study demonstrated that high $[CO_2]$ would increase the biomass production of big bluestem at temperature below optimum (<26 °C), but has no influence on biomass accumulation at higher temperatures, under the well-watered conditions of this study. As mentioned previously, a lower temperature optimum at high $[CO_2]$ may be due to increase in respiration as a result of decreased stomatal conductance, more number of young leaves and increased senescence, a response that would favor more growth at cooler than at warmer temperatures (Morison and Lawlor, 1999). The response of reproductive components to high $[CO_2]$ was lower in the optimum temperature range and equal at extreme temperature treatments. This suggests that under projected $[CO_2]$ conditions, the growing temperature will play a major role in determining the biomass, seed set and yield of big bluestem. The allocation of biomass under high $[CO_2]$ and hot temperature conditions is greater to leaves with a decrease in allocation to culms, roots and seed. This suggests less carbon was sequestered into plant parts that can be used for long-term storage. In concurrence, a SPAR study testing the effect of different temperatures and $[CO_2]$ on eastern gamagrass [*Tripsacum dactyloides* L.] also revealed higher amounts of carbon assimilated in above-ground biomass than in roots under high $[CO_2]$ conditions (Krizek et al., 2004).

Because potential changes in growth and development of big bluestem were clearly defined under controlled environment conditions, the observed changes and functional relationships

could be used to model and project the growth and development of big bluestem under current and future climates. Current dynamic global vegetation models (DGVMs) that simulate the net ecosystem production and net primary productivity of grasslands are mechanistic representations of photosynthesis, respiration, canopy energy balance and the allocation of carbon and nitrogen within the plant (Cramer et al., 2001). They also utilize the plant functional types (e.g. grasses, shrubs, trees) and their proportions in different ecosystems to define the structural characteristics of the vegetation in space and time (Woodward and Cramer, 1996; Cramer, 1997). In spite of their robustness, the DGVMs lack the mechanisms to account for species dispersal through propagules such as seeds and rhizomes (Cramer et al., 2001). In the present study, a severe decrease in seed number was recorded above/below the identified temperature optimum of 26 °C. The identified temperature response functions at ambient and high [CO₂] for parameters such as tiller number, panicle bearing tillers, panicle bearing nodes, panicles per plant and seed number per panicle can be incorporated into the DGVMs to predict more accurately the species dispersal and population establishment.

In conclusion, the present study provided temperature response functions for growth, development and reproduction of big bluestem that can be incorporated into the current DGVMs to provide a more accurate picture of prairie ecosystem dynamics. We found the cardinal temperatures under high [CO₂] were lower compared to those under low [CO₂]. The study also found that reproduction is more sensitive to temperature than vegetative growth in big bluestem and independent of [CO₂]. The temperature optima for seed set was 2.6 °C lower than the optima for biomass accumulation that is most commonly used in ecosystem models, which calls for a re-evaluation of the predictions of ecosystem productivity under projected climates. Further studies with big bluestem would be required simulating natural growing conditions such as with irrigation regimes [CO₂], UV-B radiation and ozone and their interactions to provide process-level data that can be used to improve the functionality of DGVMs to predict the biomass and reproductive performance of big bluestem in a changing climate.

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