

Response of soybean yield components and allocation of dry matter to increased temperature and CO₂ concentration

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Abstract

Future climatic scenarios can influence crop yield levels and induce hunger if no actions are taken. In this study, we evaluated the effect of increased temperature and CO₂ concentration on soybean yield components and biomass partitioning, that ultimately determine the crops productivity. This is conducted for two soybean genotypes that differ in their canopy and life cycles. Experiments were set as follows: a) T1 - ambient temperature and 390 $\mu\text{molCO}_2\cdot\text{mol}^{-1}$, b) T2 - ambient air temperature +2.7°C and ambient CO₂, and c) T3 - ambient air temperature + 2.7°C and 750 $\mu\text{molCO}_2\cdot\text{mol}^{-1}$. Results indicate that soybean under elevated CO₂ and temperature (T3), were taller and grains weighed more than under the ambient conditions in both cultivars types. However, yield has not increased substantially due to reductions in the ratio of number of branch/plant, pods/branch and grains/branch which lead also to a lesser number of total pods and grains per plant. The increase of temperature favored the number of pods and grains on branches in the modern type cultivar, and on racemes in the old cultivar. This results in more yield in both cultivars versus plants grown in the current ambient, and higher CO₂ concentration plus temperature. In both cultivars, the pods and grains partition were higher on the ontogenically oldest four branches and racemes, with decrease in the other upper ones. In addition, the biomass allocation in vegetative tissues was higher than reproductive biomass, with intensity cultivar dependent. We concluded that in future the yield could be limited by reduction of the numbers of branches and racemes in plant, and by alteration at source-sink relation, thus, indicating that changes in canopy architecture are needed to better take advantage of the increasing concentration of CO₂.

Keywords: yield components; dry matter allocation; high temperature and CO₂; growth environment; open-top chambers.

Abbreviations: CO₂_carbon dioxide gas, [CO₂]-carbon dioxide gas concentration, IPCC_intergovernmental panel on Climate Change, TGW_Thousand grains weight, OTC_open top chamber, FACE_free-air CO₂ enrichment, IRGA_infrared gas analyzer, %V_percent base saturation, Ca_calcium ion charge, Mg_magnesium ion charge, P₂O₅_phosphorus pentoxide fertilizer, K₂O_potassium oxide fertilizer.

Introduction

Global climate models predict increases in air temperature by up to 2°C (Houghton et al., 2001; IPCC, 2013) due to CO₂ concentrations higher than 500 $\text{mmol}\cdot\text{mol}^{-1}$ by the end of this century. This has urged the scientific community to investigate, among other issues, the impact of CO₂ and temperature changes in the crop system. Indeed, it has been found that several C₃ crops will respond to CO₂ enrichment with increased photosynthesis (Kimball and Idso, 1983; Vu et al., 2001; Rogers et al., 2004; Prior et al., 2011), growth rates and production (Long et al., 2004; 2006; Ainsworth and Long, 2005; Juknys et al., 2011). Meanwhile, the magnitude of changes also depend on the technology used to simulate future conditions (Ainsworth et al., 2008). In the case of soybean, CO₂ enrichment environments (between 550 and 700 $\mu\text{molCO}_2\cdot\text{mol}^{-1}$) has shown increased photosynthesis by up to ~30% (Griffin and Luo, 1999; Rogers et al., 2004; Bernacchi et al., 2005; Prior et al., 2011), and yield by up to 13% (Morgan et al., 2005; Long et al., 2006). However,

increases in photosynthetic rates can be smaller under long-term exposure to high CO₂ due to photosynthetic acclimation (Bernacchi et al. 2005; Bloom, 2009). It should be noticed that higher photosynthesis does not necessarily indicate increased productivity because the yield depends ultimately on the biomass partitioning and harvest index (Richards, 2000). As important as the CO₂-fertilization effect, the diurnal thermal regime determines the soybean production and its quality in non-limiting water and adequate nutrient conditions (Wolf et al. 1982; Oh-e et al., 2007; Setiyono et al., 2010). The growth of soybean plants has an ideal daytime temperature between 29 and 31°C (Ziska and Bunce, 1993, 1995; Setiyono et al., 2010), allowing increases in soybean production and higher final protein content (Wolf et al. 1982; Oh-e et al., 2007, Kumagai et al., 2012). Some studies report lower thresholds of 10°C (Avila et al., 2013), 11°C (Sinclair et al., 2005) and 14°C (Schoffel and Volpe, 2002) for soybean in Brazil. Temperatures near or greater than 40°C

lead significant reduction on the growth rate and retention of legumes (Avila et al., 2013).

Although the effects of high temperatures and $[CO_2]$ are known at the physiological and molecular levels, it is necessary to complement this knowledge with field studies to assess weather-related changes in genotypes, their yield components, and dry matter partitioning over longer time periods. Moreover, the understanding of yield components variables is necessary to improve breeding programs for development of new cultivars aiming to cope with weather/climate changes while maintaining high productivity.

The partitioning of biomass and yield components can differ among cultivars depending on the genetic basis and environmental stability for a particular climatic region (Ziska et al., 1995; 2001; Prasad et al., 2005; Rahman and Hossain, 2011). It is well known that environmental conditions influence plant production through the alteration of the amount of yield components that ultimately define the plant production.

The Brazilian soybean cultivars have great diversity in canopy characteristics such as plant size, architecture, branch and raceme level, and leafiness of plants (Priolli et al., 2002; Oliveira et al., 2003; Miranda et al., 2007; Mulato et al., 2010, Oliveira et al., 2012). These characteristics are genetic base dependent. Thus, environmental interactions can result in plant responses to CO_2 and to temperature elevations which may differ from what has been found in other latitudes and soybean producers.

This study evaluates the influence of high $[CO_2]$ and temperature on soybean yield components for two cultivars with different architecture and growth characteristics. In particular, we evaluated the plant height, number of branches and racemes, total pods and grains per plant, thousand grain weight, partitioning of biomass, and yield productivity. The identification of the chain in which yield components and dry-matter partitioning are altered by elevated $[CO_2]$ plus temperature according to specific growth characteristics can improve our selection for genotypes that can be better adapted to future environmental conditions.

Results and Discussion

Meteorological conditions

Mean daily temperature during the experimental season was 25.0, 27.6 and 27.8 °C in T1, T2 and T3 trials. The increase of temperature in T2 and T3 was due to heat accumulation, rising the air temperature effectively by 2.7 °C on average (Fig 2). In January, the sensible heat and soil evaporation played an important role for the temperature increases when plants occupied a minor soil area. In the following months, latent heat dictates the temperature distribution due to biomass accumulation and its increasing transpiration rate.

During night hours, temperatures in T2 and T3 have been remarkably higher (around +5°C) than those collected in T1. The day/night temperatures in T2 and T3 can be explained by the energy partitioning and balance, deriving of the heat accumulation on soil, vegetative tissues respiration, and lower air movement. The condition of higher mean temperatures could increase day/night respiration and the carbon use (Frantz et al., 2004). It has also been shown that soybean grown under high $[CO_2]$ experiences leaf respiration increase by a factor of 2.5 when the night average temperature increases between 18 and 26 °C (Bunce, 2005). Thus, it may be assumed that higher consumption of photo-assimilates are synthesized during daylight interval.

The mean relative humidity (RH) increased from January to March, with values of 79.4 ± 1.8 ; 87 ± 10.2 and 87.3 ± 10.6 in T1, T2 and T3, respectively. The highest RH in T2 and T3 were due to absence of advective flow and hence accumulation of water vapor from evapotranspiration in the Open Top Chamber (OTC), which kept the regime of RH (day/night) greater than in the T1 experiment.

Plant height, branches and racemes distributions

Discussion on plant architecture is fundamental due to its link with the distribution of carbon allocation. Moreover, the understanding of plant shape allows for identification of plant features which are strongly affected by environmental conditions such as CO_2 and weather parameters. Plants grown with higher CO_2 and temperature (T3) are taller in both cultivars than the plants in field conditions (T1; Fig 3). In the cultivar Conquista this increase was 28% (46%). Therefore, it is clearly shows that CG7484 cultivar response to high temperature or/and both high temperature plus elevated $[CO_2]$ is stronger than in Conquista.

The temperature regime influences the growth and development of plants, mainly affecting cell division, elongation rates, metabolic rates of photosynthesis and respiration in the daily cycle (Francis and Barlow, 1988; Tardieu et al 2000, Tardieu and Granier 2000; Bruhn, 2002). A mean temperature range of 29-31°C has been indicated as the optimum range for soybean vegetative growth (Ziska and Bunce, 1995; Setiyono et al., 2010), and the mean temperature of T2 and T3 were close to this range. Similarly, the main stem plastochron interval decreases and the final main stem node number increases in soybean with higher $[CO_2]$ ($660 \mu\text{molmol}^{-1}$), accompanied by a rise in mean temperature between 22.5 and 32.5 °C (Baker et al (1989).

Statistical analysis, demonstrated a positive correlation in Conquista ($r = 0.67$; $P \leq 0.001$) between the plant height and the number of racemes, indicating that these plants had more internodes as they had increase the racemes/plant ratio (see Table 1). Castro et al (2009) found similar response and significant increases in the number of nodes of soybean plant grown with a $[CO_2]$ of $548 \mu\text{mol.mol}^{-1}$. However, the correlation was lower in CG7484RR ($r = 0.34$; $P \leq 0.05$). Thus, the increase in height in the latter cultivar occurs through longer internodes since the racemes number was similar (Table 1). It can be argue that the interaction between elevated $[CO_2]$ and temperature in soybean influences the plant weight in two different ways. It is important to note that changes in the plant height should induce modification in the configuration of other plant components, such as branches, pods and racemes.

This is discussed below. The number of branches, racemes and total pods are the most important components for yield, and exhibit the highest correlation with the total yield (Pires et al., 2002; Perini et al., 2012). In the Conquista cultivar, the number of branches/plant decreased by 18.5% in T3 compared to T1 (Table 1). A similar tendency happened in the number of pods/branch and grains/branch, with 35.1% and 35.2% decrease. However,, the number of grains/pods on branches remained unaltered. For the CG7484RR cultivar, only T2 had higher number of pods/branch and grains/branch, with up to 12% increase in both components compared with plants in the other treatments. Based on previous studies one may anticipate that the increase of $[CO_2]$ and warmer conditions may not contribute to the increase

Table 1. Yield components over branches and stem-racemes of two soybean cultivars growing in three environmental conditions.

Yield components	Cultivar					
	Conquista			CG7484RR		
	T1	T2	T3	T1	T2	T3
BRANCHES						
Branches/plant	7.25 A	6.83 A	5.91 B	5.08 a	5.08 a	5.00 a
Pods/branch	5.81 A	6.14 A	3.77 B	4.80 b	5.38 a	4.38 b
Grains/branch	14.61 A	15.21 A	9.46 B	12.35 b	13.87 a	10.93 b
Grains/pod	2.48 A	2.46 A	2.49 A	2.52 a	2.38 a	2.50 a
RACEMES						
Racemes/plant	4.58 B	4.00 B	6.33 A	10.17 a	9.83 b	9.42 b
Pods/racemes	3.12 B	3.73 A	2.42 C	2.44 a	2.33 a	2.50 a
Grains/racemes	7.30 B	9.00 A	5.93 B	6.43 a	6.21 a	6.40 a
Grains/pod	2.31 A	2.41 A	2.41 A	2.64 a	2.69 a	2.57 a
PLANT						
Pods per plant	43.29 A	44.75 A	39.50 B	43.32 a	44.02 a	40.35 a
Grains per plant	109.42 A	117.24 A	101.46 B	112.72 a	115.05 a	109.12 a
TGW	134.44 B	140.04 B	152.63 A	109.91 b	122.18 a	124.72 a
Yield	15.64 B	17.88 A	15.93 B	14.48 a	16.32 a	15.40 a

T1 (plants grown in field conditions), T2 (plants grown under present [CO₂], and T3 (plants grown under 750±25 μmol.mol⁻¹ of CO₂). The mean temperature in T2 and T3 were 2.6 ±1.9 °C and 2.8±2.1 °C above T1 (25.0±3.2 °C), respectively. TGW = Thousand grains weight. Similar letters, capital or lowercase, in each line do not differ statistically by Scott-Knott test (*P*<0.05). The mean of each treatment is based on data from 40 plants.

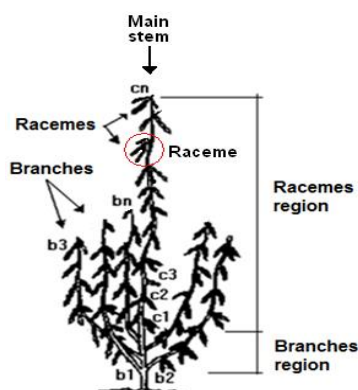


Fig 1. Plant structure scheme with the branches and racemes regions considered in this experiment. Branches position (b1, b2, b3... bn) and racemes position (c1, c2, c3 ...cn).

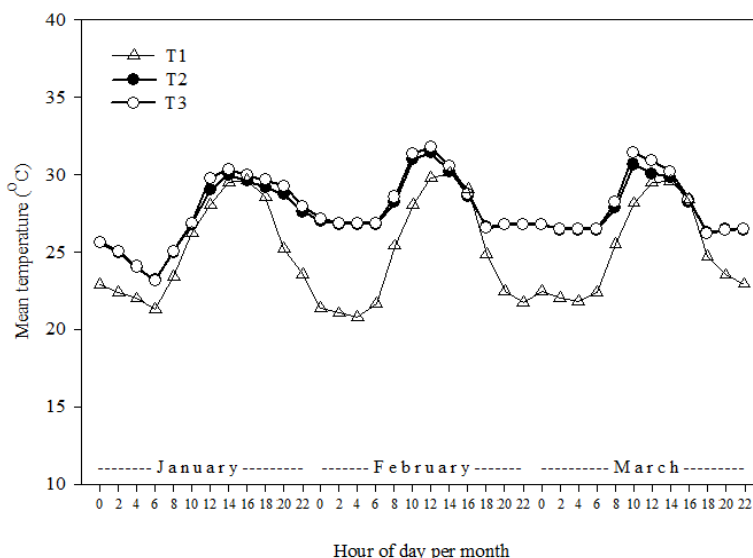


Fig 2. Profile of mean temperature by hour of day measured in T1 (plants grown in field conditions), T2 (plants grown under present [CO₂] plus elevated temperature), and T3 (plants grown under elevated temperature plus 750±25 μmol.mol⁻¹ of CO₂). The mean temperature in T2 a T3 were 2.6 ±1.9°C and 2.8±2.1°C above T1 (25.0±3.2°C), respectively. Each point represents the mean for a specific hour in a month.

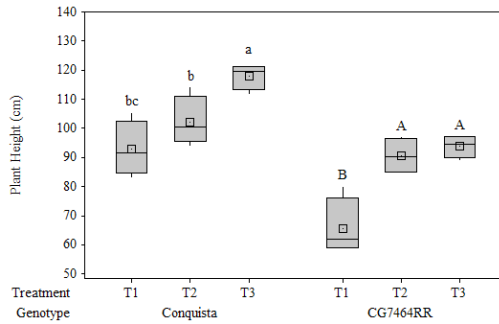


Fig 3. Mean height of soybean plants grown in T1 (plants grown in field conditions), T2 (plants grown under present [CO₂] plus elevated temperature), and T3 (plants grown under elevated temperature plus 750±25 μmol.mol⁻¹ of CO₂). The mean temperature in T2 and T3 were 2.6 ±1.9°C and 2.8±2.1°C above T1 (25.0±3.2°C). Similar lowercase (Conquista) and capital (CG7484RR) letters do not differ statistically by Scott-Knott test (*P*<0.05). The box length represents the scattering of dates. Lines across the bars correspond to the medians and the squares into bars represent the mean of the treatment. Each bar is based on data from 40 plants.

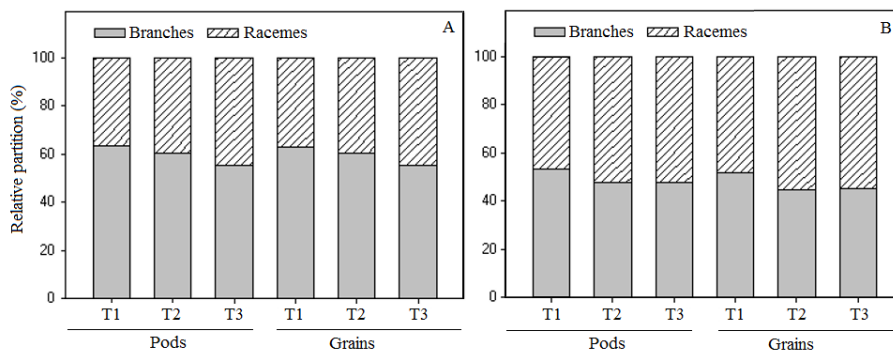


Fig 4. Relative partitioning of pods and grains in branches and racemes regions of soybean plants of cv. Conquista (A) and cv. CG7484RR (B) grown in T1 (plants grown in field conditions), T2 (plants grown under present [CO₂] plus elevated temperature), and T3 (plants grown under elevated temperature plus 750±25 μmol.mol⁻¹ of CO₂). The mean temperature in T2 and T3 were 2.6 ±1.9°C and 2.8±2.1°C above T1 (25.0±3.2°C). Each bar is based on data from 40 plants. The vertical bars are the standard errors.

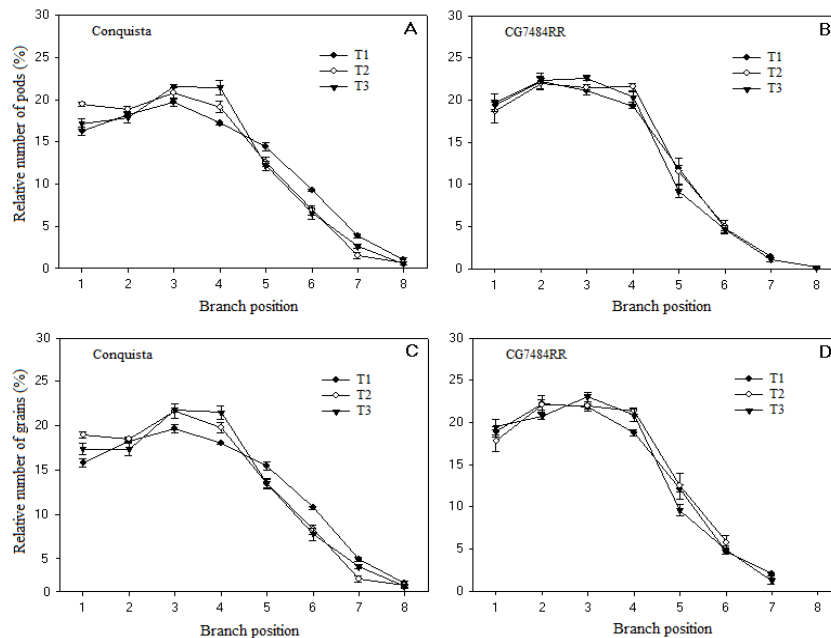


Fig 5. Average relative number of pods and grains within their position in the branches, for soybean cv. Conquista (A, C) and cv. CG7484RR (B, D) grown in T1 (plants grown in field conditions), T2 (plants grown under present [CO₂] plus elevated temperature), and T3 (plants grown under elevated temperature plus 750±25 μmol.mol⁻¹ of CO₂). The mean temperature in T2 and T3 were 2.6 ±1.9°C and 2.8±2.1°C above T1 (25.0±3.2°C). The branch in position 1 corresponds to the lowermost branch in the branch region of the plant. Each point represents the average of 40 plants. The vertical bars are the standard errors.

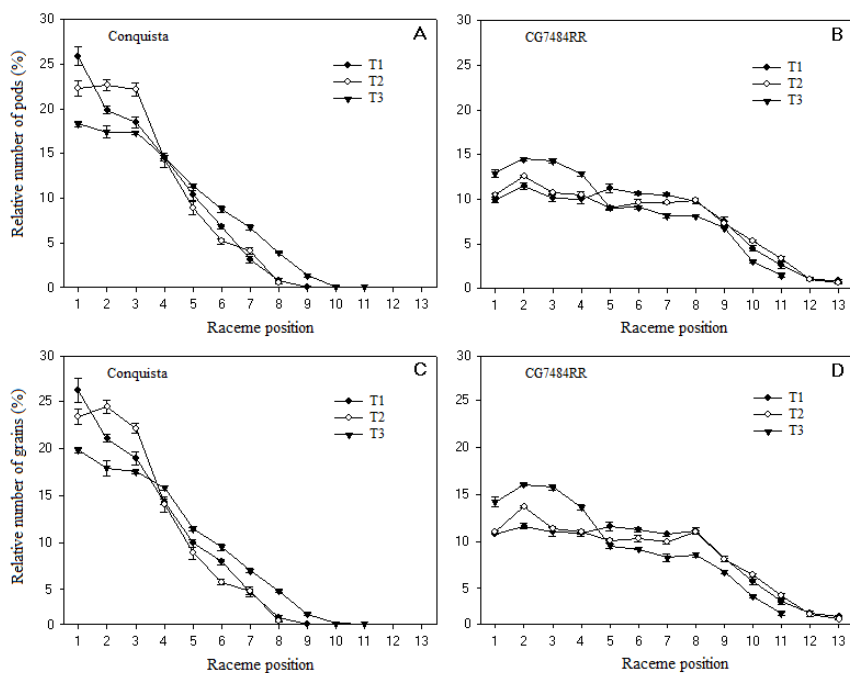


Fig 6. Average relative number of pods within their position in the racemes, for soybean cv. Conquista (A, C) and cv. CG7484RR (B, D) grown in T1 (plants grown in field conditions), T2 (plants grown under present [CO₂] plus elevated temperature), and T3 (plants grown under elevated temperature plus 750±25 μmol.mol⁻¹ of CO₂). The mean temperature in T2 and T3 were 2.6 ±1.9°C and 2.8±2.1°C above T1 (25.0±3.2°C). Each point represents the average of 40 plants. The vertical bars are the standard errors.

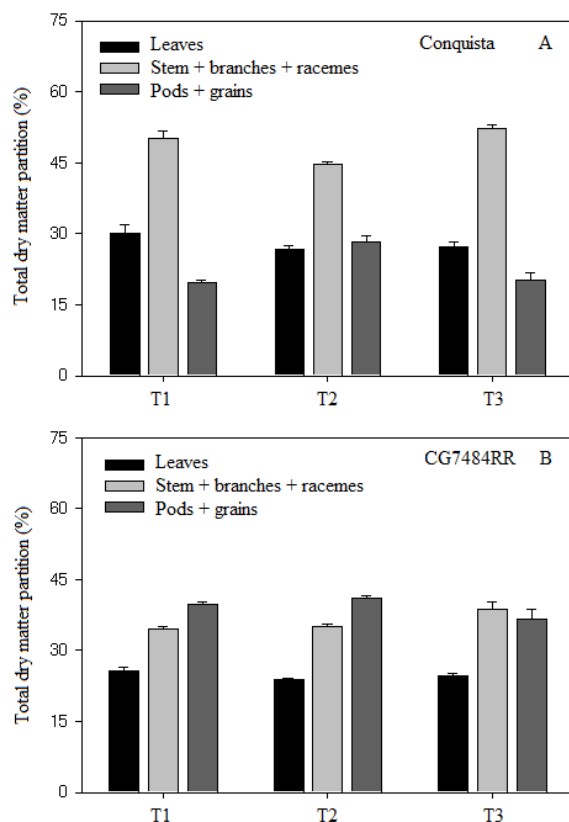


Fig 7. Total biomass partition in soybean plants of the Conquista (A) and CG7484RR (B) cultivars grown in T1 (plants grown in field conditions), T2 (plants grown under present [CO₂] plus elevated temperature), and T3 (plants grown under elevated temperature plus 750±25 μmol.mol⁻¹ of CO₂). The mean temperature in T2 and T3 were 2.6 ±1.9°C and 2.8±2.1°C above T1 (25.0±3.2°C). Each bar with standard deviations is based on from 40 plants.

yield due to reduction in the number of pods and grains in branches. This will be further discussed in more detail. The number of the racemes per plant and the number of pods or grains per raceme also respond to higher temperature and CO₂, which is cultivar dependent (Table 1). The number of the racemes/plant in Conquista increased by 27% and 37% in T3 as compared to T1 and T2, respectively. The thermal treatment (T2) had positive effect on pods/raceme and grains/raceme compared with T1 and T3. In T2 the pods/raceme increased by 35% and 16% versus T3 and T1, respectively. Similar increases were found in grains/raceme. This similarity is due to the close relationship between pods and grains number. On the other hand, the number of grain/pod-raceme did not differ between the different treatments. Differently from the Conquista cultivar, the number of racemes/plant in CG7484RR was reduced by 3% in T2 and 7% in T3, compared with the control T1 trial. There were no differences between T2 and T3. The other yield components associated with the racemes, such as pods/racemes, grains/racemes and grains/pod-raceme, were not different between treatments. It may be assumed that the Conquista cultivar is more affected than CG7484RR insofar plant height, branches or racemes per plant, pods or grains in branches, or racemes are concerned. This useful serves to highlight the high plasticity of Conquista to changes in CO₂ and temperature. Additionally, there is a positive correlation between plant height and the number of racemes in Conquista ($r = 0.67$; $P \leq 0.005$). A higher number of racemes leads to more pods and grains, which implies that a higher number of racemes in the main stem could partially compensate for the loss of pods and grains by the absence of lateral branches (Table 1). These cultivars are very stable in terms of changes of the total number of grains/pods grown on branches and racemes. They do not differ among all treatments for both genotypes. In general, the number of seeds per pod can vary between 2.1 and 2.5 (Peluzio et al., 2009; OSU, 2012). This has been classified independently of the cultivar and cultural practices, the most stable yield characteristics in soybean (Rodrigues et al 1998; Pires, 2002; Dalchiavon et al, 2012). Responses such as reduction in the number of branches, increase in racemes, and higher plant height observed in Conquista is typically a response of cultivars under competition, which occurs by inhibition of axillary buds in early vegetative stages (Ritchie et al, 1985). Previous works with soybean under high CO₂ and temperature have also shown increased photosynthesis and higher availability of photo assimilates (Leakey et al., 2009), and an increase in the number of racemes in the main stem (Castro et al., 2009). Our results indicate that higher [CO₂] and temperature might have influenced the growth of the canopy in Conquista, implying that the typical row spacing used resulted in intra-specific competition. In this sense, for this cultivar, wider row spacing and lower plant densities would be necessary for achieving substantial canopy growing. However, such practices are contradictory to the more than 50 years of breeding strategy that has aimed to decrease plant height, increase plant density, and harvest index to increase productivity (Morrison et al., 2000; Jin et al, 2010). We conclude that as an immediate and important strategy to get advantage of the higher [CO₂] without reducing the number of branches is to substitute cultivars as Conquista for others less sensitive to environmental changes, such as CG7484RR.

3. Pods, grains and the thousand grain weight per plant

The integrated changes to plant level, such as total pods and grains per plant have been shown to cause to differences among treatments only in the Conquista cultivar. In this cultivar, the number of pod/plants and grains/plants ratios were reduced by 9% and 7%, in T3 compared with T1. These yield components were 12% and 13% lower in T3 versus T2 (Table 1). These reductions are coherent with the observed reductions in pods and in grains for branches and racemes in this cultivar (Table 1). For the CG7484RR cultivar, no significant differences have been found among treatments for pods/plant and grains/plant. Furthermore, the magnitude of observed changes in pods and grains/branch, and the racemes/plant stimulated by the T2 and T3 treatments, did not result in reasonable increases in yield components at integrated plant level. Changes reported above affected the matter partition among the plant components, and may change the Thousand Grain Weight (TGW). Evaluation of the T1, T2 and T3 experiments revealed that the TGW increased by up to 11% in T2 compared to T1, in the CG7484. Under higher [CO₂] and temperature (T3 trial) the increase was up to 13.5% in both cultivars (Table 1). Increases in the weight of grains have also been reported by Heinemann et al. (2006), and Hikosaka et al. (2011) in soybean plants grown in an environment with elevated CO₂ independent of the changes in thermal regime even below the optimal growth temperature. However, high thermal regimes, such as day/night temperatures of 40/30 °C, can result in a strong fall in the seed mass without any influence of elevated [CO₂] when compared with optimal 32/22 °C day/night temperatures (Thomas et al., 2003).

The weight and number of grains per pod are characteristics with less variability, high heritability and greater positive effect on production (Sudarić et al., 2002). Besides the thermal regime influence, the long-term exposures of soybean plants to elevated [CO₂] can also change source-sink relations, (Ainsworth et al., 2004), and grain filling (Isopp et al., 2000; Kumagai et al., 2012). This further result in high weight of seeds. We found ratios of seed mass per plant (seed mass in elevated CO₂ vs seed mass in ambient CO₂) for both cultivars of 1.13, coherent with the range from 0.93 to 1.87 previously reported by Hikosaka *et al.* (2011). It has also been verified that higher [CO₂] and favorable temperature regime increase the TGW, through enhancements of sink-force of grains. However, the question remains whether this increase in sink-force is the same in all grains regardless of the position they occupy in the soybean plant. The variation in the number of pods and grains within their position in the branches and racemes explain how and where in the plant the changes occurred in relation to treatments.

In Conquista the branches, the partitioning of pods and grains in T2 and T3 versus T1 increased until the fourth branch decreasing thereafter. In the first four branches Conquista accumulated 78.3% and 78.1% of the total amount of pods in T2 and T3, respectively, which were increases by up to 7% in pods relative to plants grown in T1.

However, in the following branches T1 plants exhibits around 7% more pods than delivered by the T1 and T2 treatments. In the cultivar CG7484RR, there is not substantial changes in the distribution of pods and grain within branches among the treatments (Figure 5b, d). Pods and grain partition in the racemes as delivered by T3 and T1 exhibit different behavior between the cultivars. In Conquista for T3, pods and grains were lower (~8% for pods) than in T1 for the four first racemes, with higher number of pods and grains in the following racemes. The largest concentration of pods and grains in the first branches (Conquista) or racemes

(CG7484RR) can contribute to altering pod and grain competition between racemes. For example, there is evidence that the sequence of flowers influences the competition intra and inter-racemes for carbohydrates (Brun and Betts, 1984; Spollen et al., 1986; Stockman, 1988; Mosjidis et al., 1993; Kokubun, 2011). Thus, the increase in pods and grains in the first racemes of the T3 treatment of CG7484RR can potentially increase the competition for resources, explaining the observed variations (Fig. 6).

When the relative partitioning of pods and grains in branches or racemes is compared between T3 and T1 (Figure 4), there is a negative change in both cultivars for the pods and grains on branches, and a positive change for the pods and grains in racemes. This behavior is consistent with negative correlation found between the number of racemes vs. branches ($r = -0.71$, $P \leq 0.01$) in Conquista. While in Conquista changes in partition were driven by the decrease in the number of branches and the increase in racemes, in the CG7484RR trends were driven by the reduction of racemes per plant alone ($r = 0.15$, $P \leq 0.32$).

Although cultivar dependent, future changes in $[CO_2]$ and air temperature besides modifying the relation of total number of pods and grains when the number of branches and racemes are altered, coupled to the relative partitioning of pods over the branches and racemes position on plant, and this could be partly cultivar dependent. Identification of how these alterations are organized in the plants are important for genetic manipulation and improvement.

Dry matter plant partitioning and soybean yield

Changes in dry matter plant partitioning, displayed in Figure 7 (a-b), indicate that for both genotypes exposure to long-term CO_2 conditions altered the plant source-sink relations. The stem (stem plus branches and petioles) is the plant component with the highest carbon allocation in Conquista (Figure 7a), as this cultivar has thicker and longer branches and petioles. The high stem biomass is related to the lower number of branches per plant, pods/branch and pods/racemes as shown in Table 1.

The reduction in the number of branches, pods/branch, pods/racemes and total number of grains observed in plants under long-term high CO_2 plus high temperature exposure can be explained in different ways. For Conquista, supplemental CO_2 is favorable for growth during the vegetative phase, and adverse in the reproductive phase, because of the reduction of production units such as branches, pods and the total number of grains at the expense of creating larger main and secondary stems. According to Clough et al. (1981) and Peet (1984), in CO_2 -enriched soybean, a higher photosynthetic rate is observed during the first weeks under the treatment, with subsequent photosynthesis inhibition of ending up with dry matter values similar to non-enriched plants. The decrease in photosynthetic capacity under high $[CO_2]$ has been attributed to insufficient demand for carbohydrates to balance the higher carbon supply, or the saturation of rubisco when photosynthesis is under RuBP limitation (Bernacchi et al., 2005; Ruiz-Vera et al., 2013).

The main stem can be a temporary storage of photo-assimilates, wherefrom the available photoassimilates are translocated for the growth of pods and grains in soybean (Borrás et al., 2004; Liu et al., 2010). In fact, the common pool of assimilates are moving continuously through the stem (Larcher, 2000, Liu et al., 2010). It is likely that high temperature plus CO_2 enrichment conditions increase the accumulation of stem photoassimilates, as observed in the

CG7484RR cultivar (Figure 6). Frantz et al. (2004) found an increase of 4.0%/°C in the plant respiration in soybean, along with decrease in leaf and root biomass with reduction in the carbon fraction of the leaves; while stem biomass increased significantly without alteration in carbon fraction.

Therefore, as a result, the alteration of biomass allocation in the T2 and T3 treatments did not provide an increase in reproductive tissues. Commonly, the yield in soybean plants depend on the number of pods per plant, since the number of grains per pod is usually around 2.6 grains/pod. Thus, a higher seed weight is one way to increase the yield.

A decrease in the number of branches per plant and grains in T3, observed particularly in the Conquista cultivar, can be attributed to weaker sink-force of the reproductively favored plant components. This weakening does not directly contribute to raising the number pods or grains, and consequently the yield.

Increases in temperature up to an optimum level can contribute to yield increase. However, if the temperature rises above such optimum temperature, high decreases would be observed in the yield (Kucharik and Serbin, 2008). Justino et al. (2013) also demonstrated that the mean productivity of soybean could experience high inter-annual variability due to future climate changes in temperature, likely with the interaction genotype x environment continuing to direct the median production.

Evaluation of the soybean yield based on T1, T2 and T3 experiments revealed that in spite of reasonable changes of the plant characteristics, there are no significant changes in the productivity. Yield change relies heavily on yield components affected, essentially on branches and racemes and their pod numbers. Changes in these characteristics should effectively reduce the yield under unfavorable temperature and $[CO_2]$ conditions during various stages of development.

On the other hand, it has been found a positive effect on yield due to temperature rise in T2 over T1 and T3 in both cultivars. There were increase of 12.5% and 11% in Conquista, and 11.2% and 5.6% in CG7484 in T2 over T1 and T3, respectively. This positive effect of temperature is achieved because the thermal regime did not go above the optimal temperature in the T1 experiment. This implies that the increase in $[CO_2]$ can alter the biomass partitioning in the canopy by modifying the number of branches and number of pods above the internodes of the branches, as shown in Fig.6. However, nonlinear temperature effects could impose severe damages to crop yields under climate change (Schlenker and Roberts, 2009). A meta-analysis of 12 FACE experiments with soybean and several species showed a response to CO_2 enrichment by an increase of up to 17% (Ainsworth and Long, 2005). Smaller than predicted responses have been reported previously for soybean grown at elevated $[CO_2]$ within the SoyFACE experiment (Morgan, 2004).

Recent results of Ruiz-Vera et al. (2013) in a FACE study did not show increase in the production and harvest index of soybean plants due to the interaction between the $[CO_2]$ and temperature, if the latter exceeds a threshold. It may be argued that the increase in temperatures in combination with elevated $[CO_2]$ can lead to either increased or decreased yields. This is related to the impact of $[CO_2]$ and temperature on metabolism and photo-assimilates partitioning in a genotype.

Bishop et al. (2014) discussed the soybean response to $[CO_2]$ and temperature, concluding that among 18 genotypes there are variations in soybean response to elevated $[CO_2]$, with some cultivars showing only small yield response. The alteration on the source/sink relation can drive the yield

differences between soybean cultivars by changing the number of branches, racemes and pods, which are the characteristics that are most sensitive to environmental changes (Borrás et al., 2004; Liu et al., 2006). Still, the environmental effect can be more intense in an old cultivar (Liu et al, 2006) such as Conquista compared with the modern and more environmentally stable cultivar, such as CG7484RR due to the genetic selection process for environmental stability.

Our findings indicate that the first positions of branches and racemes can likely be targets for increase in production per plant unit in the newest developing cultivars, characterized by smaller plants and high concentration of pods and few branches and racemes. Different responses between Conquista and the hybrid CG7464RR genotypes may arise from the genetic plasticity to the environment, with CG7464RR being environmentally more stable and Conquista environmentally more plastic. Increases in [CO₂] in soybean changed the source-drain relationship, with an enhanced sink capacity of the first four branches and racemes.

Materials and Methods

Facilities and controllers

The study was conducted at the experimental located at the Agricultural Engineering Department Research Area at the Universidade Federal de Viçosa, in Viçosa, MG, Brazil (20° 45 ' S, 42° 45 ' W) during the 2012/2013 growing season. The soybean plants were cultivated inside Open Top Chamber (OTC) facilities used by Silva et al., (2012), composed by rectangular modules of 2.0 m height and 1.4 x 1.8 m section, with a pyramidal top that has a height of 0.5 m and a 19% of exchange-area relative to the base area. Each chamber had a steel structure covered with a transparent plastic film and opposite side vents to match the internal microclimate to natural environmental conditions. Outside of each chamber, there was a fan propeller of 0.2 m diameter and a motor of 1/16 cv power to inject pure CO₂ gas through the ventilator tubing. This tubing was connected to circulating pipe diffusers inside the bottom chambers with a nominal diameter of 50 mm, with holes spaced at 25 and 7mm and directed 25° relative to the ground plane, to achieve a low-medium canopy region. The pressure and flow of CO₂ stream were controlled by a solenoid and pressure valves at the outlet of CO₂ cylinders and valve-regulators with fine adjustment at the inlet OTC to ensure the desirable [CO₂] in the chambers. The time that plants were exposure to elevated CO₂ and the target [CO₂] in each chamber were controlled by a timer and monitored daily with a [CO₂]-meter (Testo 535 model; previously calibrated with the LCpro IRGA equipment).

Soil and plant management

Inside the chambers, lysimeters (1.0 x 1.4 m section and 0.8 m depth) were filled with Red-Yellow Dystrophic Latosol soil, a very clayey textural class (70% clay, 9% silt, 12% coarse sand, and 9% fine sand). The soil acidity and fertility of the lysimeters were corrected to soybean culture requirement. The soil percent base saturation (%V) was elevated to 60%, to ensure a Ca:Mg ratio of 3.5: 1 and a pH of 6.6. The fertilization management was equivalent to applying 30-80-90 of N-P₂O₅-K₂O kilograms per hectare and applied according to Ribeiro et al. (1999). The plants were irrigated with dripping tapes to maintain the soil at a stable

field capacity (FC, 33.62%). The soil water content was monitored by a TDR (Time Domain Reflectometer) with probes positioned at 0.20 and 0.40 m depth. Chewing insects were controlled with 200 ml/ha of Decis ® EC 25 (Bayer CropScience). Soybean rust and other diseases were prevented with two 2.0 kg/ha applications of Manzate ® 750 (UPL), followed by 0.7 L/ha of Opera ® (BASF).

Plant material

The Conquista and the CG7484RR were the cultivars used in this study. They were sown on the 26th of December in 2012, each one occupying half of the area of the lysimeter and at a rate of 34 plants/m². These cultivars were different in their developmental cycle, canopy architecture and genetics. The Conquista (MG/BR 46) cultivar is a determinate 8.1 maturity group cultivar with ~130-days cycle. It has a strong pyramidal leafy canopy which is open at the base with strong lower branches and a plant height around 0.95m (Priolli et al., 2002). The CG7484RR cultivar is a semi-determinate 7.4 maturity group cultivar with ~110-days cycle. It has a thin and median canopy, and plant height around 0.75m, as modern cultivar type.

Treatments

The treatments were named as T1 = plants grown as field (ambient [CO₂] and temperature), T2= plants grown under ambient [CO₂], and T3 plants grown under 750±25 mmolmol⁻¹ of CO₂. The T2 and T3 treatments had air mean temperature increased 2.7°C above the T1 during the whole growing season. To maintain field conditions, the lateral vents were kept open for T1. The CO₂ enrichment was performed daily from 6:30 a.m. to 18:00 p.m., from the emergence of the first trifoliolate leaf (V2 stage) until full maturity of the pods (R8 stage), similar to Fehr and Caviness (1977). The temperature rise inside the chambers was achieved by closing the vent side windows. The daily thermal regime was monitored by probes linked to a portable weather station model Vantage 2Pro (Davis®).

Data collected and statistical analysis

Shortly after physiological maturity, ten whole plants above the soil were harvested from each cultivar and experimental unit. For each plant, their height (from the transition soil-atmosphere zone to the shoot apical meristem) and their characteristics of the yield components, such as number of lateral branches, number of shoot axillary racemes from the main stem (Fig.1), number of pods and grains per branch and raceme, and number of grains per pod and for the whole plant was measured. The yield for each plant was obtained from the dry weight of grains adjusted to fresh weight with 12% of humidity. Dry matter of stem, leaves, and reproductive parts of each plant were weighed after being dried at 70°C for 72 hours in a forced air circulation oven. A similar procedure was realized to assess the Thousand Grains Weight (TGW) to better estimate plant production without interference of differences in grain humidity.

The partitioning of pods and grains related to branches and racemes, and pods/grain ratio according to the position in the branch and in the plant racemes were estimated from the observed data. Similarly, the relative partitioning of leave+petioles, stem+branches+racemes without pods and grains, as well as pods+seeds relative to the total biomass were calculated from their dry matter weights. The root dry matter was neglected due to high fragmentation and

intercrossing of medium and fine roots of neighboring plants in the first 10 cm, a depth with 50% or more of the roots in the soybean plants (Pivetta, 2012)

Collected data and the calculated indexes were analysed in completely randomized designs by F-test ($p \leq 0.05$) and Scott-Knot-test ($p \leq 0.05$) using the SAEG 9.0 software developed by Viçosa Federal University.

Conclusions

The [CO₂] increment resulted in poor increased of the yield. However, the isolated effect of higher air temperature led to higher productivity because the thermal regime was comprised above of the optimal mean temperature. Moreover, it has been found that the joint effect of elevated [CO₂] and temperature negatively alter the biomass partition in the whole plant and grain partition over branches and racemes, reducing yield.

Severe alteration of specific yield components and source-sink relationship as a response to CO₂ increase in warmer climate is noticed; at the level of branches, pods and grains, in particularly for the ontogenetically first branches and racemes of the plant. A better understanding of the response of soybean cultivars production, or for genotype screening, requires an evaluation of yield components, mainly in the branch level. Such is necessary to improve our understanding of sensible yield components in soybean genotypes and their ability to tolerate the impacts of the future climates.

Acknowledgments

This research was supported by the National Postdoctoral Program CAPES-PNPD/2010, Ministry of Education of Brazil and the Applied Meteorology Postgraduation Program of Viçosa Federal University. Research grant has also been supported by the CiXPAG – Interaction of Climate Extremes, Air Pollution and Agro-ecosystems, coordinated by CICERO Climate Centre, UiO/MET Norway, Oslo, Norway. We also acknowledge the useful conversation with Dr. Bill Almann on the agriculture and climate relationship.

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