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# Analysis of Maize Photosyntheis Parameters and Whole Plant Oxidative Damage Under Long-term Drought

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## Abstract

We test if maize maintain yield under long-term drought throught improvement of photosyntheis (*A*) coupled with up-regulation of the antioxidant system induced by increase in levels of abscisic acid (ABA). Four maize genotypes with constrasting drought tolerance: BRS1010 and 2B710 (sensitive) and DKB 390 and BRS1055 (tolerant) in two soil water levels, field capacity (FC) and water deficit (WD) were used. WD was applied at the pre-flowering stage for 12 days, and oxidative damage was measured as malondialdehyde (MDA) accumulation in whole plant. Plants from tolerant genotypes DKB390 and BRS1055 showed higher *A* and had no signal of oxidative damage compared to sensitive genotypes 2B710 and BRS1010 under WD, resulting in a higher yield attributes. For our surprising, it was dissociated from up-regulation of the antioxidant system ABA-mediated. In turn, plants from two sensitive genotypes under WD showed compared to FC consistent reduction of *A* due to mesophyll conductance ($g_m$) limitation. Only WD plants from sensitive genotype BRS1010 presented leaf ABA levels increased related to its counterparts under FC; however, due to the inactivation of catalase activity the oxidative damage control was not effective, resulting a hardly MDA acumulation in both leaves and roots. The maize tolerance under long-term drought is linked to scape of $g_m$ decline.

**Keywords:** Antioxidant system; Mesophyll conductance; Malondialdehyde; Photorespiration; Abscisic acid

## Introduction

The world's most important crops in terms of total yield in 2014/15 is maize (*Zea mays*), with 1014 Mt [1], and its productivity is greatly constrained by drought with depending upon the genotype, growth stage, duration and intensity of stress [2,3]. The period in which maize is particularly sensitive to water stress is one week before to two weeks after flowering [4]. Plant breeders and major seed companies have developed maize genotypes with enhanced yields in water deficient environments, and phenotypic traits, such as anthesis silking interval, yield, grain number, carbon allocation to roots, leaf rolling and leaf chlorophyll content, has been used to select drought tolerant maize germplasm [4]. Successful drought resistant genotypes improved commercial maize yields under water limiting conditions by up to 15% and, importantly, yields under water sufficient conditions were only marginally less than control genotypes [5,6]. Although we know a great deal about the agronomic performance of drought tolerant maize genotypes, much less is known about the physiological mechanisms that contribute to desiccation tolerance in these genotypes.

Maize responses to drought usually includes stomata closure [7,8], a shift from shoot to root growth [7], decreasing photosynthetic activity [7,8] and altering carbohydrate [9] and amino acid metabolism [7,9]. Drought is also known to induce oxidative stress directly, by generating reactive oxygen species (ROS) during the conversion of its valence forms, or indirectly, by inactivating antioxidant system [10]. The ameliorative effect of *A* on tolerant maize genotypes exposed to drought is believed to occur, to a large extent, through counteracting oxidative stress via modulating antioxidant enzymes at leaf level, including superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR) and glutathione peroxidase (GPX), as well as antioxidant molecules [8,11]. Failure of the antioxidant defense system may result in leaf damage when metabolites and components of the cellular machinery react with ROS [8,11], resulting in lipid peroxidation [10], thus ultimately impairing *A* and yield [12].

The higher yield in a maize genotype tolerant to drought was coupled with up-regulation of the ABA- mediated antioxidant system at leaf level, mainly CAT [10]. However, like leaves, roots exposed to drought are potential producers of ROS, and thus could counteract oxidative stress via modulating antioxidant enzymes [13]. To the best of our knowledge, little attention was paid to how ABA- mediated antioxidant system antioxidant in root affects *A* in successful drought tolerant genotypes. It is therefore tempting to speculate that signaling ABA pathways are tightly interregulated with antioxidant system at the whole-plant level to increase water uptake, in a manner that allows the maintenance of higher *A* and productivity.

The aim of this study was to test if long-term drought tolerant genotypes could maintain yield under water limiting conditions through improvements of the *A* coupled with up-regulation of ABA-mediated antioxidant system at whole plant level.

## Material and Methods

### Plant material, cultivation conditions and experimental design

The experiment was conducted in a greenhouse at the National Maize and Sorghum Research Center (19°28' S, 44°15'08" W, 732 m a.s.l.), and the plant material consisted of four open-pollinated maize genotypes with contrasting drought tolerance: two tolerant (DKB 390 and BRS1055) and two sensitive (BRS1010 and 2B710). The choice of genotypes was based on results of previous field experiments performed

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by researchers from the breeding program of the National Maize and Sorghum Research Center, who over the years, has accumulated experience in maize phenotyping for drought tolerance. Under WD, DKB390 and BRS1055 showed higher flowering synchronization and yield compared to BRS1010 and 2B710 [14,15].

Plants were grown in plastic pots containing 20 kg of **typical** dystrophic Red Latosol soil. The water content in the soil was monitored daily between 9:00 a.m. and 3:00 p.m., with a moisture sensor (GB Reader N1535; (Measurement Engineering, Australia) installed at the center of each pot with the aid of a screw auger at a depth of 20 cm. These sensors detect the water content in the soil based on electrical resistance and are coupled to digital meters. Water replacement by irrigation was based on the data obtained with the sensor and water was added to reach FC during the period preceding the imposition of the treatments. The water replacement calculations were performed with a spreadsheet and based on a soil water retention curve. In parallel, all necessary cultural and phytosanitary treatments were performed.

At the pre-flowering growth stage, half of each initial treatment was subjected to WD the other half continued to receive daily irrigation in order to maintain soil moisture close to FC, with a soil water tension of −18 kPa. WD was imposed by daily provision of 50% of the total available water until the soil water tension reached at least −138 kPa. After twelve days under these conditions, the leaf gas exchange and chlorophyll *a* fluorescence were measured in ear leaf with an infrared gas analyzer equipped with a fluorometer (LI-6400-40; LI-COR, USA) [16]. Samples of corn ear-leaves and roots tips (2 cm lenght) washed from the soil were collected at beginning of silking. Subsequently, samples were stored in liquid nitrogen for determination of antioxidant enzymes activity, levels of ABA, as well as cellular damage based on MDA accumulation. The water supply was then restored and maintained at optimum levels until physiological maturity. At harvest, the agronomic parameters associated with productivity were analyzed according to the methodology detailed in the "Agronomic parameters" section. The experimental unit was the pot containing two plants, with six replications per treatment.

For the statistical analysis, the results were submitted to variance analysis and the means were compared by the Scott-Knott test at 5% probability.

### Enzymatic assays

The activity of the enzymes of the antioxidant system, named dismutase SOD (EC 1.15.1.1), CAT (EC 1.11.1.6), and APX (EC 1.11.1.11) were determined from plant material extracted in a medium containing potassium phosphate buffer 0.1M (pH 6.8), 0.1 mM EDTA, 1 mM DTT, 1 mM PMSF and 1% PVPP (w/v). Total SOD activity was determined by measuring the ability of this enzyme to inhibit the photochemical reduction of *p*-nitro-blue-tetrazolium chloride by superoxide at 560 nm. The activity of CAT was estimated by measuring the rate of decomposition of $H_2O_2$ at 240 nm, while total APX activity was determined by monitoring the decline in absorbance at 290 nm. Additional details are described in ref. [10]. The levels of ABA was performed using immunoenzymatic assay kits (Phytodetec ABA Enzyme Immunoassay Test Kit—Sigma-Aldrich). The MDA accumulation was estimated as the content of total 2-thiobarbituric acid-reactive substances [10].

### Photosynthetic gas exchange measurements

The leaf gas-exchange parameters *A*, stomatal conductance to water vapor ($g_s$), internal $CO_2$ concentration ($C_i$) and transpiration rate (*E*) were measured simultaneously chlorophyll *a* fluorescence parameters from 10:00 a.m. to 1:00 p.m., when *A* is at its maximum, under artificial *PPFD* of 1500 μmol photons $m^{-2}s^{-1}$ at the leaf level, 400 mol $CO_2$ mol $air^{-1}$ and 21% $O_2$. During the measurements, the leaf-to-air vapor pressure deficit was ca. 1.0 kPa and a leaf temperature of 25°C. Based on relationship between *A* and *E*, the water use efficiency (*WUE*) was calculated.

The equipment was programed to make curves $A/C_i$, varying sequentially $CO_2$ partial pressure: 40, 30, 20, 10, 5, 40, 60, 80, 100, 120, 140 and 160 Pa. Estimations of $g_m$ were performed using the combined gas exchange/fluorescence data [15]. $A–C_i$ curves were converted into $A–C_c$ curves for estimation of the maximum rate of carboxylation of Ribulose 1,5 bisphosphate (Rubisco, $V_{cmax}$) and phospoenolpyruvate and pyruvate orthophosphate dikinase (PEPc and PPDK, $V_{pmax}$), as well as the maximum rate of carboxylation limited by electron transport ($J_{max}$) [16]. The maximum efficiency of photosystem II ($F_vF_m$) was determined through a fluorometer (Plant Efficiency Analyser. Hansatech Instruments King's Lynn, UK) in leaves adapted to dark. Leaf conditioning was carried out with the help of leaf clips with the light intensity in the sensor being 60 % of the equipment's total capacity, for a period of 5 s at each reading. Rates of ATP and NADPH consumption, as well as $H^+$ requirement were estimated based on ref. [17].

Additionally, nitrogen (N) allocated in the photosynthetic machinery was accessed as ref. [18], including the N partition between fractions involved in carboxylation enzymes ($N_{Rubisco}$, $N_{PEPc}$ and $N_{PPDK}$), light harvesting (Ni) and bioenergy (Nb).

### Agronomic parameters

Total leaf area per plant (LA) was measured with an area meter (LI-3100; LI-COR, USA), in six plants per treatment. The plants were then partitioned into roots, stems, leaves, tassel, ears (cob, husk, and grains), and dried in an oven with forced air circulation at 70 °C for 72 h. Based on the dry weights of the different parts, the dry grain biomass (DGB), total dry biomass (TDB), harvest index (HI) were estimated.

Additionally, a group of 50 kernels was soaked overnight in ethylenediamine (10%, *w*/*v*) and longitudinally cut with a knife to evaluate possible changes in embryo size, depending on the treatment. Photographs were obtained using a stereoscopic microscope and the Image J program was used to calculate the ratio between the areas of the endosperm and the embryo (EM: E).

## Results and Discussion

The activity of enzyme SOD was not significantly different among different genotypes and water levels (data not shown). The activity of APX was higher in BRS1055 compared to other genotypes independent of water level while CAT activity was decreased only in sensitive genotypes under WD, compared to FC (Figure 1). In WD plants from BRS1010, the decrease in CAT activity was acompained by increase in leaf level of ABA (Figure 1), as well as increase in MDA levels (Figure 1), both in leaves and roots. In WD plants from 2B710 the increase in MDA levels was verified only at root level, dissociated of changes in antioxidant enzyme activity enzyme in this organ (Figure 1). The WD plants from DKB390 and BRS1055 didn't change activity of antixidant system enzymes nor ABA levels compared to its counterparts under FC (Figure 1), and even the counteraction of oxidative stress via modulating antioxidant enzymes ABA-mediated was not active, the MDA levels with remained unchanged related to FC.

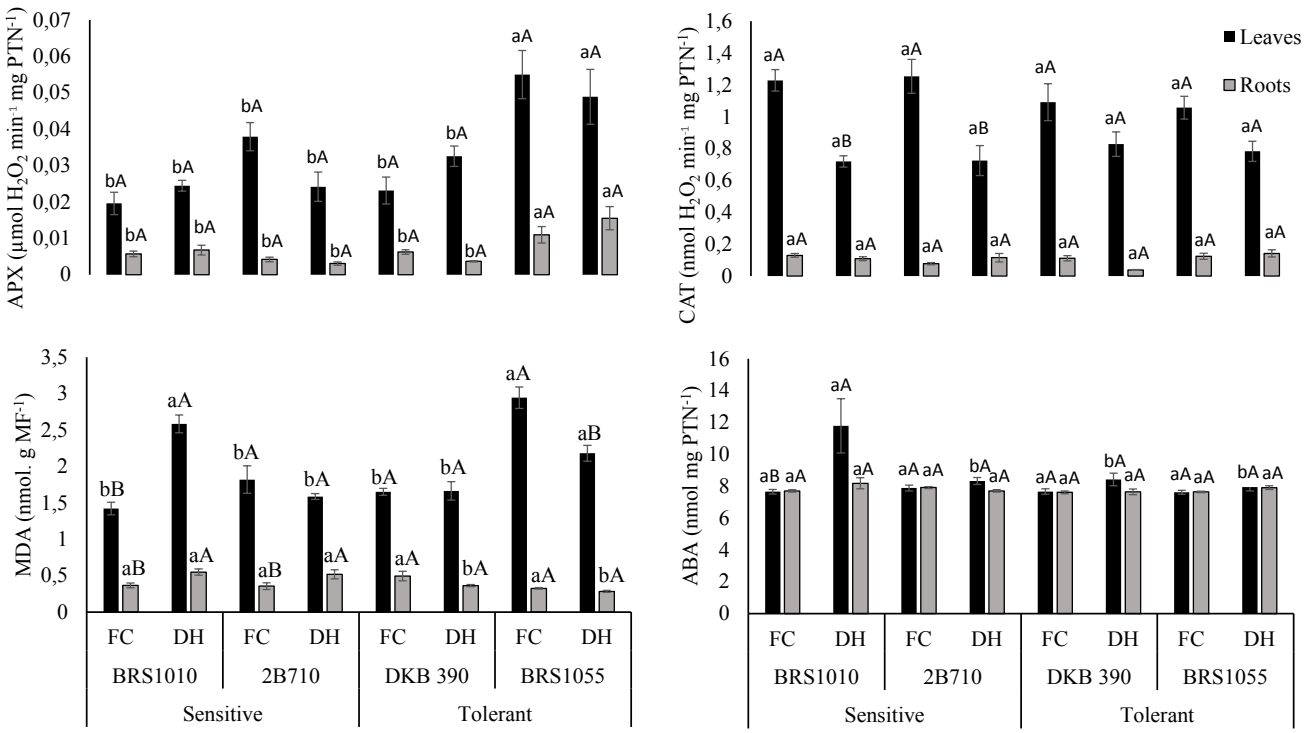


**Figure 1:** Activity of antioxidante enzymes ascorbate peroxidase (APX) and catalase (CAT), levels of abscisic acid (ABA) and cellular damage based on malondialdehyde (MDA) accumulation in ear-leaves and roots tips of four maize genotypes with contrasting characteristics for drought tolerance (BRS1010 and 2B710 - sensitive; DKB390 and BRS1055 - tolerant) grown under different water contents in the soil (field capacity - FC, and water deficit - WD) (n=6). Means followed by the same letter are not statistically different from each other. Lowercase letters denote comparisons between genotypes within the same water level soil, and uppercase letters denote comparisons between the water levels in the soil within the same genotype. Means were compared by Scott-Knott test at 5% probability.

Antioxidant enzymes activity has been reported to increase in plants exposed to various environmental stresses, including drought [11,10]. As a result, the activity of these enzymes has been used as an indirect selection criterion for screening drought-resistant plant materials. The protective effect of ABA on *A* is with due to its the ability to enhance the elimination system for ROS, as measured in terms of antioxidant enzymes such as SOD, CAT and APX [10]. The ABA aplication has no influence on antioxidant enzymes in maize under early-term drought, with exception of CAT activity, which, with ABA application had its activity elevated resulting in higher values, especially in tolerant hybrid DKB 390 [10]. In addition, the activity of antioxidant enzymes at the beginning of stress was high, while at the tenth day under drought the enzymatic activity decreased [10], corroborating our results. Maybe, both CAT and ABA were deactivated due long exposure to drought, and yet *A* and yield in DKB 390 and BRS1055 was influenced in less extent than BRS1010 and 2B710 under WD, demonstrating the effectiveness of the oxidative stress control in these genotypes under long-term was due to another tolerance mechanism that not drought-related enhancement of the antioxidant defense capacity ABA-mediated.

Only plants from sensitive genotype BRS1010 after 12 days under WD presented higher ABA levels than its counterparts under FC (Figure 1); however, due to the inactivation of ABA-mediated antioxidant system and absense of another tolerance mechanism the stress control was not effective. In this genotype, the CAT activity in leaves decreased and lipid peroxidation increased, as shown by higher MDA concentrations in both leaves and roots (Figure 1). With the increase of water stress, $H_2O_2$ participation in the Haber–Weiss/Fenton reaction as free radical attacking the cell membranes [19]. This way, a scavenging to diminish these molecules becomes necessary, but this capability was not found in the sensitive genotype BRS1010 because it was not able to diminish the $H_2O_2$ content.

Regardless genotype, there was a significant reduction of *A* and $g_s$ in plants exposed to WD compared to with well irrigated plants (Table 1). By the way, there was a strong correlation between these two variables (data not shown) while $C_i$ and $C_c$ values increased (Table 1). Plants of the tolerant genotypes DKB390 and BRS1055 under WD showed *A* and $g_s$ values of, respectively, 70.33 % and 64.66 % higher, as well as larger values of *E*, compared to those values observed in plants from the sensitive genotypes 2B710 and BRS1010 grown in the same condition (Table 1). The N partition between fractions involved in $N_{Rubisco}$, $N_{PEPc}$ and $N_{PPDK}$, Ni and Nb were significantly affected by the soil water level, with lower values on WD compared to those obtained under FC (Table 2). Such information helps to explain the declines in $V_{p,max,}$ $V_{c,max}$ and $J_{max}$ in WD plants (Table 1), demostrating lower $CO_2$ use by the enzymes $PEP_c$ and Rubisco. In contrast, the *PR* was slightly increased (Table 1), in parallel decreases in rate of ATP and NADP comsumption, as well as $H^+$ requeriment.

The carbon fixation, which generally represents the main sink for absorbed light in chloroplasts, was found to be depressed in all genotypes under drought by photoinhibition, mainly BRS1010 (Table 1). Drought resistant genotypes with high yield can release more water through the stomata openings, which in turn promotes a higher canopy cooling to escape from photoinhibition [10]. Plants from BRS1010 under WD restrict latent heat loss by *E*, with possible increased leaf temperature, leading photoinhibition, which in turn, impair *A*. As a result of the decrease in both *A* and *E* values, the *WUE* was severely

| | Sensitive | | | | Tolerant | | | |
|---|---|---|---|---|---|---|---|---|
| **Parameter** | **BRS1010** | | **2B710** | | **DKB 390** | | **BRS1055** | |
| | FC | WD | FC | WD | FC | WD | FC | WD |
| *A* | 23,20cA | 0,152bB | 28,06bA | 1,187bB | 27,72bA | 2,257aB | 33,62aA | 2,257aB |
| $F_vF_m$ | 0,803aA | 0,762bB | 0,790aA | 0,757bB | 0,800aA | 0,757bB | 0,801aA | 0,784aB |
| $g_s$ | 0,102cA | 0,007aB | 0,145bA | 0,010aB | 0,138bA | 0,023aB | 0,189aA | 0,023aB |
| *E* | 2,107cA | 0,088aB | 3,886aA | 0,192aB | 2,347cA | 0,499aB | 2,979bA | 0,498aB |
| $C_i$ | 75,27aB | 357,8aA | 31,64aB | 158,9cA | 43,38aB | 215,5bA | 67,94aB | 214,4bA |
| *A/E* | 11,99aA | 1,645bB | 7,315bA | 6,508aA | 11,81aA | 4,592aB | 11,28aA | 4,599aB |
| $g_m$ | 55,17bA | 0,830bB | 124,0aA | 22,41bB | 61,62bA | 83,79aA | 74,65bA | 86,63aA |
| $C_c$ | 63,67aB | 357,8aA | 17,61bB | 158,3cA | 29,52bB | 214,4bA | 51,13aB | 213,3bA |
| *PR* | -1,91aB | 0,619aA | -4,32cB | 1,501aA | -2,63aB | 1,122aA | -3,38bB | 1,122aA |
| $V_{pmax}$ | 38,26cA | 12,54aB | 43,50bA | 14,01aB | 42,60bA | 14,94aB | 48,81aA | 14,94aB |
| $V_{cmax}$ | 64,84cA | 50,66bB | 67,80bA | 51,36bB | 67,60bA | 52,03aB | 71,10aA | 52,03aB |
| $J_{max}$ | 231,8cA | 71,29aB | 267,7bA | 76,40aB | 260,0bA | 81,56aB | 312,5aA | 81,57aB |
| ATP | 1,280aA | 0,882aB | 1,078bA | 0,844aA | 1,322aA | 0,963aB | 1,436aA | 0,963aB |
| NADP | 3,970cA | 3,637cB | 4,035bA | 3,656bB | 4,033bA | 3,674aB | 4,088aA | 3,674aB |
| $H^+$ | 3,842aA | 2,647aB | 3,233bA | 2,531aB | 3,965aA | 2,889aB | 4,308aA | 2,888aB |

Abreviatures: photosynthetic rate (*A*), stomatal conductance to water vapour ($g_s$), maximum efficiency of photosystem II ($F_vF_m$), transpiration rate (*E*), internal $CO_2$ concentration ($C_i$), relation of water use efficiency (*A/E*), mesophyll conductance ($g_m$), chloroplastidic $CO_2$ concentration ($C_c$), photorespiration rate (*PR*), maximum rate of carboxylation of phospoenolpyruvate ($V_{pmax}$), maximum rate of carboxylation of Rubisco ($V_{cmax}$), maximum rate of carboxylation limited by electron transport ($J_{max}$).
Means followed by the same letter are not statistically different from each other. Lowercase letters denote comparisons between genotypes within the same water level soil, and uppercase letters denote comparisons between the water levels in the soil within the same genotype. Means were compared by Scott-Knott test at 5 % probability.

**Table 1:** Leaf gas exchange obtained *in situ* and derived from *A*-$C_c$ curves in four maize genotypes with contrasting characteristics for drought tolerance (BRS1010 and 2B710 - sensitive; DKB390 and BRS1055 - tolerant) grown under different water contents in the soil (field capacity - FC, and water deficit - WD) (n=6).

| | Sensitive | | | | Tolerant | | | |
|---|---|---|---|---|---|---|---|---|
| **Parameter** | **BRS1010** | | **2B710** | | **DKB 390** | | **BRS1055** | |
| | FC | WD | FC | WD | FC | WD | FC | WD |
| $N_{Rubisco}$ | 37,57bA | 29,58aB | 53,84aA | 33,30aB | 40,44bA | 30,97aB | 54,25aA | 37,21aB |
| $N_{PEPc}$ | 0,410bA | 0,140aB | 0,630aA | 0,170aB | 0,470bA | 0,160aB | 0,690aA | 0,200aB |
| $N_{PPDK}$ | 2,110bA | 0,720aB | 3,240aA | 0,860aB | 2,410bA | 0,840aB | 3,530aA | 1,010aB |
| Nb | 1,250bA | 0,780aB | 1,840aA | 0,890aB | 1,380bA | 0,830aB | 1,910aA | 1,000aB |
| Ni | 8,920aA | 8,820bA | 6,650bA | 5,290cA | 4,500cA | 4,760cA | 8,990aB | 12,74aA |
| Nt | 50,25bA | 40,05bB | 66,20aA | 40,50bB | 49,20bA | 37,56bB | 69,37aA | 52,16aB |

Abreviatures: Nitrogen investments in carboxylation enzymes (Rubisco- $N_{Rubisco}$, Phosphoenolpyruvate- $N_{PEPc}$ and Pyruvate Orthophosphate Dicinase- $N_{PPDK}$), light harvesting (Ni), bioenergetics (Nb) and total (Nt).
Means followed by the same letter are not statistically different from each other. Lowercase letters denote comparisons between genotypes within the same water level soil, and uppercase letters denote comparisons between the water levels in the soil within the same genotype. Means were compared by Scott-Knott test at 5 % probability.

**Table 2:** Nitrogen partitioning within the photosynthetic machynary in four maize genotypes with contrasting characteristics for drought tolerance (BRS1010 and 2B710 - sensitive; DKB390 and BRS1055 - tolerant) grown under different water contents in the soil (field capacity - FC, and water deficit - WD) (n=6).

decreased in WD plants of BRS1010 (Table 1). Notably, the *A* values in WD plants of BRS1010 genotype was 7.81 times lower than genotype 2B710, while *E* was only 2.2 times lower, which explain the quite similar *WUE* values of 2B710 WD compared to those verified in DKB 390 and BRS 1055 genotypes under same condition.

Adjustment of light capture, use and dissipation is required to provide photoprotection to the photosynthetic apparatus [20]. In our study we showed that Chl *a* fluorescence parameters declined under WD, but plants of BRS1055 genotype under drought had $F_v/F_m$ values higher than the others genotypes, corroborating the highest Ni value (Tables 1 and 2). It may be suggested that photoprotection of the PSII reaction center by xanthophyll engaged in sustained thermal energy dissipation are likely to have occurred in this genotype, which in turn, delays the degradation of the D1 protein, the main polypeptide of PSII reaction center. In addition, the $V_{p,max}$, $V_{c,max}$, $J_{max}$, $N_{Rubisco}$, ATP, NADP and $H^+$ values declined in all genotypes under drought in parallel to increases in *Ci*, *Cc* and *PR* (Table 1).

In fully hydrated leaves, the $CO_2/O_2$ ratio in bundle sheath cells of $C_4$ species is three to six times higher than in mesophyll cells under atmospheric levels of $CO_2$ and $O_2$ [21]. Therefore, the oxygenase activity of Rubisco, and consequently the *PR*, is low [22]. Under drought conditions, the $C_i$ may decrease because of decreased $g_s$ and should cause *PR* increase [22]. However, *PR* has been shown to neither increase nor contribute to the limitation of *A* in $C_4$ grasses under drought stress [22]. In contrast, this study demonstrated a slight increase in *PR* even when $C_i$ is substantially increased under drought, due partial deactivation of carboxylation capacity at Rubisco catalytic site. Adjustments to even mild disturbances in redox status, caused by a deficiency in ascorbate, AOX or chloroplastic NADP-malate dehydrogenase, comprise increases in photorespiratory components such as catalase, P-protein of glycine decarboxylase complex and glycine content [23]. Therefore, a strong interaction between the chloroplast redox status and *PR* to induce scape mechanism against ROS formation defense under severe drought is not surprising. Overall, these evidences conffirm that carboxylation capacity at Rubisco catalytic site at least was partially deactivated in WD plants.

Recently Centritto et al. [24] have posited that under drought conditions, $g_m$ also plays an important role in determining *A* because rice genotypes with inherently higher $g_m$ are capable of maintaining a

| | Sensitive | | | | Tolerant | | | |
|---|---|---|---|---|---|---|---|---|
| **Parameter** | **BRS1010** | | **2B710** | | **DKB 390** | | **BRS1055** | |
| | FC | WD | FC | WD | FC | WD | FC | WD |
| LA | 0.529bA | 0.480bB | 0.567bA | 0.486bB | 0.559bA | 0.553aA | 0.630aA | 0.576aA |
| DGB | 90.74bA | 53.83cB | 104.0aA | 58.33cB | 99.87aA | 98.92aA | 90.02bA | 71.63bB |
| TDB | 261.0aA | 197.1bB | 261.2aA | 192.1bB | 259.4aA | 243.9aA | 279.3aA | 244.9aB |
| HI | 0.349bA | 0.270bB | 0.401aA | 0.303bB | 0.384aA | 0.405aA | 0.324bA | 0.294bA |
| EM:E | 0.200aA | 0.156aB | 0.225aA | 0.165aB | 0.229aA | 0.228aA | 0.194aA | 0.187aA |

Abbreviatures: Leaf area (LA), dry grain biomass (DGB), total dry biomass (TDB), harvest index (HI), embryo: endosperm relationship (EM: E).
Means followed by the same letter are not statistically different from each other. Lowercase letters denote comparisons between genotypes within the same water level soil, and uppercase letters denote comparisons between the water levels in the soil within the same genotype. Means were compared by Scott-Knott test at 5 % probability

**Table 3:** Agronomic production in four maize genotypes with contrasting characteristics for drought tolerance (BRS1010 and 2B710 - sensitive; DKB390 and BRS1055 - tolerant) grown under different water contents in the soil (field capacity - FC, and water deficit - WD) (n=6).

higher *A*. To the best of our knowledge, the current study is the first to report a direct effect of sink strength on $g_m$ in a $C_4$ cereal species. The goal of present study was finding effects of long-term drought on photosynthetic resource economy in maize were associated with a mesophyll and nor a biochemical limitation. As the role of $g_m$ was never taken into account in $C_4$ species, previous studies have considered that non-stomatal due to a decrease in carboxylation capacity overrides in maize genotypes under under long-term drought.

Changes in $g_m$ were significantly correlated with the drought-induced change in *WUE*, what proves the importance of $g_m$ in optimizing resource use under water restriction period [25]. The ABA has long-lasting effects on plant hydraulic properties via aquaporin activity, which contributes to the maintenance of a favorable plant water status; if so, such decrease in $g_m$ only in drought sensitive genotypes might be linked to impaired root aquaporin activity, as these proteins are an important component controlling $g_m$ in herbaceuos plants such as maize [26]. When root aquaporin activity is affected by WD, leaf elongation rate decreases and becomes more sensitive to changes in evaporative demand [27], and only the two sensitive genotypes under WD showed lower LA values compared to FC (Table 3). These assumptions might provide a mechanistic link to at least partially explain the ameliorative effects of drought tolerant genotypes DKB390 and BRS1055 on *A* via scape of $g_m$ decline under WD (Table 1). As $g_s$ was reduced in all WD plants, and only plants from sensitive genotypes BRS1010 and 2B710 declined $g_m$ values in parallel, we believe that $g_m$ compensates reductions in $g_s$ in tolerant genotypes. We showed that the N was invested in the photosynthetic apparatus, including carboxylation enzymes, electron transport and light harvesting declined under drought in all genotypes. The N is required for building aquaporins or other proteins that contribute to $g_m$, and ongoing costs of maintaining such proteins [28]. Only WD plants in sensitive genotypes $g_m$ was limited by lower N investment. Perhaps, the tolerant genotypes just declined $g_s$ from the need to limit *E* and to prevent runaway xylem embolism, which in turn, favoured a shift of N from carboxylation enzymes to $g_m$.

The oxidative damage whole plant effect in *A* and yield attributes caused by WD is remarkable. Under WD, the genotypes DKB 390 and BRS 1055 showed similar values of *A* and TDB, but the DGB was 28% higher in the DKB 390, resulting in a higher HI when compared to BRS 1055 (Table 3). At first instance, the lower HI values in BRS1055 would be interpreted as a low tolerance for WD. However, when compared to its counterpart under FC a decrease of only 9.3% occurred in HI for BRS 1055 under WD. The sensitive genotypes BRS 1010 and 2B710 under WD presented reductions of 22 and 24% in HI, respectively (Table 3). In fact, plants from BRS 1010 and 2B710 presented LA, EM:E and DGB reduced under WD compared to FC (Table 3), indicating the occurrence of a low photoassimilate flow to the grain in these two maize genotypes under WD, compared to genotypes DKB 390 and BRS 1055. The results found in DKB390 and BRS1055 for HI confirmed its higher tolerance to drought compared to BRS1010 and 2B710.

## Conclusion

The failure of the antioxidant defense system ABA-mediated in WD plants result in oxidative damage only when genotypes doesnt present another drought tolerance mechanism, resulting in lipid peroxidation increase, thus ultimately impairing *A* and yield. The unknown tolerance mechanism in tolerant genotypes under long-term drought is linked to scape of $g_m$ decline.

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