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Received: 21 Jan 2014 | Accepted: 18 Mar 2014 | Published online: 24 Apr 2014

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# Efficient Regulation of $CO_2$ Assimilation Enables Greater Resilience to High Temperature and Drought in Maize

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Table of Contents

Abstract
Introduction
Materials and Methods
Results
Discussion
Acknowledgments
References
Supplementary Material
Keywords
Citation
Share
Export to Reference Manager

## Abstract

Maize is one of the most important crops worldwide, representing 30% of the total cereal production and 67% of the total harvested area dedicated to cereals. Although the majority of this production is consumed as food (human change (GHG), water restrictions and heat waves are among the major expected risks for food production in some of the major growing regions. Rubisco, the enzyme that catalyzes the first step of photosynthetic $CO_2$ assimilation, is inefficient and slow, and photosynthesis is limited by the supply of $CO_2$ and by the activities of Rubisco and other enzymes. To improve the maize yield in a changing climate, and ensure food security for the increasing world population, it is important to develop crops with improved photosynthetic efficiency, greater resilience and water availability, tested for traits that confer resilience to heat and drought stress, and developing genetic resources for breeding.

Photosynthetic efficiency and resilience to heat and drought stress were assessed in four C4 maize hybrids, varying in yield and water use in greater detail. Furthermore, when subjected to high temperature, plants usually exhibit a decline in photosynthesis, which is in part due to the inhibition of Rubisco activity by its inhibitor protein Rubisco activase. Rubisco activase is a molecular chaperone that uses ATP hydrolysis to remove sugar phosphates from active Rubisco sites, and is a target for improving crop resilience to heat stress. Transgenic plants with reduced amounts of Rubisco activase were also tested for their response to heat and drought stress, and develop genetic resources for breeding.

Photosynthesis was measured in 9-DAP mature enzymes (3-PGA) and ribose-5-phosphate (R5P) in the Calvin-Benson-Bassham (CBB) cycle, and in the photosynthetic electron transfer chain (PETC) components, and photosynthetic efficiency was determined by measuring the assimilation activity of Rubisco, and corresponding photosynthetic rates in the leaves. Rubisco activase was also tested for its ability to remove sugar phosphates from active Rubisco sites, and to promote the activation of Rubisco. Finally, the amount of Rubisco activase was quantified in the leaves, and the amount of Rubisco was also quantified in the leaves, and the amount of Rubisco was also quantified in the leaves, and the amount of Rubisco was also

A broad genetic variation of the trait related to transpiration rate response to VPD conditions was extensively investigated by Sinclair and collaborators in several crops, including maize (Sinclair, 2017, 2018; Sinclair et al., 2017). Using an experimental system that allowed precise control of VPD (VPD chamber, Gholipoor et al., 2013), it was found that some maize genotypes showed early closure of stomata as VPD increases, decreasing transpiration (TRlim) and saving soil water. The trait TRlim was considered beneficial for maize production under limited water supply and therefore was genetically incorporated in the DuPont Pioneer AQUAmax hybrids (e.g., P0023, Gaffney et al., 2015). However, TRlim was found to be thermal sensitive in maize plants grown at high temperature (32°C versus 25°C, Yang et al., 2012), and in another study, some genotypes lost this characteristic when exposed for 2 days at 38°C (Shekoofa et al., 2016).

Our results demonstrated that a reduced transpiration rate was maintained in plants of P0023 acclimated to high temperature/VPD without substantial damage to carbon assimilation. Moreover, this characteristic acted beneficially as a stress avoidance mechanism when WD was associated (WD38), by maintaining high leaf hydration (Figure 2A) and photosynthetic efficiency (Figure 1).

Giuliani et al. (2005) found that maize lines with a greater concentration of roots in shallow soil layers had increased the leaf abscisic acid concentration, causing reduced stomatal conductance. Consequently, TRlim could be associated with changes in the root system, as plants with a more robust root system can explore and obtain water from deeper soil layers (Hammer et al., 2009; Adee et al., 2016). The decrease of above-ground biomass and RGR in P0023 under WD38 (Figures 2C,D) besides higher photosynthetic efficiency than B73 can also suggest that photosynthetic resources in P0023 are being used in root development.

Furthermore, aquaporins can also be associated with the regulation and expression of the TRlim trait (Choudhary et al., 2015), as several authors proposed aquaporins in the same way as key players in converting chemical signals (e.g., ABA) to hydraulic response and transmembrane $CO_2$ transport (Flexas et al., 2006; Shatil-Cohen et al., 2011; Sade et al., 2014; Moshelion et al., 2015; Grondin et al., 2015; Secchi et al., 2017; Ding et al., 2020).

## Phosphoenolpyruvate Carboxylase Activation and Phosphorylation Status Contributed to the Maintenance of Photosynthesis Efficiency Under Water Deficit at High Temperature

A possible throwback of decreasing the transpiration rate under high temperature is the potential harmful increase in leaf temperature, as generally, plants use evaporative cooling to reduce it (Carmo-Silva et al., 2012; Costa et al., 2013). It is generally accepted that enzymes of CCM and Rubisco are unaffected by changes in the range of temperatures faced by plants in our experiment (Casati et al., 1997; Crafts-Brandner and Salvucci, 2002; Salvucci and Crafts-Brandner, 2004b). However, the decrease of the Rubisco activation state is usually associated with high temperatures due to an increase in catalytic misfire inhibition and decline of the regulation by heat-sensitive Rca (Salvucci and Crafts-Brandner, 2004c; Carmo-Silva and Salvucci, 2011).

Under WW38, no significant changes on the Rubisco activation state were observed (Figures 4C,D), which can be explained by the fact that in maize Rubisco is exclusively located in the chloroplast of BSC, surrounding the vascular tissue, that can offer a superior exposure to the evaporative cooling capacity, buffering the BSC temperature rise (Lundgren et al., 2014; Pignon et al., 2019). Another possible explanation is that the long-term acclimation to high temperature experienced by these plants allowed the expression of Rca isoforms more active under high temperature repairing catalytic misfire inhibition, as reported in other studies (Crafts-Brandner and Salvucci, 2002; Yin et al., 2014; Zhang et al., 2019; Kim et al., 2021).

On the other hand, the catalytic activity of carboxylating and decarboxylating enzymes was modulated by WW38 on both genotypes relative to WW25, but more extensively in B73 (Supplementary Figures 4C,D and Figures 4C,D). A possible reason for the decrease of the PEPC activation state was inhibition of physiological activity due to increased sensitivity to the inhibitor L-malate (Figure 5 and Supplementary Figure 1A), known to be mainly regulated by the PEPC kinase phosphorylation (Jiao et al., 1991; Bakrim et al., 1992; Nimmo, 2003). Nevertheless, in B73 a strong negative correlation between the PEPC maximal capacity (Vmax) and the maximum quantum yield of PSII (Fv/Fm, Supplementary Figure 4C) and a positive correlation between PEPC activation and ETR (Figure 4C) can also suggest a relation to the decline of ATP production and possible reduction of PEP regeneration by pyruvate phosphate dikinase (PPDK) in the chloroplast of the MCs, that is ATP dependent (Edwards et al., 1985; Chastain et al., 2011; Chen et al., 2014). The higher NADP-ME maximal activity (Supplementary Figures 4C,D) and lower activation state (Figures 4C,D) at high temperature mimic the changes in PEPC enzymatic capacities and respond to carbon supply and flux between MCs and BSCs (Maier et al., 2011; Wang et al., 2014). Moreover, the more considerable extent of increase of the PEPC maximal capacity than NADP-ME in both genotypes (Supplementary Figures 4C,D) can suggest that PEPC activity can be involved in the carboxylation of $CO_2$ from sources other than atmospheric provenance, as the recycling of $CO_2$ from BSC leakage or photorespiratory processes, usually associated with exposure to high temperatures (Hatch et al., 1995; Sage et al., 2010; Kromdijk et al., 2014).

Under WD38, when compared to WW25, both genotypes presented a decreased Rubisco activation state, due to the initial lower activity relative to total activity (Figures 4E,F and Supplementary Figure 3). This might be due to the slightly increased leaf temperature (Figure 3C), caused by the decline of gs and evaporative cooling (Figures 1B, 3), making the increase in the Rubisco catalytic activity insufficient to overcome enzyme inactivation (Crafts-Brandner and Salvucci, 2002). The substantial decrease of ETR (Figure 1C) and the consequent decline in the ADP:ATP ratio in the chloroplast might have also contributed to the observed decrease in Rubisco activation, as the repair of misfire inhibition by Rca is ATP dependent (Salvucci and Crafts-Brandner, 2004c; Carmo-Silva and Salvucci, 2011), also supported by the correlation between the Rubisco activation state and ETR in B73 (Supplementary Figure 4E). Nevertheless, P0023 increased the total activity and B73 maintained near the same as WW25 (Supplementary Figures 3, 4E,F), showing a higher physiological capacity in P0023. There was low correlation between the decrease of activation and the reduction of net photosynthetic assimilation and ETR in this genotype than B73 (Figures 1A, 5E,F).

The increase in the PEPC activation state in P0023 (Figures 4E,F) corresponds to the decrease in the sensitivity to malate (Figure 5), suggesting a different level of PEPC phosphorylation between genotypes and higher physiological functionality of PEPC in P0023. Regulation of PEPC activity by phosphorylation has been hypothesized to provide a possible link between PEPC activity and coordination of CCM upon drought and salt stress in $C_4$ plants (Foyer et al., 1998; García-Mauriño et al., 2003; Marques da Silva and Arrabaça, 2004; Carmo-Silva et al., 2008). Increase of PEPC phosphorylation and activation under WD38 in P0023 suggest a higher $CO_2$ assimilation efficiency, maintaining the carboxylation rate in MCs and the supply of $C_4$ acids to BSCs adequate for Rubisco activity. Therefore, an increase in PEPC phosphorylation could be regarded as a regulatory mechanism to maintain high photosynthetic activity under WD38. Nonetheless, the differences between PEPC catalytic activity can be explained by other regulatory mechanisms, such as other post-translational modifications (Luís et al., 2016; Ruiz-Ballesta et al., 2016).

The NADP-ME maximal activity was reduced by half, relative to WW38, demonstrating the negative effect of drought at 25°C (Supplementary Figures 4A,B) and 38°C (Supplementary Figures 4C,D relative to Figures 4E,F). Several authors reported the decrease of NADP-ME activity under WD (Du et al., 1996; Marques da Silva and Arrabaça, 2004; Carmo-Silva et al., 2008), but to the best of our knowledge, no changes in NADP-ME activity have been previously reported in maize plants acclimatized to high temperature and subjected to WD. Nevertheless, the plasticity of the decarboxylating process in maize plants under stress conditions was identified by other authors (Chapman and Hatch, 1981; Wingler et al., 1999; Bellasio and Griffiths, 2014), and alternative decarboxylating processes, as the synthesis of aspartate as a major translocated $C_4$ acid, can compensate the decrease of NADP-ME decarboxylating activity under our experimental conditions (Furbank, 2011; von Caemmerer and Furbank, 2016).

## Electron Transport Rate Stability Near Vascular Tissues Contributed to the Supply of Chemical Energy for an Effective $CO_2$ Concentrating Mechanism Under Water Deficit at High Temperature

The P0023 genotype showed a higher maximum quantum yield of PSII (Figure 1D) and stable quantum yield of the electron transport flux until the PSI electron acceptors (Supplementary Figure 5A) under high temperatures and a higher contribution of MV ETR to whole L ETR under WD38 (Figure 6C). These results demonstrated the higher efficiency in producing chemical energy (ATP and reduction power) in this genotype under higher temperature. The maize MVs are anatomically characterized by highly differentiated BSCs surrounded by MCs, forming concentric circles around the vasculature (Lundgren et al., 2014). Adenosine triphosphate and reduction power are cofactors of most photosynthetic enzymes, and reduction power is moved from MCs to BSCs through malate decarboxylation (Furbank, 2011) and the shuttle of 3-PGA and triose phosphate (Hatch, 1987; Bräutigam and Weber, 2010). Thus, the observed superior ETR stability in these zones (MVs) and the maintenance of the physical integrity components of the photosynthetic apparatus in MCs and BSCs can be regarded as crucial for successful acclimation of photosynthesis to high temperature. Moreover, reduction of stomatal conductance under high temperature as a water-saving mechanism in P0023 and maintenance of hydraulic conductance can also act preventing desiccation and maintenance of highly productive MCs and BSCs surrounding the vascular tissues (Figures 1B, 6D; Sunita et al., 2014; Sade et al., 2014; Moshelion et al., 2015).

## Conclusion

In summary, the limited transpiration rate under high temperature/VPD, together with higher efficiency in the regulation of CCM contributed to the maintenance of a better physiological status in P0023 under high temperature and/or extended drought. These characteristics can allow water conservation in initial periods of soil drying, without substantial crop production damage. Genotypes with the same traits may be suitable for crop production in environments with high temperature that experience regular water shortage periods. Furthermore, high throughput screening of maize hybrids under similar experimental settings, but mimicking field light conditions, can select genotypes with the same characteristics and potential for more stable production in warmer and drier conditions, helping to overcome future throwbacks in food production.

## Data Availability Statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

## Author Contributions

PC planned and carried out the experiments, analyzed, interpreted the results, and took the lead in writing the manuscript. EC-S and JS contributed to the interpretation of the results and supervised the research. AS and MV provided critical feedback. All authors discussed the results and contributed to the final manuscript.


## Funding

The financial support provided by UIDB/04046/2020 and UIDP/04046/2020 Centre grants from FCT (BioISI), FCT research project INTERPHENO (PTDC/ASP-PLA/28726/2017) is gratefully acknowledged. Pedro Correia (PMPC) acknowledges FCT (Portugal) for the financial support via a fellowship from the BioSys Ph.D. programme PD65-2012 (Ref SFRH/PD/BD/130973/2017).


## Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Acknowledgments

We would like to thank Luís Grifo (Pioneer Hi-Bred Sementes de Portugal S.A.) for the supply of P0023 seed and Hamilton Chiango for help with plant growth.


## Supplementary Material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2021.675546/full#supplementary-material

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**Keywords:** crop improvement, drought tolerance, food security, maize, global warming, heat tolerance, water deficit, *Zea mays*

**Citation:** Correia PMP, da Silva AB, Vaz M, Carmo-Silva E and Marques da Silva J (2021) Efficient Regulation of $CO_2$ Assimilation Enables Greater Resilience to High Temperature and Drought in Maize. *Front. Plant Sci.* 12:675546. doi: 10.3389/fpls.2021.675546

**Received:** 03 March 2021; **Accepted:** 28 June 2021;
**Published:** 26 July 2021.

Edited by:
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