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Short communication

Response of maize photosynthesis to high temperature: Implications for modeling the impact of global warming

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ABSTRACT

Negative impacts of increased temperature on maize yield are anticipated using simulation models. However, some temperature functions are parameterized with partial information. There is limited information on photosynthesis response to high temperature in modern maize hybrids. Improved photosynthesis-temperature functions are key for realistic yield simulations. Our experiment was aimed at building a functional relationship between photosynthesis and air temperature exploring temperature ranges relevant for global warming simulations. Maize hybrids from cold, temperate, and subtropical regions were included in the study to assess genetic adaptation. Results showed a trilinear response to temperature with an optimum of 40 °C. No genetic adaptation was observed among the diverse set of hybrids evaluated. Results contrast with common temperature-limiting functions indicating a decline in carbon assimilation above 30–33 °C. Our results suggest possible overestimations of negative impacts of global warming on maize yield due to the use of inadequate response functions relating carbon assimilation to temperature.

1. Introduction

Global warming is associated with high temperature events projected to increase in magnitude, duration, and frequency (IPCC, 2014). Concern exists on how global warming will impact food security in the future and particularly maize production. Several crop modelling studies have predicted substantial reductions in maize yield due to elevated temperature (Lobell et al., 2013; Bassu et al., 2014; Schauberger et al., 2017). Predicted yield reduction in the US Midwest was associated with degree-day accumulations over 30 °C (Lobell et al., 2013). Across four maize production regions in the world, a 0.5 Mg ha^{-1} yield reduction was simulated for each 1 °C temperature increase (Bassu et al., 2014). A 6% yield reduction for each day with average temperature greater than 30 °C was predicted for dryland maize in the United States (Schauberger et al., 2017). Globally, 7% maize yield reduction was predicted per 1 °C increase relative to current mean temperature (Zhao et al., 2017). Confidence in these projections of the effect of global warming on maize production relies on crop simulation models correctly capturing physiological responses to high temperature.

From a physiological perspective, different mechanisms explain maize sensitivity to high temperatures. Implicated mechanisms include sensitivity of flowering to heat stress (Bolanos and Edmeades, 1996), reduction in duration of crop cycle (Parent and Tardieu, 2012), increased water stress due to increased atmospheric demand (Lobell et al., 2013), and decline in photosynthesis at increased temperature (Crafts-Brandner and Salvucci, 2002). Accuracy in maize yield projections associated with global warming rely on precise temperature-limiting functions affecting these processes. It is recognized that more realistic temperature functions are key to improve simulations of global warming effects. For example, improved temperature functions based on experimental data reduced wheat yield simulation error by up to 50% (Wang et al., 2017). They demonstrated that improving temperature response functions allowed crop models to better capture the impact of temperature change on grain yield, leading to a higher confidence in crop yield projections under global warming scenarios.

The response of leaf photosynthesis to light plays a pivotal role in the simulation of canopy carbon assimilation during the growing season and, ultimately, in the determination of crop yield (Boote and Pickering, 1994; Hammer and Wright, 1994). Measurements of light-saturated leaf photosynthesis provide the basis for scaling carbon assimilation from leaf to canopy (Farquhar et al., 1980). Currently, there is a paucity of light-saturated maize leaf photosynthesis assessments over a temperature range relevant to global warming simulations. Past assessments failed to explore the effect of supra-optimum temperatures relevant to global warming simulations (Bennet et al., 1982; Tollenaar,

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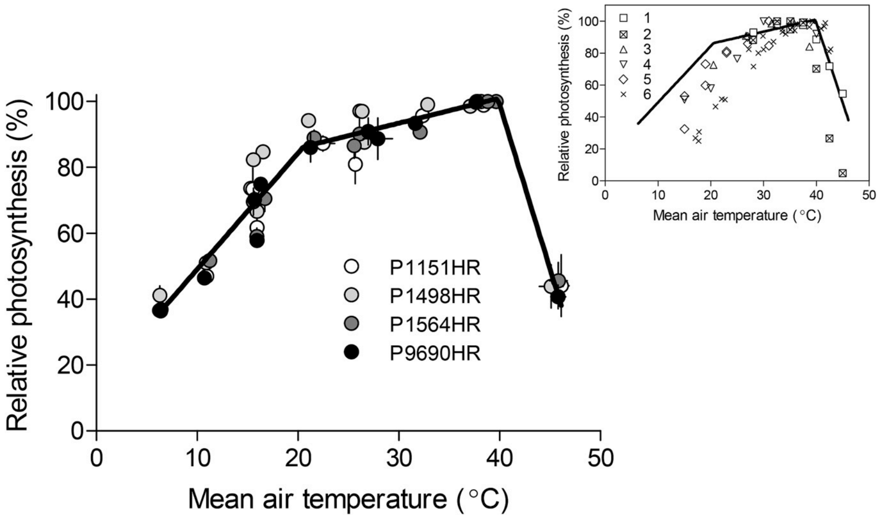

Fig. 1. Relative leaf photosynthesis response to temperature. Trilinear response of relative maize leaf photosynthesis across different air temperature treatments in growth chamber conditions for four hybrids adapted to cold and tropical regions. Function parameters are presented in Table 2. Each point is the average of three replications. Errors bars are standard errors. Inset includes the trilinear response and relative leaf photosynthesis from previously published works. References: 1. Crafts-Brandner and Salvucci (2002) with acclimation; 2. Crafts-Brandner and Salvucci (2002) without acclimation; 3. Kim et al. (2007); 4. Massad et al., (2007); 5. Tollenaar (1989); 6. Bennet et al. (1982).

1989; Kim et al., 2007). Only one study reported supra-optimal photosynthesis responses up to 45 °C (Crafts-Brandner and Salvucci, 2002), but this response was tested only in one hybrid that might not be representative of current maize germplasm. Therefore, a comprehensive temperature response function for a diverse set of modern maize genotypes adapted to different regions is critically needed for accurate maize yield simulations in global warming scenarios. The objective of our study was to evaluate in controlled conditions the response of light-saturated maize leaf photosynthesis to a broad range of air temperature spanning from 6 to 45 °C on modern commercial hybrids from cold, temperate, and subtropical regions.

2. Materials and methods

Four maize (*Zea mays* L.) commercial elite hybrids adapted to cold (P9690HR), cold-temperate (P1151HR), temperate-temperate/subtropical (P1498HR), and temperate/subtropical (P1564HR) regions (Loeffler et al., 2005) were grown in ~4-L pots in a greenhouse located in Johnston, Iowa. Artificial lights were used to expose plants to PAR at a minimum of 600 μmol m^{-2} s^{-1}, with 25 and 20 °C for day and night greenhouse temperature, respectively. Pots were irrigated and fully fertilized to avoid any growth limitation. Two independent experiments were carried out. Experiment 1 explored five temperatures, while experiment 2 explored six temperatures. Temperature treatments started at developmental stage V7 by placing 3 potted plants per hybrid (12 pots total) in a temperature controlled growth chamber. Temperature and relative humidity were monitored constantly and recorded at the moment of measurement. One chamber was used for each experiment and temperature was increased on consecutive days for the same plants. Before measurements, plants were acclimated for 24 h at each specific treatment temperature to avoid any short-term stress effect (Crafts-Brandner and Salvucci, 2002). Light intensity in the growth chamber was 600 μmol m^{-2} s^{-1} PAR. Relative humidity in the controlled growth chamber was maintained between 60 and 80% using commercial air humidifiers. Vapor pressure deficit (VPD) inside the growth chamber was calculated using air temperature and relative humidity. Leaf measurements were made using a portable gas exchange system (Li-Cor 6400, Li-Cor). The system was zeroed using anhydrous calcium carbonate to eliminate water, and soda lime to remove carbon dioxide from the air entering the system. Measurement irradiance intensity was set at 2500 μmol m^{-2} s^{-1} using red-blue light source in an integrated chamber. Flow rate was set at 300 mmol s^{-1}, and ambient CO_2 concentration of 380 mmol mol^{-1}. Each measurement was logged after reaching three stability criteria. These criteria were that slopes with time (seconds) were < 1 for CO_2 concentration of the sample cell (CO_2S parameter, mmol mol^{-1}) and water concentration (H_2OS parameter, mmol mol^{-1}), and < 0.5 for g_s (stomatal conductivity, mol m^{-2} s^{-1}).

A trilinear function was fitted using a nonlinear mixed-effects model by maximum likelihood using the nlme package from R (Pinheiro et al., 2017; R Core Team, 2017). The model included the parameters of the trilinear function as fixed effects, and experiments and individual plants as random effects. Model selection for testing hybrid effect on function parameters was made by the Akaike's Information Criterion (AIC; Akaike, 1998) and the Bayesian Information Criterion (BIC; Schwarz, 1978). Both AIC and BIC rank models based on both model fitting and model complexity. They deal with the trade-off between the goodness of fit of the model and the simplicity of the model, though BIC tends to favor simpler models than AIC. Under both criterions, the most parsimonious model will be the one with smallest value. Analysis was carried out for relative photosynthesis calculated as the proportion of maximum photosynthesis observed for each individual plant across temperature treatments.

3. Results and discussion

Temperature treatments explored in this experiment allowed evaluation of both supra- and sub-optimal leaf photosynthesis responses using a trilinear function (Fig. 1). No differences were observed in response function parameters across hybrids as shown by the model selection procedure (Table 1). Even though hybrids were adapted to regions with different temperature regimes, it was not possible to find any evidence of local adaptation to either high or low temperature treatments. For wheat, however, Monneveux et al. (2003) reported substantial genotypic variation in tolerance to high temperature when evaluating leaf photosynthesis. Even though there was no genetic variation in photosynthetic response to temperature, other evidence suggest that maize yield loss associated with increased temperature is

Table 1
Nonlinear mixed-effects model fit by maximum likelihood. Comparison of the trilinear fit for three alternative models. Model 1 includes replications and hybrids as random factors in all the trilinear model parameters. Model 2 excludes hybrids and keep replications accounting for variation in all the trilinear model parameters. Model 3 is a simpler version of model 2 including replications as random factors but only accounting for variation in the intercept and third slope. AIC and BIC indicate Model 3 is the best model.

Model	df	AIC	BIC	logLik	Test	L.Ratio	p-value
1	19	1004.4	1060.8	−483.2			
2	13	995.2	1033.8	−484.6	1 vs 2	2.83	0.830
3	9	987.2	1014.0	−484.6	2 vs 3	0.00	1.000

Table 2
Photosynthesis response to temperature. Parameters of the trilinear temperature limiting function for maize leaf photosynthesis (Fig. 1). *** indicates *P* value < 0.005.

Parameter	Value	Std. Error	df	t-value
y-intercept	13.8%	2.89	115	4.76***
First slope	3.5% °C^{-1}	0.21	115	17.12***
Breakpoint 1	20.5 °C	0.80	115	25.39***
Second slope	0.8% °C^{-1}	0.02	115	5.92***
Breakpoint 2	39.8 °C	0.36	115	111.00***
Third slope	−10.0% °C^{-1}	1.13	115	8.80***

overestimated if adaptation to temperature is not taken into consideration (Butler and Huybers, 2013). Our results suggest that adaptation as proposed by Butler and Huybers (2013) originates from processes other than carbon assimilation.

For this diverse set of modern elite hybrids, temperature breakpoints were at ~20 °C and ~40 °C (Table 2). Relative photosynthesis increased from the lowest temperature evaluated to the first breakpoint at 3.5% per °C. Between 20 and 40 °C, relative photosynthesis increased slightly to reach the maximum at 40 °C. At this optimum temperature, maximum actual photosynthesis was 42.0, 38.1, 40.4, and 40.4 μmol m^{-2} s^{-1} for P1151HR, P1498HR, P1564HR, and P9690HR, respectively. The only significant difference among hybrids for maximum photosynthesis was between P1151HR and P1498HR ($P < 0.05$). After the optimum, a sharp decline was observed at a rate of −10% per °C when air temperature was greater than 40 °C. Interestingly, at 45 °C maize plants retain almost 40% of maximum relative photosynthetic rate. This finding is consistent with the only previous report that tested ~45 °C treatments (Crafts-Brandner and Salvucci, 2002). However, that study assessed only one hybrid released > 20 years ago that might not be representative of current germplasm. Our study indicates that current elite maize hybrids, regardless of background adaptation, are well suited to support photosynthesis in high temperature environments. Leaf photosynthesis might still be occurring at relatively high rates at temperatures beyond the explored ranges in previous work (Bennet et al., 1982; Tollenaar, 1989; Kim et al., 2007; Massad et al., 2007). Relative leaf photosynthesis results from these previous works are shown as inset in Fig. 1 to highlight comparison. Interestingly, germplasm evaluated in the present study showed higher photosynthetic rates at low temperature compared to previous published works (inset Fig. 1). There is evidence that despite its tropical origins maize is not inherently cold-sensitive and that substantial genetic variation exists for photosynthesis at low temperature (Sobkowiak et al., 2016). Studies have demonstrated the genetic and molecular controls of this trait (Fracheboud et al., 2004; Sobkowiak et al., 2014). Therefore, it can be speculated that some of the observed response at low temperature in this modern germplasm can be explained by selection in US mid-western environments (Greaves, 2007).

Although relative humidity inside growth chambers was maintained between 70 and 80%, temperature treatments affected VPD. There is evidence indicating that some maize hybrids have a non-linear transpiration response to VPD, with reduced transpiration rates at high VPD (Gholipoor et al., 2012). This is associated with reductions in leaf hydraulic conductivity leading to partial stomatal closure even in well-watered plants. Our results, however, showed that transpiration rate was linearly related to VPD (Fig. 2). This is consistent with results indicating that expression of limited transpiration is reduced at high temperature (> 38 °C) (Yang et al., 2012; Shekoofa et al., 2016). Consequently, in our experiments, high VPD was induced by high temperature possibly preventing the expression of limited transpiration. Therefore, the decrease in photosynthesis observed in our study above 40 °C cannot be attributed to a direct effect of VPD on stomatal conductance.

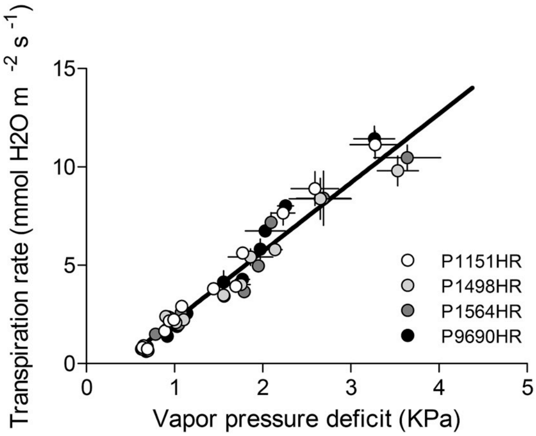

Fig. 2. Transpiration response to vapor pressure deficit. Linear response of maize leaf transpiration rate to vapor pressure deficit evaluated in growth chamber conditions for four hybrids adapted to cold and tropical regions. Each point is the average of three replications. Errors bars are standard errors.

An important aspect of leaf photosynthesis response to temperature is whether the high temperature inhibition is reversible or not when temperature is reduced (Feller, 2016). Currently, the response to temperature is assumed reversible from a simulation model perspective. From a physiological perspective, the inhibitory effect of high temperature on leaf photosynthesis was usually associated with the inability of Rubisco activase activity to keep pace with a faster rate of Rubisco inactivation as temperature is increased (Crafts-Brandner and Salvucci, 2000). At moderately high temperature Rubisco activase is reversibly inactivated; at higher temperature, the enzyme is irreversibly inactivated and degraded. However, the loss of leaf photosynthesis at high temperature (mediated by reduced Rubisco activase activity) may still be reversible as new Rubisco activase is produced by *de-novo* protein synthesis (Feller, 2016). As a consequence, the assumption of reversible temperature effects on leaf photosynthesis is likely correct and holds valid for modeling purposes. However, further experimentation needs to be done for properly testing temperature reversible effects. Alternatively, the negative impact of high temperature on leaf photosynthesis can be explained by the effect of temperature on the maximal electron transport rate (J_{max}) (Massad et al., 2007). These authors found that J_{max} was the most reduced photosynthesis parameter at high temperature compared other parameters like V_{cmax} or V_{pmax} (maximum carboxylation rate of ribulose 1–5 bisphosphate and of phosphoenolpyruvate, respectively) (Massad et al., 2007).

Author contribution

C.M. conceived the presented idea and carried out the experiment. T.T. performed the statistical analysis. J.R. wrote the paper with input from all authors.

4. Conclusions

Previous assessments of global warming effects on maize productivity using physiological models have been based on optimal temperatures for photosynthesis well below those found in this study. Estimated reductions in maize yields under global warming scenarios could have been overestimated due to, in part, inadequate parameterization of photosynthesis response to temperature. This study contributes fundamental knowledge about the response of leaf photosynthesis in maize to a wide range of temperatures and for contrasting germplasm based on their adaptation background. Integrating this knowledge with physiological models will facilitate increased realism in future assessment studies and assist the design of mitigation strategies.

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