Effect of atmospheric water vapor on photosynthesis, transpiration and canopy conductance: A case study in corn

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ABSTRACT

The effect of atmospheric water vapor (AV) on plants has mostly been neglected in climate impact studies. The objectives of this study were to determine the effect of AV on photosynthesis (P_n), dry matter production (DM), transpiration (T_r), leaf conductance (g_l) and water use efficiency (WUE), in climate controlled chambers. The relative humidity (RH) was held near 30, 60, and 85%. DM and WUE increased with RH. δDM/δRH ~ 0.3 from 30% to 60% and ~2.2 from 60% to 85%, δWUE/δRH ~0.2 for all RH's. The improved WUE at a rate of 0.2 units for each percent of increased RH resulted from a synergy between larger g_l and lower T_r at high RH. This conclusions carries a bleak message to dry regions.

Keywords: growth chambers, water use efficiency; relative humidity; vapor pressure deficit; absolute humidity

Yield is linearly related to transpiration (Hanks 1974) and consequently to leaf to air vapor pressure deficit (VPD) (Anderson 1936). Others (Tanner and Sinclair 1983, Hoffman and Jobes 1978, Zangvil et al. 2004) concluded that crop production and water use efficiency (WUE) in a humid climate is greater than in a dry, arid climate.

Due to the diurnal fluctuation of relative humidity (RH) and leaf water conductance (g_l) (Vialet-Chabrand et al. 2013), in field trials it was difficult to isolate it and determine causality of crop response to atmospheric water vapor (AV). However, several studies (Bell 1982, Ball et al. 1987, Bunce 1996, Campbell and Norman 1998, Buckley et al. 2003, Wang et al. 2009) showed that stomatal closure occurs as VPD and transpiration (T_r) increase. The mechanism underneath is based on the effect of water-loss rate on the turgor of the guard cells (Mott and Parkhurst 1991); due to the balance between water loss to the atmosphere and water gain from the epidermis (Shope et al. 2008). Unfortunately, many studies of crop response to RH were not combined with in-depth stomata response but determined correlative and empirical relationships (Timlin et al. 2008), so it was difficult to quantify the relationship between yield and stomatal behavior.

Monteith (1995) re-interpreted stomatal responses to humidity by showing that g_l maximized when transpiration is minimized and the derivation of g_l with respect to T_r was linearly negative. However, this theory was open to criticism because g_l is affected by many other environmental factors such as photosynthetic photon flux density

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(PPFD), CO_2 concentration in the air, temperature and plant species (Bunce 1998a, b).

These multivariate natural fluctuations can be eliminated by experiments in growth chambers (Twizeyimana et al. 2007, Thongbai et al. 2010, Manzoni et al. 2011) and thus, enhancing the effect of selected individual factors variations like air temperature (T_a), RH or CO_2.

The objective of this study was, therefore, to use closed environmental chambers as a tool for the understanding of interactions between biotic and abiotic components on WUE, T_r, photosynthesis (P_n) and g_l of corn by isolating the effect of three RH treatments under stabilized temperature, irradiance, and CO_2 concentration.

MATERIAL AND METHODS

Experimental conditions and measurements. This study was conducted in the Georgia Envirotron facility. Three growth chambers equipped with the Conviron dehumidifier systems were used. The AV were absolute humidity (AH), relative humidity (RH) and vapor pressure deficit (VPD). The three are exchangeable because temperature was stabilized with minimal variations close to 30°C (coefficient of variation (CV) ~0.06). RH were 30 ± 3%, 56 ± 9%, and 84 ± 14%. Sweet corn (*Zea mays* L. var. *rugosa*) was grown in 1.5 L plastic containers from planting (21 November, day of the year (DOY): 325) to harvest (9 February, DOY: 43), a total of 84 days. Air-dried Georgia sand with a particle size up to 0.5 mm was employed as growth media; the bulk density varied between 1100 and 1300 kg/m^3. Miracle Gro 24-8-16% NPK (equivalent to 3 mg N/kg soil) was applied with the irrigation water. Each container had one dripper with a discharge rate of 1 L/h. Irrigation was controlled by computer and applied four times a day. The major properties of the chambers are summarized in Table 1.

Table 1. Average physical properties of the chambers[1]

Chamber #	Units	1	2	3
RH[1]	%	30	60	85
Area	m^2	3.5	3.5	3.5
Height	m	1.8	1.8	1.8
Wind speed	m/s	0.5	0.5	0.5
Irradiance[2]	W/m^2	310 ± 10	300 ± 10	320 ± 10
PPFD[2]	µmol/m^2/s	740 ± 28	743 ± 28	740 ± 28

[1]Temperature ≈30/25°C and CO_2 concentration 300/450 µmol/mol during 14 light/10 dark(h); [2]Irradiance and PPFD increased linearly with height

The average daily solar radiation during January is 11.7 MJ/m^2/day and in the growth chamber it was about 11.1 MJ/m^2/day. The measurements of P_n and T_r were obtained with the PTM-48M (photosynthesis transpiration monitor, Bio Instruments, Chisinau, Moldova). Four replications of continuous 24 h measurements in each chamber were taken once a week.

Additional supporting sensors to monitor meteorological conditions and soil water content included were: photosynthetic active radiation (PAR), T_a, leaf temperature (T_l), RH and time domain reflectometry to maintain optimal moisture condition. All data were collected from four young fully developed leaves on four different plants in each growth chamber.

Environmental conditions. The course of two RH treatments is displayed in Figure 1 during two sampling days. The highest RH treatment was 87% while the average RH of the lowest was 31%. The four peaks of RH during the daylight hours were caused by the four daily irrigations that are shown by the heavy dark line.

Long-term averages inside the growth chambers are given in Table 2.

For the low RH, T_l-T_a was large while for high RH it was negligible because of minimal evaporative cooling.

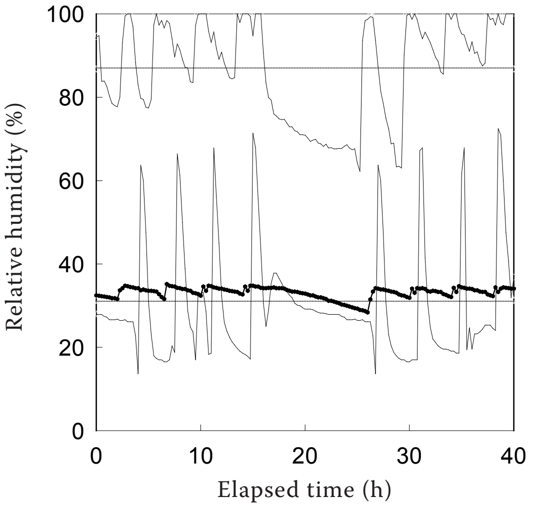

Figure 1. The course of two relative humidity treatments during 40 h

Table 2. Long-term average relative humidity (RH) inside the growth chambers and their associated meteorological values

Treatment[1]	RH (%)	Air temperature (°C)	AH[2] (g/m^3)	$T_l - T_a$(°C)	VPD (kPa)
30	30 ± 3	27.2 ± 1.7	7.9	−1.4 ± 0.7	2 ± 0.4
60	56 ± 9	29.8 ± 2.5	16.8	−0.5 ± 0.3	1.9 ± 0.6
85	84 ± 14	30.3 ± 2.9	26.0	−0.05 ± 0.03	0.7 ± 0.7

AH – absolute humidity; T_l – leaf temperature; T_a – air temperature; VPD – vapor pressure deficit; [1]Proposed RH; [2]The corresponding AH of the averages RH

It should be noted that T_a was not absolutely constant. This is due to inherent difficulties to control a precise combination of fixed T_a and RH. However, RH dominated the experiment because of the extreme differences between RH treatments (CV ~ 0.5) compare to the small CV (~ 0.06) in T_a. The cooler temperature in the 30% RH treatment and its associated lower VPD resulted in slightly better growth conditions than expected, offsetting some of the AV effects.

Data analysis. Eight measuring cycles from the V1 stage (when the collar of the first leaf is visible) to the R3 stage (when kernels are filled with a white, milky fluid) were averaged and analyzed statistically. The effect of RH on the daily sum of P_n and T_r was used to calculate WUE (g CO_2/g H_2O) and TC (transpiration coefficient = 1/WUE). At the end of the experiment the biomass of six plants from each growth chamber was determined.

Pillar analysis. In order to derive the most benefit from about 2000 data points, P_n and T_r, were plotted as a function of absolute humidity (AH). It created three pillar-like histograms, one for each humidity treatment.

Statistical analysis. The P_n and T_r measurements were analyzed for standard deviation (SE). Regression was used to present the best fit line of linear development of fresh matter. The graphics software (SigmaPlot 10; Systat Software Inc., Chicago, USA) was used for *t*-test, and the least significant difference (*LSD*) between the treatments.

Leaf water conductance: Theoretical analysis. Jackson et al. (1981) included T_l-T_a in P-M and this was modified here to replace resistances by leaf and aerodynamic conductance model:

$$T_l - T_a = \frac{[A/(\rho cp)/g_l] \times (1 + g_l/Ca)}{[\Delta + \gamma(1 + Ca/g_l]} - VPD/[\Delta + \gamma(1 + Ca/g_l] \qquad (1)$$

Where: A – net available energy (W/m^2); Δ – slope of saturated vapor pressure with respect to temperature (Pa/K); ρ – air density (1.21 kg/m^3); cp – specific heat of air [1010 J/(kg K)], VPD (kPa); γ – psychrometric constant (0.066 kPa/°K); Ca and g_l – respective aerodynamic and the canopy conductance to water transfer (m/s).

Combining Eq. (1) and P-M model we obtained a closed form that was solved in two stages, first g_l and Ca were obtained iteratively using Eq. (1) (Ben Asher et al 2013) and then g_l and Ca were used to calculate T_r according to P-M model. Input data are given in Tables 1 and 2 (300 W/m^2 and with estimated losses of 100 W/m^2 we used (a) A = 200 W/m^2), (b) T_a = 30°C; (c) T_l-T_a was changed gradually from −5 to +5 (d), RH was changed gradually from 10% to 90%. The outputs were Ca and g_l from Eq. (1) and T_r from the known P-M model.

Table 3. Biomass (g/plant) at the end of the experiment and its change with respect to relative humidity (RH)

RH (%)	Total above ground		Leaves		Stem		Ears		Roots	
	DM	$\frac{\delta DM}{\delta RH}$	fresh	dry	fresh	dry	fresh	dry	fresh	dry
30	70 ± 19	–	90 ± 8	21 ± 10	98 ± 4	25 ± 6	154 ± 13	24 ± 3	7 ± 2	2 ± 1
60	80 ± 30	0.3	100 ± 2	23 ± 9	97 ± 9	38 ± 10	105 ± na	19 ± 11	6 ± na	2 ± 4
85	134 ± 27	2.2	104 ± 9	44 ± 9	108 ± na	61 ± 15	185 ± 9	29 ± 3	16 ± 5	5 ± 2
LSD	45/33	–	17/12	17/13	18/13	21/15	26/19	7/5	11/8	2

LSD is given in *P* = 0.05/*P* = 0.1; na – SE not available

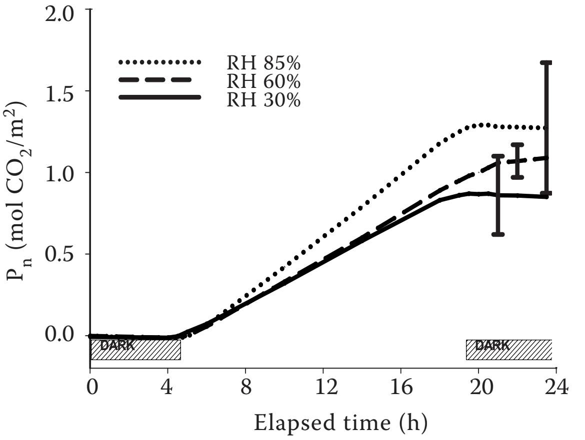

Figure 2. Cumulative CO_2 assimilation for three relative humidity (RH) levels

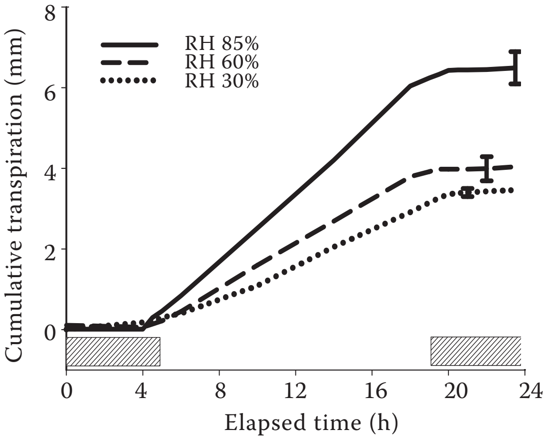

Figure 3. Cumulative transpiration (T_r) based on three levels of relative humidity (RH)

RESULTS AND DISCUSSION

Plant biomass. Weight of dry matter (DM) of maize under 85% RH was greater than 30% RH ($P = 0.05$), and fresh biomass under 85% was also larger than 30% but the significance level was $P = 0.1$ (Table 3).

The results of fresh and dry biomass under 60% RH were between RH 85% and 30%. Total vegetative biomass (leaves + stem) was 212, 197 and 188 g/plant for RH = 85, 60, and 30%, respectively. δDM/δRH indicates that the one percent increase in RH from 30% to 60% was associated with increase of only 0.3 g/plant but from 60% to 85% it was 2.2 g/plant.

The effect of RH on P_n and T_r. Daily gross assimilated CO_2 is equivalent to 56, 48, and 38 g/m² for the high, medium, and low RH, respectively. This is comparable to 72 g CO_2/day measured by Usuda et al. (1987) and to 67 and 52 g CO_2/day measured by Kalt-Toress et al. (1987) under very similar conditions. $LSD_{0.05}$ between RH 85% and 60% was 4.2 g CO_2/m^2 and between RH 60% and 30% it was 17.3 g CO_2/m^2. It emphasized the positive contribution of RH to the photosynthetic process.

The daily T_r in Figure 3 was 3.4, 3.9, and 6.4 mm ($LSD_{0.05}$ = 0.4 mm) for 85, 60 and 30% RH, respectively.

Leaf water conductance (g_l). To clarify the causality of the advantages of high RH it is imperative to quantify the control exerted by stomata over T_r, P_n and the resulting yield. This causality question was addressed by 'Penman-Monteith' (P-M) and Kim's models (Monteith et al. 1965, Allen et al. 1998, Kim and Leith 2003).

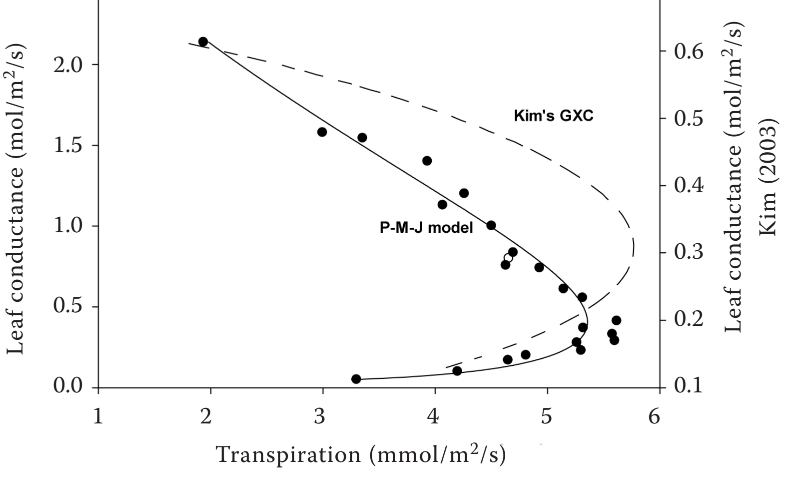

Figure 4. The relationships between leaf conductance (g_l) and transpiration (T_r) based on P-M-J transpiration models and Kim's GXC (gas exchange calculator). The T_r range from 0 to 6 mmol/m²/s is equivalent to a range of 0 to 0.39 mm/h and the g_l range from 0 to 2.5 mol/m²/s is equivalent to a range of 0 to 162 mm/h

Table 4. Mass and molar water use efficiency (WUE)

		Relative humidity treatment (%)			$LSD_{0.05}$
		30	60	85	
Mass basis calculations					
CO_2	g /m^2/day	38	48 (17.3)	56 (4.2)	in parenthesis
H_2O	kg/m^2/day	6.4	3.9	3.4	0.4
WUE^2	g CO_2/kg H_2O	6	12	16	
TC	g H_2O/g CO_2	168.4	81.3	62.5	
Molar basis calculations^1					
CO_2	mol CO_2/m^2/day	0.9	1.1	1.3	0.69
H_2O	mol H_2O/m^2/day	355.6	216.7	194.4	22
WUE	mmol CO_2/mol H_2O	2.4	5.0	6.5	

^{1}Molar masses of CO_2 is 44 and H_2O is 18 g/mol; $^2\delta$WUE/δRH ~ 0.2; TC – transpiration coefficient

The effect of T_r on g_l was evaluated though the relationship between RH and T_r knowing that at high RH, T_r is low and vice versa.

Kim's model is based on thermodynamic and molecular considerations with a linear relationship between g_l and RH following Ball et al. (1987) while P-M model is based on biophysical considerations (Eq. 1), resulting in different g_ls. Quantitatively, both models reached a turning point at $\delta T_R/\delta g_l = 0$ when ET ~ 5.5 mmol/m^2/s and RH ~ 50% (not shown here). The two models characterize arid environment by RH < 50% when T_r is increasing with g_l. Conversely, humid environment is characterized here by RH > 50%, when stomatal aperture is increasing with reduced T_r. Consequently, when RH > 50%, CO_2 intake and hence DM production are intensifying. Thus, under humid conditions the plant strategy to ensure high WUE is to increase both stomatal aperture and CO_2 intake at a low transpiration cost. When RH > 50%, the negative linear section in P-M model ($g_l = -5.1 \times T_r + 3.1$; $r^2 = 0.94$) suggests that g_l can be maximum 3.1 mol/m^2/s (201 mm/h). The control exerted by stomatal aperture over T_r and P_n can therefore provide a reasonable causality for the advantages of high RH and the resulting yield. Specifically, in Table 3 at RH = 30% DM yield was only 70 g/plant compared to 134 g/plant at RH = 85% and in Table 4, WUE was 2.4 and 6.5 mmol CO_2/mol H_2O, respectively.

AH and WUE. A summary of all positive values collected for P_n and T_r is displayed in Figure 5 as three pillar-like histograms that reflect the three RH treatments.

In Figure 5 P_n increased slightly as AH increased from near 15 to 28 g/m^3 while T_r reduced by about 70% with the increased AH. From Figure 5 $\delta P_n/\delta T_r$

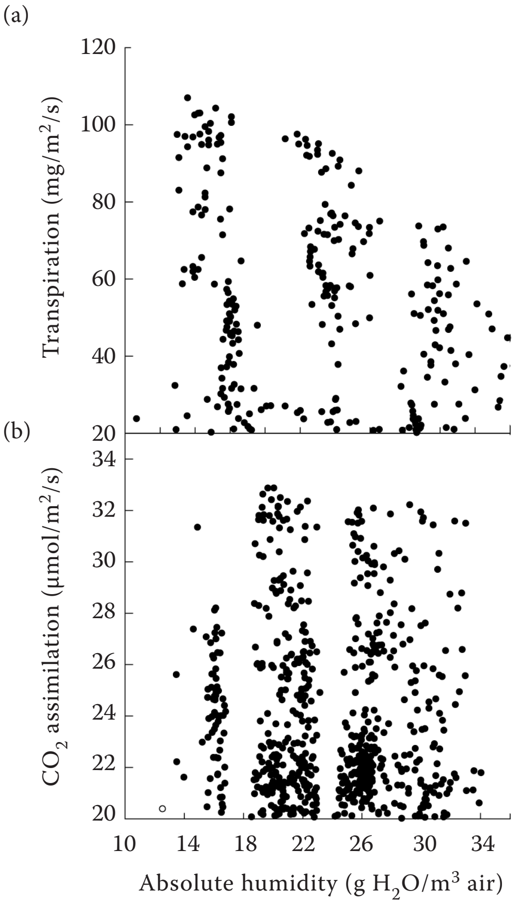

Figure 5. Scatter plot of transpiration (a) and assimilation (b) as a function of absolute humidity

was approximated as the upper limit of WUE and it yielded 8.2, 6.4 and 5.2 mmol CO_2 produced by 1 mol H_2O, respectively from high to low RH. The values are higher than the daily average of WUE in Table 4 but acceptable as upper limits.

The integrated values of WUE in Table 4 show a significant ($P = 0.05$) difference in WUE between 85, 60 and 30% which is complementing the results in Figure 5. In the entire range of RH one percent increase in RH resulted in an increase of 0.2 mass units of WUE.

Concluding remarks. Physically P_n is accompanied by T_r through the open stomata and both are linearly linked to each other (Hanks 1974) but the slope $\delta P_n/\delta T_r$ that can be defined as WUE was higher under RH = 85% than under 30%. The improved WUE is explained by a synergy between larger g_l associated with reduced T_r (Monteith 1995) and a reduced driving force (VPD) for transpiration in humid environment. The environmental relevancy of this study is strengthened by global average estimates of RH = 60% (Dai 2006) that was used here and global WUE of 3.2 ± 0.9 mmol CO_2/mol H_2O (Jasechko et al. 2013) that agrees with the range from 2.4 to 6.5 for RH 30–85% (Table 4). This synergy resulted in DM production at a low water cost and explained the agronomic and ecological importance of humid environment. On the other hand it carries a bleak message to dry regions where water is naturally limited.

The positive response of corn (as a case study) to high RH indicates that in arid habitats, where water supply is limited and RH is low, water use would be less efficient compared to humid habitats where RH is high and water is abundant.

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