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Large Day to Day Variation in V_{Cmax} During Mid-Season in Soybean and Wheat Crops Related to Water Vapor Pressure Deficit

James Arthur Bunce *

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Large Day to Day Variation in V_{Cmax} During Mid-Season in Soybean and Wheat Crops Related to Water Vapor Pressure Deficit

James Bunce

Adaptive Cropping Systems Laboratory, USDA-ARS, Beltsville, MD, USA; buncejames49@gmail.com

Abstract

Most modelling of photosynthesis of higher plants utilizes the Farquhar, Von Caemmerer, Berry photosynthesis model of C_3 photosynthesis. At current air levels of CO_2, C_3 photosynthesis at high photosynthetic photon flux density is most often limited by the maximum capacity of RuBisco carboxylation, V_{Cmax}. This study tested whether experimentally determined values of V_{Cmax} corrected for variation in measurement temperature were consistent from week to week during mid-season in two major C_3 crop species, soybean and wheat. Gas exchange was measured on single upper canopy leaves near mid-day on sunny days, at the current air temperature and humidity, every 3-9 days during mid-season for two years and was used to estimate V_{Cmax}. It was found that V_{Cmax} values corrected to the same temperature sometimes varied by a factor of about 1.5 in both species from day to day. Variation in V_{Cmax} was not associated with prior 4-day means of temperature, or cloudiness, or with day of year in either species. However, V_{Cmax} in both species and years was significantly negatively correlated with the leaf to air difference in water vapor pressure (VPD) at the time of measurement. The results indicate a strong negative impact of high VPD on mid-day leaf photosynthesis which was not evident from sub-stomatal CO_2 concentrations, which varied little from day to day. Because VPD increases with global warming, these results indicate that increasing VPD could diminish crop growth beyond any direct effects of warming.

Keywords: photosynthesis; Rubisco; vapor pressure deficit; climate change; wheat; soybean

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1. Introduction

Models of photosynthesis of higher plants are often used in diverse agronomic and ecological applications to predict the income of fixed carbon into ecosystems. Updated versions of the original Farquhar, von Caemmerer, Berry C_3 photosynthesis model [1] are very widely used [e.g., [2–6]]. The model parameter, the maximum rate of carboxylation (V_{Cmax}), along with stomatal conductance (g_s), are the rate limiting parameters at current air levels of CO_2 and high light, under most environmental situations. V_{Cmax} increases exponentially with temperature over a wide range of temperatures. The temperature dependency of V_{Cmax} may vary considerably among species and with prior temperature exposure within species [e.g. [7–9]]. While the temperature dependency of V_{Cmax} is an important issue, this paper focuses on a more fundamental issue, the degree of variation in V_{Cmax} in the middle of a growing season, after accounting for different measurement temperatures. This study focused on the temporal variation in midday V_{Cmax} at high light for soybean and wheat crops during mid-season.

The Farquhar, von Caemmerer, Berry model [1] initially did not consider mesophyll conductance, and in many applications the model is still used without incorporating mesophyll conductance, because values for mesophyll conductance and its possible variation with C_i [10] remain unknown for most species. In wheat, estimates of V_{Cmax} made with and without estimates of mesophyll conductance produced very similar seasonal patterns [5].

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Variation in leaf photosynthetic capacity with the light and temperature environment during leaf development, "acclimation", is well known [11,12], with cool temperatures, above some lower limit, and high light generally leading to higher photosynthetic capacity when measured at moderate temperatures [9,13,14]. In this study, near mid-season, both soybean (an indeterminate cultivar) and wheat were still producing new leaves, so measurements of upper canopy leaves made over time were on leaves at higher nodes, with similar leaf ages of all measured leaves. This approach differs from prior studies of soybean and wheat [15,16] which compared leaves throughout a growing season, and where leaf age was more variable.

In wheat, Sun et al. [5] found that when measured at a constant 25 ^{o}C, V_{Cmax} ranged from about 80 to 125 mmol m^{-2} s^{-1} over the season, using the standard FVC model, and from about 70 to 115 mmol m^{-2} s^{-1} using the FVC model separating out mesophyll conductance. In that study, V_{Cmax} values generally decreased as growing degree days increased. In another study of wheat [15] maximum assimilation rates at midday measured at ambient temperatures ranged from 17 to 25 mmol m^{-2} s^{-1}, with no clear seasonal pattern. In soybean, Bernacchi et al. [16] measured assimilation rate at ambient CO_2 and temperature near midday in upper canopy leaves 4 to 6 times per year for three years, and found that rates varied from about 17 to 31 mmol m^{-2} s^{-1}, with no clear seasonal pattern, although measurement temperature was also not constant in that study.

At high light, photosynthesis in plants with C_3 metabolism may be limited by V_{Cmax}, Jmax, or TPU [17]. Limitation by the last two parameters is evident from little or no increase in photosynthesis with increased CO_2. In this study we confirmed limitation of photosynthesis by V_{Cmax} each day by measuring photosynthesis of each leaf first at current air levels of CO_2 (380 mmol mol^{-1}) and then at 570 mmol mol^{-1}of CO_2. In all cases, photosynthetic rates were higher at the higher CO_2 concentration by 20 to 40% for temperatures ranging from 17 to 32 ^{o}C. This test indicated that photosynthesis measured at the lower CO_2 concentration was limited by V_{Cmax} in all cases.

Global warming not only increases air temperature, but, because of the exponential increase in saturated water vapor pressure with temperature, warming also increases the daytime leaf to air difference in water vapor pressure (VPD) [18]. VPD is the driving force for transpiration. It is becoming recognized from observations of crop yields and weather variables over time, as well as crop modelling studies that high VPD often reduces crop yields in current and projected warmer environments, sometimes more so than would increased air temperatures [18–26].

2. Results

Photosynthetic carbon dioxide assimilation rates (A) measured at ambient temperature, humidity, and carbon dioxide concentration in full sunlight varied greatly from day to day in both wheat and soybean (Figure 1), with no clear relationship between A and temperature in either species. Measurements in wheat, in the spring, covered a wider range of temperatures than the summer measurements in soybeans.

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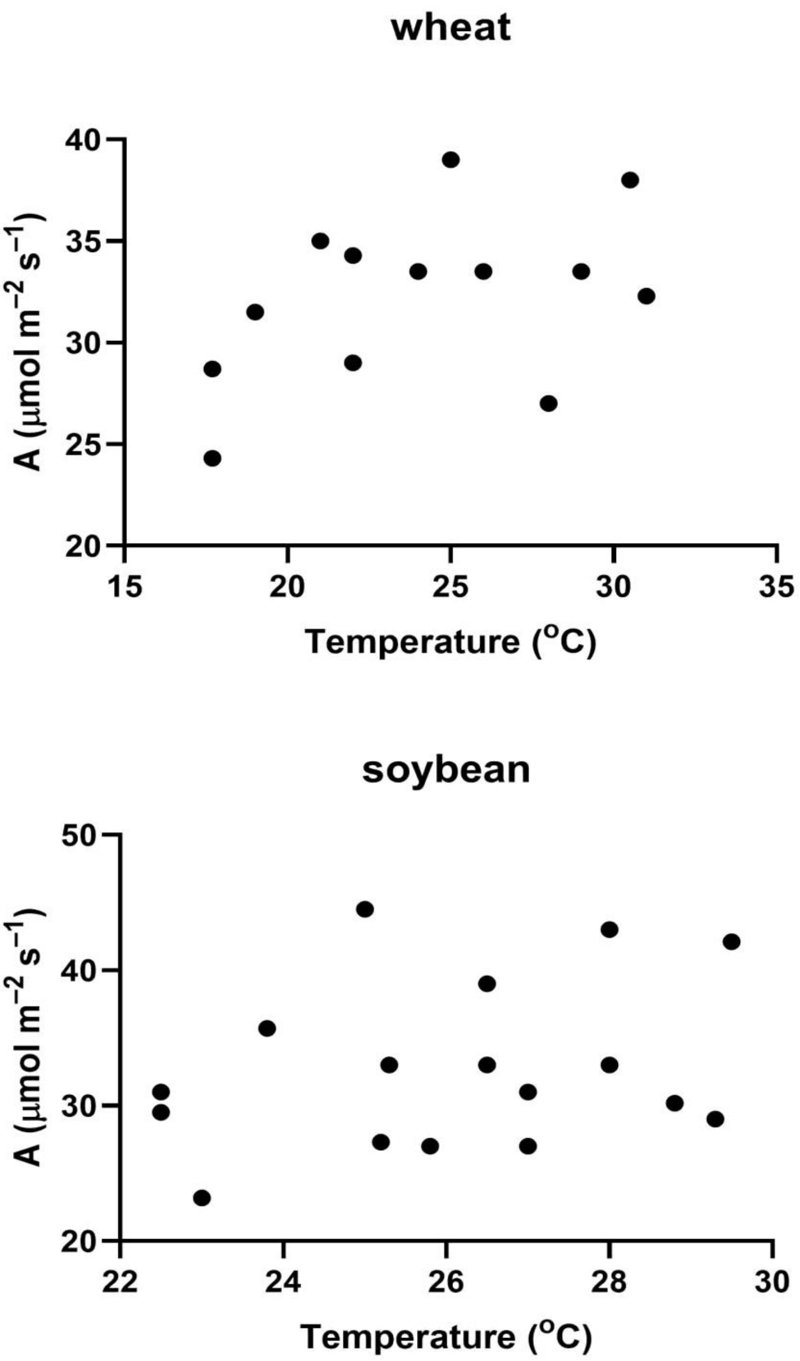

Figure 1. Midday carbon dioxide assimilation rates (A) in single, upper canopy leaves of wheat and soybeans as a function of measurement temperature. Combined data for 2013 and 2014 are presented.

In both species, V_{Cmax} generally increased with the measurement temperature, but with very large variability among days within the same year (Figure 2). Figure 2 also includes the modelled response of V_{Cmax} to temperature for both species, with the values of V_{Cmax} for each species set to approximately match the upper limit of measured values. Clearly, while a few of the measured values matched this upper limit in each species over a wide range of temperatures, most of the measured values were lower, with several values only 60% of this upper limit. In wheat, the values of V_{Cmax} averaged 83% of the upper limit of values in Figure 2, and in soybeans they averaged 75% of

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the upper limit of values. Therefore, for both species, day to day variation in V_{Cmax} values substantially reduced midday photosynthesis.

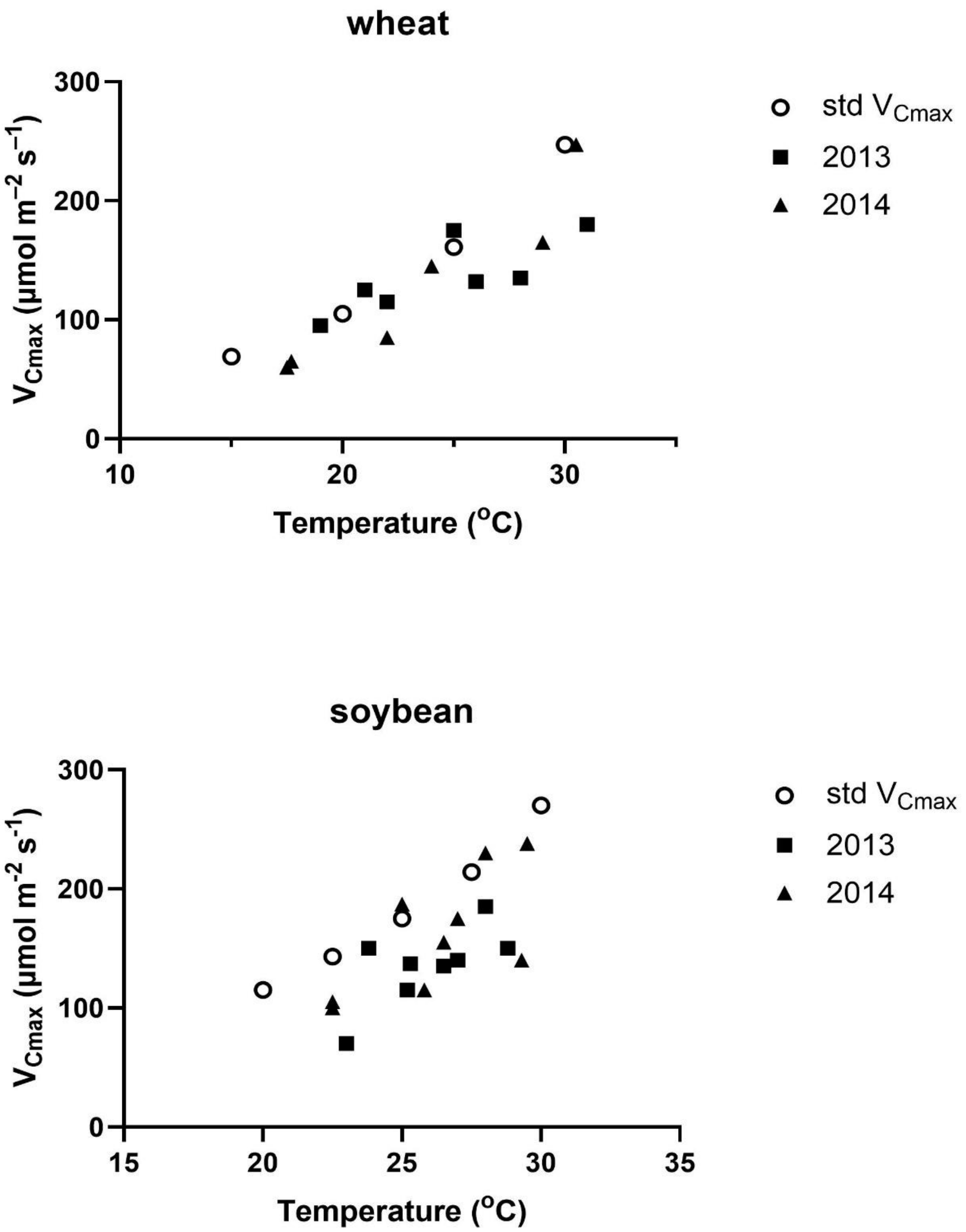

Figure 2. Relationships between V_{Cmax} and measurement temperature on different days in 2013 and 2014 in single, upper canopy leaves of wheat and soybean measured in full sunlight, and the standard response of V_{Cmax} to temperature, with the standard V_{Cmax} value set for each species to approximate the highest observed values of V_{Cmax}.

Possible causes of variation in V_{Cmax} across measurement days were explored by regressions of the actual V_{Cmax} on a given date relative to that expected from the measurement temperature taken from Figure 2 against the variables of a) the difference between the measurement temperature and the mean temperature of the prior four days, b) the amount of photosynthetically active radiation

(PAR) averaged over the four days prior to the measurements day of year, and c) day of year. The four-day interval was chosen based on the high correlation between the light and temperature environment of the four days before reaching full expansion to the photosynthetic capacity of fully expanded soybean leaves [28]. No comparable information was found for wheat. No linear regressions between the fraction of V_{Cmax} and these three environmental variables were significant at P = 0.05 in either soybeans or wheat (Figures 3–5). Multiple linear regressions of the fraction of V_{Cmax} on these three environmental variables were also not significant in either species.

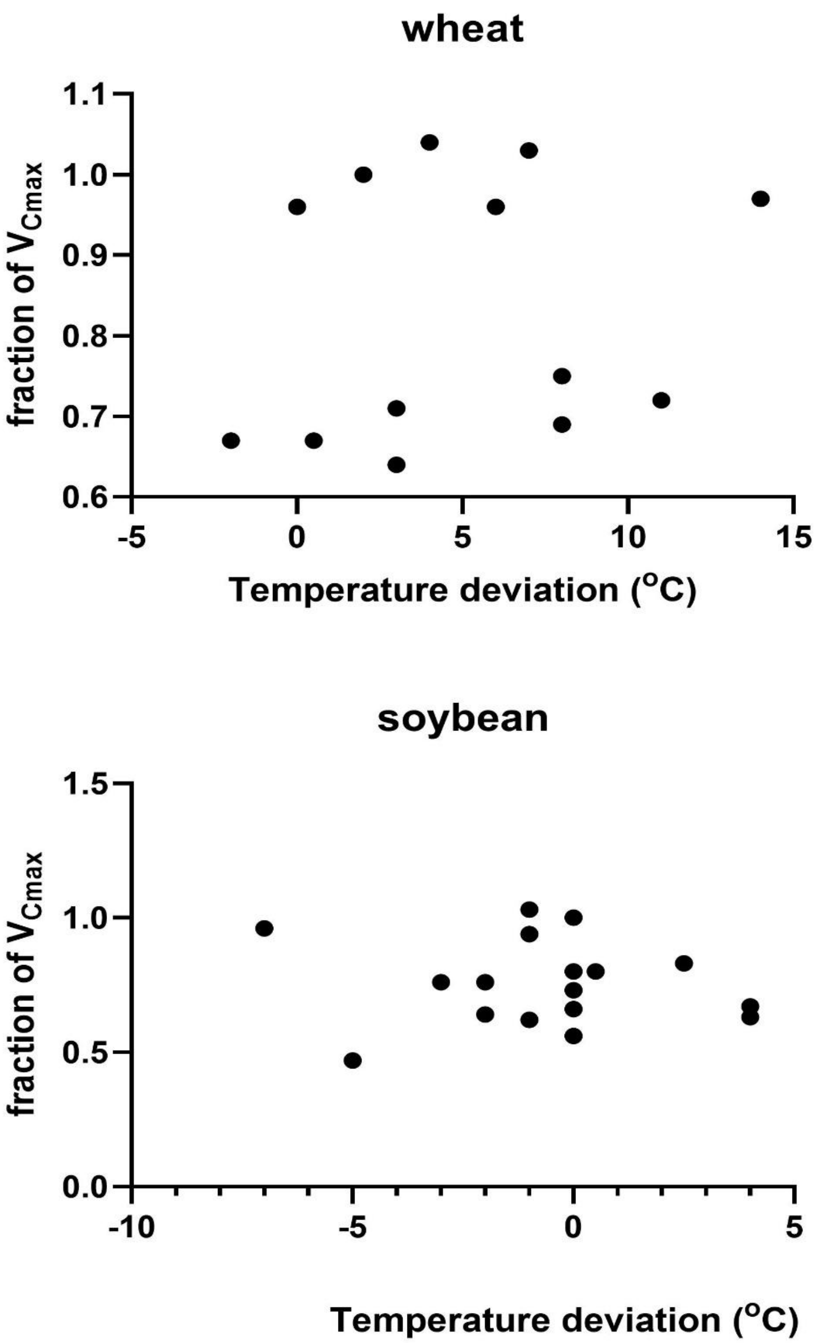

Figure 3. The fraction of the theoretical value of V_{Cmax} from Figure 1 observed on each measurement date in relation to the temperature deviation for the four days prior to the measurement day compared with the temperature on the day of measurement. Correlations were not significant in either species.

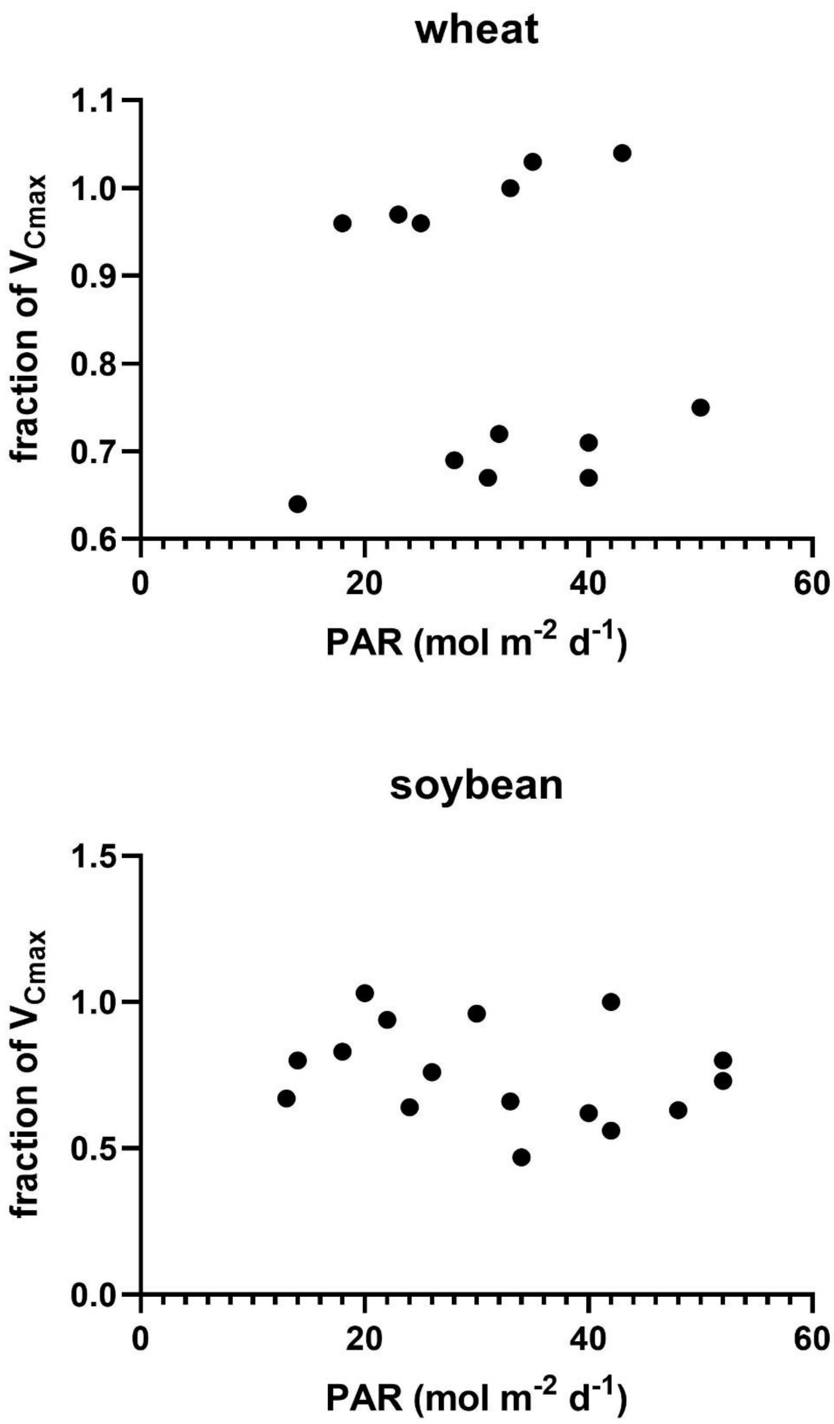

Figure 4. The fraction of the theoretical value of V_{Cmax} from Figure 1 observed on each measurement date in relation to the mean daily photosynthetically active radiation for the four days prior to the measurement day. Correlations were not significant in either species.

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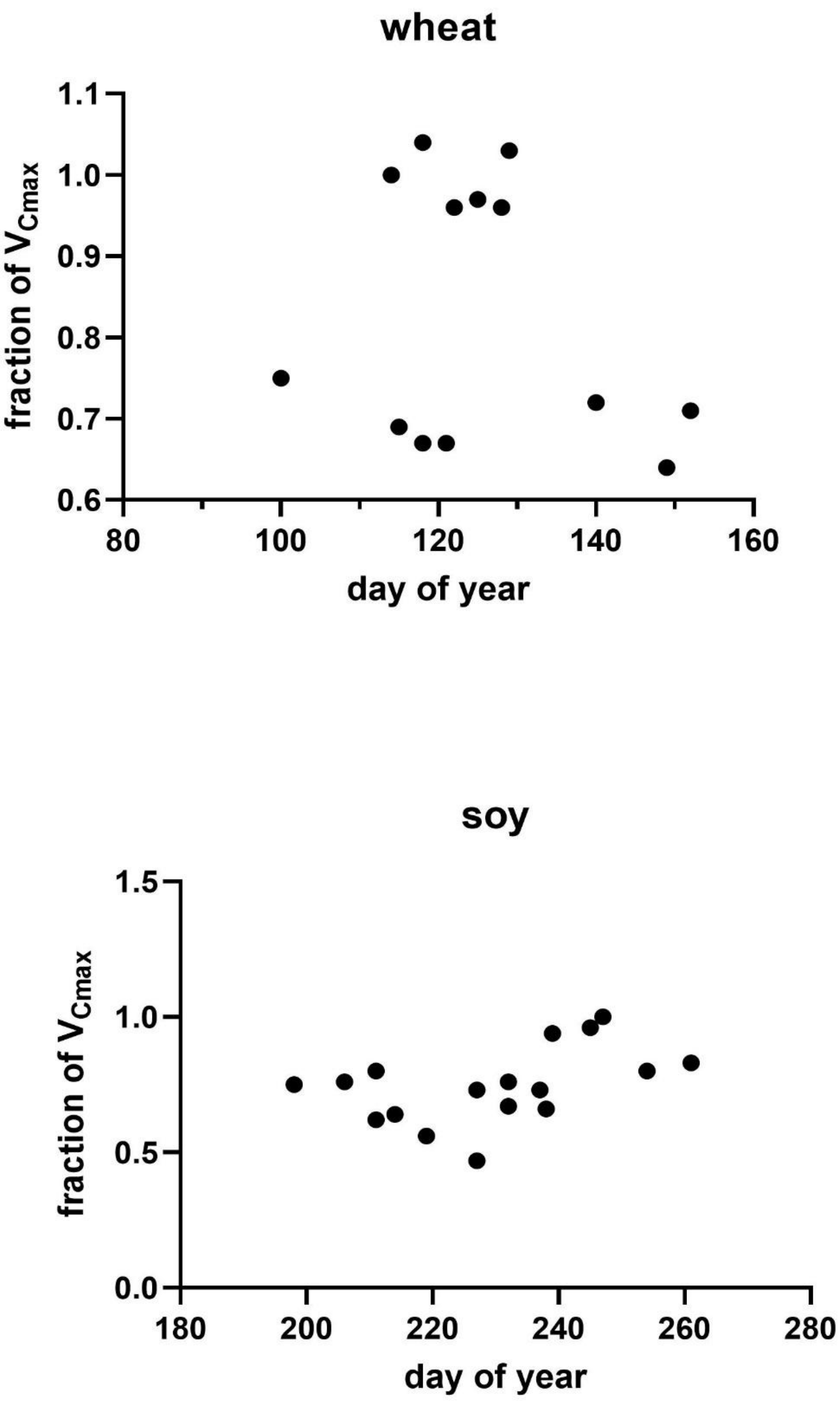

Figure 5. The fraction of the theoretical value of V_{Cmax} from Figure 1 observed on each measurement date in relation to the day of year of the measurement of V_{Cmax}. Correlations were not significant in either species.

Variation in C_i across measurements dates showed no clear relationship with VPD in either species (Figure 6). Mean C_i values ranged from about 260 to 320 mmol mol^{-1} in wheat and 280 to 330 mmol mol^{-1} in soybean on the different measurement dates.

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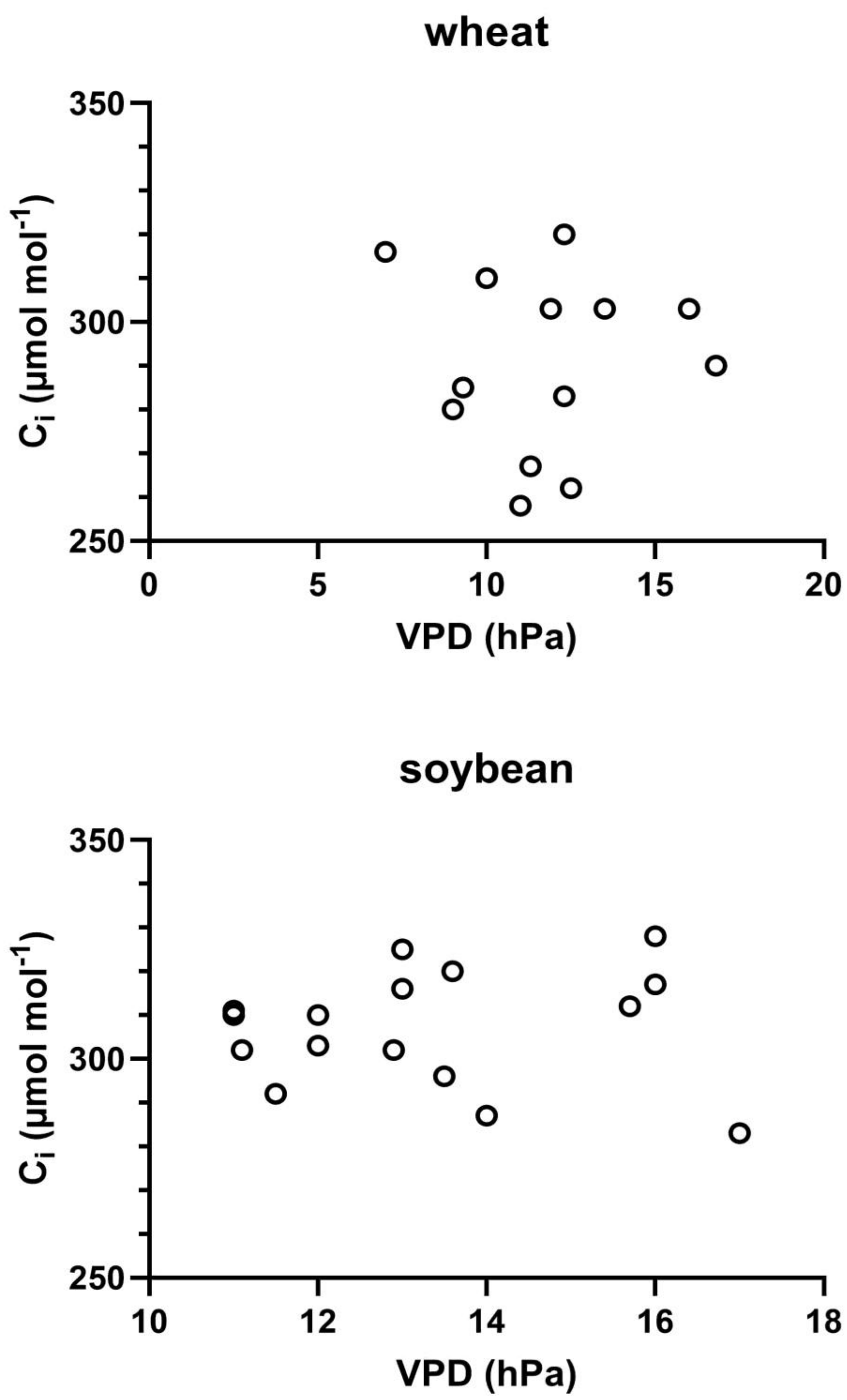

Figure 6. Internal CO_2 values (C_i) as a function of VPD on all measurement days in wheat and soybean. Correlations were not significant in either species.

In both species and in both years, the ratio of the observed V_{Cmax} to that expected based on the measurement temperature decreased linearly with the VPD on the day of leaf gas exchange measurement (Figure 7). Values of r^2 of the linear regressions ranged from 0.72 to 0.91 for the two species and two years of data, and all of the slopes were significant at the P = 0.05 level (Table 1). Combined over the two years, the r^2 values were 0.517 (P = 0.0056) for wheat and 0.612 (P = 0.0003) for soybean. The overall mid-season means of 17 to 25% reductions in midday V_{Cmax} values for these two species (Figure 2) occurred for average VPD values of only 12-13 hPa, and the maximum VPD values were about 17 hPa in both species.

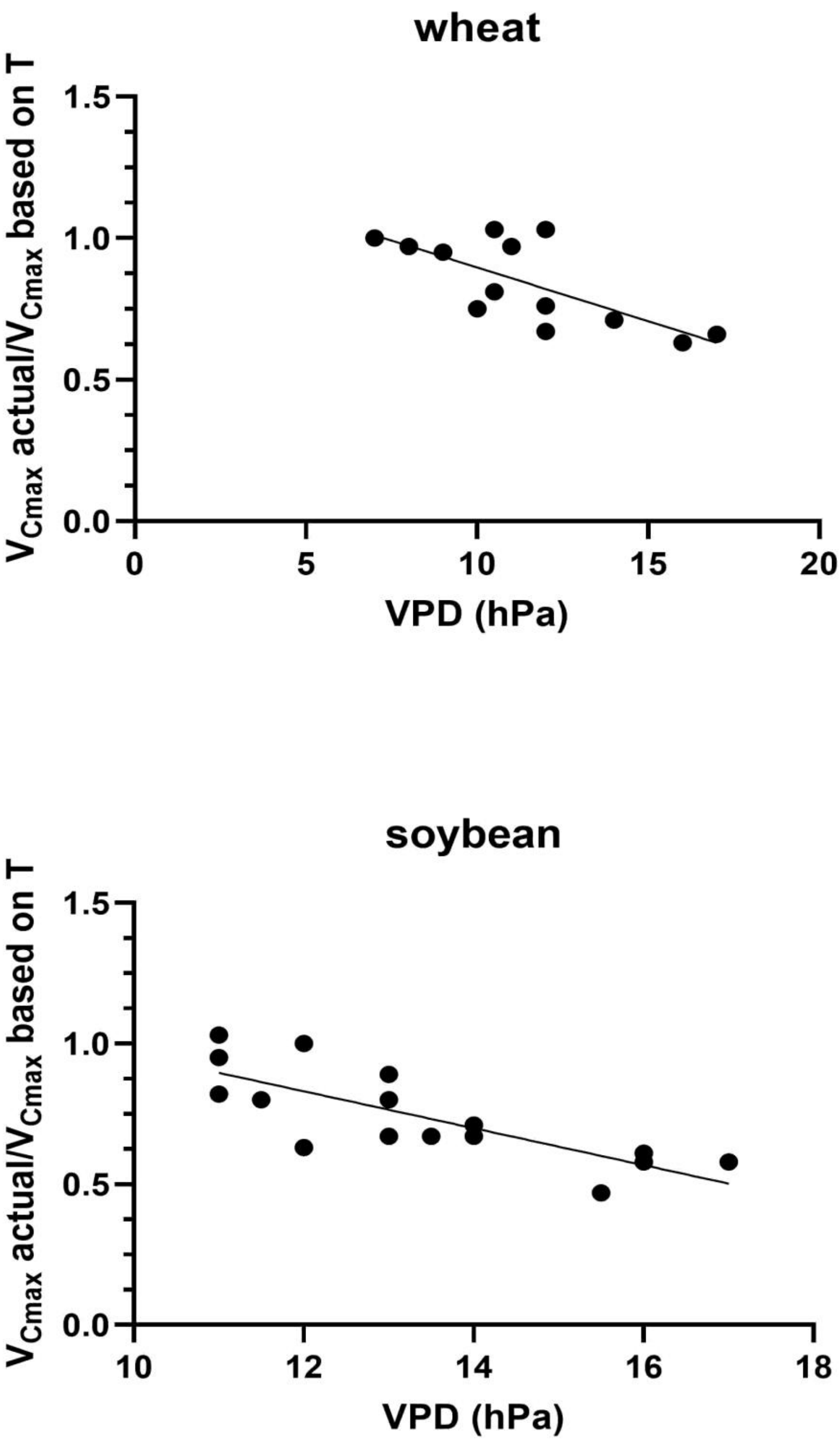

Figure 7. The ratio of observed V_{Cmax} on each measurement day relative to the maximum V_{Cmax} expected for that temperature in relation to the VPD at the time of measurement of V_{Cmax} on each day. r^2 values were 0.517 for wheat and 0.612 for soybean.

Table 1. Slopes and r^2 values of linear regressions of (actual V_{Cmax})/(V_{Cmax} based on temperature) against VPD for each year of the wheat and soybean measurements.

Species	Year	Slope	r^2	Probability value
Wheat	2013	-0.055	0.72	0.0160
Wheat	2014	-0.063	0.81	0.0146
Soybean	2013	-0.050	0.83	0.0016
Soybean	2014	-0.093	0.91	0.0002

3. Discussion

Reductions in photosynthesis at high light caused by increases in VPD are well-known consequences of reduced stomatal conductance at high VPD [18,28–31]. Reductions in stomatal conductance with increasing VPD result in progressively lower internal CO_2 concentrations, which in turn reduce photosynthesis. Such experiments have almost exclusively been conducted on individual leaves or parts of leaves, where the VPD around the rest of the plant has been constant. Results of these types of experiments are generally consistent with a constant V_{Cmax} over the range of experimental VPDs, and contrast with the results presented here, where V_{Cmax} significantly decreased with increasing VPD. A clear difference between the results presented here and previous experiments in which single leaves or parts of leaves were exposed to high VPD, is that in this study, the day-to-day variation in the VPD values for the measured leaves also occurred for the whole plants. This distinction is important, because exposure of whole plants to increased VPD would likely increase whole plant transpiration, which in turn would decrease leaf water potential and thereby also decrease V_{Cmax}, as in typical soil water stress responses. The concept of high VPD reducing V_{Cmax} by lowering leaf water potential of whole plants is supported by reports of high VPD reducing canopy photosynthesis in C_4 species such as maize and sorghum [18,32,33], because in single leaves of C_4 species, high VPD generally does not decrease photosynthesis substantially despite reducing stomatal conductance, since photosynthesis in C_4 leaves is usually nearly saturated for CO_2 at ambient CO_2 concentrations [34,35]. Reductions in photosynthesis at a given C_i value caused by high VPD were previously reported in potato (C_3 metabolism) and sorghum (C_4 metabolism) under field conditions [36], although those reports were not analyzed in terms of changes in parameters of photosynthesis models. Reductions in photosynthesis at a given C_i value caused by high VPD occurred for both ambient and elevated CO_2 growth conditions, in both potato and sorghum [36]. The reductions in photosynthesis at saturating C_i values in potato also indicate that the photosynthesis model parameter J_{max} was also reduced by the high VPD. In cases such as potato and sorghum, rising atmospheric CO_2 did not prevent high VPD from reducing photosynthesis.

This study identified VPD as an important factor affecting day to day variation in V_{Cmax} of soybean and wheat crops in mid-season under the current climate. Because global climate change would increase VPD along with CO_2 and temperature, impacts of high VPD on these crops, and others, will become more severe. A reduction in V_{Cmax} by high VPD, as shown in these experiments, would, by itself, reduce light-saturated leaf photosynthesis at limiting CO_2 levels, with potential consequences of reducing crop growth and yield. The maximum VPD values in these observations are generally less than the daily maximum values, because the measurements presented here were all taken before solar noon in order to avoid later cloudiness, and maximum daily VPDs would coincide with maximum daily air temperatures, which normally occur a few hours after solar noon. Therefore, the maximum impacts of high VPD on photosynthesis of these two species were likely larger than the impacts reported here, and they probably would also be larger in less humid climates.

Because V_{Cmax} is reduced by high VPD applied to the whole plant, climate warming would decrease V_{Cmax} and whole plant photosynthesis by increasing VPD, regardless of direct impacts of high temperature on photosynthesis. Reduction in whole plant photosynthesis by rising VPD would decrease plant growth in general, and agronomic yield. Observations of reduced photosynthesis by high VPD even at elevated CO_2 concentrations in potato and sorghum [37], suggest that rising atmospheric CO_2 concentrations would not overcome negative effects of rising VPD on photosynthesis and plant growth due to climate warming.

4. Materials and Methods

Both crops were grown at the South Farm of the Beltsville Agricultural Research Center, in Beltsville, Maryland USA. The 5m x 5m plot used for both crops (39 ^{O}N, 77 ^{O}W, elevation 30 m) has a Codorus silt loam soil. This plot was surrounded by extensive (several hectare) soybean and wheat crops which were not part of the experiment. The row width was 30 cm for soybean, with a planting density of 40 plants m^{-2}, and for wheat the row width was 20 cm, and the plant density was 120 plants m^{-2}. Wheat plots were fertilized with 10-10-10 NPK at the rate of 25 g N m^{-2} in early spring. No pesticides were applied to either crop species, and weeds were pulled by hand. The plots were not irrigated, but frequent precipitation prevented any significant soil water deficits. A weather station adjacent to the plot recorded light, air temperature, humidity and precipitation. The mean air temperatures for these soybean and wheat growing seasons were 24.9 and 23.2 ^{o}C for soybean, and 10.5 and 13.3 ^{o}C for wheat, which are close to the long-term mean temperatures at this location at those times of year.

Measurements of leaf gas exchange on soybean (*Glycine max* L. cv. Spencer) and wheat (*Triticum aestivum* L. cv. Choptank) were conducted during the spring (wheat) and summer (soybean) in 2013 and 2014. Choptank is a winter wheat variety, and was planted in late October of 2012 and 2013 for leaf gas exchange measurements in the springs of 2013 and 2014. The soybean crops were planted in the same plots after the wheat crops were harvested, in late May of 2013 and 2014 for measurements of leaf gas exchange in mid-summer of 2013 and 2014. The plot was tilled with a rotary tiller a few days before the planting of each crop. Weeds were removed by hand pulling.

Leaf gas exchange was measured using a CIRAS-3 portable gas exchange system, with a leaf cuvette with a 2.5 cm diameter circular window. The cuvette air temperature was set to match that of the outside at the beginning of gas exchange measurements each day. Measurements were confined to mid-morning to noon on clear days, and no lamp was used. The PPFD inside the cuvette was at least 1500 mmol m^{-2} s^{-1} for all measurements. Air entering the cuvette was partly dried, so that air within the cuvette had nearly the same water vapor pressure as that of the outside air. Leaves to be measured were selected as recently fully expanded leaves which had been fully illuminated by the sun for at least several minutes just before enclosure in the leaf cuvette. Each leaf was first measured at a CO_2 concentration of 380 mmol mol^{-1} and then at 570 mmol mol^{-1}. On each measurement date, three leaves were measured at both CO_2 concentrations. Steady gas exchange rates occurred within about a minute of enclosure in the cuvette, and time was allowed for stomatal conductance to decrease to a new stable value after shifting to the higher measurement CO_2 concentration. For wheat, leaf gas exchange measurements were made from days of year 100 to 152, and for soybean, from days of year 198 to 261.

From the observed means values of A, C_i, and leaf temperature measured at the external CO_2 concentration of 380 mmol mol^{-1} for each species and measurement date, values of V_{Cmax} were calculated from the Farquhar, von Caemmerer, Berry photosynthesis model [1] not incorporating mesophyll conductance, because mesophyll conductance values and their temperature dependence were not known. The 20 to 40% increase in A when external CO_2 was increased to 570 mmol mol^{-1} indicated that A at the lower C_i was limited by V_{Cmax} in all cases.

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Data Availability Statement: Data not contained in the article are available from the author upon request.

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Conflicts of Interest: The author declares no conflicts of interest.

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