

Leaf Photosynthesis and Conductance of Selected *Triticum* Species at Different Water Potentials¹

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RICHARD C. JOHNSON*, DOLORES W. MORNHINWEG, DAVID M. FERRIS, AND JAMES J. HEITHOLT
Department of Agronomy, Oklahoma State University, Stillwater, Oklahoma 74078

ABSTRACT

Leaf gas exchange characteristics of a desert annual (*Triticum kotschy* [Boiss.] Bowden) and the wheat cultivar TAM W-101 (*Triticum aestivum* L. em Thell) were compared over a range of leaf water potentials from -0.50 to -2.9 megapascals. At an ambient $[\text{CO}_2]$ of 330 microliters per liter, *T. kotschy* had higher conductance and CO_2 assimilation (A) at a given water potential than *T. aestivum*. Under well watered conditions, A versus internal CO_2 concentration (C_i) response curves for both species were similar in shape and magnitude, and the higher A of *T. kotschy* at an ambient $[\text{CO}_2]$ of 330 microliters per liter was mostly related to the higher stomatal conductance of *T. kotschy*. The higher conductance of *T. kotschy* than *T. aestivum* under well watered conditions was associated with higher C_i and lower water use efficiency. Under water deficits, however, C_i at 330 microliters per liter ambient $[\text{CO}_2]$ did not differ significantly between species. *T. kotschy* had higher A under water deficits than *T. aestivum* primarily because its A versus C_i response curves had higher A at C_i values above about 150 microliters per liter. The results show that conductance played an important role in the high A of *T. kotschy* under well watered conditions, but under water deficits the high A of *T. kotschy* was related more to the maintenance of a higher capacity for mesophyll photosynthesis.

For some time it was thought that reduced photosynthesis under water deficits was to a significant extent mediated by stomatal closure, causing reduced CO_2 concentrations inside the leaf. Recently, however, it has been shown that reductions in mesophyll photosynthetic capacity and reductions in stomatal conductance under water deficits may, to a significant degree, be coupled (7). As a result, leaf C_i is relatively stable and reduced stomatal conductance is not considered the major cause of reduced photosynthesis under water deficits (7, 14). Stomata may still, however, play an important role in determining and explaining differences in the photosynthetic rate and water use efficiency between given plant species.

Many wild diploid and tetraploid *Triticum* species have photosynthetic rates that are considerably higher than domestic hexaploid wheats (*Triticum aestivum*), yet the physiological basis for these differences is not well understood (1). *Triticum kotschy* is a tetraploid desert annual with reportedly higher photosynthesis both under well watered conditions and at reduced water potentials compared to *T. aestivum* (13). Although *T. kotschy*

appears to maintain a higher degree of relative stomatal opening at reduced water potentials than *T. aestivum*, it is not clear if this is the only factor involved in the control of photosynthesis (13). In this study, we report that stomata had an important role in causing the relatively high photosynthetic rates of *T. kotschy* under well watered conditions, but under water deficits the mesophyll capacity for photosynthesis was more important.

MATERIALS AND METHODS

Plant Material. *Triticum aestivum* L. em Thell. (cv TAM W-101) and *Triticum kotschy* (Boiss) Bowden are both herbaceous annuals. The tetraploid *T. kotschy* grows in the Negev desert of Israel (13) and the *T. aestivum* cultivar TAM W-101 is a hexaploid winter wheat grown widely in the southern Great Plains of the United States.

Unvernalized plants were grown in growth chambers at 20°C , 60% RH, and 14 h light ($600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR at pot level). Three seeds were planted per pot about 1.5 cm deep in pots holding 1 L of sterilized sand. Emerged seedlings were thinned to 1 per pot after a week and the remaining plants watered daily with 25% Hoagland solution until the stress treatments were imposed. In the first experiment plants of *T. kotschy* and *T. aestivum* were grown under well watered conditions for 42 d after which gas exchange measurements were made as described below. The experiment was randomized in complete blocks with five replications. In a second experiment plants of the two species were grown for 35 d under well-watered conditions before water deficits were imposed by withholding water from pots. The experiment was randomized in complete blocks with four replications with genotype and water stress level (days without water) as experimental factors. Gas exchange measurement for the four water levels were made over a 5-d period with a given stress level completed each day. Plants of each species were measured at 0, 2, 3, and 4 d after withholding water from pots. The measurement order for stress level and species within a stress level was randomized. In a third experiment water deficits were applied to *T. kotschy* and *T. aestivum* over a more prolonged period. The water-holding capacity of the sand was determined and the weight of each pot, filled with equal volumes of dry sand, was recorded. The pots were weighed daily and their percent water calculated. Plants were watered to the maximum water holding capacity each day before the start of the stress treatment. For the stress treatment, plants were grown under well watered conditions for 24 d and then allowed to dehydrate to just below 20% of pot water-holding capacity, which took 4 d, and then were watered each day thereafter up to 20% of pot water-holding capacity for a 10-day period. Thus, the stress treatment consisted of a 4-d dehydration period followed by 10 d of prolonged stress. Pots from well watered treatments were watered daily to their pot water holding capacity. The experiment was completely randomized with three replications.

Gas Exchange Measurements. Simultaneous measurements of

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² Abbreviations: C_i , internal CO_2 concentration; A, CO_2 assimilation.

A and transpiration (E) per unit leaf area were made on intact leaves using a stirred, temperature and humidity controlled reaction chamber described by Bingham *et al.* (2) and Coyne *et al.* (4). Humidity was measured inside the chamber with a condensation dew-point hygrometer (General Eastern 1100DP, Watertown MA) and [CO₂] by passing chamber exhaust through a differential CO₂ gas analyzer (Horiba PIR 2000 R, Irvine CA). Leaves were measured at 1800 $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$, 20°C, 21% O₂, and 1 KPa vapor pressure (for some of the water stressed treatments with low E, vapor pressure was somewhat lower than 1 KPa). For each plant, gas exchange was measured on a single fully emerged leaf of a given tiller. In the first experiment all measurements were made at an ambient CO₂ concentration of 330 $\mu\text{L/L}$. In the second experiment A *versus* C_i curves were developed by measuring A at different ambient CO₂ concentrations of 0, 75, 160, 315, 330, 380, 480, and 573 $\mu\text{L/L}$. Values of A, E, diffusive conductance, and C_i were calculated according to von Caemmerer and Farquhar (3).

Water Potential. Immediately after gas exchange measurements were completed on a given leaf, leaf water potential was measured as described by Johnson *et al.* (8). Two 0.24 cm² leaf discs were removed using leaf cutter psychrometers, sealed in a psychrometer chamber, and allowed to come to temperature and vapor equilibrium in a 30°C water bath. Wet bulb depression was then determined using a microvolt meter (Wescor HP-115, Logan, UT). The resulting readings were used to calculate water potential for the individually calibrated psychrometers.

Stomatal Frequency. In experiment 2, adaxial and abaxial leaf impressions were made by applying clear fingernail polish to the midportions of fully emerged leaves. After removing the dried transparent images, the number of stomata in a 6.5 mm² grid were counted under a microscope. For each species, four different leaves were counted on each plant from each of the four blocks.

RESULTS

Under well watered conditions and at an ambient [CO₂] of 330 $\mu\text{L/L}$, *T. kotschyi* had a higher rate of A than *T. aestivum* (Table I). The higher A of *T. kotschyi* was associated with higher conductance, lower water use efficiency, and higher values of C_i compared to *T. aestivum* (Table I). The lower water use efficiency and higher C_i of *T. kotschyi* was again observed under well watered conditions in experiment 2 (data not shown).

Reduction in water potential significantly decreased A without a significant interaction with species—that is, the average difference in A between *T. aestivum* and *T. kotschyi* was, within experimental error, maintained as water potential declined (Fig. 1). As expected, the reduction in leaf water potential led to a reduction in leaf conductance (Fig. 1). The higher conductance of *T. kotschyi* than *T. aestivum* observed under well watered conditions (Table I) was also observed at lower water potentials and, as with A, there was no significant water potential \times species interaction. Although the difference was smaller as water poten-

tial declined, the higher A and conductance of *T. kotschyi* than *T. aestivum* was maintained over the entire range of water potential values from -0.5 to -2.9 MPa. The stomatal frequency for leaves of *T. kotschyi* (34 per mm² adaxial and 42 abaxial) and *T. aestivum* (32 per mm² adaxial and 43 abaxial) were nearly identical, so the difference between species in conductance was not directly related to stomatal frequency. The higher C_i observed in *T. kotschyi* than *T. aestivum* under well watered conditions (Table I) was not observed under water deficits. There was, however, a significant effect of water potential on C_i. The average C_i of both species first declined as water potential declined but then increased sharply past -1.9 MPa (Fig. 2).

In a separate experiment, A *versus* C_i response curves were developed to determine more precisely the role of conductance as compared to the capacity for mesophyll photosynthesis under well watered and stressed conditions. As in previous experiments, *T. kotschyi* had significantly higher A at an ambient [CO₂] of 330 $\mu\text{L/L}$ under both well watered and lower water potentials than did *T. aestivum* (Fig. 3). Under well watered conditions the A *versus* C_i response curves of the two species were quite similar. *T. kotschyi* did have somewhat higher A values than *T. aestivum* at C_i values above about 150 $\mu\text{L/L}$. Nevertheless, most of the higher A of *T. kotschyi* under well watered conditions measured at an ambient [CO₂] of 330 $\mu\text{L/L}$ (Fig. 3) was associated with the higher conductance of *T. kotschyi* (0.46 mol H₂O m⁻² s⁻¹) than *T. aestivum* (0.24 mol H₂O m⁻² s⁻¹). This higher conductance apparently led to the higher C_i in *T. kotschyi* compared to *T. aestivum* at an ambient [CO₂] of 330 $\mu\text{L/L}$ (Fig. 3). Thus, under well watered conditions, the higher stomatal conductance of *T. kotschyi* than *T. aestivum*, which was also observed in previous experiments, apparently led to most of the higher A in *T. kotschyi*. In the stressed treatments, however, the higher A of *T. kotschyi* than *T. aestivum* at an ambient [CO₂] of 330 $\mu\text{L/L}$ was mostly the result of differences in the A *versus* C_i response curves rather than conductance. Under water deficits, *T. kotschyi* had a higher A mostly because its response curve had a higher A plateau at a given C_i than that of *T. aestivum* (Fig. 3). As in the second experiment (Fig. 2) there was a shift upward in the C_i at an ambient [CO₂] of 330 $\mu\text{L/L}$ under stress. Water deficits also caused an increase in the CO₂ compensation concentration from about 25 to 65 $\mu\text{L/L}$ (Fig. 3).

DISCUSSION

Our results showing *Triticum kotschyi* to have higher A than *Triticum aestivum* at near current atmospheric CO₂ concentrations and over a range of water potentials is consistent with the results of Shimshi *et al.* (13). In that study, however, they could not attribute the higher A to stomatal control or to a higher cellular or subcellular capacity for photosynthesis. Since the A *versus* C_i response curves under well watered conditions were quite similar between species (Fig. 3), the higher conductance of *T. kotschyi* resulted in a higher C_i at 330 $\mu\text{L/L}$ ambient [CO₂]

Table I. Leaf Gas Exchange Characteristics for the Leaves of Two Triticum Species

The measurements were under well watered conditions at 20°C, 1800 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$, 21% O₂, and an ambient vapor pressure of 1 KPa.

Species	Ploidy	CO ₂ Assimilation per Unit Leaf Area	Leaf Conductance to H ₂ O Vapor (g _s)	WUE ^a	C _i
				$\frac{\mu\text{mol CO}_2}{\text{mmol H}_2\text{O}}$	
		$\mu\text{mol m}^{-2} \text{s}^{-1}$	$\text{mol m}^{-2} \text{s}^{-1}$	ratio	$\mu\text{L L}^{-1}$
<i>T. kotschyi</i>	4 \times	27.9	0.48	4.0	225
<i>T. aestivum</i>	6 \times	24.3	0.37	4.9	201
LSD = 0.05 ^b		3.5	0.10	0.8	20

^a Water use efficiency as the ratio of A to leaf transpiration. level.

^b Least significant difference at 5% probability level.

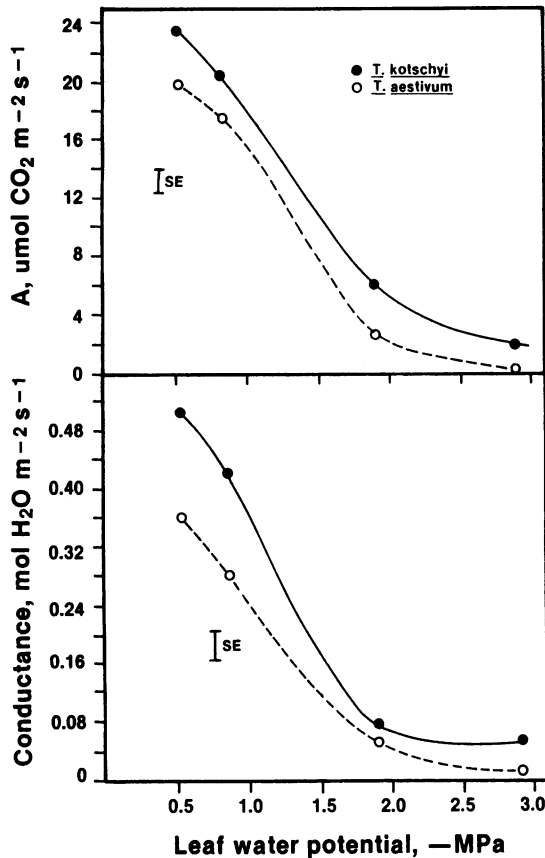


FIG. 1. Assimilation of CO_2 (A) and conductance to water vapor as a function of leaf water potential for *T. kotschy* and *T. aestivum*. Measurements were made at $330 \mu\text{L/L}$ ambient $[\text{CO}_2]$ concentration, a leaf temperature of 20°C , $1800 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$, $21\% \text{O}_2$, and an average vapor pressure of 1 KPa. There was no significant effect of species on leaf water potential at a given water potential level ($P = 0.93$) so water potentials were averaged within each water potential level. Both species and dehydration effects were highly significant for A and conductance ($P < 0.01$) but there was no significant species \times dehydration level interaction for either A ($P = 0.81$) or conductance ($P = 0.64$). Each point is the mean of measurements of four recently emerged leaves from different plants.

than in *T. aestivum*. *T. kotschy* had more CO_2 available to mesophyll tissue than *T. aestivum*, which lead to a higher rate of A. Thus, leaf conductance was more important in controlling A than the mesophyll capacity for photosynthesis under well watered conditions.

Under water deficits, however, there was little difference in the C_i at an ambient $[\text{CO}_2]$ of $330 \mu\text{L/L}$ between species (Figs. 2 and 3) and the higher A of *T. kotschy* appeared to be associated with its ability to maintain a higher mesophyll capacity for photosynthesis expressed as a higher plateau in the A versus C_i response curve (Fig. 3). Interpretation of the higher A plateau using the model of Farquhar *et al.* (6) suggests a maintenance of ribulose biphosphate regeneration capacity in *T. kotschy* under water deficits, which could in turn be related to a number of factors. Mayoral *et al.* (11) report that ribulose biphosphate carboxylase activity, electron transport rates, and photophosphorylation of isolated chloroplasts of *T. kotschy* were maintained to lower water potential levels than in *T. aestivum*.

With moderate water deficits C_i declined as water potential declined (Fig. 2) indicating that reductions in conductance were relatively greater than reductions in the mesophyll capacity for photosynthesis. This could result in an increased stomatal limi-

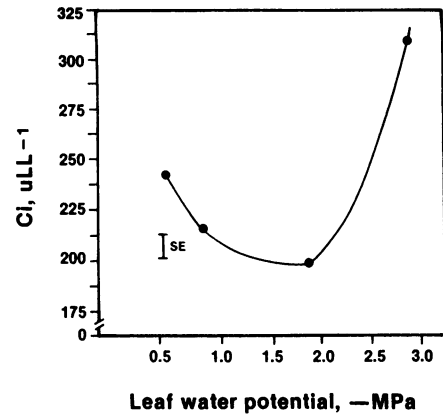


FIG. 2. Average internal $[\text{CO}_2]$ (C_i) as a function of leaf water potential for *T. kotschy* and *T. aestivum*. The species effect was not significant ($P = 0.80$) so the average C_i for the species is presented for each water potential level. Water potential level had a significant effect on C_i ($P < 0.01$) without a significant species \times C_i interaction ($P = 0.64$). Measurement conditions were those given in Figure 1. Each point is the mean of eight recently emerged leaves from different plants.

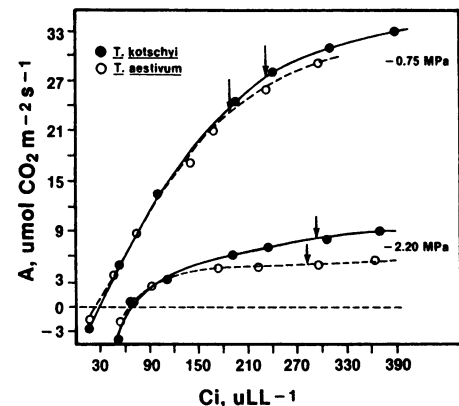


FIG. 3. Assimilation of CO_2 (A) as a function of internal $[\text{CO}_2]$ (C_i) in leaves of two *Triticum* species under well-watered (-0.75 MPa , $\text{SE} = 0.11$) and water stressed (-2.20 MPa , $\text{SE} = 0.18$) conditions. The arrows show the C_i value corresponding to an ambient $[\text{CO}_2]$ of $330 \mu\text{L/L}$. Other measurement conditions were those given in Figure 1. Each point is the mean of three determinations on recently emerged leaves of different plants for the well watered treatment and two determinations for water stress treatment.

tation to A. Nevertheless, the reduction in C_i from an average of 242 to $196 \mu\text{L/L}$ at -1.9 MPa was only 19%, whereas the average decline in A associated with that decline in water potential was 79% (Figs. 1 and 2). Thus, nonstomatal inhibition—damage to the plant's internal photosynthetic capability—was apparently the dominant factor reducing A under water deficits in both species. A faster relative decline in the mesophyll photosynthetic capacity than in conductance apparently occurred below -1.9 MPa , resulting in an increase in C_i values (Fig. 2). Even though C_i was not constant, there was still a close linear relationship between A and conductance ($r = 0.96$) observed in the second experiment (Fig. 1). The mechanism by which A and conductance are coupled is not known, but given the lack of coupling between C_i and conductance, C_i does not appear to be the principal controlling factor.

There was a shift in the CO_2 compensation concentration resulting from water deficits (Fig. 3). This has been previously reported for *T. aestivum* when the compensation concentration was measured by placing a leaf in an illuminated closed chamber until steady state CO_2 concentration was reached (9). A similar

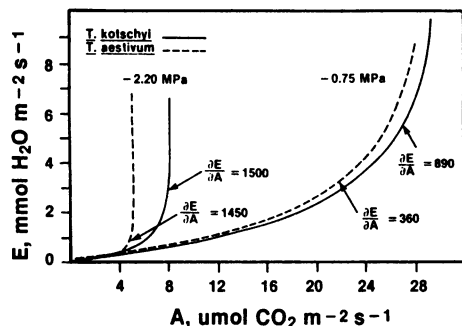


FIG. 4. Relationship between transpiration (E) and CO_2 assimilation (A) in leaves of two *Triticum* species calculated as described by Dubbe *et al.* (5). Curves were developed using simultaneously measured values of A , E , and conductance associated with data from Figure 3. Arrows indicate the values for leaves undergoing gas exchange at an ambient $[\text{CO}_2]$ of $330 \mu\text{l/L}$ and from species at a water potential of -0.75 MPa (well watered) and at -2.20 MPa (stressed). Measurement conditions were those given in Figure 1.

increase was observed by Mawson and Colman (10) in osmotically stressed isolated mesophyll cells by *Phaseolus* and *Lycopersicon*. The increase in the CO_2 compensation concentration under water deficits could stem from an increase in dark respiration (9) or a decrease in the rate of carboxylation relative to oxygenation (10, 12).

If the partial differential $\partial E/\partial A$ —the ratio of environmental gains of transpiration and assimilation—is large but constant, leaf carbon assimilation is maximal and the amount of water loss is high (5). When $\partial E/\partial A$ is small, carbon assimilation is reduced, but the water loss required to take up carbon is minimized. Under well watered conditions the maintenance of higher conductance in *T. kotschyi* results in an $\partial E/\partial A$ that is higher than that of *T. aestivum* (Fig. 4). Under water deficits there was an increase in $\partial E/\partial A$ for both species, but *T. aestivum* increased more than *T. kotschyi*, and there was little difference in this gain ratio between species at reduced water potential levels. The ecological significance of this could be related to the adaptation of *T. kotschyi* to its desert environment. When water is available *T. kotschyi* apparently maximizes carbon gain at the expense of water conservation. But when water becomes limiting it has the ability to maintain more carbon assimilation than *T. aestivum* at a similar gain ratio.

Even though the gain ratio was not constant—it increased in association with water deficits—*T. kotschyi* was as conservative with water for a given amount of A as was *T. aestivum* under

water deficits (Fig. 4). In an agricultural setting, provided that the boundary layer conductance in a crop canopy was large enough so that stomata had a significant influence over transpiration, the popular idea of developing wheat with higher water conservation potential—that is, higher water use efficiency—must be considered carefully. High water use efficiency, especially if it resulted from a greater capacity for mesophyll photosynthesis so that a high rate of A was maintained, may benefit productivity under water limited conditions. But as exemplified by *T. kotschyi*, lower water use efficiency results in maximum carbon assimilation when water is adequate and can be coupled with the maintenance of higher assimilation when water is limited. In certain drought prone environments, especially when the time for growth is limited, this may be a more effective way to maximize crop production than strict water conservation.

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