



Transpiration-use efficiency of barley

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Abstract

Transpiration-use efficiency, the ratio of biomass (Y) produced per unit of water transpired (T) by a crop, depends on crop characteristics and on the environment in which crops develop. Transpiration-use efficiency has been described as $Y/T = k_c/D_a$, where k_c is a crop dependent constant and D_a is the daytime air vapor pressure deficit. Our objectives were to determine Y/T and k_c of barley grown in Pullman, WA, and to analyze the variation in Y/T and k_c of barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) reported in the literature. Transpiration and biomass accumulation of barley crops were measured in the years 2000 and 2001. The coefficient k_c was estimated as the slope of the regression between cumulative values of biomass and T/D_a . It ranged from 6.6 ± 0.4 to 6.9 ± 0.2 Pa. These figures are greater than 5.8 Pa obtained by applying equations developed by Tanner and Sinclair [Tanner, C.B., Sinclair, T.R., 1983. Efficient water use in crop production: research or re-research. In: Taylor, H.M., et al. (Eds.), Limitations to Efficient Water Use in Crop Production. ASA, Madison, WI, pp. 1–27]. Data on k_c reported in the literature, although scarce, ranged from 3.0 to 5.9 Pa for barley, and from 2.8 to 6.7 Pa for wheat, with the lower values occurring at low D_a (<1 kPa). This variability seems to associate with the response of the internal (leaf) to external (bulk air) CO₂ concentration ratio (c_i/c_a) to changes of the leaf-to-air vapor pressure deficit (D_l), suggesting that k_c rather than a constant could be a function of D_l . The evaluation of more field data on k_c , the field validation of the response of c_i/c_a to D_l , and testing this approach for different species and cultivars is needed to improve the understanding of the Y/T determination at the canopy level. © 2005 Elsevier B.V. All rights reserved.

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1. Introduction

Transpiration-use efficiency is the ratio of biomass produced per unit of water transpired by a crop.

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Bierhuizen and Slatyer (1965) proposed that, at the leaf level, transpiration-use efficiency is represented by:

$$\frac{A}{E} = \frac{k_1}{D_l}, \quad (1)$$

where A is the CO₂ assimilation rate per unit of leaf area, E is the rate of evaporation per unit leaf area, k_1 is a constant for leaves of a given crop, and D_l is the leaf-to-air vapor pressure deficit. Bierhuizen and Slatyer

(1965) argued that k_1 could be scaled up to the entire canopy (k_c), since the leaf temperature appears to be within $\pm 2\text{--}3$ °C of air temperature, and as first approximation the vapor pressure deficit of the air (D_a) could be a surrogate of D_l ; hence:

$$\frac{Y}{T} = \frac{k_c}{D_a}, \quad (2)$$

where Y is crop biomass production, T is crop transpiration, and k_c is a canopy level constant for a given crop.

Tanner (1981) presented a rich discussion on the scaling of leaf (A/E) to canopy (Y/T) transpiration-use efficiency. He pointed out that k_c should be a conservative parameter (at least within a location), considering that the ratio between the internal (leaf) and the external (bulk air) concentration of CO_2 (c_l/c_a) is reasonably constant, an idea previously expressed by Bierhuizen and Slatyer (1965). Figures for this ratio reported by Wong et al. (1979) were around 0.7 for C_3 crops and 0.3 for C_4 crops. Tanner (1981) also indicated that k_c should be lower than k_1 for two reasons. First, there is a loss of CO_2 due to maintenance and growth respiration. Second, if the effectively photosynthesizing leaf area of a canopy is less than the effectively transpiring leaf area, k_c is further decreased below k_1 .

Tanner and Sinclair (1983) expanded the analysis of Tanner (1981). They developed equations to represent biomass production and transpiration of a canopy from which k_c can be explicitly calculated. Since we will use these equations throughout our analysis, they are summarized in this section. Scaling up from leaf to canopy, they concluded that biomass production could be represented by the following expression (their Eq. 11):

$$Y = \frac{abcc_a PAI_d}{1.5r_d}, \quad (3)$$

where a is the ratio of molecular weights of carbohydrates to CO_2 (0.68), b is a conversion coefficient from hexose to biomass and varies from near 0.8 for crops with high accumulation of sugar or starch (e.g. sugarcane and potato) to near 0.45 during the seed growth of crops with high accumulation of oil (e.g. sunflower), $c = (1 - c_l/c_a)$, PAI_d is the sunlit plant area index, c_a is the CO_2 atmospheric concentration (g m^{-3}), and r_d is the sum of boundary layer and stomatal resistance to

water vapor flux for sunlit leaves. The fundamental assumptions to develop Eq. (3) were: (1) c is reasonably constant (Wong et al., 1979) and (2) the photosynthesis of the shaded leaves is roughly equivalent to the maintenance respiration of the whole canopy.

Separating canopy foliage as sunlit and shaded leaves, Tanner and Sinclair (1983) expressed transpiration as (their Eq. 12b):

$$T = \frac{\rho \varepsilon D_a [PAI_d D_l / D_a + (PAI - PAI_d) r_d / r_s]}{Pr_d}, \quad (4)$$

where ρ is the density of the air, ε is the vapor to air molecular weight ratio, P is the atmospheric pressure, and r_s is the sum of boundary layer and stomatal resistance to water vapor flux for shaded leaves. As indicated by Tanner and Sinclair (1983), the term in brackets is the effective transpiring leaf area (PAI_t). Assuming that the ratio r_d/r_s is approximately 0.3 for $PAI = 4$, they calculated that PAI_t would be around 2.2 ± 0.2 for $PAI > 3$, unless the ratio D_l/D_a departs appreciably from unity. The fundamental assumption to develop Eq. (4) was that the shaded leaves are at air temperature.

The quotient between the equations for biomass and transpiration is Y/T ; then k_c is:

$$k_c = \frac{abcC_aP}{(1.5\rho\varepsilon)} \frac{PAI_d}{PAI_t}. \quad (5)$$

The merit of the Tanner and Sinclair (1983) analysis is widely recognized; after its publication almost every paper dealing with transpiration-use efficiency refers to it. Several simulation models estimate daily growth (Stockle et al., 1994; Sinclair and Seligman, 1995) and transpiration (Keating et al., 1999) based on k_c and Eq. (2).

Sinclair (1994) argued that, since the c values that Tanner and Sinclair (1983) used are probably in the upper limit for C_3 and C_4 , k_c estimated with their equations should be close to the maximum attainable. Barley and wheat k_c can be evaluated by taking $b = 0.74$ (as used for corn by Tanner and Sinclair, 1983), $PAI_d = 1.4$, $PAI_t = 2.2$, the current c_a at sea level (0.67 g m^{-3}), and the atmospheric pressure at sea level, giving k_c of $5.8 \text{ Pa g biomass g}^{-1} \text{ water}$ (hereafter we express k_c in Pa). Sinclair and Seligman (1995) used this value in a wheat growth model.

However, field-measured k_c values for barley are scarce and the available data shows great variability. In Table 1 we summarized data of Y/T and k_c of barley and wheat reported or calculated from the literature, assuming that they would be similar for both crops. Different techniques were employed by different authors to obtain k_c . Tanner (1981) indicated that k_c should be calculated as the slope of the linear regression between biomass and the daily integration of the quotient between transpiration and daytime D_a , and that was the method employed by Condon et al. (1993) and Marcos (2000). The other estimates in Table 1 are the product of Y/T times a seasonal average of daytime D_a , which can give slightly different values than the daily integration method. Hubick and Farquhar, 1989 presented data for several cultivars obtained in glasshouse experiments. We only show data for the cultivar with the highest k_c (Table 1); other cultivars had k_c 20% lower. For the water stressed treatment k_c was 5.9 Pa, almost identical to the theoretical value obtained above; however, for the irrigated treatment k_c was 4.7 Pa. Higher Y/T in water stressed than in unstressed crops was reported in field grown potatoes (Vos and Groenwold, 1989), and in pearl millet (*Pennisetum glaucum* [L.] R. Br.) in pot experiments (Brück et al., 2000), suggesting that k_c of water stressed crops could be higher than that of unstressed crops. Gregory et al. (1992) and Siddique et al. (1990) estimated k_c for barley from field experiments (Table 1). Gregory et al. (1992) estimated k_c as the product of Y/T times D_a . However, they indicated that D_a varied from around 0.51 kPa at the beginning of the season to 1.4 kPa in the last 4 weeks of growth. Siddique et al. (1990) reported the ratio Y/T at crop maturity but did not report D_a . We estimated D_a from a paper reporting the meteorological conditions for the same experiment (Siddique et al., 1989); it varied from around 0.8 to 1.2 kPa. The k_c reported for Gregory et al. (1992) range from 3.16 to 3.58 Pa and the k_c calculated from Siddique et al. (1990) is 5.14 Pa. For wheat, reported k_c ranges from 2.80 Pa (Gregory et al., 1992) to 6.7 Pa (Angus and van Herwaarden, 2001). This variability cannot be attributed entirely to genotypic variation; for the wheat cultivar Gutha k_c ranged from 2.80 to 4.74 Pa, and for Timgalen ranged from 3.83 to 5.18 Pa (Table 1). Although the data is insufficient to compare barley and wheat, the range of

variation of k_c for both species is similar. Condon et al. (1993) found a correlation between genotypic variation in k_c and ^{13}C discrimination in wheat, strongly suggesting that the genotypic variation in k_c is explained by variation in c (Condon et al., 2002). Interestingly, Angus and van Herwaarden (2001) reported a higher k_c postanthesis compared to preanthesis. In that study, D_a was also higher postanthesis compared with preanthesis (Table 1), suggesting that the environment could affect k_c . To the best of our knowledge, there has been no previous attempt to explain this variability in k_c .

Our objectives were to: (1) estimate k_c of barley from field measurements of biomass accumulation and transpiration and (2) analyze the variability in barley and wheat k_c reported in the literature in terms of the assumptions used by Tanner and Sinclair (1983) to develop their theoretical estimate of k_c .

2. Materials and methods

Measurements of crop growth and biomass accumulation were obtained from a larger field experiment designed to study radiation interception and radiation-use efficiency of barley. Briefly, field experiments were conducted in 2000 and 2001 at the Palouse Conservation Field Station (lat 46.8°N, long 117.2°W, elevation 756 m), located 5 km NW of Pullman, WA, on a Palouse silt loam (Fine-silty, mixed, mesic Pachic Ultic Haploxerolls). Treatments consisted of a factorial combination of two cultivars of spring barley (Baronesse, a two-row barley and Steptoe, a six-row barley), two seeding densities and two seeding dates, arranged in a complete randomized block design with four replications in 2000 and three replications in 2001. Each plot (2.2 m × 12 m) was seeded with a no-till drill rows 20 cm apart. At seeding, each crop received 157 kg ha⁻¹ of nitrogen and 51 kg ha⁻¹ of phosphorus. The sowing dates were 27 April and 6 June in 2000, and 26 April and 13 June in 2001. Target densities were 100 and 250 plants m⁻². Plots were irrigated with sprinklers. Weeds were controlled by hand. Diseases and insect damage were prevented or controlled with insecticides and fungicides.

In 2000, we monitored water use and crop growth in Baronesse seeded at the highest density in two

Table 1

Barley and wheat transpiration-use efficiency (Y/T) and k_c as reported or calculated from data obtained in the literature (the average daytime vapor pressure deficit (D_a) during the period of biomass growth and transpiration measurement is also reported)

Source ^a	Site	Species and cultivar	Y/T (g kg ⁻¹)	D_a (kPa)	k_c (Pa)	Observations ^b
(1)	Pullman, WA	Barley, cv. Baronesse	4.99	1.39	6.89	2000, normal seeding date
			3.20	1.93	6.67	2000, late seeding date
		cv. Steptoe	4.12	1.63	6.72	2001, normal seeding date
			4.29	1.63	7.00	2001, normal seeding date
(2)	Australia (glasshouse)	Barley, cv. Proctor	3.37	1.4	4.72	Irrigated, shoot + roots
			4.22	1.4	5.91	Water stressed, shoot + roots
(3) ^c	Merredin, Australia	Barley, cv. O'Connor	5.35	0.96	5.14	1987
		Wheat, cv. Gutha	4.93	0.96	4.74	
(4)	East Beverley, Australia	Barley, cv. Beecher	5.43	0.63	3.42	1988, shoot + roots
		cv. O'Connor	5.69	0.63	3.58	
		cv. Syrian	5.01	0.63	3.16	
		Wheat, cv. Gutha	4.45	0.63	2.80	
(5) ^c		Wheat, cv. Timgalen	5.75	0.82	4.69	1973, D1, preanthesis
			4.30	1.19	5.10	1973, D1, postanthesis
			5.64	0.92	5.18	1973, D2, preanthesis
			3.90	1.23	4.80	1973, D2, postanthesis
			4.14	1.07	4.45	1973, D3, preanthesis
			3.10	1.35	4.20	1973, D3, postanthesis
			4.83	0.91	4.38	1975, D1, preanthesis
			4.10	1.17	4.80	1975, D1, postanthesis
			3.91	0.98	3.83	1975, D2, preanthesis
			3.40	1.39	4.73	1975, D2, postanthesis
(6) ^c	Werribee, Australia	Wheat, cv. Bank	7.06	0.70	5.07	1984
			8.06	0.64	5.16	1985
		cv. Quarrion	7.75	0.68	5.28	1984
			9.21	0.61	5.63	1985
(7)	Moombooldool, Australia	Wheat, cv. Gutha	8.16	0.54	4.37	1985, preanthesis
		cv. Quarrion	6.75	0.71	5.51	
(8) ^c	Toowoomba, Australia	Wheat, cv. Hartog	4.2	1.18	4.9	1993
(9)	Pucawan, Australia	Wheat, average of cv. Comet, Janz and Kulin	7.13	0.51	3.95	Preanthesis, low N
			5.98	0.51	3.10	Preanthesis, high N
			4.3	1.54	6.7	Postanthesis, low N
			3.9	1.54	6.0	Postanthesis, high N
(10) ^c	Nottinghamshire, UK	Wheat, cv. Soissons	5.66	0.60	3.68	1994
			6.17	0.63	4.01	1995
		cv. Maris Huntsman	6.63	0.60	4.31	1994
			6.66	0.63	4.32	1995
(11)	Pullman, WA	Wheat, cv. WB926R	4.59	1.13	5.90	Pooling 1998/1999 data

^a (1) This study; (2) Hubick and Farquhar, 1989; (3) Siddique et al. (1990), D_a from Siddique et al. (1989); (4) Gregory et al. (1992); (5) Doyle and Fischer (1979) showed data from year 1974 too, but these were excluded because of occurrence of heavy frosts; D_a was estimated as 2/3 of the maximum saturation deficit, that is approximated as the difference in vapor saturation between maximum and minimum temperature, both obtained from the average monthly temperature reported and a daily thermal amplitude of 12 °C; (6) Connor et al. (1992) showed data for four sowing dates per year but we excluded the last sowing date for Quarrion because it showed irregular phenological development; D_a was estimated as in (5) with the reported maximum and minimum temperatures; (8) Meinke et al. (1997); (7) Condon et al. (1993); (9) Angus and van Herwaarden (2001); (10) Foulkes et al. (2001) they had irrigated treatments but indicated that the irrigation added uncertainty to the transpiration estimates; we only show data for non-irrigated crops; (11) Marcos (2000).

^b Shoot + roots indicates that roots were sampled and included in the computation of biomass; to make a rough accounting of root biomass when it was not measured, Y/T and the resulting k_c were multiplied by 1.15 (sources 5 and 7) and by 1.07 (see text) for the preanthesis and the entire crop cycle data, respectively. No apportioning of biomass to roots was made for postanthesis data.

^c Indicates that k_c was estimated as the product of Y/T times D_a .

replications at both sowing dates. In 2001, we monitored water use and crop growth between booting and the beginning of grain filling (June 28 to July 13) for Baronesse and Steptoe seeded at the highest density in the first seeding date. The techniques employed to estimate water use in each year differed. In 2000, soil water content was measured from emergence to physiological maturity with water reflectometer probes (model CS615-L, Campbell Scientific Inc., Logan, UT). In each plot, five probes were installed to a depth of 1.5 m at 0.3 m interval. An additional sensor was installed in the first layer at angle of 20° from the soil surface to monitor water content in the first 0.1 m of the soil profile. Each probe was connected to a datalogger (CR10x, Campbell Scientific Inc., Logan, UT), and the signal recorded at midnight. Each probe was calibrated against measured volumetric water content. Gravimetric water content was measured four times during the growing season to a depth of 1.8 m at 0.3 m interval. The samples were taken at crop emergence, beginning of stem elongation, heading and harvest. Volumetric water content was estimated as the product of the gravimetric water content and the bulk density of the layer. Bulk density was measured to a depth of 1.8 m at 0.3 m intervals by taking three soil cores of 2 cm in diameter and 20 cm long in spring.

A weather station located in the border of the experimental area recorded hourly precipitation, temperature, relative humidity, and wind speed. Radiation interception was measured using one tube solarimeter (70 cm) per plot (Marcos, 2000). After the plants reached the two- to three-leaf stage, the solarimeters were placed below the canopy in areas representative of the plot. Each solarimeter was connected to a datalogger, and the signal recorded every 20 min. Simultaneously, solar radiation was measured at a height of 2.5 m with a pyranometer (LI200X, Licor Inc., Lincoln, NE, USA). The pyranometer and the solarimeter outputs were integrated to obtain daily solar irradiance and daily solar radiation transmitted through the canopy, and the values used to calculate daily fractional radiation interception (f_i). The seasonal variation in f_i was reported in Kemanian et al. (2004). The replicates of each treatment for f_i showed very low variability (data not shown), consistent with the observations that the crop stand was homogenous and that the plants tillered

aggressively, compensating minor unevenness in the plants distribution.

Daily evapotranspiration (ET) was calculated from a water balance for the soil profile:

$$ET = PP + I - DP - R - \Delta S, \quad (6)$$

where, PP is precipitation, I is irrigation, DP is deep percolation, R is runoff, and ΔS is the change in storage to a depth of 1.8 m. Runoff did not occur during the course of the experiment. Deep percolation was only evident at the beginning of the measurement period in the first sowing date, when the sensors at 1.2 and 1.5 m of depth showed a slight decrease in water content, but thereafter the signal stabilized until the crops started to uptake water from that layer towards the end of the crop growth cycle. Daily ET was partitioned into soil evaporation and crop transpiration on a daily basis. Soil evaporation was taken as the minimum of the change in storage at the first 0.1 m soil and the product $(1 - f_i)ET$. The remaining fraction of ET was apportioned to transpiration. Above-ground biomass was estimated from samples of two adjacent 0.5 m length rows (0.2 m^{-2}) per plot, at intervals of 6–10 days until physiological maturity. Samples were dried at 60 °C for 72 h and the dry weight recorded.

In the year 2001, measurements were taken between flowering and beginning of grain filling (June 28 to July 13). We selected this period because it shows the highest growth and water depletion rate of the crop cycle, the crops fully cover the ground ($f_i \approx 0.9$) minimizing soil evaporation and then errors in the estimation of transpiration, and the probability of occurrence of precipitation are low. No irrigation was applied during that time interval. In each plot at high density (three replications), two sections of about 1 m^2 were flagged. The sections were visually identical. We carefully avoided borders, areas with uneven plants distribution or populations unusually high or low. Aboveground biomass samples of two adjacent rows 1 m long were taken at the beginning and at the end of the selected period; one of the flagged areas was sampled at each time. Samples were dried at 60 °C for 72 h and the dry weight recorded. Concurrently, gravimetric water content was measured to a depth of 1.5 m at 0.3 m interval. An additional sample was taken in the first 5 cm. Each sample was a composite of two cores 30 cm long

(5 cm in the top layer) and a diameter of 2 cm. There was a rain of 3.3 mm during that period but there was no runoff and we assumed deep percolation to be negligible. Therefore, ET was approximated as the change in storage plus the precipitation during the period June 28 to July 13. The change in storage of the first 5 cm was attributed to soil evaporation and the remaining fraction of ET apportioned to transpiration.

In 2000, the transpiration efficiency (Y/T) was estimated as slope of the linear regression between cumulative Y against cumulative T , and the coefficient k_c was estimated as the slope of the linear regression between Y and daily cumulative T/D_a . We considered that the estimations of T for $Y > 100 \text{ g m}^{-2}$ (f_i of approximately 0.35) were more accurate than the estimations of T for $Y < 100 \text{ g m}^{-2}$. Therefore, although in theory the regression should pass through the origin, we prioritize honoring the actual data and did not set the intercept to zero. In 2001, Y/T was calculated as the biomass gained in the period divided by the estimated transpiration, and k_c was calculated as the product of D_a times Y/T , where D_a was averaged for the period considered.

3. Results and discussion

In the year 2000, crop water uptake was restricted to a depth of 1.5 m; no change in the water content between 1.5 and 1.8 m was detected between heading

and maturity (data not shown). Biomass accumulation was linearly related to both cumulative transpiration (slopes of 4.7 ± 0.4 and $3.0 \pm 0.6 \text{ g biomass kg}^{-1}$ water for the first and the second sowing date) and cumulative transpiration normalized by D_a (Fig. 1). As observed by Tanner (1981) in potatoes, the normalization of T by D_a decreased the scatter of the data; the slopes of the first and second sowing dates were indistinguishable giving a common k_c of $6.2 \pm 0.4 \text{ Pa}$ (cv. Baronesse). If an accounting for roots is made assuming that on average over the entire crop cycle about 7% of the biomass is allocated belowground, then $k_c = 6.6 \pm 0.4 \text{ Pa}$. The 7% figure comes from the following calculation. Gregory et al. (1978) indicated that roots represent about 15% of the total biomass at anthesis and that root growth stops thereafter. In this area, spring cereals duplicate the aboveground biomass from beginning of anthesis to maturity. Therefore, if root biomass is kept constant, it amounts to about 7% of total biomass at harvest. Another calculation that gives a similar estimate is converting root density measurements to root biomass based on a root length density of 240 m g^{-1} (Gregory et al., 1978). With a maximum root density at the surface of 4 cm cm^{-3} (see the review table by de Willigen and van Noordwijk, 1987, p.88) and an exponential decrease in root density (Dwyer et al., 1998) to a depth of 1.5 m, root biomass would represent slightly less than 7% of the total biomass for a crop with 10 Mg ha^{-1} of aboveground biomass. In the year

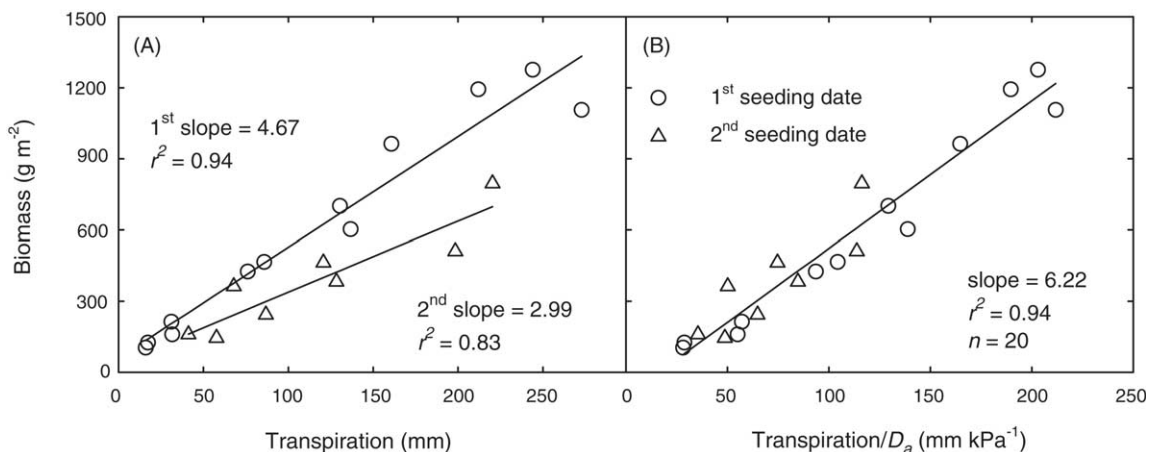


Fig. 1. Biomass as a function of cumulative transpiration (panel A) and cumulative transpiration normalized by the air vapor pressure deficit (D_a) (panel B), of spring barley cv. Baronesse grown at Pullman, WA, year 2000.

2001, the average ET for the period considered was 115 ± 7 mm, the average T was 106 ± 7 mm, and the average crop growth rate was $29.4 \pm 1.2 \text{ g m}^{-2} \text{ d}^{-1}$. The average k_c estimated was $6.9 \pm 0.2 \text{ Pa}$ ($n = 6$); the estimates for Baronesse and Steptoe, although not statistically different, are shown separately in Table 1. No accounting for root biomass was made in the year 2001 as root growth stops around anthesis (Gregory et al., 1978).

Comparing the values that we obtained for barley with the values summarized in Table 1, Y/T values are within the range reported in the literature, while k_c values of 6.6 and 6.9 Pa are in the upper limit reported in the literature for both barley and wheat, and so are the D_a values. Furthermore, while some k_c presented in Table 1 are similar to the 5.8 Pa obtained by applying Eq. (5), others are noticeable lower. We graphed Y/T of Table 1 against the daytime D_a (Fig. 2) and found that, as suggested by Bierhuizen and Slatyer (1965), Y/T seems to be an inverse function of D_a , that is well represented by the model $Y/T = 4.9D_a^{-0.59}$ ($r^2 = 0.97$, $n = 38$, $P < 0.001$). The upper envelope of the data departs from the Y/T predicted by Eq. (2) using $k_c = 5.8 \text{ Pa}$, particularly at $D_a < 1 \text{ kPa}$, where predicted Y/T is much higher than the observed Y/T ,

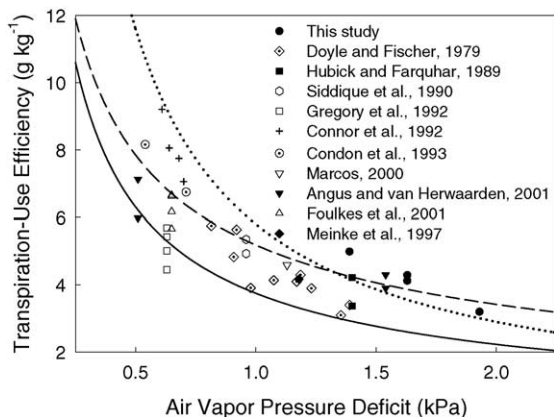


Fig. 2. Transpiration-use efficiency (Y/T , $\text{g biomass kg}^{-1} \text{ H}_2\text{O}$) as a function of the vapor pressure deficit of the air. The points are the Y/T reported in the literature for wheat and barley (Table 1); the dotted line is for $Y/T = 5.8/D_a$; the solid line is for Y/T calculated using $c = 1 - (0.85 - 0.05D_1)$ (Eq. (7), see text) and (Eqs. (2), (5), (8) and (9)); the dashed line is for Y/T calculated using $c = 1 - (0.85 - 0.12D_1)$; see text for explanations. The solid line is well approximated by $Y/T = 3.8/D_a^{3/4}$ and the dashed line by $Y/T = 5.2/D_a^{3/5}$.

except the highest Y/T reported by Connor et al. (1992) (Fig. 2). We suspect that Connor et al. (1992) underestimated T . The information presented in their paper allows calculating Y/T for different phenological stages, and we found that in the third seeding date of 1984, the cultivar Quarrion Y/T was $17 \text{ g biomass kg}^{-1} \text{ H}_2\text{O}$ in the period between floral initiation and anthesis. This value is unusually high, even for a C_4 plant, and may be indicative of an underestimation of transpiration and consequently an overestimation of Y/T . There is also considerable scattering in the data of Fig. 2, and although part of this scattering could be genetic variation, it is probably better explained by uncertainties in measuring transpiration and growth. However, the upper and lower envelopes of the data are almost parallel, suggesting that they are truly depicting the trend of Y/T as a function of D_a (Fig. 2). The significant conclusion here is that, to make the reported Y/T compatible with Eq. (2), k_c cannot be a constant but rather decrease with decreasing D_a , which is in fact the trend observed in Table 1.

One of the fundamental assumptions of Bierhuizen and Slatyer (1965) and Tanner and Sinclair (1983), was that the ratio c_i/c_a , and hence c , is fairly constant. However, there is evidence that c varies in response to physiological and environmental factors. Among these factors, it is well documented that c_i/c_a decreases as water stress increases in field-grown potatoes (Vos and Groenwold, 1989), wheat (Whitfield, 1990), and sorghum (Williams et al., 2001). Indirect evidence of that response to water deficit and the associated decrease in stomatal conductance is the decrease in the ^{13}C discrimination in water stressed plants (e.g. Hubick and Farquhar, 1989; Condon et al., 1992). Interestingly, there is also evidence that the ratio c_i/c_a decreases with increasing D_1 (Table 2), and effect suggested in the analysis by Condon et al. (1992). Farquhar et al. (1982) concluded that when assimilation rate is reduced by a decrease in the stomatal conductance, c_i should decrease. Then, the response of c_i/c_a to D_1 could be explained by a reduction in stomatal conductance at increasing transpiration rates (Mott and Parkhurst, 1991), caused in turn by increasing D_1 .

The magnitude of the response of c_i/c_a to D_1 seems to be associated to the photosynthetic metabolism. While the extrapolated c_i/c_a at $D_1 = 0$ is approximately

Table 2

Relation between the ratio leaf-to-ambient CO₂ concentration (c_i/c_a) and the leaf-to-air vapor pressure deficit (D_l) for several species (the D_l at which the plants were exposed during the measurements is reported)

Source ^a	Species	Intercept	Slope (kPa ⁻¹)	r^2	n	D_l range (kPa)
C₃ plants						
(1)	<i>Nicotiana glauca</i>	0.81	-0.051	0.63	10	0.5–3.0
(2)	<i>Gossypium hirsutum</i>	0.83	-0.120	0.99	5	1.5–3.4
(3)	<i>Phalaris aquatica</i>	0.95	-0.093	0.97	4	0.4–2.0
	<i>Oryza sativa</i>	0.91	-0.120	0.97	4	0.4–2.0
(4)	<i>Phaseolus vulgaris</i>	0.84	-0.065	0.97	6	0.8–3.0
(5)	<i>Ricinus communis</i>	0.90	-0.070	0.97	6	0.2–2.0
		0.83	-0.126	0.81	4	0.2–2.0
(6)	<i>Encelia farinosa</i>	0.89	-0.027	0.85	28	1.0–4.0
(7)	<i>Solanum tuberosum</i>	0.93	-0.070	0.55	32	0.9–3.0
	Average C ₃	0.88	-0.082			
C₄ plants						
(3)	<i>Zea mayz</i>	0.85	-0.203	0.99	4	0.4–2.0
	<i>Paspalum plicatulum</i>	0.93	-0.179	0.98	4	0.4–2.0
(6)	<i>Pleuraphis rigida</i>	0.80	-0.101	0.88	21	1.0–4.0
(7)	<i>Sorghum bicolor</i>	1.00	-0.246	0.79	22	1.0–2.5
	Average C ₄	0.90	-0.182			

^a (1) Farquhar et al. (1980), their Fig. 4, plants grew in growth chamber, $c_a \approx 330 \mu\text{mol mol}^{-1}$, photosynthetic photon flux density (PPFD) $\approx 480 \mu\text{mol m}^{-2} \text{s}^{-1}$; (2) Sharkey et al. (1982), their Fig. 2, plants grew at $c_a \approx 1900 \mu\text{mol mol}^{-1}$, measurements were at $c_a \approx 350 \mu\text{mol mol}^{-1}$; (3) Morison and Gifford (1983), their Fig. 8, plants grew in growth chamber at $D_a \approx 0.95 \text{ kPa}$, $c_a \approx 340 \mu\text{mol mol}^{-1}$, -1 , and PPFD $\approx 670 \mu\text{mol m}^{-2} \text{s}^{-1}$; (4) Commstock and Ehleringer, 1993, their Fig. 2, plants grew in glasshouse with $D_a \approx 2.5 \text{ kPa}$, $c_a \approx 350 \mu\text{mol mol}^{-1}$, and maximum PPFD $\approx 1600 \mu\text{mol m}^{-2} \text{s}^{-1}$; (5) Dai et al. (1992) plants grew in growth chamber $D_a \approx 1.3 \text{ kPa}$, $c_a \approx 345 \mu\text{mol mol}^{-1}$, and PPFD $\approx 600 \mu\text{mol m}^{-2} \text{s}^{-1}$, measurements at 20°C and at PPFD of 1000 and 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ shown here; (6) Zhang and Nobel (1996), field and growth chamber study, $c_a \approx 380 \mu\text{mol mol}^{-1}$, maximum PPFD $\approx 1600 \mu\text{mol m}^{-2} \text{s}^{-1}$, measurements made several times over daytime; (7) Bunce (personal communication, 2003), field study, D_a varied day-to-day, measurements were on plants grown at c_a of 350 and 700 $\mu\text{mol mol}^{-1}$, the regressions were identical for both CO₂ levels and were pooled, PPFD $> 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$; for potatoes, the regression was not significant for instantaneous D_a variation.

0.90 for both C₃ and C₄ plants, the slope of the response is on average 0.08 kPa^{-1} for C₃ and 0.18 kPa^{-1} for C₄ plants (Table 2). Choudhury (1986) calculated c_i for field grown cotton based on measured net photosynthesis and other biophysical considerations; we estimated that the slope of c_i/c_a versus D_l was 0.07 kPa^{-1} (Choudhury, 1986, Fig. 5), very similar to the average of 0.08 kPa^{-1} for C₃ crops shown in Table 2. Hence, the empirical relation between c_i/c_a and D_l appears robust and could be included in an analysis of Y/T . Zhang and Nobel (1996) developed a simple model to explain the response of A/E to D_l , explicitly considering the linear response of c_i/c_a to D_l . However, there is no report integrating this response to the canopy level Y/T .

We calculated Y/T (and k_c) using Eq. (5) but allowing c to vary linearly with D_l :

$$c = 1 - \frac{c_i}{c_a} = 1 - (d_0 + d_1 D_l), \quad (7)$$

where d_0 and d_1 are the intercept and slope, respectively, of the regression of c_i/c_a versus D_l (Table 2). Since there is no report of the response of c_i/c_a for barley and wheat, we can only assume that the response would be somewhere within the range indicated by the data gathered in Table 2. We calculated Y/T using the average of the three steepest slopes ($d_1 = -0.12 \text{ kPa}^{-1}$) and the average of the three less steep slopes ($d_1 = -0.05 \text{ kPa}^{-1}$) for the C₃ species summarized in Table 2. In both cases the average d_0 was 0.85. The Y/T obtained with the steepest d_1 would

approximate an upper boundary for C_3 , while the Y/T obtained with the less steep d_1 would represent a lower boundary. With $d_1 = -0.12 \text{ kPa}^{-1}$, the value of c of 0.3 used by Tanner and Sinclair (1983) is achieved at $D_1 = 1.25 \text{ kPa}$. Vos and Groenwold (1989) reported $c_i/c_a \approx 0.77$ ($c = 0.23$) at $D_a \approx 1.4 \text{ kPa}$ for the potato cv. Saturna; assuming that D_1 is approximated by D_a , Eq. (7) predicts $c = 0.22$ ($d_1 = -0.05 \text{ kPa}^{-1}$) and $c = 0.32$ ($d_1 = -0.12 \text{ kPa}^{-1}$).

Two more responses to change in the vapor pressure deficit should be considered for completeness in applying Eq. (5): (1) the response of the stomatal resistance and thus the ratio r_d/r_s , and (2) the canopy evaporative cooling and thus the ratio D_1/D_a . Choudhury and Monteith (1986) summarized information showing that the stomatal resistance increases with increasing D_1 . Due to the exposure of sunlit leaves, we can expect that the increase in resistance with rising D_1 be more acute in the sunlit leaves, increasing the ratio r_d/r_s . Since we did not find experimental information, we assumed that a linear function could approximate this effect:

$$\frac{r_d}{r_s} = 0.2 + 0.8 \frac{D_1}{7}. \quad (8)$$

This function assumes that when $D_1 = 0 \text{ kPa}$ the ratio of resistances is 0.2, and increases until a maximum of 1 for $D_1 = 7 \text{ kPa}$. The limit of 7 kPa was taken from Choudhury and Monteith (1986), who assumed by extrapolation of published data that stomata of arable crops close at D_1 of approximately 7 kPa. We did not perform any calculation above 5 kPa, which is a reasonable upper limit for the D_1 experienced by field crops. Although field measurements of resistance of both sunlit and shaded leaves should be performed to test the validity of this approximation, the use of an intercept of 0.2 seems to be consistent with some available measurements. For example, this equation predicts that the ratio r_d/r_s equals 0.3 at a D_1 of $\sim 0.9 \text{ kPa}$, the ratio assumed by Tanner and Sinclair (1983) for their computations of k_c . Kjelgaard (1993) reported the stomatal resistance for both sunlit and shaded leaves of irrigated corn (average $PAI = 3.7$, range 2.0–4.5). From this data, we calculated that the ratio r_d/r_s averaged 0.4 for an average D_a of 1.7 kPa, while Eq. (8) yields 0.39.

The leaf-to-air vapor pressure deficit depends on the canopy temperature and the air vapor pressure.

Although the canopy temperature depends on the energy balance of the foliage, Idso (1982) showed that for well-watered crops the difference between canopy and air temperature (ΔT) is a linear function of D_a . Even more, Idso et al. (1987) showed that this relationship is weakly affected by doubling c_a from 330 to 660 $\mu\text{mol mol}^{-1}$. For barley Idso (1982) reported that:

$$\Delta T = 2.01 - 2.25D_a. \quad (9)$$

For potato and sunflower the slopes reported by Idso are also near 2.0 C kPa^{-1} . We used this equation to calculate the ratio D_1/D_a assuming that it gives the sunlit leaves temperature and that the shaded leaves are at the air temperature.

It is of interest to analyze the behavior of PAI_t as a function of D_a after the introduction of these changes. Increasing D_a causes PAI_d to be cooler than the air and consequently a decreasing ratio D_1/D_a than under the isothermal condition ($D_1/D_a = 1$), and an increasing ratio r_d/r_s . Hence, on the computation of PAI_t the weight of the sunlit leaf area decreases while the weight of the shaded leaf area increases, keeping the value reasonably bounded. For instance, for a dew point temperature of $10 \text{ }^\circ\text{C}$, air temperatures varying from 15 to $30 \text{ }^\circ\text{C}$, $d_1 = -0.12 \text{ kPa}^{-1}$, a PAI of 4 and a PAI_d of 1.4, PAI_t is 2.1 ± 0.2 , reasonably close to the 2.2 used by Tanner and Sinclair (1983). For this set of conditions, c ranges from 0.22 to 0.39. Then, the adjustment of c by D_a will cause a greater impact on k_c than the adjustment of PAI_t by D_a .

The resulting Y/T calculated with variable k_c follows approximately the lower envelope ($d_1 = -0.05 \text{ kPa}^{-1}$, Fig. 2, solid line) and the upper envelope ($d_1 = -0.12 \text{ kPa}^{-1}$, Fig. 2, dashed line) of the data gathered from the literature. The calculated k_c decrease with decreasing D_a as suggested by the data of Table 1; for instance, using $d_1 = -0.12 \text{ kPa}^{-1}$, Eq. (5) gives $k_c = 3.9 \text{ Pa}$ for $D_a = 0.5 \text{ kPa}$ and $k_c = 6.8 \text{ Pa}$ for $D_a = 2.0 \text{ kPa}$. The differences in Y/T suggested by the so-called upper and lower boundary could represent both differences among species or cultivars. In comparing two cultivars of potatoes, Vos and Groenwold (1989) found that the cultivar Bintje (high stomatal resistance) had Y/T about 14% higher than the cultivar Saturna (low stomatal resistance). Genetic differences in Y/T were also reported for barley (Hubick and Farquhar, 1989) and wheat

(Condon et al., 1993). Therefore, although the information presented is not conclusive, it strongly suggests that the variability observed in Y/T could be associated to the variation of c as a function of D_a , and that k_c is not constant.

Both a constant or a variable k_c imply that the water use efficiency increases with decreasing D_a , but the advantage in biomass production at low D_a compared with high D_a predicted by the variable k_c is smaller than that predicted by a constant k_c of 5.8 Pa (Fig. 2). Tanner and Sinclair (1983) warned that under low D_a the departure of the ratio D_1/D_a from unity due to canopy temperature rising above the air temperature could cause deviation from their calculations. The additions presented here to their equations seem to account explicitly for that effect. Testing this approach under high D_a would be of major interest. However, due to the season at which barley and wheat are grown, average $D_a > 2$ kPa are rarely obtained for a long period of time. Consequently, we could not find data in the literature reporting Y/T at $D_a > 2$ kPa.

The set of equations presented can be used to speculate on the effect of water stress on k_c . The temperature of a water stressed canopy can be 2–4 °C above the air temperature. This would cause a rise in both c Eq. (7) and PAI_t Eq. (4). We tried several combinations of dew point, air and canopy temperatures, and found only a marginal variation of k_c . This is in disagreement with some investigations showing that Y/T tends to increase with increasing water stress (e.g. Vos and Groenwold, 1989). The reason is that in addition to the effect on c through an increase in D_1 , water stressed plants close the stomata to prevent dehydration, a response attributed to an abscisic acid-mediated root signal (Davies and Zhang, 1991), which causes a further increase in c . This would explain an increase in Y/T of stressed crops, and suggests that k_c of Eq. (2) should be calculated independently for stressed and unstressed crops.

4. Conclusions

The coefficient k_c of barley (cv. Baronesse) measured at Pullman ranged from 6.6 ± 0.4 to 6.9 ± 0.2 Pa. Thus, in this environment and for the cultivars selected, k_c is greater than the 5.8 Pa estimate obtained from Tanner and Sinclair (1983) Eq. (5). This

difference, as well as the variability reported in Y/T and k_c in the literature, seems to be accounted for by allowing the ratio c_i/c_a to vary as a function of D_1 in the Tanner and Sinclair (1983) derivation. However, both the quality and the quantity of available data on k_c of barley (and wheat) preclude being conclusive. The evaluation of more field data on k_c , the field validation of the response of c_i/c_a to D_1 , and testing this approach for different species and cultivars is needed to improve the understanding of the transpiration-use efficiency determination at the canopy level.

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