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RESEARCH

ASSESSING THE TRANSFERABILITY OF TRANSPIRATION-USE EFFICIENCY MODELS OF BIOMASS PRODUCTION

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Transpiration-use efficiency (w), defined as the ratio of biomass produced per unit water transpired, has been used to evaluate crop performance under limited water supply. However, the lack of consistency of w values through different environmental conditions has not allowed, using it as a transferable parameter. Thus, simple approaches have been developed, including: 1) $w = k_{Da}\ D_a^{-1}$ and; 2) $w = k_{Eto}\ ET_0^{-1}$ where k_{Da} and k_{ETo} are crop-dependent parameters, with the underlying concept that normalization by D_a or ET_0 would accounts for the effects of climate variations on w, while these parameters would be reasonably constant across diverse environments. The objective of this study was to assess the transferability of k_{Da} and k_{ETo} for wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.). The scarcity of experimental information and discrepancy of the methodology used, justified the use of a canopy transpiration and photosynthesis model which was developed, tested, and fitted with weather data from eight environmentally different locations to simulate values of w, k_{Da} and k_{ETo}. The results indicated that k_{Da} and k_{ETo} were more variable than expected; suggesting that calibration would be desirable. A consistent trend of change of the parameter values as function of D_a or ET_0 was found, which can be represented by mathematical functions, allowing transferring w, k_{Da} and k_{ETo} (maize). In contrast, the k_{ETo} for wheat correlated weakly with D_a and ET_0, but a low overall coefficient of variation (10%) allowed using an average value as a reasonable predictor of w.

Key words: Transpiration-use efficiency, models of biomass production.

Agriculture is challenged by the scarcity of water resources in many regions of the world, problem that is compounded by climate variability and expected to worsen in the future. There is a raising need for tools to evaluate crop productivity as a function of water to better guide development policies and field management practices aimed at producing "more crop per drop".

Mechanistic simulation models of canopy photosynthesis and transpiration appear as suitable tools to evaluate the effect of interacting factors on water-use efficiency and productivity of crops. However, demanding parameterization and computing requirements of these models limit their applicability for long-term analysis that includes multiple species across the globe. As a result, there is a renewed interest in simple, transpiration-based models of crop productivity that can be readily applied to a large number of crop species across the range of climatic conditions where these crops are grown. Although these models were introduced as early as the beginning of the previous century, the experimental determination of the parameters (typically just one parameter) used in the models has been relatively scarce, probably due to the need of measuring crop transpiration for their determination. As a result of scarce experimental information, it is not easy to assess the variability and transferability among locations of the parameters of these simple transpiration-based models.

Attempts to develop simple relationships to predict w for different crops and climates can be traced back to the early 20th century and later (Brigss and Shantz, 1914; Shantz and Piemeisel, 1927; de Witt, 1958; Arkley, 1963; Bierhuizen and Slatyer, 1965; Tanner, 1981; Ritchie, 1983; Tanner and Sinclair, 1983; Steduto and Albrizio, 2005). The underlying assumption has been that the parameters of these relationships are relatively constant across diverse climatic conditions, and assumption that has not been well evaluated.

Early work by Bierhuizen and Slatyer (1965) led the way to the development of a comprehensive physiologically-based description of transpiration use efficiency as follows:

$$N_l\,T_l^{-1} = \Delta C r_{CO2}^{-1}\left[\left(\rho\varepsilon P_a^{-1}\right)\left(D_l r_v\right)\right]^{-1} \qquad [1]$$

where N_l is the net leaf photosynthesis, T_l is the leaf transpiration, ΔC is the CO_2 concentration difference between the atmosphere and the CO_2 compensation point, r_{CO2} is the leaf resistance to CO_2 diffusion from the surrounding air into the leaf and into the cells of the chloroplasts, ρ is the density of the air, ε is the vapor

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to air molecular weight ratio, D_l is the vapor pressure difference between the leaf and the surrounding air, P_a is the atmospheric pressure, and r_v is the summation of the partial resistances to water vapor flux from the leaf. Bierhuizen and Slatyer (1965) showed that the ratio $N_l T_l^{-1}$ is determined largely by D_l based on the following assumptions: (1) ΔC is a relatively constant crop-dependent parameter, and (2) the $r_v\ r_{CO2}^{-1}$ ratio is fairly constant in active leaves when the water stress is not severe. The authors redefined Equation [1] in a simpler expression:

$$N_l T_l^{-1} = k_l D_l^{-1} \quad [2]$$

where:

$$k_l = P_a \Delta Cr \left[\rho \varepsilon_{CO2}\right]^{-1} \quad [3]$$

here k_l is considered constant for leaves in a given crop. The authors also argued that $N_l T_l^{-1}$ should be proportional to canopy $B\ T^{1}$ (where B is canopy dry matter and T is canopy transpiration) and, therefore, k_l could be scaled up to the entire canopy k_{Da} and that D_l could be well represented by the air vapor pressure deficit D_a since the leaf temperature appear to be within ± 2-3 °C of air temperature. Hence:

$$w = BT^{-1} = k_{Da} D_a^{-1} \quad [4]$$

where k_{Da} is obtained experimentally as the slope of the linear regression between cumulative biomass and the daily integration of the quotient TD_a^{-1}.

Tanner and Sinclair (1983) extended the work initiated by Bierhuizen and Slatyer (1965) and Tanner (1981), developing equations to represent biomass production and transpiration of the sunlit and shaded fractions of the canopy, essentially leading to a re-derivation of Equation [4].

Although Equation [4] has been adopted as a reasonable predictor of biomass accumulation (Stöckle *et al*., 1994; Sinclair and Seligman, 1995), concerns have been raised about the transferability of k_{Da} (Kemanian *et al*., 2005). These authors argued that k_{Da} is not a "constant" for a crop, but it rather changes with environmental conditions, most noticeable D_a.

Steduto and Albrizio (2005) presented field data and a discussion of the concept and mechanism of determination of k_{Da}, including C_3: chickpea (*Cicer arietinum* L.), sunflower (*Helianthus annuus* L.), wheat (*Triticum aestivum* L.), and C_4: sorghum (*Sorghum bicolor* (L.) Moench subsp. *bicolor*) species in one location (Bari, Italy; 41º03' N, 16º52' E, 72 m a.s.l.). They found that their k_{Da} values had large variability among species and did not match data for the same species from literature. Two explanations to their findings were mentioned: 1) the error introduced by scaling D_l to D_a, especially in low D_a conditions where leaf temperature can be several degrees larger than air temperature, and 2) the effectiveness of D_a normalization to represent D_l since the latter is defined by the transpiration flux, which changes as the physiological stage of the crop changes. They proposed an alternative methodology, similar to the original work by de Witt (1958), where w is a function of the evaporation rate of a reference condition as:

$$w = BT^{-1} = k_{ETo} ET_0^{-1} \quad [5]$$

where ET_0 is the reference crop evaporation computed as proposed by Allen *et al*. (1998) and k_{ETo} is the slope of the linear regression between cumulative biomass and the daily integration of the quotient TET_0^{-1}. Steduto and Albrizio (2005) claim that this method would work better than Equation [4] and that k_{ETo} appeared transferable among different climatic zones. However, this claim was based on limited data and has not been verified.

The main objective of this work was to evaluate the transferability across diverse climatic condition of k_{Da} and k_{ETo} of wheat and maize. However, experimental data allowing the calculation of k_{Da} and k_{ETo} is scarce and does not cover well the wide array of environmental conditions where wheat and maize are grown. In addition, the available data include differences in cultivars, crop management, methods to estimate transpiration, sampling methods for biomass, and other sources of variability and experimental error, making it difficult to evaluate the constancy of the parameters. For that reason, a canopy transpiration and photosynthesis (CTP) model was developed and tested (Kremer, 2006), and used as reference to obtain simulated values of w, k_{Da}, and k_{ETo} under variable climatic conditions while crop and soil characteristic were held constant, allowing a more consistent evaluation of the transferability of these parameters.

MATERIALS AND METHODS

The model

An hourly time step canopy transpiration and photosynthesis (CTP) model, separating sunlit and shaded fractions of the canopy, was developed as a tool to obtain simulated values of k_{Da} and k_{ETo}. The model simulates C assimilation (g CO_2 m^{-2} ground area), and crop transpiration (kg H_2O m^{-2} ground area) in response to climatic conditions, soil and plant water status, and atmospheric CO_2 concentration. Transpiration, photosynthesis, stomatal conductance, and plant water uptake are solved simultaneously through an iterative numerical procedure. Daily measurements of global solar radiation, air temperature, air humidity, and wind speed are inputs to the model. Additional inputs include green leaf area index (LAI), maximum crop height, maximum LAI, assimilation rate as a function of intercellular CO_2 concentration, stomatal conductance response to air vapor pressure deficit and leaf water potential, and soil characteristics (hydraulic parameters, bulk density, depth, and number and thickness of soil layers). Model performance was tested using meteorological and crop data (wheat and maize) collected at the Conservation and Production

Research Laboratory, Bushland (35º11’ N, 102º06’ W; elevation 1170 m a.s.l.), Texas, USA, indicating the suitability of the model for the application presented in this research. A more detailed description of the CTP model and parameters for the simulation of wheat and maize transpiration-use efficiency is presented in Kremer (2006). For this study, soil water content, LAI, crop height, and crop parameters for photosynthesis and stomatal conductance were held constant during the entire simulation period at all the locations. Thus, only daily weather was variable.

Meteorological data

To generate a highly diverse set of conditions, daily weather data from eight locations were selected. The data were composed of daily measurements of global solar radiation (MJ m^{-2} d^{-1}), maximum and minimum air temperature (ºC), maximum and minimum air relative humidity, and average wind speed (m s^{-1}), encompassing the period day of the year (DOY) 120 through 239 for a year selected at random in the following locations: Concepcion del Uruguay (32°28’ S, 58°16’ W; elevation 20 m a.s.l.), Argentina; Landriano (45°18’ N, 9°15’ E; elevation 78 m a.s.l.), Italy; Temple (31°7’ N, 97°4’ W; elevation 208 m a.s.l.), Texas, USA; Pullman (46°45’ N, 117°1’ W; elevation 756 m a.s.l.), Washington, USA; Prosser (46° N, 119°7’ W; elevation 380 m a.s.l.), Washington, USA; Ankara (40°7’ N, 32°59’ E; elevation 948 m a.s.l.), Turkey; Aleppo (36°1’ N,37°18’ E; elevation 430 m a.s.l.), Syria; and DOY 166 through 239 for Maricopa (33°49’ N, 112°1’ W; elevation 359 m a.s.l.), Arizona, USA. The main climatic characteristics of the selected period in the eight locations are presented in Table 1.

Determination of k_{Da} and k_{ETo}

Daily transpiration and photosynthesis for wheat and maize were simulated for all locations using the CTP model and assuming well-developed and unstressed crops. The parameters k_{Da} (g CO_2 kg^{-1} H_2O kPa) and k_{ETo} (g CO_2 m^{-2}) were estimated as the slope of the linear regression between cumulative photosynthesis and the accumulation of the transpiration to daytime D_a quotient (Tanner, 1981; Condon *et al*., 1993) and transpiration to ET_0 quotient (Steduto and Albrizio, 2005), respectively. Calculations of the parameters were done for moving 15-d intervals, shifted by 5 d throughout the 120-d period. Daily ET_0 calculation was carried out as proposed by Allen *et al*. (1998).

RESULTS AND DISCUSSION

As was expected simulated w values for 15-d periods across eight locations were highly variable (Table 2), with coefficient of variation of 25% and 18% for wheat and maize, respectively, with the known implication that w values determined experimentally in one location may not be readily transferable to another. Normalization of w by D_a Equation [4] or ET_0 Equation [5] is expected to account for weather variability, with the parameters k_{Da} or k_{ETo} remaining reasonable constant. However, as shown in Table 2 k_{Da} and k_{ETo} (maize) present more variability than desirable for transferring values derived in one location to another with k_{Da} variability being greater than that of k_{ETo}.

As pointed out by Tanner (1981) and Steduto and Albrizio (2005), a drawback associated with D_a normalization is usually related to the degree of error introduced on the assumption that D_a is a fair

Table 2. Mean (x), standard deviation (sd), number of data (n), and coefficient of variation (CV) for simulated values of transpiration-use efficiency (*w*), and the crop parameters k_{Da} and k_{ETo} from eight locations.

Parameters	n	x	sd	CV (%)
w, g CO_2 kg^{-1} H_2O				
Wheat	159	10.71	2.69	25.09
Maize	159	17.50	3.07	17.53
k_{Da}, g CO_2 kg^{-1} H_2O Pa				
Wheat	159	15.99	4.35	27.21
Maize	159	27.70	9.66	34.88
k_{ETo}, g CO_2 m^{-2}				
Wheat	159	55.87	5.68	10.16
Maize	159	94.37	16.79	17.80

Table 1. Mean (x) and standard deviation (sd) of weather data from eight locations and selected periods.

Variables		Concepción	Landriano	Temple	Pullman	Prosser	Ankara	Aleppo	Maricopa
T_{max}	x	27.8	26.0	31.2	22.6	27.0	27.9	34.7	38.9
	sd	4.0	4.7	3.3	6.8	6.3	6.1	4.9	2.5
T_{min}	x	16.9	14.2	20.6	8.4	9.3	14.3	17.5	24.3
	sd	3.3	3.4	2.9	4.2	4.2	4.7	5.3	2.1
S_R	x	21.5	22.5	21.1	23.3	25.7	21.1	27.2	27.6
	sd	7.8	6.5	5.8	5.9	5.2	4.4	2.3	3.6
RH_{max}	x	99.7	85.5	92.0	81.4	61.7	63.1	67.4	78.7
	sd	2.2	21.4	6.3	12.4	14.5	14.3	15.0	17.0
RH_{min}	x	64.8	46.7	47.6	32.8	43.4	31.7	25.7	25.1
	sd	13.3	21.3	12.9	13.0	9.2	15.3	7.2	11.2
Wind	x	3.0	1.2	2.7	2.1	1.5	1.8	4.8	2.2
	sd	1.3	0.6	1.1	1.0	0.5	0.7	1.9	0.5
ET_0	x	4.3	4.3	5.3	4.4	4.8	5.0	9.0	7.7
	sd	1.5	1.2	1.3	1.2	1.1	1.3	2.0	1.2
D_a	x	0.8	1.0	1.5	1.1	1.3	1.8	2.6	3.2
	sd	0.3	0.4	0.6	0.6	0.6	0.8	0.8	0.9

T_{max} and T_{min}: maximum and minimum air temperatures (ºC), S_R: global solar radiation (MJ m^{-2} d^{-1}), RH_{max} and RH_{min}: maximum and minimum relative humidity, ET_0: reference evapotranspiration (mm d^{-1}), D_a: day time air vapor pressure deficit (k_{Pa}) estimated as: $D_a = 2/3\ e_s(T_{max})\ (1 - R_{min})$, where $e_s(T_{max})$ is the saturation vapor pressure of the air in kPa at maximum air temperature.

representation of D_l, especially in humid environments. In these environments, transpiration rate is expected to be lower, and as a result leaf temperature should increasingly depart from air temperature making D_l larger than D_a. To test this assumption, the values of k_{Da} obtained in environments with D_a less than 1 kPa were not included in the coefficient of variation (CV) analysis. Some improvement on CV was obtained for both crops however the variability still remained (wheat: 18.75%, and maize: 26.18%).

Figures 1 and 2 present w as a function of the average D_a and ET_0, of each corresponding 15-d interval. Both figures show that w is not constant across environments characterized by D_a and ET_0, and has an important non-linear response to D_a and ET_0 (Abbate *et al*., 2004; Kemanian *et al*., 2005). Fitted power equations appear good estimators of w, with D_a explaining 94% and 90% of the w variability for wheat and maize, respectively, and ET_0 explaining 89% and 72%, respectively. The dispersion around the fitted lines represents variability due to climate that is not accounted for D_a or ET_0. This effect of other weather variables is less important with D_a and ET_0 greater than 2 kPa and 7 mm d^{-1}, respectively.

Figure 3 reaffirms that the variability in Table 2 is not random, but can be explained to a large extent when k_{Da} values are plotted vs. D_a or ET_0. A linear equation was fitted to the k_{Da} values and included in the figure. It seems that D_a was able to explain k_{Da} variability better than ET_0, which presented a larger scattering, particularly for wheat. These results confirm that: 1) k_{Da} is not a constant value and, 2) k_{Da} increases when D_a and ET_0 increases. The significant conclusion is that the use of Equation [4] to estimate w has to considerer local calibration of k_{Da} to be transferable. The linear response obtained for k_{Da} should facilitate transferability through field calibration based on a few points across the environmental range. The fitted linear equations included in each figure, can be used as k_{Da} estimators for climatic conditions characterized by different D_a or ET_0.

In an attempt to explain k_{ETo} variability, k_{ETo} values were plotted vs. D_a and ET_0 (Figure 4). Fitted linear equations are included in the Figure 4, which shows that k_{ETo} variation in wheat does not correlate well with variations in climatic conditions represented by D_a or ET_0. However the relatively low CV and standard deviation (sd) determined that a mean value of 55.87 (g CO_2 m^{-2}) can be used as a constant regardless of the climatic environment, supporting the view of Steduto and Albrizio (2005). Nevertheless, some response of k_{ETo} for wheat when the ET_0 gradient is increasing was observed (Figure 4), suggesting some benefit of using the fitted equation in situations with high evaporative demand.

A different scenario was found in maize (Table 2). Figure 4 shows that k_{ETo} (maize) did not correlate well with variations in D_a, and that the variability was better explained by ET_0, although ET_0 alone was not able to account for the entire variability due to weather. It can be concluded that k_{ETo} is not a constant and, therefore, experimental values cannot be transferred among locations with different climate. The linear equation presented here to estimate k_{ETo} as function of ET_0 for maize should be taken as first approximation to overcome the transferability problem.

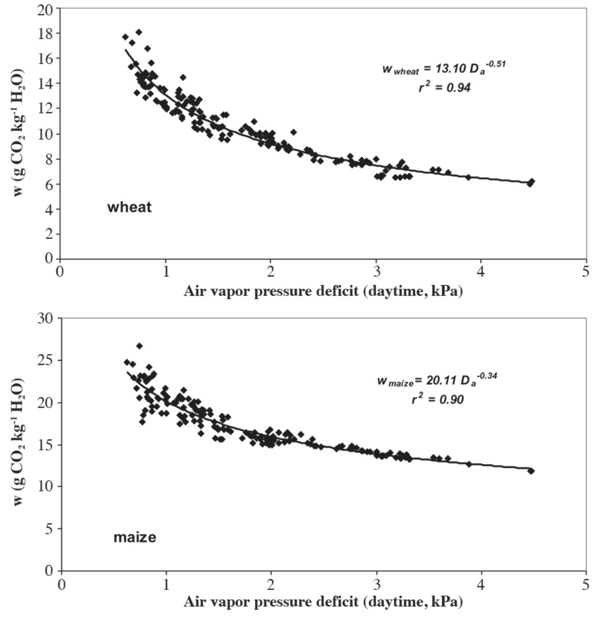

Figure 1. Transpiration use efficiency (w, g CO_2 kg^{-1} H_2O) as a function of the air water vapor pressure deficit (daytime, kPa) for wheat and maize.

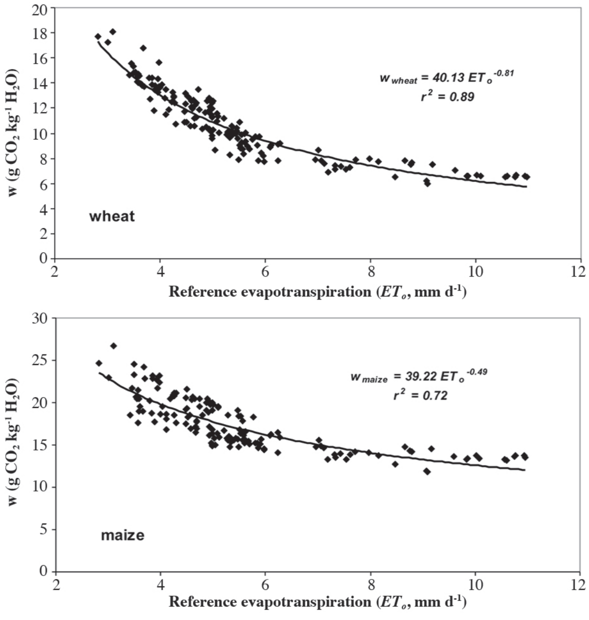

Figure 2. Transpiration use efficiency (w, g CO_2 kg^{-1} H_2O) as a function of reference evapotranspiration (ET_0, mm d^{-1}) for wheat and maize.

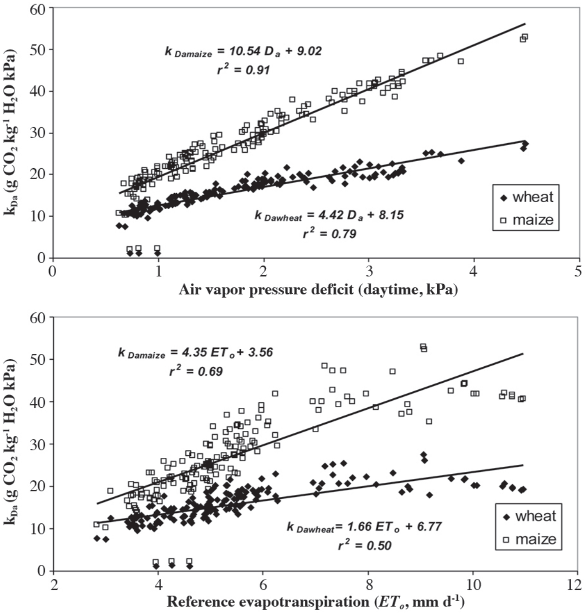

Figure 3. Variability of the crop dependant parameter k_{Da} (g CO_2 kg^{-1} H_2O kPa) as a function of the daytime vapor pressure deficit (D_a; kPa), and the reference evapotranspiration (ET_0, mm d^{-1}) for wheat and maize.

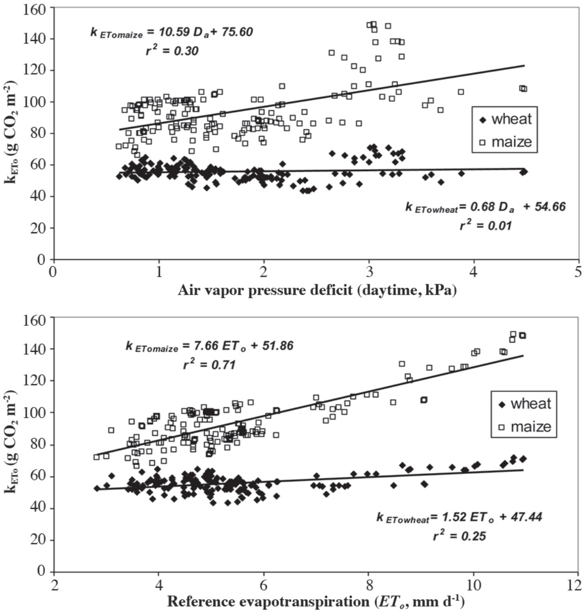

Figure 4. Variability of the crop dependant parameter k_{ETo} (g CO_2 m^{-2}) as a function of the daytime vapor pressure deficit (D_a; kPa), and the reference evapotranspiration (ET_0, mm d^{-1}) for wheat and maize.

CONCLUSIONS

The simulation results showed as was expected that w is not constant across climatic environments, so that values determined in one location cannot be readily transferred to another. However, w as a function of D_a and ET_0 was well described by a power function, with D_a explaining 94% and 90% of the w variability for wheat and maize, respectively, and ET_0 explaining 89% and 72%, respectively. The dispersion around the fitted lines was much lower with D_a and ET_0 greater than 2 kPa and 7 mm d^{-1}, respectively.

Normalization of the k_{Da} and k_{ETo} parameters of two simple transpiration-use efficiency models by D_a and ET_0 was not able to properly account for the effect of weather variability, resulting in parameters still too variable to be readily transferred across locations for both wheat and maize.

It was found that the transferability of these parameters can be dramatically improved when they are plotted against D_a (in the case of k_{Da}) or ET_0 (in the case of k_{ETo}), with linear functions describing well the relations and explaining 79% and 91% of k_{Da} variability for wheat and maize, and 71% of k_{ETo} variability for maize. The k_{ETo} for wheat correlated weakly with ET_0, explaining only 25% of its variability. However, the overall coefficient of variation of this parameter across eight locations was about 10%, so that the use of a constant k_{ETo} value is not unreasonably, although is not a perfect solution.

The simulation-based equations presented here are offered as a first approximation to overcome the spatial transferability of w, k_{Da}, and k_{ETo}, but field validation will be required before adoption is recommended.

Comprobando la transferibilidad de modelos para la producción de biomasa basados en la eficiencia del uso de la transpiración. Eficiencia del uso de la transpiración (w), definida como la relación entre biomasa producida por unidad de agua transpirada, se ha utilizado para evaluar productividad bajo condiciones limitadas de agua. Sin embargo, la falta de consistencia de valores w bajo condiciones climáticas distintas no ha permitido su uso como parámetro transferible. Consecuentemente, aproximaciones simples han sido desarrolladas, incluyendo: 1) $w = k_{Da} D_a^{-1}$ y; 2) $w = k_{ETo} ET_0^{-1}$ donde k_{Da} y k_{ETo} son parámetros dependientes del cultivo, y sustentado en que la normalización por D_a o ET_o absorbería el efecto del clima en la determinación de w, mientras que estos parámetros se mantendrían razonablemente constantes. El objetivo de este estudio fue determinar la transferibilidad de k_{Da} y k_{ETo} para su uso en trigo (*Triticum aestivum* L.) y maíz (*Zea mays* L.). La escasez de información experimental y metodologías usadas, justificó el uso de un modelo para estimar transpiración y fotosíntesis, el cual fue desarrollado y probado con datos de ocho regiones climáticamente distintas para simular valores de k_{Da} y k_{ETo}. Los resultados indicaron que estos parámetros poseían mayor variabilidad de la esperada, sugiriendo que una calibración previa sería necesaria. Además, el cambio de estos parámetros como función de D_a o ET_0 tiene una tendencia consistente, representable por funciones matemáticas, permitiendo transferir w, k_{Da} y k_{ETo} (maíz).

Por otro lado, valores de k_{ETo} en trigo se correlacionaron débilmente con D_a y ET_0, pero un bajo coeficiente de variación (10%) permitiría el uso de un valor promedio como un predictor razonable de w.

Palabras clave: eficiencia en el uso de la transpiración, modelos de producción de biomasa.

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