

Variability in crop radiation-use efficiency associated with vapor-pressure deficit

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ABSTRACT

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The ratio of the amount of crop dry-matter produced per unit of intercepted photosynthetically active radiation is usually referred to as radiation-use efficiency (RUE). Large within-species variability in RUE has been reported for a number of species growing with adequate moisture and nutrients. This variability raises questions concerning the generality of the approach for plant-growth analysis and modeling. Available data suggest that increased vapor-pressure difference between substomatal air and the air surrounding the leaves may lead to reductions in leaf conductance and photosynthetic capacity of well-watered plants, and therefore to RUE reductions. The coefficient of determination (r^2) of linear regressions of reported RUE values as a function of daily saturation vapor-pressure deficit (Δe) were calculated for sorghum (*Sorghum bicolor* (L.) Moench) and maize (*Zea mays*). Decreased RUE was associated with increased Δe in well-watered conditions, explaining a large portion of the RUE variability. Effects of Δe should be considered when the RUE concept is used to estimate biomass accumulation.

INTRODUCTION

Cumulative dry-matter production of crops supplied with adequate moisture and nutrients has been shown to be linearly related to intercepted photosynthetically active radiation (Q_{pa}) (e.g., Gallagher and Biscoe, 1978; Gosse et al., 1986; Hamdi et al., 1987). The slope of this relationship represents the amount of dry-matter produced per unit of intercepted Q_{pa} . This slope, or 'radiation-use efficiency' (RUE), has been reported to be reasonably stable for several crop species (Hughes et al., 1987; Monteith, 1989). Such apparent stability has made RUE an attractive parameter for crop simulation models

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(e.g., Charles-Edwards, 1982; Stapper, 1984; Williams et al., 1984; Ritchie, 1985; Jones and Kiniry, 1986; Rosenthal et al., 1989). Recently, however, large within-species variability in RUE has been reported for a number of species growing with adequate moisture and nutrients (Kiniry et al., 1989). This variability raises questions concerning the generality of the approach.

In this paper, we briefly review the evidence showing that an increase in the vapor-pressure difference between the air in the substomatal cavities and the air surrounding the leaves may decrease leaf conductance and photosynthesis of well-watered plants, making vapor-pressure difference a likely candidate to explain variability in RUE under nonstressed conditions. We then assess the possible contribution of leaf/air pressure difference, approximated by the saturation vapor-pressure deficit (Δe) of the air above the canopy, to variability in RUE using data from several sites (Kiniry et al., 1989).

BACKGROUND

It is commonly accepted that environmental stresses reduce RUE, and that such stresses must be accounted for when modeling biomass accumulation (Shibles and Weber, 1966; Hughes and Keatinge, 1983; Hughes et al., 1987). Drought decreases photosynthetic capacity and leaf conductance (Zou and Kahnt, 1988). Nitrogen deficiency reduces the photosynthetic capacity of crop canopies (Sinclair and Horie, 1989) and may alter the plant/water relations (and affect leaf conductance) by decreasing root permeability to water (Radin and Mauney, 1986). Water stress has been shown to increase the partitioning of carbon to the roots (Blum, 1988; Wilson, 1988), decreasing shoot growth proportionately more than total growth. A similar alteration of the root:shoot partitioning of carbon occurs in response to nutrient stress (Wilson, 1988). All these factors contribute to reduce RUE of stressed crops. Under nonstressed conditions, however, RUE is often assumed to be reasonably stable (Hughes et al., 1987; Monteith, 1989).

Dynamic interactions between plants and their environment make the definition of nonstressed conditions difficult. Diurnal and seasonal changes in microclimate, soil water availability, and plant growth continuously change the status of the plant/environment system. Plant water status is the result of the balance between the rates of water supply and evaporation loss at the sites of evaporation within the leaf (mainly substomatal cavities). The supply is controlled by soil water availability, rooting characteristics, root radial and axial resistances, xylem resistance, leaf resistance, and the gradient of water potential between soil and leaves, with the leaf water potential (which also influences leaf conductance) constantly adjusting to maintain the balance. The evaporation rate depends on the vapor-pressure difference between the air in the substomatal cavities and the air surrounding the leaf, and on the magnitude of leaf (stomatal and cuticular) and boundary-layer conduc-

tances. The difference in vapor pressure between leaf and surrounding air is the result of dynamic interactions between the leaf energy balance, leaf conductance, boundary layer and aerodynamic conductances, and the vapor pressure of the air above the canopy.

When conditions are conducive to potentially large evaporation rates that cannot be met by the supply rate, as is likely to occur under large Δe conditions, plant tissues dehydrate and leaf conductance and photosynthesis decrease. Sharkey (1984) reported that high transpiration rates decreased photosynthesis in several species, presumably by causing a localized leaf water-deficit. Bunce (1985) presented evidence supporting the hypothesis that direct epidermal evaporation (as opposed to stomatal evaporation) controls stomatal response to Δe , which may cause stomatal closure even at high leaf water-potential. In the field, the equilibrium between supply and evaporation is adjusted throughout the day, with evaporation losses often exceeding supply for short periods even in well-watered conditions (Hanson and Hitz, 1982).

Changes in leaf conductance and photosynthetic rate in response to changes in Δe have been extensively documented in the literature (Ludlow, 1980; El-Sharkaway et al., 1984; Schulze, 1986), although the response of leaf conductance to Δe may be small in some species (Bunce, 1988). According to Farquhar and Sharkey (1982), a reduction in leaf conductance in response to increased Δe may be the main cause of reduced assimilation rate with Δe increase. However, reduction in photosynthesis as a result of increased Δe has been observed in field-grown tomato with minimum effect on leaf conductance, suggesting that nonstomatal inhibition is also possible due to localized dehydration (Bunce, 1988). Decreased leaf conductance and photosynthetic rate are likely the consequence of an imbalance between supply to and losses from the sites of evaporation, as discussed above, even though dehydration may be localized without causing a reduction in leaf bulk water-potential. The role of this imbalance is supported by the observation that the sensitivity of leaf conductance to Δe is reduced as the length of the root system, and thus the potential for water uptake, increases (Bunce, 1981).

Vapor-pressure deficit may, therefore, cause reductions of leaf conductance and photosynthesis in leaves of plants growing in well-watered soils, with and without changes of leaf bulk water-potential. El-Sharkaway et al. (1984) reported reductions of leaf conductance and photosynthetic rate of well-watered plants growing in pots when Δe was increased, although the degree of sensitivity differed among species. Figure 1 shows the Δe effect reported for sorghum. Although not discussed by the authors, the photosynthetic rate responded to changes in Δe only after Δe exceeded a threshold value. The same response was observed with seven other species, including C_3 and C_4 plants. Such threshold response, however, was not apparent with leaf conductance. This may be explained by considering that the effect of Δe on leaf conductance is largely through cuticular conductance in the lower range of Δe , while mainly

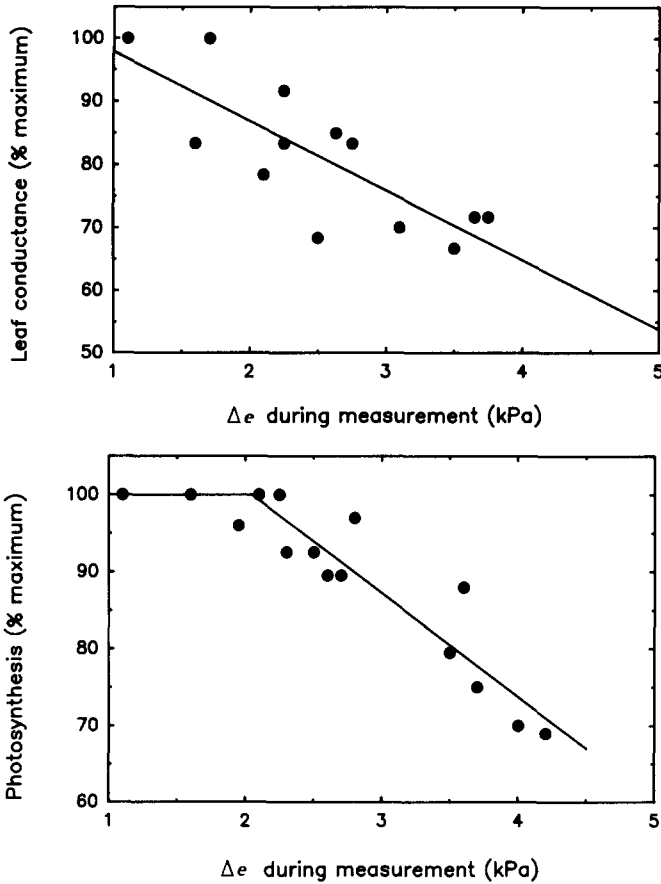


Fig. 1. (a) Sorghum leaf conductance response to vapor-pressure deficit (Δe). (b) Sorghum photosynthesis response to Δe (adapted from El-Sharkaway et al., 1984).

stomatal conductance is affected in the higher range (Zou and Kahnt, 1988). The responses to Δe reported by El-Sharkaway et al. (1984) are likely to be attenuated in the field because of more extensive root development and, therefore, larger potential water-uptake rate.

The discussed effects of Δe on conductance and photosynthesis of leaves of plants growing in well-watered soils will be likely reflected in the RUE of the whole crop, making Δe a likely candidate to explain variability of RUE of non-stressed crops across different environments. However, the magnitude of the possible effect cannot be extrapolated directly. The response of single leaves in the canopy will depend on the position in the canopy, age, and intercepted radiation, which need to be integrated to represent the whole canopy. Although the photosynthetic rate is the main factor determining dry-matter accumulation, other factors such as maintenance respiration, carbon allocation,

nutrient uptake and translocation may respond to environmental changes associated with Δe changes. In addition, Δe fluctuates diurnally and throughout the season, and the size of the root system and the canopy leaf area also changes. The degree of these fluctuations differs for different environments. Radiation-use efficiency is usually derived experimentally as a single value for the growing-season or determining separate values for vegetative and grain-filling stages. The possible response of RUE to the average Δe prevailing during the period of interest across diverse environments could not be inferred from single-leaf, short-term responses of leaf conductance and photosynthesis to Δe .

The sensitivity of RUE to Δe under nonstressed conditions has been explicitly demonstrated in a greenhouse experiment with sorghum (Hamdi et al., 1987), in which RUE decreased linearly with increased Δe although soil moisture was non-limiting. However, this apparent relationship between RUE and Δe has yet to be demonstrated with field data, where root systems are larger and the environment more variable. In the following sections, we will assess Δe as a possible cause of the variability in RUE observed in well-watered field conditions.

METHODS

Data sets with RUE estimates for sorghum (*Sorghum bicolor* (L.) Moench) and maize (*Zea mays* L.) from different international locations (Kiniry et al., 1989) were used in this analysis. These estimates correspond only to RUE for above-ground biomass production (Table 1). The data sets selected for the present analysis were reported as having no water, nutrient, or low-temperature stresses, and included all except three from the original study of Kiniry et al. (1989) that had available maximum and minimum temperature data. Two maize data sets which were not included, from Estree-Mons (France) and College Park (Pennsylvania, U.S.A.), appeared to have low temperature restricting growth and a mild drought stress, respectively. The sorghum data set not included, from College Station (Texas, U.S.A.), had a short period of apparent stress when growth nearly stopped.

Values of RUE were calculated for plant growth prior to anthesis, thus eliminating differences in RUE related to seed growth and seed composition. For this analysis, the vapor-pressure difference between substomatal air and the air surrounding the leaves was approximated by the saturation vapor-pressure deficit of the air above the canopy (Δe). This assumes that leaf and air temperature are equal, and that the air in the substomatal cavities is saturated. Leaves in a canopy, and even spots of the same leaf, have different temperatures, fluctuating a few degrees below or over air temperature. The assumption of equal leaf and air temperature introduces some error, but this is not important given the scale of the assessment intended in this study.

TABLE 1

Radiation-use efficiency (RUE; g MJ⁻¹) for above-ground biomass accumulation for sorghum and maize (adapted from Kiniry et al., 1989)

Sorghum		Maize	
Location/Year	RUE	Location/Year	RUE
Toulouse, France		Columbia, MO, U.S.A.	
1986	3.8	1978	4.4
1987	3.3		
Mead, NB, U.S.A.		Toulouse, France	
1971	3.2	1987	4.1
1972	2.7	1988	3.6
Bushland, TX, U.S.A.		Temple, TX, U.S.A.	
1986	3.0	1981	4.1
		1987	3.7
Manhattan, KS, U.S.A.		Hyderabad, India	
1965	3.0	1978	3.8
1966	2.7		
Katharine, Australia		Katharine, Australia	
1986	2.4	1986	3.2
Perth, Australia		Davis, CA, U.S.A.	
1978	2.1	1962	2.9
Mean	2.9		3.7
cv (%)	16.4		12.4

Because relative humidity data were unavailable, daily mean saturation vapor-pressure deficit was estimated from daily maximum and minimum temperatures using the approach proposed by Diaz and Campbell (1988):

$$\Delta e_d = (p' T_{\text{mean}} - p' T_{\text{min}}) / 1. - 0.3 (p' T_{\text{mean}} - p' T_{\text{min}}) \quad (1)$$

where: Δe_d is daily mean saturation vapor pressure deficit (kPa); $p' T_{\text{mean}}$, saturation vapor pressure at t_{mean} (kPa); $p' T_{\text{min}}$, saturation vapor pressure at t_{min} (kPa); T_{mean} , daily mean temperature (K); and T_{min} , daily minimum temperature (K).

Saturation vapor pressure at any temperature T ($p' T$) in degrees Kelvin was calculated from:

$$p' T = \exp(52.58 - 6790.50/T - 5.03 \ln(T)) \quad (2)$$

This approach has shown good agreement between measured and predicted Δe over a wide range of locations and environmental conditions (R.A. Diaz and G.S. Campbell, Washington State Univ., personal communication, 1989). Additional testing for a few locations was done comparing Δe_d estimated as described above, with values calculated from mean daily temperature and relative humidity.

The daily mean Δe , averaged for the period of interest, was calculated using equation 1 for each data set. The R^2 values of the linear regression of RUE as a function of the average daily mean Δe were calculated to estimate how much of the variability in RUE could be explained by Δe .

RESULTS AND DISCUSSION

As estimated by equation 1, Δe appeared reasonable and adequate for this study, as evidenced by the similarity to those calculated from temperature and relative-humidity data for six data sets (Table 2). The two Δe estimates differed by less than 9% (using method 2 as base) for all but one data set. The Pantancheru data for 1975 had a 24% difference between values. There was no significant relationship between percent difference and Δe value calculated by Method 2, indicating that systematic error was not present.

Vapor-pressure deficit appeared to be a major factor contributing to variability in RUE for sorghum (Fig. 2). Values of RUE ranged from 2.1 to 3.8 g of shoot dry-matter per MJ of intercepted Q_{pa} , with a coefficient of variation (CV) of 16.4% (Table 1). Average daily mean Δe accounted for 76% of this variability in RUE. Maize RUE ranging from 2.9 to 4.4 g/MJ and with CV of 12.4%, also appeared to be dependent on Δe , which accounted for 50% of the variability in RUE (Fig. 2). The available data for this species was concentrated at the lower and upper end of the Δe range.

While variability in Δe appears to be an important contributor to variability in RUE, an apparent discrepancy should be explained. Short-term photosynthesis has a threshold response to short-term Δe (Fig. 1b), while such is not evident in the response of RUE to mean daily Δe (Fig. 2). The probable cause of this difference relates to the time scale of the Δe values. Data sets with mean Δe estimated over several days include both the RUE response to diurnal variation in Δe as well as the response to Δe variation among days. Data points with mean Δe below the short-term threshold value of 2.0 kPa (Fig. 1b) probably experienced periods when Δe exceeded 2.0 and thus RUE

TABLE 2

Comparison of daily mean vapor-pressure deficit (kPa) estimated using equation 1 (Method 1) with values calculated based on mean daily temperature and relative humidity (Method 2)

Location/Year		Method 1	Method 2
Patancheru, India	1974	1.10	1.02
	1975	0.89	0.72
	1986	0.91	0.84
Temple, Texas	1988	1.14	1.23
Yuma, Arizona	1974	2.11	2.06
	1975	1.73	1.78

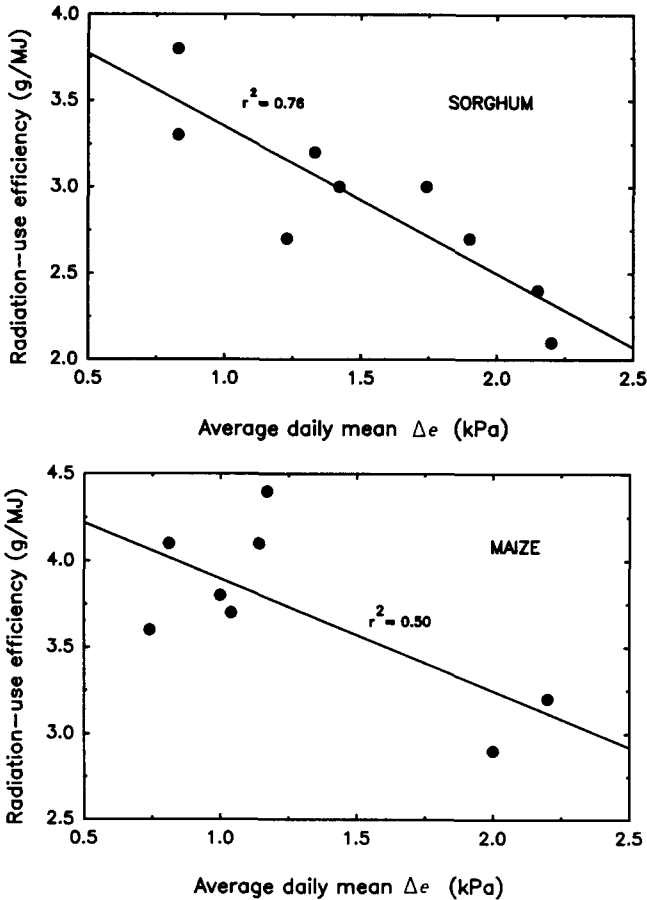


Fig. 2. Radiation-use efficiency of (a) field-grown sorghum and (b) maize as a function of estimated average daily mean saturation vapor-pressure deficit (Δe).

was reduced. This would prevent a threshold response of RUE to VPD calculated as a mean over several weeks.

The variability of RUE at given ranges of Δe , especially important at low Δe (Fig. 2), is likely a response to other sources of variability. Radiation-use efficiency of well-watered crops has also been reported to fluctuate with temperature regimes (Hammer and Vanderlip, 1989) and for different cultivars (Sivakumar and Huda, 1985; Hammer and Vanderlip, 1989). On the other hand, because the RUE estimates used in this analysis corresponded to above-ground biomass production, any condition conducive to alterations of the shoot:root ratio of the plants may also have affected the reported values. Water stress may increase the partitioning of carbon to the roots at the expense of shoot growth (Finn and Brun, 1980; Huck et al., 1986; Wilson, 1988). Increased Δe may have had a similar effect through mild transient stress cycles

(evaporation losses exceeding supply during part of the day) in otherwise well-watered plants, which would indirectly reduce RUE, calculated using above-ground biomass, when Δe increased.

Finn and Brun (1980) measured an increase of 25% in root biomass of water-stressed soybean plants, growing in pots, compared to unstressed control plants. For soybean undergoing mild stress in the field, Huck et al. (1986) reported mainly an increase in total root length, favoring a greater root length deeper in the soil profile with no change in carbon partitioning. If a fraction of 0.15 of the total biomass is assumed to be allocated to the roots at 1 kPa average daily mean Δe , increasing linearly to 0.20 at 2 kPa (a 33% increase), this would reduce RUE by 6% for the same amount of carbon assimilation. Data in Fig. 2 suggest RUE reductions in the same Δe range of about 25% and 17% for sorghum and maize, respectively, indicating that even the significant alteration of shoot:root ratio assumed in this example would not explain the bulk of the response to Δe . Alterations of the shoot:root ratio due to Δe in well-watered crops are likely to be lower.

Assuming a linear response to Δe (Fig. 2), a simple method of altering RUE could be derived; RUE for a crop could be described for a daily mean Δe value of 1.0 kPa. Such predicted RUE values for sorghum and maize were 3.35 and 3.90 g of shoot dry-matter per MJ of intercepted Q_{pa} , respectively. Predictions of RUE would be decreased or increased from these values, according to the slope of the response line, when the daily mean Δe was greater or less than 1.0 kPa, respectively. These slopes for sorghum and maize were -0.85 and -0.65 g MJ⁻¹ kPa⁻¹, respectively. However, a note of caution is necessary. Sensitivity to Δe (and, therefore, the slope of the response line) may fluctuate in the field with fluctuations in the length of the root system (Bunce, 1981), soil hydraulic conductivity, and soil/root contact (Graham and Thurtell, 1989). Significant variability in all these attributes is common. Increased boundary-layer conductance due to greater wind speed also increases sensitivity of stomatal response to Δe (Bunce, 1985). Therefore, average wind speed and associated variability may also influence Δe effects.

In conclusion, variation in Δe appeared to be an important contributor to the observed within-species variability in RUE. Inclusion of the RUE response to Δe in plant models should increase the accuracy and generality of biomass predictions. Further field research is needed to better assess the effect of Δe on RUE of different species.

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