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Comparison of Photosynthetic Water use Efficiency of Sweet Sorghum at Canopy and Leaf Scales

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Abstract: Little is known about the response of sweet sorghum to water stress. Therefore, the aim of this study was to characterize sweet sorghum physiological water use efficiency (WUE) under progressing water stress conditions, with emphasis on the canopy scale as compared with the leaf scale.

Sweet sorghum (*Sorghum bicolor* (L.) Moench) was subjected to two water stress cycles. Energy, water vapor, and CO_2 fluxes were estimated at the canopy scale by means of the Bowen ratio/energy balance/CO_2 gradient method (BREB+), and at the leaf scale with a portable photosynthesis system. Predawn (ψb) and noon-time leaf water potential (ψn) were measured by pressure chamber.

Canopy and leaf photosynthetic WUE showed parallel behavior. They decreased following an increase in leaf-to-air vapor pressure deficit (VPD) and a decrease in ψb. The variation in soil-water status, estimated by ψb, ranged from –0.2 to –1.1 MPa and in VPD from 2.3 to 5.8 kPa at the leaf scale, and from 1.4 to 5.5 kPa at the canopy scale, during the experimental period. Mean values of noon-time photosynthetic WUE were around 5 and 4.3 $mmol_{CO2}.mol^{-1}_{H2O}$ for leaf and canopy scales, respectively.

Şeker Sorgumunun Fotosentetik Su Kullanım Randımanının Bitki Örtü ve Yaprak Düzeylerinde Karşılaştırılması

Özet: Bu çalışma, su stresine karşı gösterdiği tepkiye ilişkin çok az bilginin olması nedeniyle, şeker sorgumunun fizyolojik su kullanım randımanını kısıntılı sulama koşulları altında bitki örtü ve yaprak düzeylerinde belirleyip karşılaştırılmasını amaçlamıştır.

Şeker sorgumu, iki su stres dönemi ile karşı karşıya bırakılmıştır. Bitki örtü düzeyinde enerji, su buharı ve CO_2 akıları Bowen Oranı/Enerji Dengesi/CO_2 Eğimi yöntemiyle; anılan değişkenlerin yaprak düzeyindeki değerleri ise taşınabilir fotosentez sistemi ile belirlenmiştir. Gün doğumundan önce ve öğle zamanı yaprak su potansiyelleri (ψb , ψn), basınç çemberi aletiyle ölçülmüştür.

Bitki örtü ve yaprak düzeyi fotosentetik su kullanım randımanları (WUE) paralel bir tavır göstermiştir. Bunların, gün doğumundan önce yaprak su potansiyelindeki (ψb) azalışa ve yaprak-hava buhar basıncı açığındaki (VPD) artışa karşı azaldıkları gözlenmiştir. Deneme süresince, ψb değerleri –0.2 ile –1.1 MPa, VPD değerleri ise yaprak düzeyinde 2.3 ile 5.8 kPa ve bitki örtü düzeyinde 1.4 ile 5.5 kPa arasında değişmiştir. Öğle zamanı fotosentetik su kullanım randımanının ortalama değerleri, yaprak ve bitki örtü düzeylerinde, sırasıyla, yaklaşık olarak 5 ve 4.3 $mmol_{CO2}.mol^{-1}_{H2O}$ olarak belirlenmiştir.

Introduction

Sweet sorghum is normally used as animal feed. However, recent interest in renewable energy resources, environment conservation, and the concept of sustainable development have focused increased attention on this crop. In Europe, various research programs for increasing the production and utilization of biomass for fuel production have been promoted by the European Community (1, 2).

Sorghum is one of the 5 major cultivated species in the world. It can outproduce most other cereals under marginal environmental conditions, especially under hot and dry conditions. Furthermore, it is grown in environments that are normally too harsh for other C4 plants. Most literature deals with the productivity of grain sorghum, though little is known of sweet sorghum in the Mediterranean region, where an exceptional dry matter productivity is found (3). Preliminary results indicate that sweet sorghum has a particularly high water use efficiency, but there is still insufficient information on the physiology of sweet sorghum that could explain its apparent superiority in terms of productivity, relating to water use and water stress response (4, 5, 6, 7).

In the approach to gas exchange measurements at the canopy scale, then, micrometeorological methods were used, specifically, the Bowen ratio method. Micrometeorological methods provide the proper means of measuring water vapor and CO2 exchanges at the crop level as they do not disturb the microenvironment of the crop and they minimize sampling problems by integrating fluxes over a substantial area of the field (8). Long-term estimation of net CO2 exchange rates of the vegetation is important in order to achieve a better understanding of the canopy response to environmental conditions and improve biomass production predictability on a theoretical basis. However, micrometeorological measurements above canopy do not provide any direct clues on gas exchanges at single leaf scale to test the impact of leaf physiological models on the crop scale (9, 10, 11). Therefore, leaf chamber methods are needed to estimate CO2 exchanges from leaf scale.

Investigating photosynthetic WUE is a valuable physiological approach for analysis of optimum water use by plants (12, 13); observatoins of photosynthetic WUE at the leaf scale are not sufficient. In this regard, photosynthetic WUE determinations at the canopy scale can be extremely relevant in characterizing the behavior of the underlying gas-exchange processes of the individual leaves composing the population, and of the population as a whole (14). Therefore, the purpose of the present work is to report the gas-exchange and photosynthetic water-use efficiency (WUE) responses of sweet sorghum, at both leaf (WUEl) and canopy (WUEc) scales, under progressing water stress conditions in the field.

Materials and Methods

The experiment was carried out in the experimental fields of "Istituto Sperimentale Agronomico" in Rutigliano (Bari), Southern Italy, located at latitute 41° 01' N, longitude 4° 39' E, altitude 122 m a.s.l.

The soil was a natural well drained clay soil, with a mean depth of 0.6 m, lying on a fissured rocky subsoil. The region under study has a typical Mediterranean climate, characterized by a dry summer and rainfall mainly occurring in autumn and winter. The average rainfall of the region is 600 mm per year.

Sweet sorghum, variety " Keller", was sown on 9th June 1994, in a 2ha field, at 0.6 m between rows and 0.11m on rows with a final plant density of 15 plants per m^2. In order to facilitate emergence and initial crop development, the crop was irrigated with a drip irrigation system from sowing time (9 June) to the end of July. Thereafter, irrigation was ceased in order to promote a progressive development of water-stress conditions for about 1 month. Subsequently, (end of August, beginning of September), irrigation was re-started.

Measurements were made mainly during the stress cycle. For the whole period, predawn leaf water potential (ψb) was monitored (at 4.00 a.m. solar time) as an indication of soil water content. When ψb reached a value of -1.0 MPa., the first stress cycle was assumed to be over, and irrigation started again after 85 DAP (days after planting), to allow plants to recover growth and then to undergo a second stress cycle. Fields were fertilized 2 times, the first during the sowing period and the second at about the middle of the crop cycle (12th August). The total amount of fertilizer used each time was 100 Kg/ha and 150 Kg/ha N, respectively.

A Portable Photosynthesis System, LI-6200 (Li Cor Inc., Lincoln, Nebraska, USA), was used for gas exchange measurements at leaf scale, and operated as a closed system to measure water vapor and CO_2 gas-exchange fluxes. Prior to operating, calibration of the system was done in the laboratory and in the field. In the laboratory, calibration of the zero offset and the span of the IRGA was done at least once a day with a known CO_2 concentration source. In the field, before starting each measurement, the flowmeter was calibrated to zero flow.

Transpiration, net photosynthesis, intercellular CO_2 mole fraction, epidermal conductance, leaf temperature, air temperature, relative humidity, and PAR were determined at each single measurement. The measurements were carried out from about 6.00 a.m. to 6.00 p.m. solar time, at 1-hour intervals, on 20 randomly selected leaves on the top canopy, fully expanded and fully exposed to the sun. Care was taken not to modify their actual position or orientation during the measurement. The time of measurement of each leaf was short (15 s) to avoid stomatal response to microclimatic modification within the chamber. The leaf water use efficiency was determined as follows:

$$T_l = g_{tw}.(w_i-w_a) = g_{tw}.\Delta_w \quad (1)$$

$$A_l = g_{tc}.(c_a-c_i) = g_{tc}.\Delta_c \quad (2)$$

where T is the transpiration rate per unit of leaf area ($molH_2O.m^{-2}\ s^{-1}$); gtw is the total leaf conductance to water vapor ($molH_2O.m^{-2}\ s^{-1}$); Δw is the water vapor mole fraction difference between the air at the intercellular air spaces (w_i) and the bulk air outside the leaf (w_a) ($molH_2O.molair^{-1}$); A is the rate of CO_2 assimilation per unit of leaf area ($molCO_2.m^{-2}\ s^{-1}$); g_{tc} is the total leaf conductance to CO_2 ($molCO_2.m^{-2}.s^{-1}$); and Δc is the CO_2 mole fraction difference between the air outside the leaf (C_a) and at the intercellular air spaces (c_i) ($molCO2.mol\ air^{-1}$).

$$\text{Photosynthetic } WUE_l = \frac{A_l}{T_l} \tag{3}$$

Values for WUE are expressed in $mmolCO_2 \cdot molH_2O$-1

The Bowen ratio method was used to determine water vapor and CO_2 gas exchanges at the canopy scale. The Bowen ratio energy balance (BREB) system, which in conjunction with an infra-red gas analyzer (IRGA) is referred to as BREB+, consisted of two 100-Ω platinum-resistance temperature sensors (BR-TC1, Tecno-El, Rome, Italy) having an output of about $2.5mV^0C^{-1}$ with an operational constant current of 1 mA; a differential IRGA having a resolution of 0.1 µmolCO2molair-1 (binos-100, Rosemout, Hanau, Germany); 4 soil heat-flux plates (HFT3, Campbell Scientific, Logan, UT, USA); 2 Frithshen-type net-radiometers (Q6, Radiation and Energy Balance System, Seattle, WA, USA); a dew-point hygrometer (Dew-10, General Eastern, Watertown, MA, USA). The data acquistion and control system (model 023, which included a 21x Micrologger) with proper relays, solenoid valves, and diaphragm pump to circulate the air through the hygrometer and the IRGA, was obtained from Campbell Scientific. The Bowen apparatus was located so as to ensure 160 m of upwind fetch in the direction of the dominant wind, which is extremely stable in the agricultural area where the experiment was carried out. The lower and upper arms of the apparatus were positioned at 30 cm and 130 cm, respectively, above the canopy. The output values of each sensor were stored as averages over 15-min intervals.

The BREB+ system was used to estimate evapotranspiration and net CO2 flux over the sweet sorghum canopy. Water evaporation requires relatively large amounts of energy, either as sensible heat or radiant energy. Thus, the evapotranspiration (ET) process is governed by energy exchange at the vegetation surface and is limited by the total amount of energy available.

Through the BREB+ method, the field water vapor flux (ETc) was calculated as

$$ETc = \frac{1}{\lambda}\left(\frac{R_n\text{-}G}{1+\beta}\right) \tag{4}$$

with

$$ETc = \gamma\ \frac{\Delta\theta}{\Delta e} \tag{5}$$

where λ is the latent heat of vaporization, Rn is the net radiation, G is the soil heat flux, γ is the psychometric constant and $\Delta\theta$ and Δe are the differences in potential temperature and water vapor pressure, respectively, between the two heights. Assuming the equality of the eddy transfer coefficients for water vapor and CO_2, the carbon exchange rate of the crop field (CER) was calculated (15) as,

$$CER = -\ ET_c\ \frac{\Delta CO_2}{\Delta_q} \tag{6}$$

where Δq is the absolute humiditiy. Since the crop leaf area index was higher than 3, ET_c was mostly given by the crop transpiration (T_c). Furthermore, being estimated as negligible the contribution of the soil carbon flux to the total CO_2 exchange of the crop, CER was also mostly given by the crop carbon assimilation (A_c). Therefore, with T_c=ET_c and A_c=CER, the canopy photosynthetic water use efficiency (WUE_c) was estimated as the ratio of carbon flux (A_c) to water flux (T_c),

$$\text{Photosynthetic } WUE_c = \frac{A_c}{T_c} \tag{7}$$

Results and Discussion

Leaf and Canopy Scale Responses

The evolution of photosynthetic WUEl, calculated as A_l/T_l ratio with VPD and with ψb at the leaf scale is shown in Figures 1a and b, respectively. These figures show that WUE_l decreases with increasing VPD and decreasing ψb.

This trend is similar to what has been shown at canopy scales in Figures 2a and b. With the ratio between carbon flux and water vapor fluxes, the photosynthetic canopy WUEc can be obtained for each single measured time period. As already mentioned above, both VPD and ψb variable are somehow correlated, so that we cannot say which is the relative contribution of each one to the variation observed in WUE.

The value of the photosynthetic WUE at canopy scale (WUE_c) is of 4.3 $mmol_{CO2} \cdot mol_{H2O}^{-1}$ which on average is roughly equal value of the photosynthetic WUE observed at leaf scale. The WUE value at the canopy scale is generally expected to be lower than the WUE value at leaf scale.

Comparing WUE at Leaf and Canopy Scales

Similar behavior of WUE is observed for both canopy and leaf scales with lower values for canopy due to additional respiration of non-photosynthesizing organs (e.g., stems). For comparison with progressing water stress, during the same period, predawn leaf water potential (ψb) vs DAP is reported in Figure 3c. It may be noticed that a decrease in WUE occurs any time ψb tend to decrease. Here, however, we discuss the observation reported in the previous section, where we stated that an increase in VPD of the atmosphere is correlated with a decrease in ψb, (Figure 2a and b.). In Figure 3a and b, the actual trend of WUE (Figure 3a) and the corresponding trend of the normalized WUE (Figure 3b) are reported at both leaf and canopy scales. The normalization of WUE at both leaf and canopy scale is simply a matter of multiplying WUE by the VPD occurred for the same time-period of the measurements to eliminate the effect of VPD. It appears to be quite evident that the normalization for VPD returns a more constant response of WUE to various degree of stress, although this is clearer for canopy scale than for leaf scale. These findings confirm the theoretical expectation reported in the literature by various authors (7, 16), and that VPDl rather than ψb was principally responsible for the observed variation in WUE during the stress period.

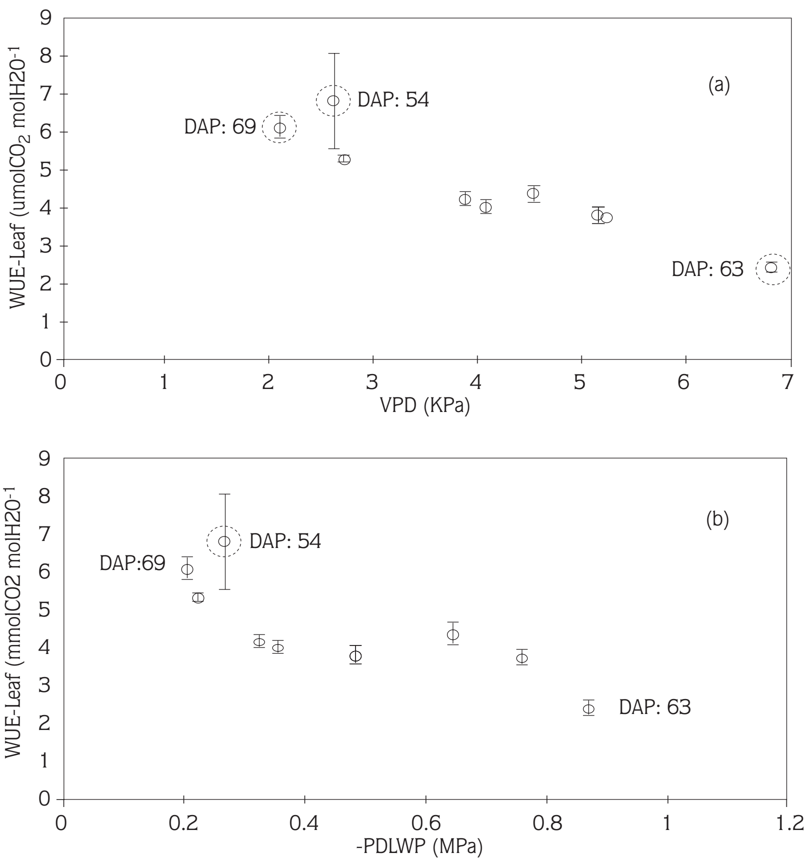

Figure 1. Relationships between photosynthetic WUE at the leaf scale (WUE_l) vs. VPD (a) and photosynthetic WUE_l vs. ψb (b).

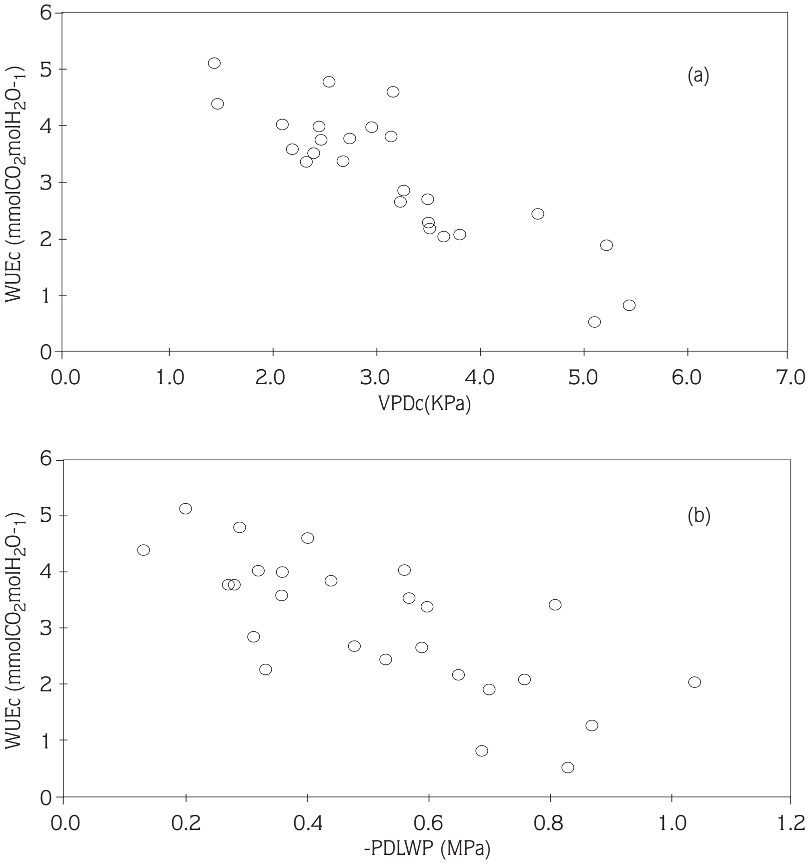

Figure 2. Relationships of photosynthetic WUE at the canopy scale (WUE_c) vs. vapor pressure deficit (VPD) (a) and photosynthetic WUE_c vs. predawn leaf water potential (ψb) (b).

Conclusions

Sweet sorghum proved to be superior to many other C4 plants in terms of water use efficiency and ability to withstand severe water stress conditions. However, these results had to be explained in mechanistic terms to identify the processes which may confer to the crop the peculiarities observed at agronomic scale.

The aim of this study was to answer some basic questions by investigation of crop gas-exchange features under progressing water stress. Previously discussed results led to the following conclusions:

a) Sweet sorghum photosynthetic water use efficiency (WUE) appeared to vary with ψb and VPD, at both leaf and canopy scales. However, once WUE values were normalized for VPD, WUE remained constant regardless of ψb status.

b) Parallel behavior occurred between leaf and canopy scales in terms of gas-exchange variables. This indicates an effective stomatal control over the whole canopy and a relatively high degree of coupling between crop and atmosphere. The Bowen-ratio system was able to detect at canopy scale the same patterns observed at leaf scale, such as midday decline in assimilation rates, higher afternoon reduction in assimilation rate relative to morning, and progressing water stress.

c) The values of the photosynthetic WUE were around 5 and 4.3 $mmol_{CO2}.mol^{-1}_{H2O}$ for leaf and canopy scale, respectively.

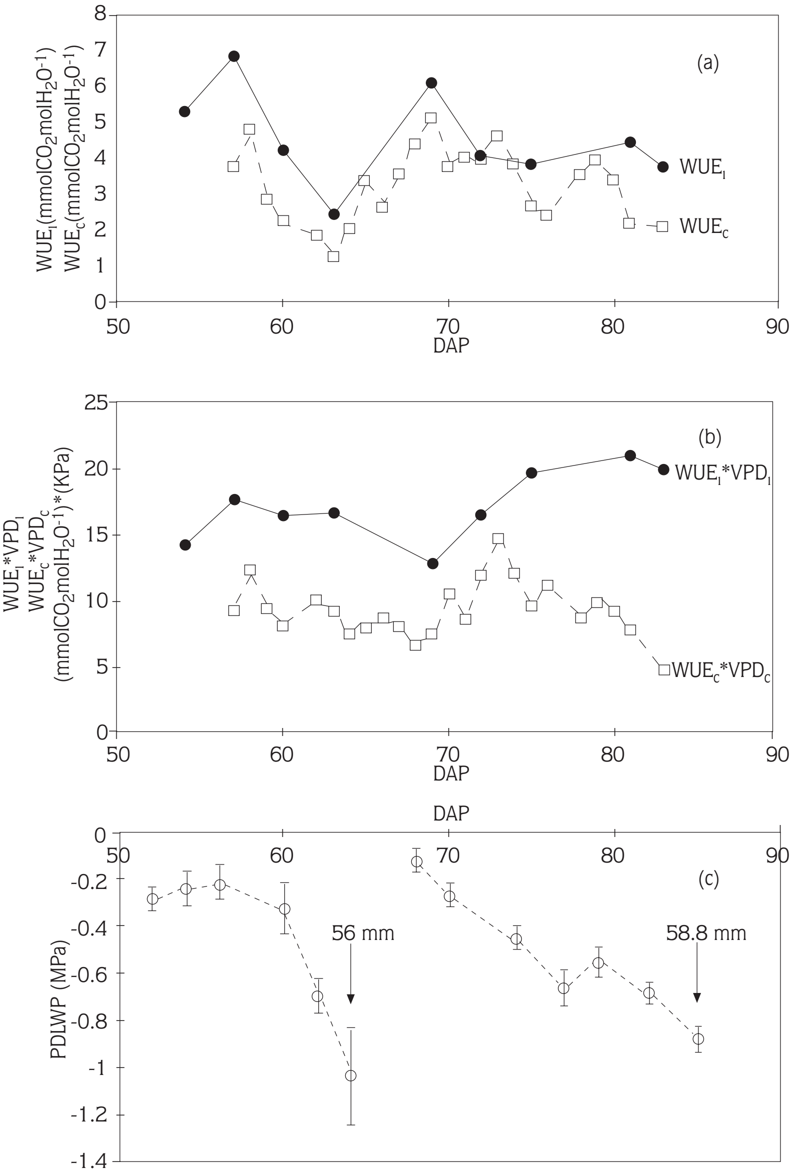

Figure 3. Variation of photosynthetic WUE at the canopy and leaf scales (a), normalized photosynthetic WUE at both leaf and canopy scales (b), and predawn leaf water potential (c), during the trial period.

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