Defoliation of sweet corn plants under irrigation depths and its impact on gas exchange

Osvaldir F. dos Santos[1], Sebastião F. de Lima[2], Vespasiano B. de Paiva Neto[3],
Gabriel L. Piati[2], Christian R. W. de S. Osório[2] & Hugo M. de Souza[2]

[1] Universidade Estadual Paulista Júlio de Mesquita Filho/Faculdade de Ciências Agronômicas/Departamento de Engenharia Rural. Botucatu, SP. E-mail: osvaldir.feliciano@gmail.com (Corresponding author)

[2] Universidade Federal de Mato Grosso do Sul/Câmpus de Chapadão do Sul. Chapadão do Sul, MS. E-mail: sebastiao.lima@ufms.br; gabrielpiati@hotmail.com; c.osorio@hotmail.com; hugo_manoel12@hotmail.com

[3] Universidade Federal do Vale do São Francisco/Câmpus de Ciências Agrárias/Colegiado Acadêmico de Engenharia Agronômica. Petrolina, PE. E-mail: vespasiano.paiva@univasf.edu.br

A B S T R A C T

The objective of this work was to evaluate leaf gas exchanges of sweet corn as a function of defoliation when submitted to different irrigation depths. The experimental design was randomized blocks in split-plot scheme, with four irrigation depths in the plots [50, 75, 100 and 125% of crop evapotranspiration (ETc)], and three levels of defoliation in the subplots (0%, control; 35%, removal of four fully expanded leaves; 100%, total removal of the leaves - section of the aerial part) with three replicates. Defoliation was manually performed when the plant had four fully expanded leaves. It was verified that the dephs of irrigation and defoliation levels affect leaf gas exchanges in sweet corn plants, allowing the conclusion that the plant tends to activate a mechanism of photosynthetic compensation, when subjected to leaf stress, which can vary according to the degree of severity and water availability to which it is submitted. The most expressive values of gas exchanges in sweet corn plants that did not have defoliation were generally observed at irrigation depths estimated between 87 and 99% ETc and, in the treatments with defoliation, regardless of the level, at irrigation depth of 125% ETc.

Desfolha em plantas de milho doce sob diferentes lâminas de irrigação e seu impacto nas trocas gasosas

R E S U M O

Objetivou-se neste trabalho avaliar as trocas gasosas foliares de plantas de milho doce em função da desfolha, quando submetidas a diferentes lâminas de irrigação. O delineamento experimental foi em blocos casualizados em esquema de parcelas subdivididas, tendo nas parcelas quatro lâminas de irrigação 50, 75, 100 e 125% da evapotranspiração da cultura (ETc) e nas subparcelas três níveis de desfolha (0%, testemunha; 35%, remoção de quatro folhas completamente expandidas; 100% remoção total das folhas - secção da parte aérea) com três repetições, sendo a desfolha realizada manualmente quando a planta apresentava quatro folhas completamente expandidas. Verificou-se que os níveis de irrigação e desfolha afetam as trocas gasosas foliares em plantas de milho doce, permitindo a conclusão de que a planta quando submetida a estresses foliares, tende a ativar um mecanismo de compensação fotossintética, podendo variar em função do grau de severidade e da disponibilidade hídrica a qual está submetida. Os valores mais expressivos de trocas gasosas em folhas de milho doce que não tiveram desfolha foram, de forma geral, observados nas lâminas de irrigação estimadas entre 87 e 99% da ETc e nos tratamentos com desfolha, independente do nível ocorrido, na lâmina de 125% da ETc.

Introduction

Sweet corn (*Zea mays* L., var. *saccharata*) is classified as special type and exclusively intended for human consumption, mainly used as green corn, both fresh and processed by industries of canned vegetable products (Oliveira Júnior et al., 2006). Its yield is directly affected by stress factors that reduce its leaf area, such as: diseases, insects, frosts, hail, wind, machinery traffic, among others, due to its low plasticity (Pereira et al., 2012; Sangoi et al., 2014).

Despite the difficulty to precisely simulate natural defoliation caused by direct and/or indirect factors, the artificial cut of leaves is currently a useful method to measure to which extent the crop can withstand leaf area reduction, being used in many crops nowadays (Oyediran & Heinrichs, 2002; Lima Júnior et al., 2010).

These injuries may lead to alteration in the source-drain relationship of the plant, because leaves are responsible for the main source of photoassimilates, which can consequently cause changes in agronomic features that affect production and physiological quality of the seeds (Karam et al., 2010; Pereira et al., 2012).

In addition to leaf injuries, inadequate water management can aggravate even more the situation of the plants, leading to a reduction in leaf water potential, loss of turgor, stomatal closure and reduction of root growth (Jaleel et al., 2009), limiting stomatal conductance and transpiration, which results in the decrease of photosynthetic rate (Silva et al., 2010).

Based on these factors, besides the importance in the cultivation of this vegetable, the information in the literature about the physiological mechanisms of response to leaf injuries due to water availability is still very scarce. Therefore, since morphological and physiological aspects have direct influence on crop yield, it becomes evident the importance of understanding this set of factors in sweet corn cultivation.

Hence, this study aimed to evaluate leaf gas exchanges of sweet corn as a function of defoliation, when subjected to different irrigation depths.

Material and Methods

The experiment was carried out in the experimental area of the Federal University of Mato Grosso do Sul, campus of Chapadão do Sul (18º 47' 39" S; 52º 37' 22" W; 820 m). The climate of the region is classified as humid tropical (Peel et al., 2007). Temperature, relative air humidity, rainfall and reference evapotranspiration during the experimental period are presented in Figure 1.

The soil where the experiment was conducted is classified as dystrophic Red Latosol (Jacomine, 2009), with clayey texture, bulk density of 1.2108 g dm^{-3} and water contents equivalent to field capacity and permanent wilting point of 0.2652 and 0.1858 dm^3 dm^{-3}, respectively. Chemical properties in the 0-20 cm layer were: 9.0 mg dm^{-3} of P (resin); 33.5 g dm^{-3} of OM; 4.9 of pH (CaCl$_2$); K$^+$, Ca^{2+}, Mg^{+2} and H + Al = 0.07; 2.40; 0.90 and 2.9 cmol$_c$ dm^{-3}, respectively, and 53.7% of base saturation.

The experiment was conducted in split-plot scheme, in which plots consisted of four irrigation depths (50, 75, 100 and 125% of crop evapotranspiration) and subplots consisted of three defoliation levels (0%, control; 35%, removal of four fully expanded leaves - first initial leaves from the soil; 100%, total removal of the leaves - section of the aerial part) with three replicates. Defoliation was manually performed by removing the leaf blade from its base, according to each treatment in the vegetative stage V4 (four expanded leaves) at 25 days after emergence (DAE). Plots were 4 m long (1-m border) and 2.25 m wide (0.9-m border), resulting in a total area of 9 m^2 and evaluation area of 4.5 m^2.

Soil tillage consisted of plowing and harrowing, and acidity correction and fertilization at sowing were performed based on soil chemical analysis and following the recommendations of Souza & Lobato (2004) for the corn crop. Top-dressing nitrogen fertilization was split and applied in the phenological stages V4 and V8 (eight expanded leaves), using urea as nitrogen source, totaling 150 kg ha^{-1} of N.

Sowing was performed on February 13, 2016, at spacing of 0.45 m between rows, adopting a density of 75,000 seeds ha^{-1}. The single hybrid Tropical Plus® (Syngenta) was used in the experiment, which shows the following features: cycle from 90 to 100 days, light-yellow color in the grains, thin pericarp and sweet taste, besides resistance to the main diseases.

Seeds were previously treated in the processing industry and, during the experiment, phytosanitary tracts performed in the crop consisted of two applications of the insecticide Methomyl (129 g a.i. ha^{-1}) and one application of the herbicides Tembotrione (100.8 g a.i. ha^{-1}) and Atrazine (1.5 kg a.i. ha^{-1}).

A drip irrigation system was used, in which emitters operated at service pressure of 98 kPa, applying a flow rate
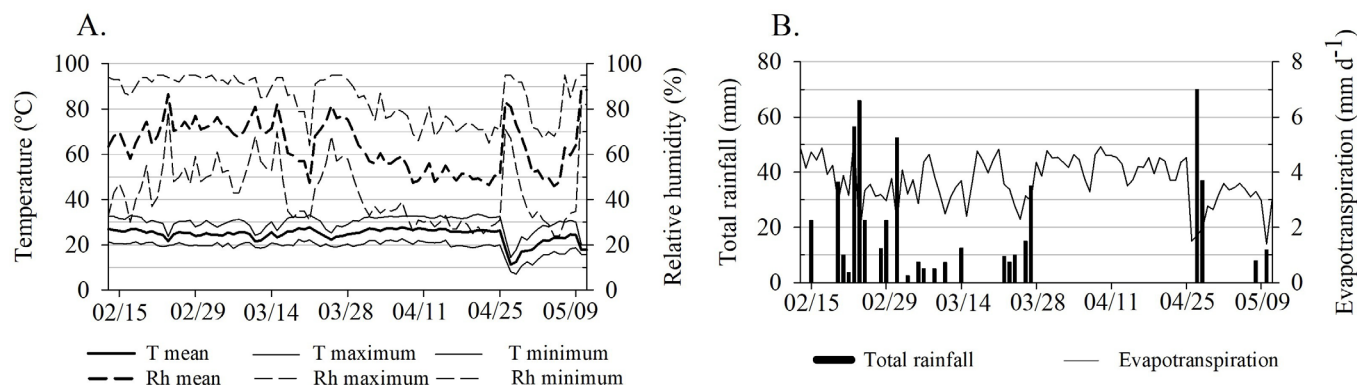

Figure 1. Daily mean values of (A) mean, minimum and maximum temperatures (ºC), relative air humidity (%), (B) rainfall (mm) and reference evapotranspiration (mm), during the experimental period

of 1.29 L h^{-1}, with spacing of 0.20 m, using one drip tape for each plant row. The actual irrigation required for the 100% ETc treatment was determined according to the parameters of climate, plant and soil, representing the actual water demand of the system (Eq. 1):

$$IRN_{LOC} = \sum_{dial}^{i} ET_O K_C K_S K_L - P_E \qquad (1)$$

where:

AIR$_{LOC}$ - actual irrigation required in localized systems, mm;

ET$_O$ - reference evapotranspiration, mm d^{-1}, Allen et al. (1998);

K$_C$ - crop coefficient, dimensionless, Allen et al. (1998);

K$_S$ - soil moisture coefficient, dimensionless, Bernardo et al. (2008);

K$_L$ - location coefficient, dimensionless, Keller & Bliesner (1990); and,

P$_E$ - effective rainfall in the period, mm.

Daily weather data used to calculate reference evapotranspiration (ETo) were obtained in an automatic surface weather station installed close to the experimental area. Crop coefficients (Kc) were 0.8 and 1.2 for the stages I and III, respectively. For stage II, linear weighting between late stage I and early stage III. Stages I, II and III lasted 16, 24 and 30 days, respectively, and stage IV from the 70th day to harvest.

Gas exchanges were evaluated at 50 and 80 DAE (in young leaves, after 25 and 55 days, respectively, from the removal of leaf blade according to each treatment), from 9 to 11 a.m., measuring the middle third of the third leaf counted from the apex. In these occasions (50 and 80 DAE), plants showed 14 fully expanded leaves (FEL) in the treatment without leaf area removal; 10 FEL in the treatment with 30% leaf area removal and 7 FEL in the treatment with 100% leaf area removal in the vegetative stage V4.

Measurements were taken using an infrared gas analyzer (IRGA) with air flow of 500 μmol s^{-1} and attached light source of 1000 μmol m^{-2} s^{-1}. The following variables were measured: net photosynthesis rate (A) (μmol of CO$_2$ m^{-2} s^{-1}), transpiration (E) (mmol of H$_2$O m^{-2} s^{-1}), stomatal conductance (gs) (mol of H$_2$O m^{-2} s^{-1}), internal carbon concentration (Ci) (μmol m^{-2} s^{-1}), and instantaneous water use efficiency (IWUE - A/E), calculated based on the relationship between net photosynthesis and transpiration [(μmol m^{-2} s^{-1}) (mmol of H$_2$O m^{-2} s^{-1})$^{-1}$].

For statistical analysis, the data were subjected to analysis of variance and regression. Models were selected based on the significance of the regression coefficients.

Results and Discussion

Water availability influenced stomatal conductance as a function of the defoliation level, showing a very similar behavior in both evaluation periods (Figures 2A and B). Stomatal conductance showed maximum values of 0.79 mol of H$_2$O m^{-2} s^{-1} with irrigation depth of 96.3% ETc at 50 DAE and 0.43 mol of H$_2$O m^{-2} s^{-1} with irrigation depth of 92% ETc at 80 DAE, a result also found by Mathobo et al. (2017), who

observed that plants exhibit higher stomatal conductance when young, with subsequent decrease along its development. These results may be associated with the reduction in the efficiency of solar radiation absorption due to leaf senescence, and also with the lower demand for photoassimilates as the plant approaches the end of its cycle.

In environments with severe water stress (50% ETc), stomatal conductance decreased in plants that did not suffer reduction in leaf area in initial growth stages, regardless of the evaluated period (Figure 2A and B). According to Nahar et al. (2016), this occurs because the decrease in soil water content reduces stomatal activity and, consequently, induces stomatal closure in the plants. However, with the occurrence of defoliation, stomatal conductance values were higher in comparison to the control in the same environment. According to Quentin et al. (2011), reduction in leaf area usually results in hydraulic improvements in the water balance of the remaining leaves, with subsequent increments in stomatal conductance, which can be even more evidenced with the increase in water availability (125% ETc).

Reduction of stomatal conductance in plants under water stress (125% ETc), in the absence of treatment with initial defoliation, results from a regulating behavior of the water balance, according to Mollard et al. (2008). These authors also claim that this mechanism is a critical response of the plant to avoid leaf dehydration in species susceptible to water excess in the soil, thus allowing their survival, for reducing the absorption of potentially toxic ions.

The results of the present study demonstrate a positive correlation between stomatal conductance and internal carbon concentration, especially when plants were in environments with water excess (125% ETc), regardless of presence or absence of reduction in leaf area (Figures 2A, B, C and D). These data corroborate those of Gupta & Thind (2015) and Silva et al. (2015), who claim that reduction in stomatal conductance can cause reduction in internal carbon concentration because the greater the stomatal opening, the higher the CO$_2$ diffusion to the substomatal chamber, and there was a higher correlation between these factors as a function of water availability in the soil.

Regarding net photosynthesis (Figures 2E and F), higher values were obtained at 50 DAE, equal to 0.81 μmol of CO$_2$ m^{-2} s^{-1} with irrigation depth of 93.29% ETc and 4.42 μmol of CO$_2$ m^{-2} s^{-1} with irrigation depth of 96.11% ETc at 80 DAE, in the treatments with absence of defoliation in the initial stages of the crop. However, in treatments with defoliation, higher values were obtained using the irrigation depth of 125% ETc, regardless of the evaluated period, equal to 40.43 and 34.52 μmol of CO$_2$ m^{-2} s^{-1} at 50 and 80 DAE, respectively, with 35% defoliation, and 41.55 and 35.47 μmol of CO$_2$ m^{-2} s^{-1} at 50 and 80 DAE, respectively, with 100% defoliation.

The behavior of photosynthetic rates observed in the present study is directly related to stomatal conductance, because water availability and accumulation of internal CO$_2$ concentration are some of the factors that control stomatal opening and closure (Silva et al., 2015). In addition, the severity of the stress will determine the relative magnitude of stomatal and non-stomatal factors in the limitation to photosynthesis (Kalariya et al., 2015).
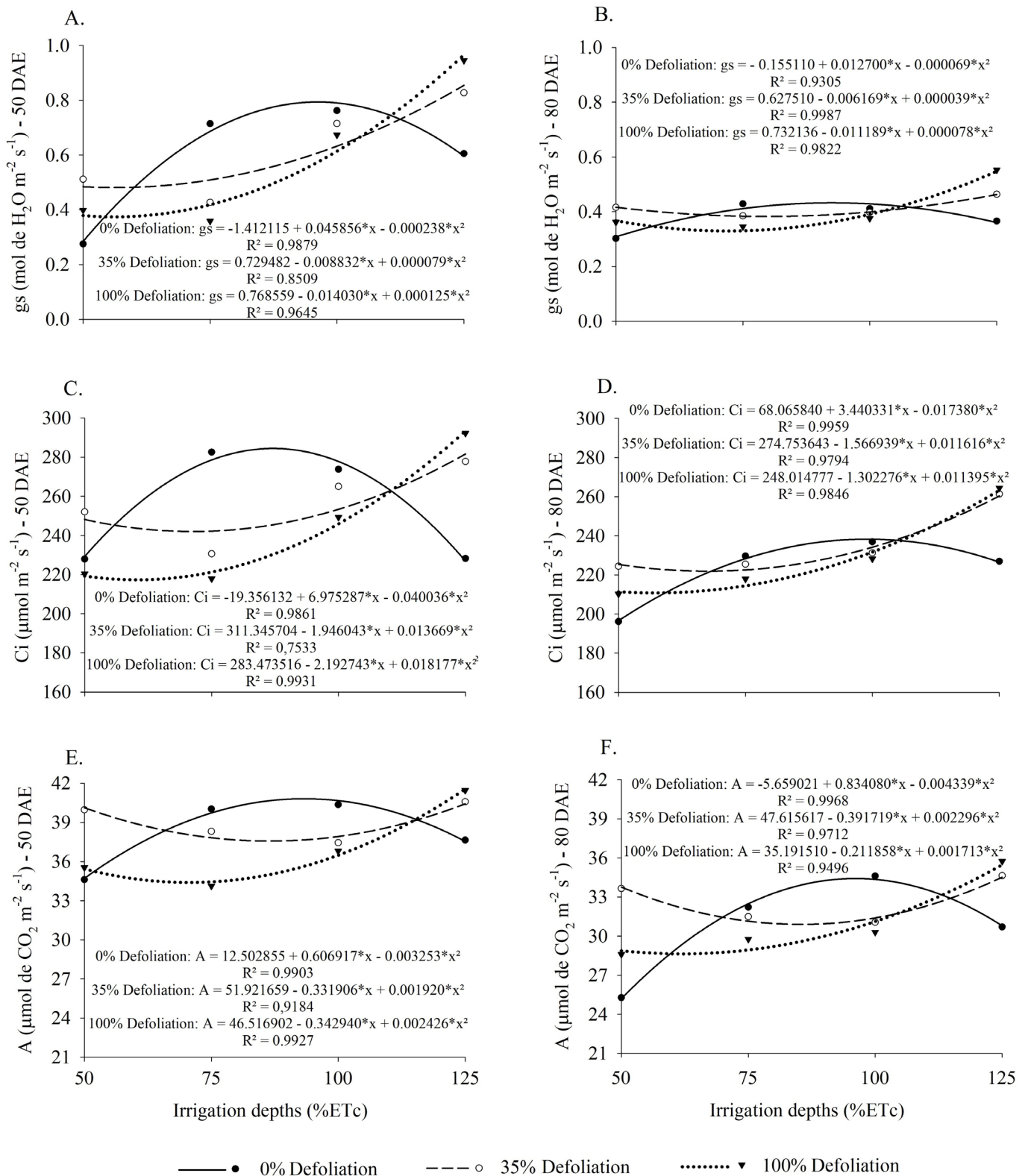
Figure 2. Estimate of stomatal conductance (gs) (A and B), internal carbon concentration (Ci) (C and D), photosynthetic rate (A) (E and F) of sweet corn subjected to different irrigation depths (LI), for different defoliation levels at 50 and 80 DAE

In addition, higher values of photosynthesis obtained in treatments with defoliation in environments with water stress (Figures 2E and F) may also be related to a mechanism of photosynthetic compensation, as reported by Thomson et al. (2003), in which the loss of leaf area results in a higher demand for carbon in the remaining leaves. Moreover, such decrease in photosynthetically active area changes the equilibrium of capture of resources below the soil and the quantity required by the plant (above the soil), resulting in a higher content of nutrients and water available per remaining leaf area, thus increasing the photosynthetic rate of the plant. However, with a drastic defoliation (100% leaf area removal in V4 stage), this compensation mechanism is reduced, probably because of the limitation in solar radiation interception by the leaves.

A.

0% Defoliation: $E = -17.065956 + 0.887010*x - 0.005000*x^2$
$R^2 = 0.9998$
35% Defoliation: $E = 25.604905 - 0.200209*x + 0.001295*x^2$
$R^2 = 0.7214$
100% Defoliation: $E = 29.843844 - 0.443213*x + 0.003091*x^2$
$R^2 = 0.9993$

B.

0% Defoliation: $E = -9.850076 + 0.492380*x - 0.002616*x^2$
$R^2 = 0.9994$
35% Defoliation: $E = 18.729054 - 0.190422*x + 0.001191*x^2$
$R^2 = 0.9594$
100% Defoliation: $E = 23.580305 - 0.392040*x + 0.002581*x^2$
$R^2 = 0.9895$

C.

0% Defoliation: $IWUE = 4.859134 - 0.070267*x + 0.000405*x^2$
$R^2 = 0.9997$
35% Defoliation: $IWUE = 2.0646$
100% Defoliation: $IWUE = 1.260840 + 0.032098*x - 0.000221*x^2$
$R^2 = 1.0000$

D.

0% Defoliation: $IWUE = 4.901708 - 0.050528*x + 0.000273*x^2$
$R^2 = 0.9858$
35% Defoliation: $IWUE = 2.7152$
100% Defoliation: $IWUE = 0.009344 + 0.080263*x - 0.000491*x^2$
$R^2 = 0.9901$

———•——— 0% Defoliation   – – – ○ 35% Defoliation   ·········▼ 100% Defoliation
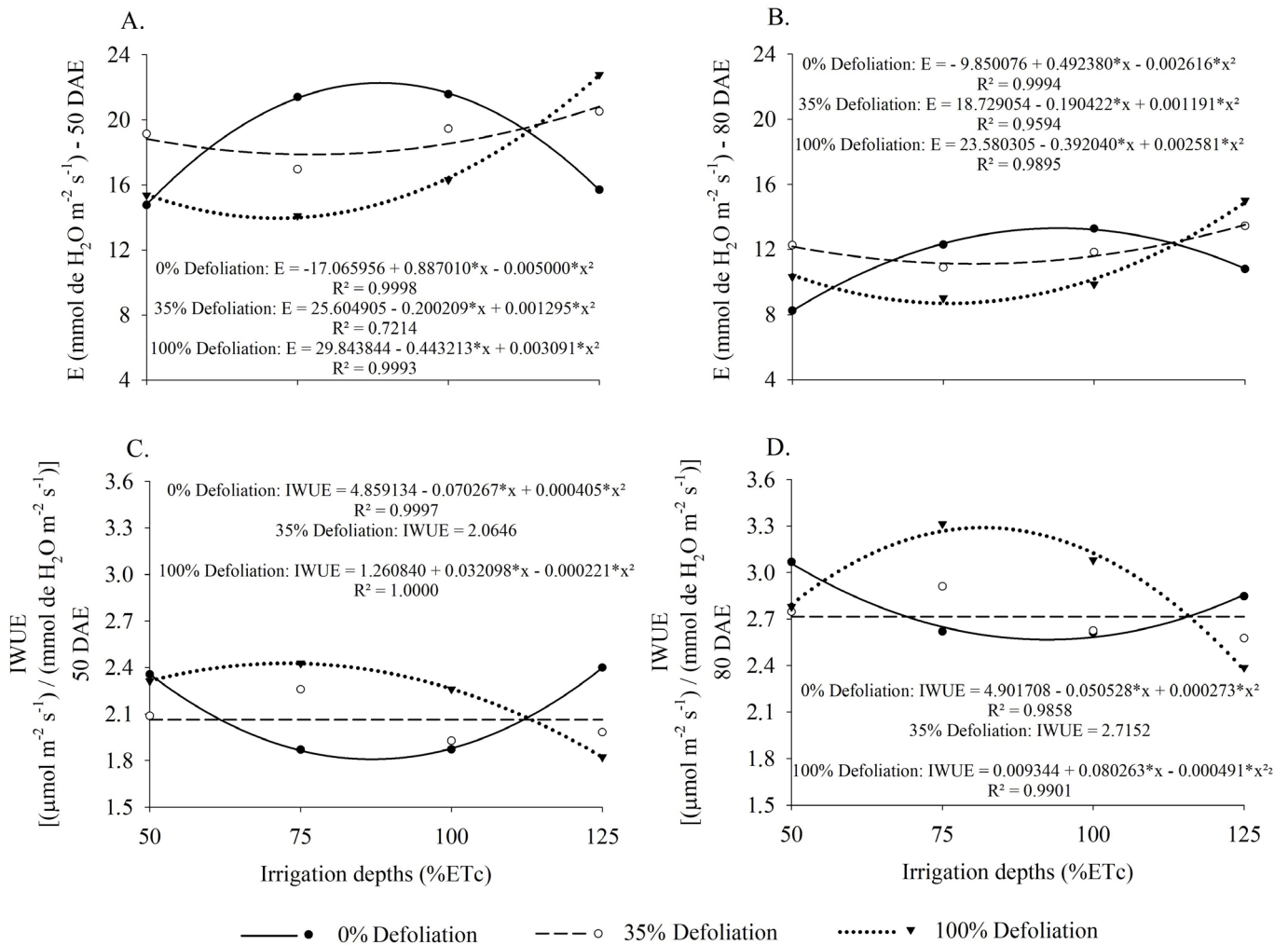
Figure 3. Estimate of transpiration (E) (A and B) and instantaneous water use efficiency (IWUE) (C and D) in sweet corn subjected to different irrigation depths (LI), for different defoliation levels at 50 and 80 DAE

In general, there was a very similar behavior between transpiration and net photosynthesis as a function of the irrigation depths at both 50 DAE (Figures 3A and 2E) and 80 DAE (Figures 3B and 2F). According to Taiz & Zeiger (2013), this is associated with the fact that, in favorable moments to perform photosynthesis, CO_2 demand inside the leaf is very high; therefore, stomatal slits open wide, decreasing stomatal resistance to CO_2 diffusion, leading to substantial water loss under these conditions. In plants under water stress (lower irrigation depths), higher values of transpiration were obtained with 35% defoliation. Plants that did not undergo any leaf stress stood out in irrigation depths between 89 and 94% ETc at 50 and 80 DAE, respectively. With water excess, total defoliation led to higher values of transpiration at both 50 and 80 DAE.

Regarding the instantaneous water use efficiency, no significant difference was between irrigation depths for the 35% defoliation level, regardless of the evaluated period (Figures 3C and D). However, with 100% leaf removal, higher efficiency was observed at 50 DAE with irrigation depths of 72.62% ETc and at 80 DAE with irrigation depth of 81.73% ETc, resulting in values of 2.43 and 3.28 (μmol m^{-2} s^{-1}) (mmol of H_2O m^{-2} s^{-1}), respectively. However, plants in which leaf area was not removed showed higher values of IWUE under adverse water conditions.

Conclusions

1. When subjected to leaf stress, the plant tends to activate a photosynthetic compensation mechanism, which may vary according to the degree of severity and water availability.

2. The most expressive values of gas exchanges (A, E, gs, Ci) in sweet corn plants in the absence of defoliation were, in general, observed at irrigation depths estimated between 87 and 99% ETc; and in treatments with defoliation, regardless of the level, at irrigation depth of 125% ETc.

Acknowledgments

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