T1992PHY22

Quantification of leaf responses to soil water content: comparative sensitivity of leaf expansion rate and leaf conductance in field-grown sunflower

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ABSTRACT. The relative importance of changes in rate of leaf expansion (LER) and leaf conductance (g_l) in the control of crop transpiration depends on the sensitivity of these factors to soil water deficits. In this paper, we have quantified the responses of LER and g_l to soil water deficits of field-grown sunflower under spring and summer conditions.

Leaf conductance was much less sensitive to soil water deficit than LER. Even under the harsh conditions of the summer experiment, no g_l changes were evident whereas marked LER reductions were observed. This field study indicates that g_l plays an irrelevant role in the control of sunflower transpiration in the pre-anthesis period. The present experiments also confirm the importance of leaf expansion in the regulation of gas exchange of expanding sunflower canopies subjected to water deficits.

INTRODUCTION. Crops subjected to water deficits can reduce transpiration (T) by two mechanisms: less interception of radiation (IR) and less transpiration per unit intercepted radiation ($T\ IR^{-1}$). Small IR may arise from a reduced leaf area index (LAI) and/or small $IR\ LAI^{-1}$. The latter is reflected, for instance, in the smaller light-extinction coefficient of wilted crops. Before anthesis, smaller LAI of stressed sunflowers arise essentially from decreased rate of leaf expansion (LER). Reduced $T\ IR^{-1}$ implies lower canopy conductance which is, in turn, related to leaf conductance (g_l).

The relative importance of changes in LER and g_l in the control of crop transpiration depends on the sensitivity of these factors to water deficits. In this paper, we have quantified the responses of LER and g_l to soil water deficits in the field. To explore the possible interactions between soil and atmospheric water status, comparisons were made of the responses measured under spring and summer conditions.

METHODS. The experiments were carried out on a deep (> 3 m) sandy-loam Typic Xerofluvent at Cordoba (southern Spain). Sunflower (cv. Sungro 380) was sown on 22/2/91 (Exp 1) and 31/5/91 (Exp 2). Plant population was 7 plants m^{-2}. Crops were irrigated frequently until treatments began. WET (trickle-irrigated daily) and DRY (non-irrigated) treatments were established at 54 days after emergence (DAE) in Exp 1 and 32 DAE in Exp 2. Treatments were laid-out in a randomized, complete-block design with four replicates.

Leaf area was estimated as length x width x 0.7. To reduce the variability in LER associated with leaf ontogeny, measurements were limited to leaves in their lineal growth phase. Average LER of 4-5 leaves were used in our analysis. Leaf conductance was measured with a steady state porometer and LWP with a pressure bomb, both at solar noon ± 1h. Soil water content was measured twice-weekly with a neutron probe at 0.15 m increments and daily values were obtained by extrapolation between measurements. Plant available water (PAW) was calculated as in Rosenthal et al.[2]. To estimate PAW-thresholds for LWP, LER, and g_l responses, a two-line model was fitted to the data[2] using PLOTIT (Scientific Programming Enterprises, Haslett, Michigan).

RESULTS AND DISCUSSION. Table 1 shows the LWP, g_l, and LER of the WET controls under the contrasting conditions of Exps 1 and 2 (Table 2). Well irrigated plants maintained similar LWP and g_l across experiments. The rate of leaf expansion of WET controls in summer was about twice that measured in spring. Most of this difference was accounted for by mean air temperature, i.e. leaves in both experiments expanded at a similar rate of 1.6 cm^2 $(C\ d)^{-1}$ [base temperature = 4 C [3]]

Leaf responses to soil drying are presented in Fig. 1. In spring, both LWP and LER of DRY plants started to decline with respect to the WET controls at a PAW-threshold ca. 0.5. The PAW-threshold for these variables in summer was 0.8. The significant ($P<0.05$) differences between the responses in spring and summer were accounted for by the differences in potential evapotranspiration during the measurement period[1].

Leaf conductance was much less sensitive to soil water deficit than LER (Fig. 1). In spring, g_l of DRY plants started to decline when the lowest PAW values where achieved at the end of the drying cycle, when leaf expansion was only ca. 20% of the controls (Fig. 1). Even under the harsh conditions of the summer experiment no g_l changes were evident whereas marked LER reductions were observed (Fig. 1).

In contrast with the conclusion of some laboratory experiments[4] this field study indicates that g_l plays an irrelevant role in the control of sunflower transpiration in the pre-anthesis period. The present experiments also confirm the importance of leaf expansion in the regulation of gas exchange of expanding sunflower canopies subjected to water deficits[5].

Table 1. Leaf water potential (LWP), leaf conductance (g_l) and rate of leaf expansion (LER) of well watered plants in Exps 1 and 2

	Exp. 1	Exp. 2
LWP (− MPa)	0.82 (0.03)[a]	0.75 (0.02)
g_l (mm s^{-1})[b]	21.3 (1.10)	20.7 (1.6)
LER (cm^2 d^{-1})	23.3 (1.9)	42.4 (1.5)

[a] s.e.m. [b] calculated from abaxial and adaxial measurements of leaf conductance

Table 2. Daily short-wave irradiance (Rad, MJ m^{-2}), maximum (T_{max}, °C) and minimum temperature (T_{min}, °C), vapour pressure deficit (VPD, kPa), and reference evapotranspiration (ET_o, mm) for Exps 1 and 2 at Cordoba 1991. Values are means (SE).

	Experiment 1		Experiment 2	
	Days after emergence		Days after emergence	
	1-54†	54-83‡	1-32†	32-42‡
Rad	9.3 (0.9)	16.0 (1.8)	21.3 (1.9)	28.2 (0.3)
T_{max}	20.8 (0.5)	28.1 (0.8)	34.7 (0.6)	41.8 (0.6)
T_{min}	8.0 (0.3)	8.9 (0.6)	16.7 (0.3)	20.1 (0.7)
VPD	0.6 (0.0)	1.3 (0.1)	2.0 (0.1)	3.2 (0.1)
ET_o	4.1 (0.2)	5.5 (0.2)	7.0 (0.3)	8.8 (0.2)

† Period from emergence to start of treatments
‡ Treatment period

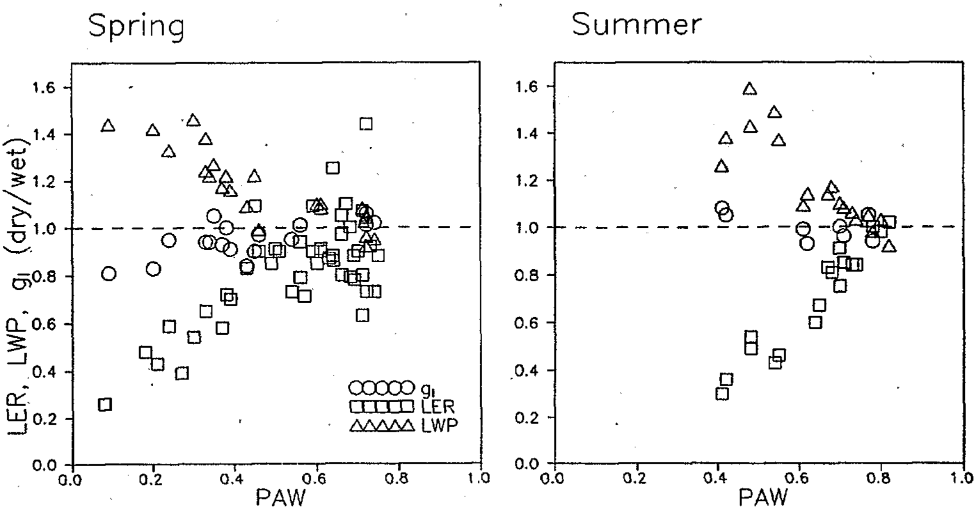

Fig. 1. Responses of dry/wet ratios of LWP, LER and g_l to PAW in Exps 1 (spring) and 2 (summer). The dashed line is the y = 1 line.

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