Wilting contributes to genotypic differences in the response of transpiration rate to soil drying

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♠ Plants respond to soil drying with different mechanisms which ultimately lead to reduced transpiration rate. Numerous studies have shown the importance of stomatal control mechanisms in the regulation of this response. The effect of changes in the position of the leaves, however, have been less studied. In sunflower, the effect of leaf wilting on transpiration rate has not been quantified. The objective of this work was to quantify the contribution of the effect of wilting to genotypic differences in the response of transpiration rate to soil drying.

♠ Two experiments were carried out: the first, for an evaluation of genotypic variability in wilting response, and the second, carried out in a growth chamber with the two most contrasting genotypes (HA89 and ND761), in which all the leaves of half the plants were kept in a horizontal position with a wire structure, while the other half of plants were untreated (control treatment). Plants were grown in a greenhouse in 2.7L pots filled with soil. For measurements, pots were irrigated to different soil water contents, covered with polyethylene to prevent water loss by evaporation, and left to dry down to a water potential of about -2 MPa. In both experiments, whole-plant transpiration rate, stomatal conductance and angle of the youngest fully-expanded leaf were measured. In experiment 2, quantum yield of photosystem II and leaf temperature were also measured.

♠ In both experiments, genotype HA89 showed a more linear response of transpiration rate to soil water deficit than ND761, along with a more marked wilting response. Keeping leaves in a horizontal position - thus eliminating the effects of wilting- increased transpiration rates at low soil water contents. The magnitude of the effect of wilting on transpiration rate was higher for HA89 than for ND761 and was closely related to the cosine of measured leaf angle. Leaf angle and temperature together explained 79% of the variability in the quantum yield of photosystem II, which decreased with increased temperature in horizontal leaves, and increased with decreasing leaf angle in control leaves. Keeping the leaves in a horizontal position increased the curvature of the fitted function of transpiration rate vs. soil water content for HA89, making it more similar to that of ND761; the effect of wilting increased this genotypic difference by 50%.

♠ Wilting contributes, in a genotype-dependent manner, to the response of whole-plant transpiration rate to soil drying by changing the shape of the response function. About one-third of the genotypic difference in the curvature of the response was explained by this mechanism. Our results confirm that this mechanism allows sunflower plants to conserve more soil water, and protects them from thermal stress and high radiation loads. This study was carried out under controlled conditions; under field conditions, the effect of wilting on transpiration would be expected to be increased by higher incident radiation but decreased by wind.

♠ These results contribute to understanding the response of transpiration rate to soil drying in sunflower, and point out a mechanism, in addition to stomatal control, regulating this response. Such adaptive traits have the potential of increasing performance under stress without yield penalties under favourable conditions. Characterization of this trait, together with the availability of public inbred lines with contrasting response, could help breeders in obtaining new sunflower varieties with increased adaptation to water deficit scenarios.

Keywords: Wilting – transpiration rate – genotypic variation – soil water potential

INTRODUCTION

Plants respond to soil drying with different mechanisms which ultimately lead to reduced transpiration rate (e.g., stomatal closure, wilting, leaf rolling, reduced growth, senescence). Numerous studies have shown the importance of stomatal control mechanisms in the regulation of this response. The effect of changes in the position of the leaves, however, have been less studied (Zhang et al., 2010). In sunflower, some authors (Rawson, 1979; Connor & Sadras 1992) cite wilting as an important mechanism in the regulation of transpiration rate, especially in advanced phenological stages. Although the response of transpiration rate has been studied in several sunflower genotypes (Casadebaig et al., 2008; Velázquez, 2011) the contribution of wilting to this response has not been quantified. Furthermore, preliminary studies show genotypic differences in wilting response to soil drying among sunflower inbred lines (Velázquez 2011).

The objective of this work was to quantify the contribution of the effect of wilting to genotypic differences in the response of transpiration rate to soil drying.

MATERIALS AND METHODS

Two experiments were carried out: the first, for an evaluation of genotypic variability in wilting response (inbred lines HA89, HA64, HAR2, HAR3, and ND761), and the second with the two most contrasting genotypes (HA89 and ND761). Eight plants per genotype were grown in a greenhouse in cilindrical 2.7 l pots filled with soil. For measurements, pots were irrigated to different soil water contents, covered with polyethylene to prevent water loss by evaporation, and left to dry down to a water potential of about -2 MPa.

In experiment 1, whole-plant transpiration rate (TR), stomatal conductance and angle of the youngest fully-expanded leaf were measured in the greenhouse.

In experiment 2, all the leaves of half the plants were kept in a horizontal position with a wire structure, while the other half of plants were untreated (control treatment). Whole-plant transpiration rate, stomatal conductance, quantum yield of photosystem II, leaf temperature and angle of the youngest fully-expanded leaf were measured in a controlled growth chamber (temperature: 25C, vapor pressure deficit: 1.3kPa, incident radiation: 500μmol.m^{-2}.s^{-1}, photoperiod: 24h).

An exponential function was fitted to the relationship between transpiration rate and soil water content in order to characterize the response of each genotype under each treatment.

$$TR=y_0+a*(1-\exp(-b*\theta_m)) \qquad \text{[Equation 1]}$$

where TR is transpiration rate per unit leaf area (g cm^{-2} h^{-1}), θ_m is mass basis soil water content (g g^{-1}), and y_0, a and b are the parameters which describe the shape of the curve.

In order to avoid confounding effects of different initial values of TR, fitted curves were standardized by dividing them by the estimated value for a θ_m of 0.24, which was considered as the initial value for each genotype x treatment combination.

The curvature (C) of this function was defined as the relationship between the estimated TR value for a θ_m of 0.19 and those for θ_m of 0.24 (i.e. maximum TR) and 0.14 (minimum TR), using the following equation:

$$C = [\, TR_{(0.19)} - TR_{(0.14)} \,] / [\, TR_{(0.24)} - TR_{(0.14)} \,] \qquad \text{[Equation 2]}$$

RESULTS

In experiment 1, genotypes HA89 and ND761 showed the most contrasting relationship between leaf angle and stomatal conductance, and were selected for further analysis in experiment 2.

In both experiments, genotype HA89 showed a more linear response of transpiration rate to soil water deficit than ND761, as shown in Figure 1.

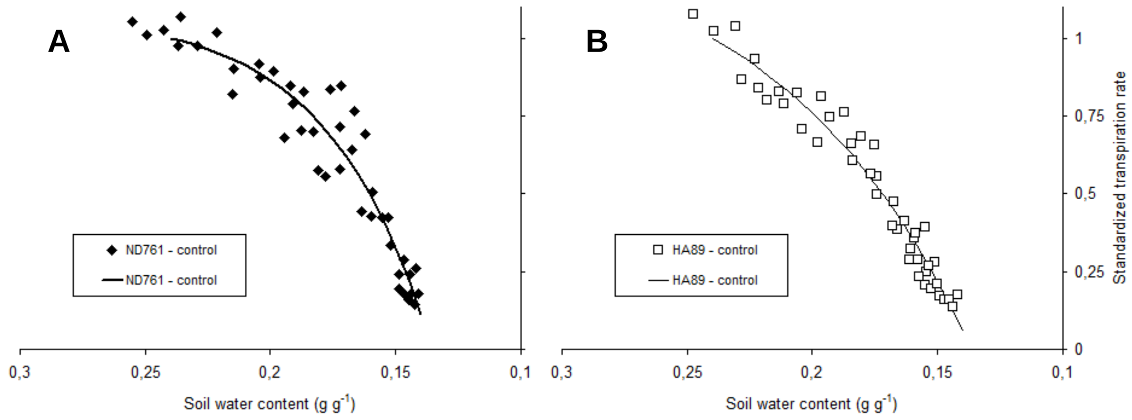

Fig. 1. Standardized transpiration rates as a function of decreasing soil water content, for genotypes ND761 (A) and HA89 (B). Data from experiment 2.

Genotype HA89 showed also a more marked wilting response to soil drying than ND761, as shown in Figure 2. Wilting started at higher water content, and leaves reached a lower final leaf angle in HA89 than in ND761.

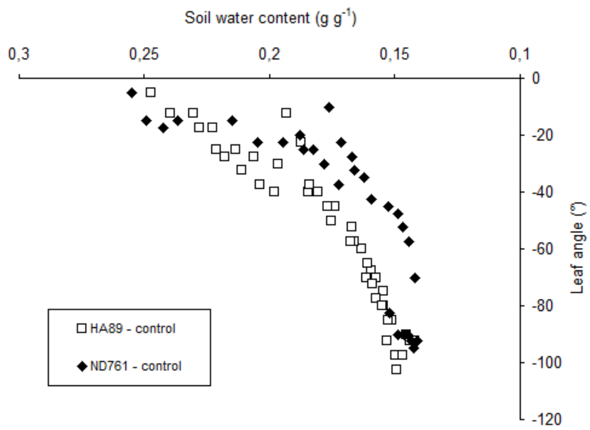

Fig. 2. Leaf angle of the youngest fully-expanded leaf as a function of decreasing soil water content, for genotypes HA89 (open symbols) and ND761 (closed symbols). Data from experiment 2.

Keeping leaves in a horizontal position -thus eliminating the effects of wilting- increased transpiration rates at low soil water contents. The magnitude of the effect of wilting on transpiration rate was higher for HA89 (Figure 3B) than for ND761 (Figure 3A). At a soil water potential of -0.64MPa wilting decreased transpiration rate by 15% only in HA89; at the minimum water potential of -2MPa, wilting decreased transpiration rate by 60 and 30% in HA89 and ND761, respectively (Figure 3C).

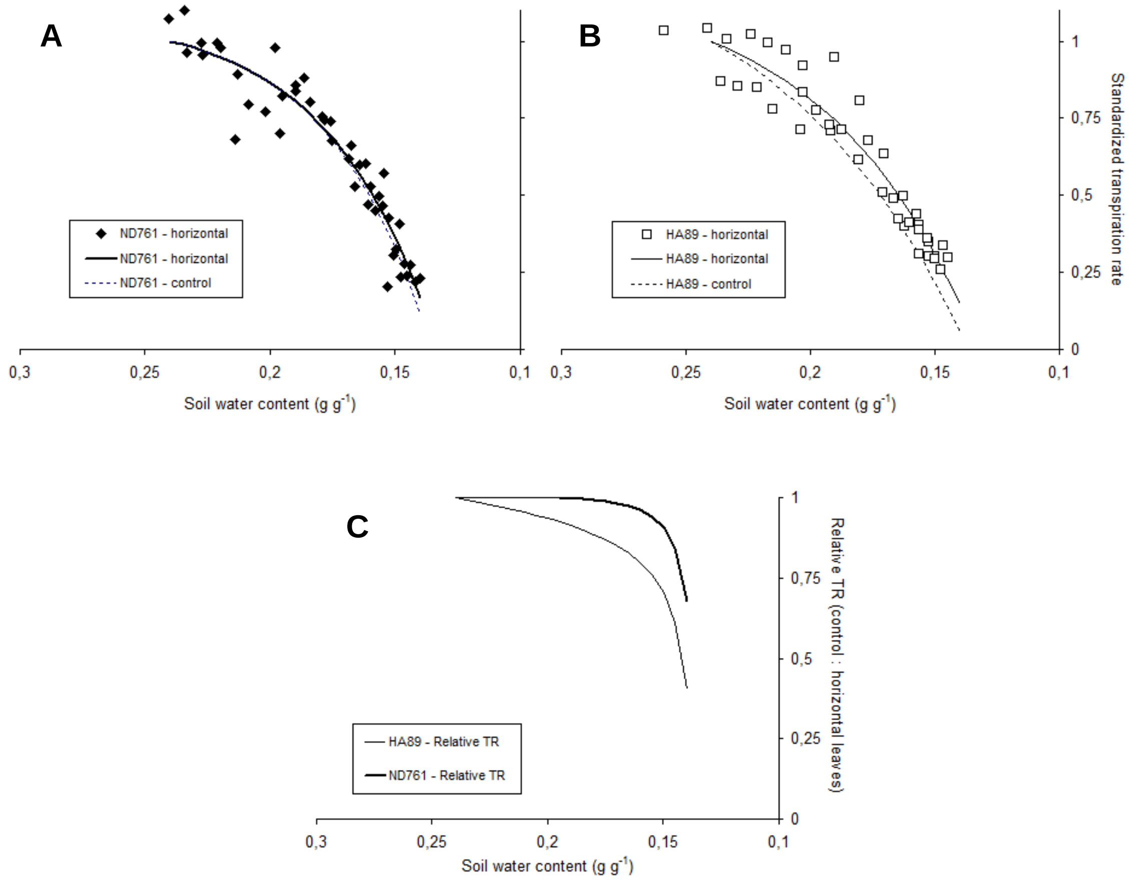

Fig. 3. Standardized transpiration rates in the treatment with horizontal leaves (symbols, solid lines) and the control treatment (dashed line) as a function of decreasing soil water content, for genotypes ND761 (A) and HA89 (B). (C) Standardized transpiration rate in the control treatment relative to that in the treatment with horizontal leaves (Relative TR), as a function of decreasing soil water content, for genotypes HA89 (thin line) and ND761 (thick line).

The effect of wilting on transpiration rate, quantified as TR in the control treatment relative to TR in the treatment with horizontal leaves (Figure 3) was closely related to the cosine of measured leaf angle of the youngest fully-expanded leaf (Figure 4).

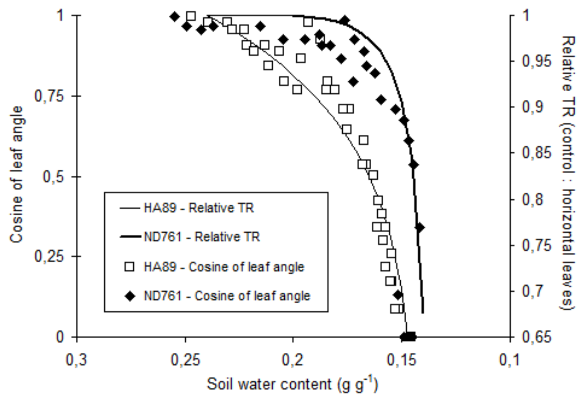

Fig. 4. Standardized transpiration rate in the control treatment relative to that in the treatment with horizontal leaves (Relative TR), as a function of decreasing soil water content, for genotypes HA89 (thin line) and ND761 (thick line), as compared to the cosine of leaf angle of the youngest fully-expanded leaf, for genotypes HA89 (open symbols) and ND761 (closed symbols). Data from experiment 2.

Leaf temperature increased with decreasing soil water content, with a much greater effect in horizontal leaves. Quantum yield of photosystem II (QY) decreased in horizontal leaves, as temperature increased (Figure 5A). On the other hand, control leaves increased QY as soil dried, which was highly correlated to leaf angle (Figure 5B). Leaf angle and temperature together explained 79% of the variability in the QY (Figure 5C).

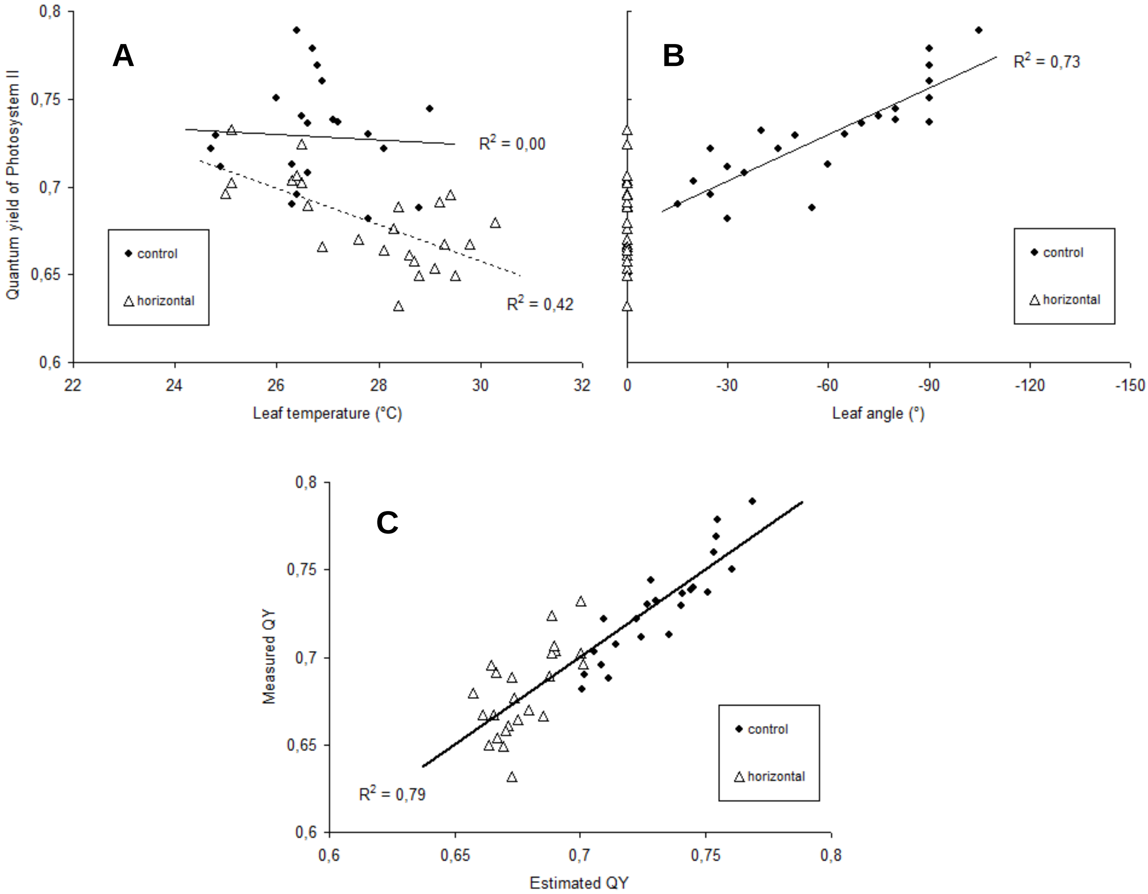

Fig 5. Quantum yield of Photosystem II (QY) as a function of leaf temperature (A) or leaf angle (B) in the youngest fully-expanded leaf, in the treatment with horizontal leaves (filled symbols) and control plants (open symbols). (C) Measured QY as a function of estimated QY based on leaf temperature (T, °C) and leaf angle (A, °): y= 0,907 – 0,00825 T – 0,00075 A.

These changes in transpiration rate due to the wilting response altered the response funtion of TR to soil drying, especially in HA89. Keeping the leaves in a horizontal position increased the curvature of the fitted function of transpiration rate vs. soil water content for HA89, making it more similar to that of ND761; the effect of wilting increased this genotypic difference by 50% (Figure 6).

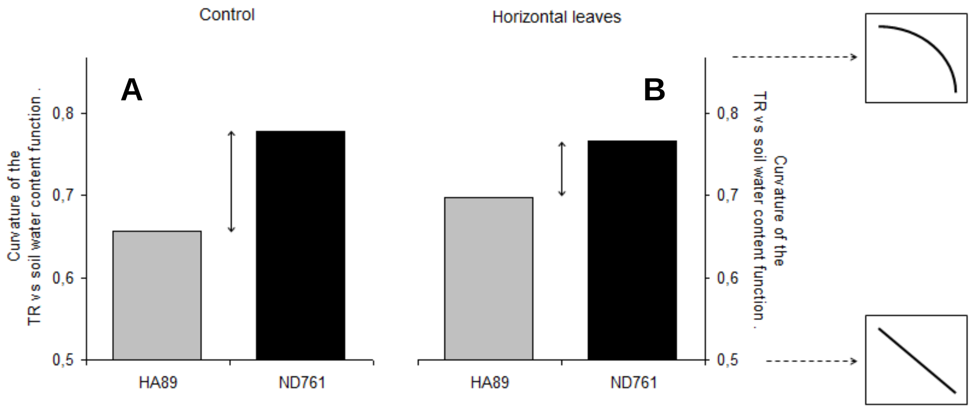

Fig. 6. Curvature of the TR vs soil water content function (Equation 2) for genotypes HA89 and ND761 in the control treatment (A) and the treatment with horizontal leaves (B). Vertical arrows indicate the extent of differences between both genotypes, under each treatment. Minimum and maximum values of the y-axis scale correspond to the curvature of a linear relationship and that of a 90-degree circular curve, respectively.

DISCUSSION

Wilting contributes, in a genotype-dependent manner, to the response of whole-plant transpiration rate to soil drying by changing the shape of the response function. About one-third of the genotypic difference in the curvature of the response was explained by this mechanism. Our results confirm that this mechanism allows sunflower plants to conserve more soil water, and protects them from thermal stress and high radiation loads.

This study was carried out under controlled conditions; under field conditions, the effect of wilting on transpiration would be expected to be increased by higher incident radiation but decreased by wind.

CONCLUSIONS AND PERSPECTIVES

These results contribute to understanding the response of transpiration rate to soil drying in sunflower, and point out a mechanism, in addition to stomatal control, regulating this response. Such adaptive traits have the potential of increasing performance under stress without yield penalties under favourable conditions.

Characterization of this trait, together with the availability of public inbred lines with contrasting response, could help breeders in obtaining new sunflower varieties with increased adaptation to water deficit scenarios.

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