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Relationships between plant and soil water status in five field-grown cotton (*Gossypium hirsutum* L.) cultivars

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Abstract

The objective of this study was to evaluate the possibility of using the fraction of transpirable soil water (FTSW) under field conditions, to analyse genotypic differences in plant responses to soil water deficit. Two years of field experiments were carried out on a sandy soil under sub-sahelian conditions in Senegal. Five cotton cultivars (*Gossypium hirsutum* L.), with similar phenology but different yield responses to drought, were compared under two irrigation treatments differentiated after flowering. Because of differences in the rainfall pattern during the pre-flowering period, the two years resulted in marked differences in soil water hydration and effective rooting depth. Soil water deficit experienced by the plants in each elementary plot was characterized with FTSW, calculated with volumetric soil water content (measured with a neutron probe) from soil surface to the estimated effective rooting depth. Despite large differences of soil water content between years and irrigation treatments, FTSW was closely related to the predawn leaf water potential measured on the same day. Plant responses to soil water deficit were analysed with leaf water potential (ψ_1), relative water content (RWC), stomatal conductance (g_s), and crop water stress index (CWSI) measured during the crop cycle. Genotypic differences for these plant variables were found on some days, but they were frequently associated with genotypic differences in FTSW. The relationships between plant variables and FTSW, over two years of measurements and contrasting soil water profiles, were adjusted to typical logistic functions, previously used in other species. Leaf water status (ψ_1 and RWC), g_s and CWSI did not change appreciably until FTSW reached 0.4–0.5. Significant genotypic differences were found in the relationships of RWC and CWSI with FTSW, which allowed the ranking of the five cultivars for dehydration avoidance. The absence of genotypic differences in the relationships between g_s and FTSW indicates that the higher dehydration avoidance of one of the cultivars (STAM F) is not linked to stomatal regulation, but probably to osmotic adjustment. Calculation of FTSW from soil water content measurements provided an efficient way to conduct genotypic comparison of plant response to drought in field conditions over two years of contrasted rainfall pattern. © 1998 Elsevier Science B.V.

Keywords: Cotton; *Gossypium hirsutum* L.; Fraction of transpirable soil water; FTSW; Soil water deficit; Plant water status; Genotypic comparison

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1. Introduction

In most tropical African countries, cotton is an agricultural product of great economic importance. In sub-sahelian regions, it is grown under rainfed conditions, and water deficit remains as a major limitation to yield (Hearn, 1994). Genetic variability in yield has been reported in cotton subjected to water deficit (Cook and El-Zik, 1993; Munk et al., 1994). This variability is difficult to analyse, as yield under drought is the result of many physiological processes involved in the carbon and water balances of the crop (Turner, 1997). Empirical relationships between available soil water and leaf expansion or stomatal conductance (Sadras and Milroy, 1996) can be interpreted from the recent findings of relationships between soil water status, ABA content in the xylem sap and stomatal conductance (Tardieu, 1996). A number of studies under controlled or field conditions report on the effects of soil water availability, assessed as extractable or transpirable soil water, on plant water status, leaf expansion or yield [Al-Khafaf et al. (1978), on cotton; Wright and Smith (1983), on sorghum; Rosenthal et al. (1987), on cotton and sorghum; Sinclair and Ludlow (1986), on grain legumes; Muchow and Sinclair (1991), on maize; Lecoeur and Sinclair (1996), on pea].

Because of the relationship between soil water status and leaf water status, genotypic comparisons for plant responses to water deficit are difficult without a control or a measurement of soil water status as it is sensed by each genotype (Ray et al., 1997; Wery et al., 1997). Blum (1974) relates the variability among 14 sorghum genotypes in some physiological responses to water stress, to differences in soil water extracted. Ray et al. (1997) showed that differences in some plant variables between two maize hybrids were related to differences in early growth and subsequent differences in water conservation. Wery et al. (1997) showed that genotypic differences observed on a given day for net photosynthesis and leaf relative water content in field or pot grown sunflowers, were accounted for by the differences of predawn leaf water potential. In this last study, the physiological differences between genotypes on a given day relied on their water consumption (probably linked to leaf area index) and not on the plant susceptibility to soil dehydration. There are few studies where two cultivars are compared in field conditions, on the basis of the relationship between plant water status and available soil water [Wright and Smith (1983), on sorghum; Erickson et al. (1991), on groundnut].

The objective of this study was to evaluate the possibility of using the fraction of transpirable soil water (FTSW) in the field, in order to analyse genotypic differences in plant responses to soil water deficit. The experiment was conducted in sub-sahelian conditions during two years on five cotton (*Gossypium hirsutum* L.) cultivars grown with and without irrigation.

2. Materials and methods

2.1. Experimental site and growth conditions

Two experiments were carried out at CERAAS (Centre d'Etudes Régional pour l'Amélioration de l'Adaptation à la Sécheresse) at Bambey (14.42°N, 16.28°W) in Senegal, during the rainy seasons of 1995 and 1996 on two adjacent fields. Soil was a deep sandy soil with low levels of clay + silt (12%) and organic matter (0.4%). A significant variability of soil texture was observed between elementary plots of the experiment (10.5 to 13.2% clay + silt averaged over the 0–1.2 m depth soil layer). Clay + silt content was also increasing with soil depth from 10.2% in the 0- to 0.2-m layer to 13.3% in the 0.8- to 1.2-m layer.

Air temperature, relative humidity, and class 'A' pan evaporation were measured in a weather station adjacent to the experimental field. Cotton was sown on 4 Aug. 1995 and 14 Aug. 1996, on a field previously fallowed for three seasons. Delinted seeds were placed in holes in 6-m long rows spaced 1 m apart, with 0.25 m between holes. After emergence, plants were thinned to one plant per hole. Fertilizer was applied at rates of 88, 69 and 42 kg ha^{-1} of N, P, and K, split between emergence (2/3) and beginning of flowering (1/3). Insecticides were applied to minimize damage to leaves and fruits, and weeds were controlled by hand.

2.2. Experimental design, genotypes, and water deficit treatments

Five cotton cultivars were grown under two water regimes (as sub-blocks) in a split-plot design with two (1995) and three (1996) blocks. Each elementary plot was 6 × 6 m, of which the 3 × 3 m central part was used for plant measurements.

The five cultivars belong to the *Gossypium hirsutum* (L.) species: 'STAM F' (further noted STF) from Togo, 'Guazuncho II' (GUA) from Argentina, 'Coker 310' (COK), 'Deltapine 90' (DEL), and 'DES119' (DES) from USA. They were chosen to cover the range of yield response to water deficit observed in a preliminary field study (Lacape, unpublished). These five cultivars had similar phenology (only four days between the earliest and latest), but they covered the existing morphological variability within cultivated types.

Plants grew under near optimal water supply (rains and two or five supplemental irrigations in 1995 and 1996, respectively) until the beginning of flowering, then water regimes were differentiated as an irrigated treatment (IR) and a non-irrigated treatment (NI). Irrigation was applied once (1995) or twice (1996) a week to meet theoretical water requirements for a cotton crop in the zone, calculated as the product of daily class 'A' pan evaporation by a crop coefficient depending on phenological stage (Dancette, 1983). Irrigation was stopped 75 and 77 days after emergence (DAE) in 1995 and 1996, respectively. This was soon after the 'cut-out' phenological stage (72 DAE in the two seasons) and prior to first boll split. Flowering of fruiting branches was followed throughout the crop cycle using NAWF (nodal position from the apical node of the fruiting branch bearing a white flower on first node). Cut-out phenological stage, corresponding to the end of leaves production, was defined as day when NAWF reached the value of 5 (Oosterhuis et al., 1992).

2.3. Soil water content

Volumetric soil water content was measured once (1995) or twice (1996) a week with a neutron probe in a 2.7-m access tube centered in each elementary plot. Counts were made every 0.1 m down to 0.6 m and every 0.2 (1996) or 0.3 m (1995) between 0.6 and 2.7 m depths. Field calibration relating the neutron counts to gravimetrically measured water contents were realized each year on the experimental site. Calibration points included a dry profile before sowing and a near-field capacity profile obtained 48 h following a heavy irrigation.

2.4. Effective rooting depth

Effective rooting depth (ERD) was derived from neutron probe data. On a given date, ERD was defined as the depth at which soil water content was not significantly different from the measurement made on the previous date, during a period of transpiration and in the absence of water supply (Silim and Saxena, 1993). This occurred at two periods in 1995 (between days 26 and 33, and between days 54 and 61) and at one period in 1996 (between days 44 and 48). The average ERD for these three periods were, respectively, 1.20, 1.90 and 1.06 m, without any significant difference (at $P = 0.05$) between genotypes (not shown). The maximal value of ERD (ERD_{max}) was determined by comparison of the driest soil profile obtained at harvest and the wettest soil profile, obtained 68 and 69 DAE in 1995 and 1996, respectively. For each experiment, the average ERD_{max} was close to the maximal depth of soil hydration, itself linked to the amount of water received by the crop. ERD_{max} was consequently higher in 1995 (2.35 ± 0.20 m) than in 1996 (1.32 ± 0.26 m). With the hypothesis that ERD was at 0.2 m at emergence and that ERD increased linearly with time after emergence, we calculated rates of ERD progression in 1995 of 30 mm day^{-1}, from emergence to 33 DAE, and 25 mm day^{-1} between 34 and 61 DAE. In 1996, the rate of ERD progression, calculated between emergence and 48 DAE, was 18 mm day^{-1}. These value are in agreement with ERD measured in field grown cotton with P^{32} uptake (Basset et al., 1970; Marini et al., 1978). ERD was calculated with this simple model at each date of soil water measurement, until the maximal value (ERD_{max}) measured in each experimental plot.

2.5. Calculation of FTSW

The total transpirable soil water (TTSW) was estimated in each elementary plot as the soil water reserve held between an upper and a lower limit from soil surface to ERD. As stated by Ritchie (1981), these limits depend not only on soil characteristics, but also on plant characteristics, and cannot only be retained as the commonly used -0.01 and -1.5 MPa matric suction limits. The upper limit of TTSW established as the soil water content was near field capacity, i.e., measured two days after a heavy supply of water. This occurred 12 days (1995) and 6 days (1996) after emergence, when the plots had received 180 mm and 75 mm of water, respectively. These amounts of water were not sufficient to restore field capacity at a depth lower than 0.3–0.5 m. The measurement taken on these dates at 0.3 m depth was used to adjust, for each plot, the overall relationship obtained in laboratory between soil water holding capacity (pressure of 0.03 MPa) and soil depth. This procedure was used to consider the previously mentioned variability of soil texture with depth and between elementary plots. For example, at 1.2 m depth, soil water content at the upper limit varied from 0.11 to 0.16 m^3 m^{-3} in the 1995 experiment, and from 0.12 to 0.18 m^3 m^{-3} in the 1996 experiment.

The lower limit of TTSW was defined as the lowest field-measured soil water content after the cotton plants had stopped extracting water (Ritchie, 1981). At each depth, the lower limit was determined as the lowest moisture content obtained during a period covering the last two weeks before harvest. As depth increases, this lower limit becomes higher than the water content at the permanent wilting point measured in the laboratory with a pressure of -1.5 MPa. As an example, the average values obtained in 1996, at 0.2–0.4, 0.4–0.8 and 0.8–1.2 m depths were 0.033, 0.051, and 0.058 m^3 m^{-3}, respectively, for field-measured lower limits, as compared with 0.037, 0.044, and 0.045 m^3 m^{-3} for laboratory measurements. Wright and Smith (1983) and Savage et al. (1996) noted such discrepancies between field and -1.5 MPa lower limits in the case of cotton and sorghum. This deviation can be accounted for by the fact that, in the deeper layers of soil, the access to water is reduced by the root density. Observations made in our 1996 experiment at harvest time showed that 87% of the total root length was concentrated in the upper 60 cm layer of soil, and no roots was observed below 1.20 m (not shown).

On each date of measurement, the total transpirable soil water ($TTSW_t$) of each elementary plot was calculated as the water reserve held between the upper and lower limits integrated over the estimated effective rooting depth (ERD_t). Because of the higher maximal ERD in 1995, the maximal TTSW was higher in 1995 (187 mm) as compared to 1996 (124 mm).

As suggested by Sinclair and Ludlow (1986), the fraction of transpirable soil water ($FTSW_t$), at a given date and at the corresponding effective rooting depth (ERD_t), was calculated as the ratio of available (ASW_t) to total transpirable soil water ($TTSW_t$). ASW_t was calculated as the difference between the amount of water measured on this day and the amount of water at lower limit, integrated over the ERD_t.

2.6. Plant water status

Leaf relative water content (RWC), leaf water potential (ψ_l), and stomatal conductance (g_s) were measured on every 3–7 days until the cut-out stage of the crop. Measurements were made between 12:30 and 14:00 (solar time) on four (1995) and three (1996) plants per plot. Leaf water potential was measured with a pressure chamber (Soil Moisture PWSC3000 Santa Barbara, CA, USA) on the uppermost fully expanded leaf (4th to 5th node from the top) and completely exposed to full sunlight. Predawn leaf water potential was measured, in each block and irrigation treatment, on the five cultivars at 69 DAE in 1995 and on two cultivars (DEL and DES) at four dates (between 44 and 65 DAE) in 1996. RWC and g_s measurements were made on the leaf immediately below the last expanded leaf. RWC was measured on a 2 cm^2 leaf sample, with a 4-h floating time in distilled water to reach turgid weight. Stomatal conductance was measured with a Licor 1600 porometer (Lincoln, NE, USA), when PAR was above 1100 $\mu mol\ m^{-2}\ s^{-1}$.

The canopy temperature (T_c°) was measured between 13:00 and 14:00 (solar time), twice a week, using a calibrated Telatemp AG42 infrared radiometer (Fullerton, CA, USA) with a 4° field of view and an emissivity set to 0.99. The radiometer readings were averaged from four measurements (from each corner) made with an oblique angle of around 30°, viewing the centre part of the plot at a distance of approximately 4.5 m. Temperature measurements started with irrigation treatments in which bare soil could be avoided from the view (LAI above 2 and more than 75% soil cover). Vapour pressure deficit (VPD) was determined from psychrometric equations using wet and dry bulb temperatures measured by a ventilated psychrometer held at about 0.5 m above the crop. Air temperature (T_a°) measured from dry bulb thermometer was used to calculate canopy minus air temperature difference ($T_c^\circ - T_a^\circ$). When using the empirical approach of Idso et al. (1981a), the calculation of a crop water stress index (CWSI) requires the definition of a linear non-water stress base line of $T_c^\circ - T_a^\circ$ as a function of air VPD. To establish this base line, several set of measurements were made in both experiments with radiometer measurements taken every 15 to 20 min between 08:00 and 17:00 on clear days following irrigation (3 dates in 1995 and 2 in 1996). No significant difference (at $P = 0.05$) was found between the five genotypes for the slope and intercept of this non-water stress base line. Base line coefficients varied with crop age and experiment (not shown). The upper limit of $T_c^\circ - T_a^\circ$, considered to be independent of the VPD (Idso et al., 1981a), was fixed at +3.8°C, the highest reading obtained in the completely wilted but non-defoliated plots in 1996. Air temperature varied between 35 and 41°C during the course of the measurements. At a given value of VPD, the CWSI was calculated as the ratio of the vertical distance of an observed $T_c^\circ - T_a^\circ$ data point above the lower (i.e., non-water stress) base line divided by the total vertical distance between the upper and lower lines.

2.7. Statistical analysis

For each date of measurement, cultivar and irrigation treatments were compared with analysis of variance of a split-plot design using the GLM procedures

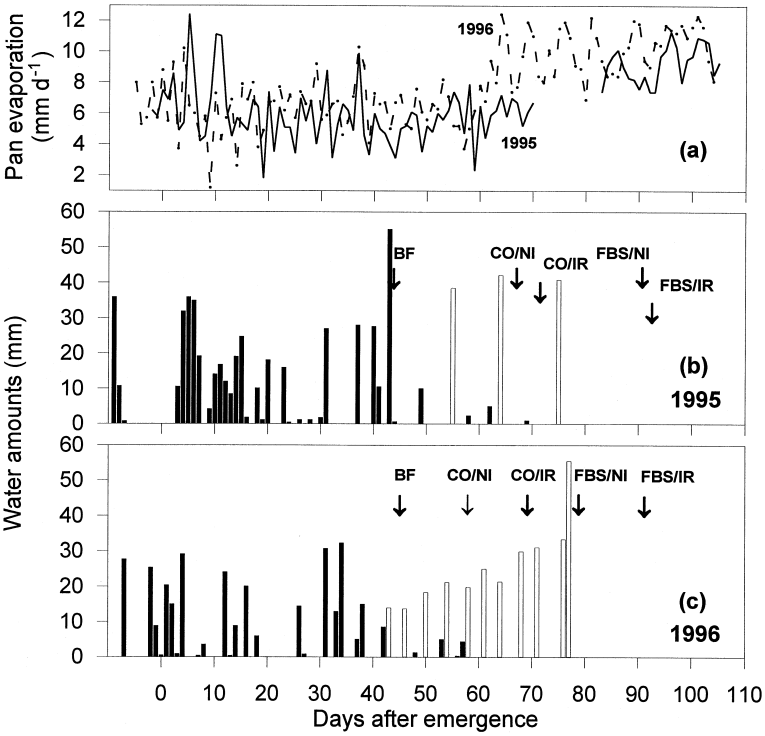


Fig. 1. Pattern of class ‘A’ pan evaporation (a) during the cotton crop cycle in 1995 (straight line) and 1996 (dashed line). Amounts of water received by irrigated (IR) and non-irrigated (NI) plots (closed bars) in 1995 (b) and 1996 (c). Additional water received by IR (open bars). Vertical arrows indicate beginning of flowering (BF), cut-out (CO), and first boll split (FBS) of the cotton crops under IR and NI treatments.

of SAS (1988). Nonlinear regressions between plant water status variables and FTSW were made with logistic equations using Table Curve 2D (Jandel Sc., San Rafael, CA, USA). Genotypic differences in the fitting curves were tested with likelihood ratio test, and a *F*-test of Snedecor was performed between

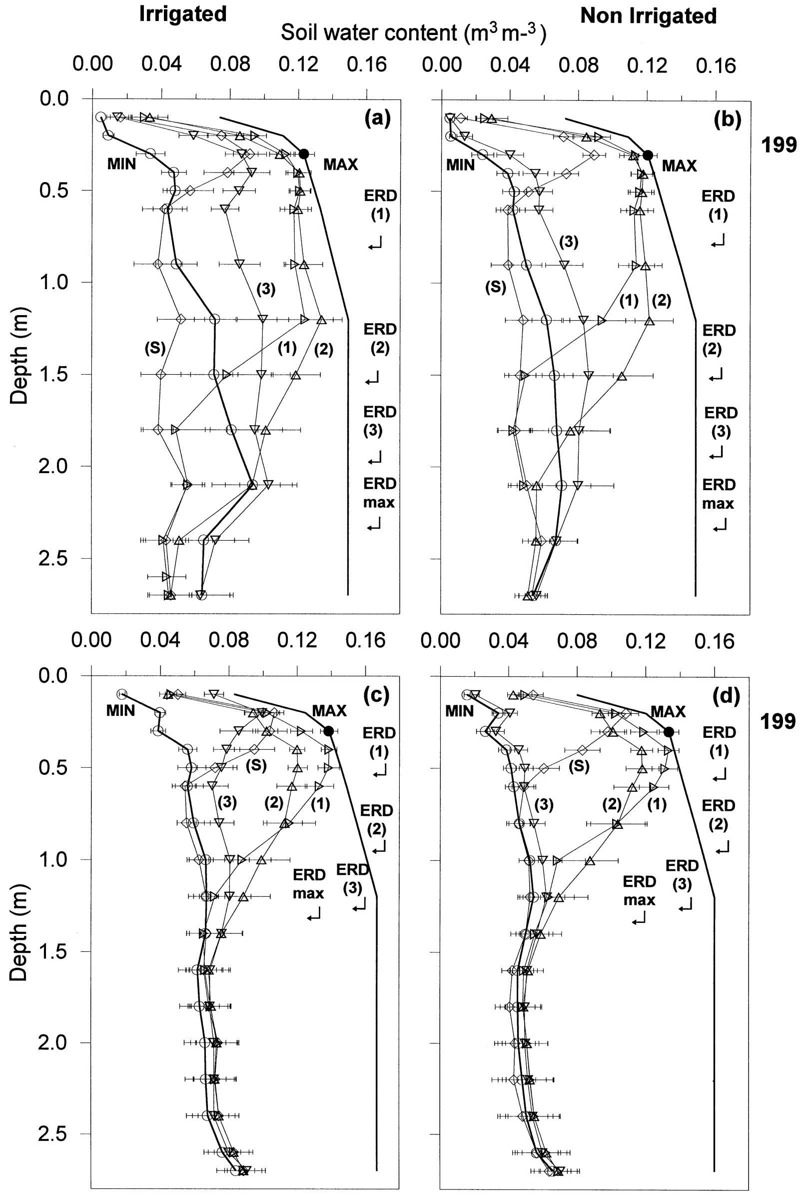


Fig. 2. Variation with depth of volumetric soil water content for irrigated (a and c) and non-irrigated (b and d) cotton, at sowing (S) and at various days after emergence (DAE). (1) Close to square initiation (20 DAE in 1995 and 1996, respectively); (2) differentiation of irrigation treatments (47 and 41 DAE in 1995 and 1996, respectively); (3) close to cut-out of the irrigated crops (69 DAE). Each point is the average of 10 (1995) or 15 (1996) measurements (one per block and cultivar). Horizontal bars indicate confidence intervals at $P = 0.05$. Horizontal arrows show the estimated effective rooting depth (ERD) on dates (1), (2), (3) and maximal ERD value ($\mathrm{ERD}_{\mathrm{max}}$). MIN: minimal soil water content measured at each depth in the two weeks before harvest. MAX: maximal soil water content measured at field capacity at 0.3 m depth and extrapolated from laboratory measurements of water holding capacity for the deeper layers.

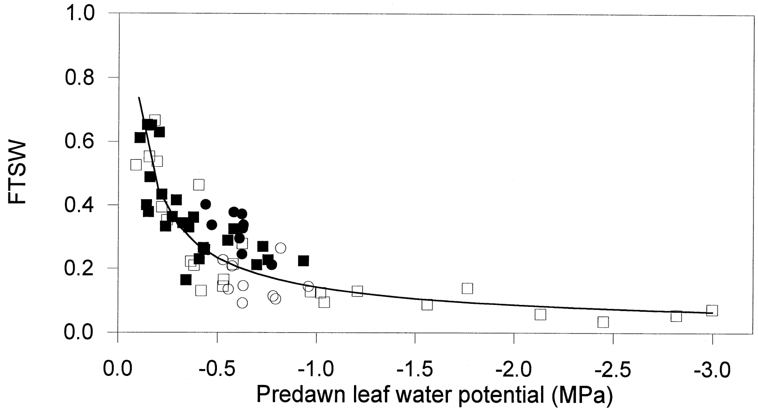


Fig. 3. Relationship between the fraction of transpirable soil water (FTSW) and predawn leaf water potential (ψ_l) measured on irrigated (closed symbols) and non-irrigated (open symbols) cottons in 1995 (circles) and 1996 (squares). Coordinates of each point are the average of two to three plants for predawn leaf water potential and the value of FTSW for each elementary plot. $\mathrm{FTSW} = 0.14^*(-\psi_l)^{-0.72}$, (CVe = 18%).

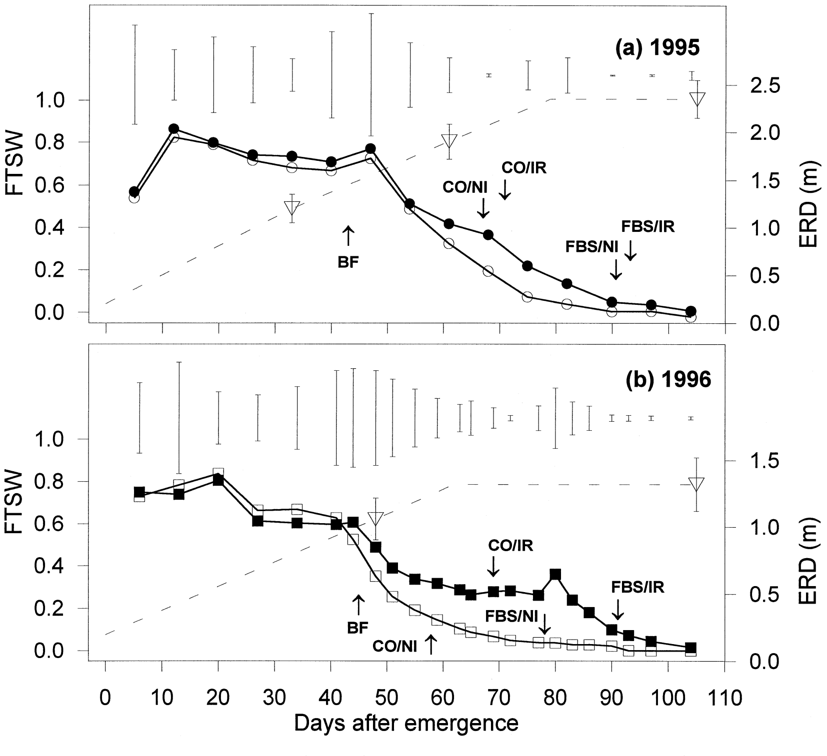


Fig. 4. Pattern of the fraction of transpirable soil water (FTSW) during the crop cycle in irrigated (IR, closed symbols) and non-irrigated (NI, open symbols) cottons in 1995 (a) and 1996 (b). Each point is the average of 10 (1995) or 15 (1996) plots (block × cultivar). Vertical bars are LSD at $P = 0.05$. The dashed curve indicate the development of the effective rooting depth (ERD) estimated from measurements at three dates on 20 plots in 1995 and at two dates on 30 plots in 1996. Vertical arrows indicate beginning of flowering (BF), cut-out (CO), and date of first boll split (FBS) of the cotton crops. Irrigation was stopped at BF in NI plots and one week after CO in IR plots.

single models grouping all the genotypes and individual or sub-groups of genotypes. When mentioned, LSD or confidence intervals are given for the 0.05 probability level.

3. Results and discussion

3.1. Amounts of water applied and soil water content

Pan evaporation was slightly higher in 1996 than in 1995 (Fig. 1a). Air VPD measured at 13:00–14:00 varied between 2 and 3 kPa during the first part of the crop season, and after around day 60 after emergence (end of rains), it regularly increased to 6 kPa (not shown). The amount of water received by the cotton crops was the same for the irrigated (IR) and the non-irrigated (NI) plots until the beginning of flowering, but it was lower in 1996 (293 mm) than in 1995 (489 mm), because of differences of rainfall between the two years (Fig. 1b and c). On IR plots, irrigation was stopped between cut-out and first boll split stages. The amount of water received by IR plots after the beginning of flowering was larger in 1996 (310 mm) than in 1995 (129 mm). Over the two years, the total amount of water received by the IR plots during the crop cycle was the same (618 mm in 1995 and 603 mm in 1996), but the distribution between pre- and post-flowering periods was quite different. Because of a higher rainfall in the pre-flowering period of 1995, the NI treatment received more water in 1995 (497 mm) than in 1996 (304 mm). In both years, the NI plots received almost no water after the beginning of flowering.

At sowing, the soil water content was close to the soil permanent wilting point, except in the first 0.4 m previously rehydrated by the pre-sowing irrigation and rainfall (Fig. 2). Even in irrigated plots, the

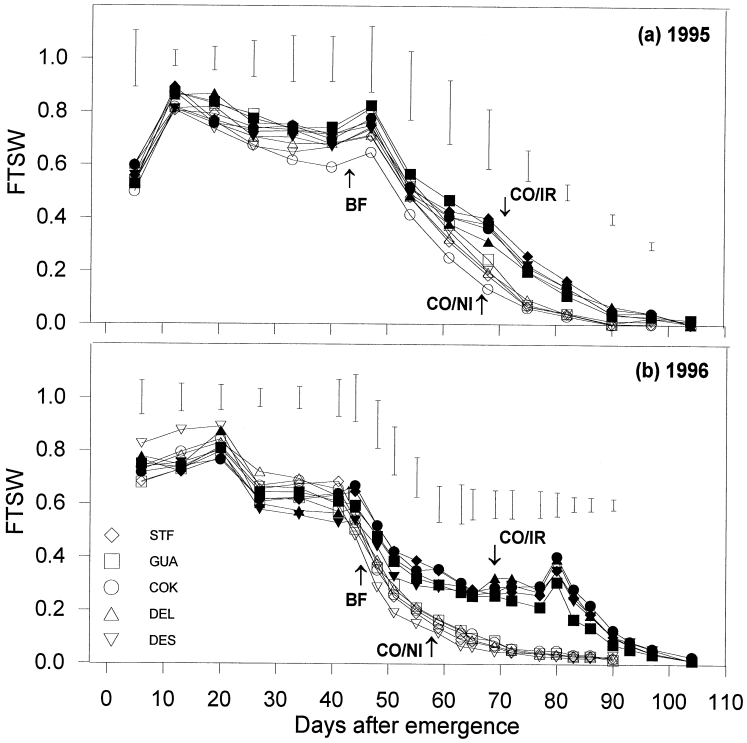


Fig. 5. Comparison of the five cultivars for the pattern of the fraction of transpirable soil water (FTSW) during the crop cycle in irrigated (IR, closed symbols) and non-irrigated (NI, open symbols) cottons in 1995 (a) and 1996 (b). Each point is the average of two (1995) or three (1996) measurements. Vertical bars indicate LSD at $P = 0.05$. Vertical arrows indicate beginning of flowering (BF) and cut-out (CO) of the cotton crops.

amount of water applied was not sufficient to reach the maximum soil water content (field capacity). The marked difference in the seasonal pattern of water application between the two years resulted in quite different soil water profiles (Fig. 2). Compared to the measurements made at sowing, the wetting front reached the bottom of the neutron probe access tube (2.7 m) in most of the IR plots in 1995, although it remained above 1.8 m in 1996.

The minimum soil water content (MIN) for the cotton crop in this soil was reached at first boll split in both years. In 1995, MIN was higher than the initial soil water content at sowing (S), indicating that a part of the water received during the cycle was not used by the crop, even in NI plots. The maximum effective rooting depth (ERD_{max}), calculated from the comparison between MIN and soil water content at date 3, was on average 2.3 m in 1995 (Fig. 2), which is close to the rooting potential of cotton (Hearn, 1994). In 1996, the average ERD_{max} remained at 1.3 m depth, probably because root development was stopped at this depth by the low soil water content (Fig. 2c and d). As a consequence, the maximum TTSW was smaller in 1996 (124 mm) than in 1995 (187 mm). Soil water content remained the same in IR and NI plots until the beginning of

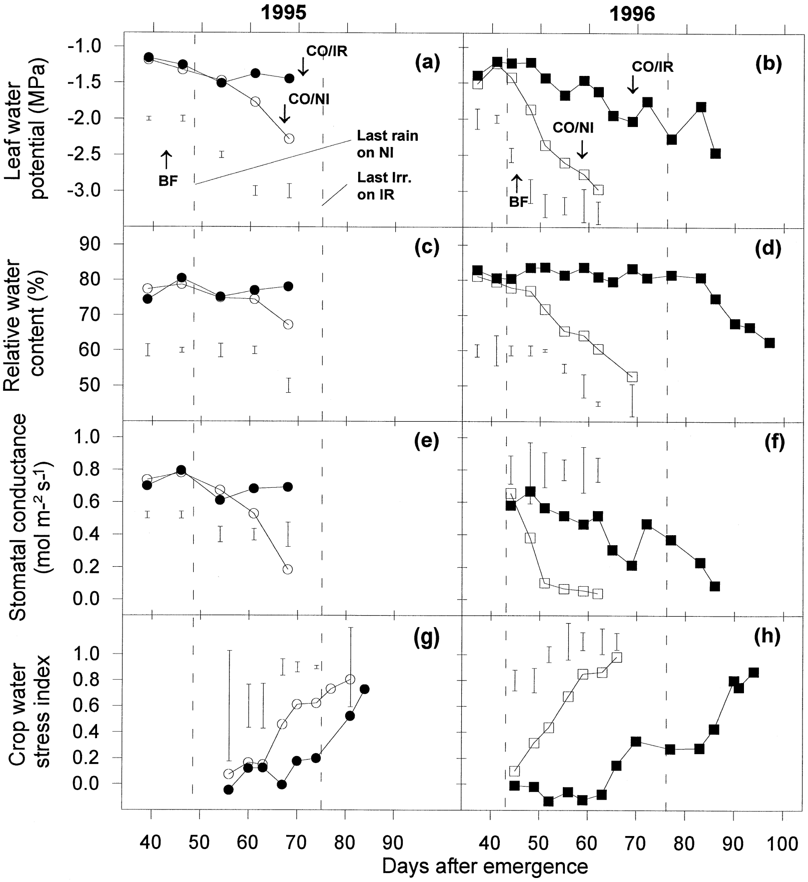


Fig. 6. Development with time of midday leaf water potential (ψ_l, a and b), relative water content (RWC, c and d), stomatal conductance (g_s, e and f), and crop water stress index (CWSI, g and h) of irrigated (IR, closed symbols) and non-irrigated (NI, open symbols) cottons. Each value of ψ_l, RWC, and g_s is the average of 40 (1995) or 45 (1996) measurements (plant × block × cultivar). Each value of CWSI is the average of four infrared radiometer readings in each of 10 (1995) and 15 (1996) elementary plots (block × cultivar). Vertical bars indicate LSD at $P = 0.05$. Vertical arrows indicate beginning of flowering (BF) and cut-out (CO) of the cotton crops. Dashed vertical lines indicate dates of last rain on NI plots and of last irrigation on IR plots.

flowering (dates 1 and 2 in Fig. 2). Then, it was markedly reduced in NI plots compared to IR plots at least until 1.0 m depth (date 3). This soil dehydration of NI plots was more pronounced in 1996 because of the lower amount of water applied (Fig. 1b and c).

3.2. Relationship between FTSW and predawn leaf water potential

The fraction of transpirable soil water (FTSW), calculated from the measurements of soil water content and the estimated effective rooting depth, was used to quantify the soil water deficit experienced by the crop (Sinclair and Ludlow, 1986). As shown in Fig. 3, FTSW was closely related to predawn leaf water potential (predawn ψ_l), which is itself linked to the soil water potential in the rooting zone (Dwyer and Stewart, 1984). The six lowest values of predawn ψ_l, ranging from -1.5 to -3.0 MPa, correspond to the 65 DAE measurements made on NI plots in 1996. This date was 22 days after the cessation of irrigation, and by that time plants had passed cut-out phenological stage. In plants with anisohydric behaviour such as cotton, predawn ψ_l can be used to quantify the soil water deficit experienced by the crop (Guo et al., 1994). A linear relationship has been shown between ψ_l and ABA content of the xylem sap, which is itself related to stomatal conductance and leaf carbon exchange rate [Tardieu et al. (1996); Wery et al. (1997), in sunflower]. From the overall relation between FTSW and predawn ψ_l, it can be concluded that FTSW gives, in our experiments, a good estimate of soil water deficit experienced by the plants, despite the large differences in soil water status between the two years.

3.3. Evolution of FTSW during the plant cycle

During the pre-flowering period, irrigation and rainfall maintained FTSW between 0.7 and 0.8 in 1995 and between 0.6 and 0.7 in 1996 (Fig. 4), a range which is generally considered as optimal for leaf water status, transpiration and leaf expansion (Lecoeur and Sinclair, 1996; Sadras and Milroy, 1996). After the beginning of flowering, FTSW rapidly fell down to 0.3, even in IR plots, because the increase of ERD (between dates 2 and 3 in Fig. 2) occurred in soil layers not restored to field capacity at flowering (date 2). A value of 0.3 for FTSW has been cited as a lower limit below which cotton yield is limited by water deficit (Cull et al., 1981). After cessation of irrigation (around day 76) FTSW progressively dropped to near-zero at first boll split stage. This indicates that IR plots experienced a progressive terminal water deficit after the beginning of flowering. In NI plots, irrigation was stopped earlier than on IR plot (beginning of flowering) and FTSW rapidly fell down to near-zero values. This reduction was more pronounced in 1996, because the amount of water stored in the soil during the pre-flowering period was lower than in 1995 (Fig. 2).

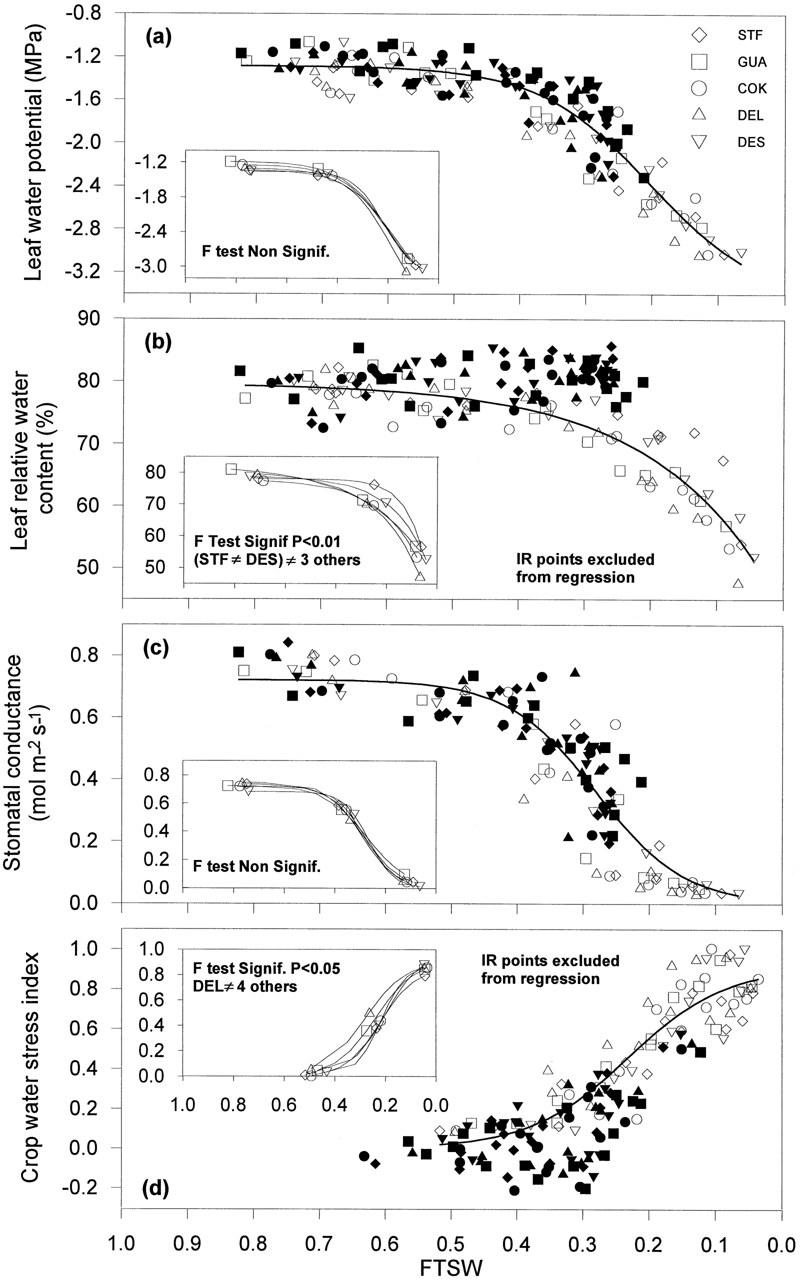
Although significant genotypic differences for FTSW were found by analysis of variance on some dates of measurement (not shown), the evolution of FTSW during the crop cycle was similar for the five cultivars, both in IR and NI plots (Fig. 5). In 1995, cv. COK had a consistently lower FTSW in NI plots

Fig. 7. Relationship between the fraction of transpirable soil water (FTSW) and midday leaf water potential (ψ_l, a), relative water content (RWC, b), stomatal conductance (g_s, c), and crop water stress index (CWSI, d) of irrigated (closed symbols) and non-irrigated (open symbols) cottons in 1995 and 1996. Each point of ψ_l, RWC, and g_s is the average of eight (1995) or nine (1996) measurements made on each cultivar. Each point of CWSI is the average of four infrared radiometer readings in each of two (1995) and three (1996) elementary plots of each cultivar. The corresponding FTSW is the average of two (1995) and three (1996) elementary plots. Curve fitting of the whole set of data was made by nonlinear regressions, as follows.

$\psi_l = -3.48 + 2.20/(1 + \exp(-(\mathrm{FTSW} - 0.2)/0.085))$ (CVe = 11.0%)
$\mathrm{RWC} = 43.46 + 36.21 * (1 - \exp(-(\mathrm{FTSW} * 5.62)))$ (CVe = 4.4%)
$g_s = 0.72/(1 + \exp(-(\mathrm{FTSW} - 0.28)/0.07))$ (CVe = 21.6%)
$\mathrm{CWSI} = 0.92/(1 + \exp(-(\mathrm{FTSW} - 0.23)/-0.07))$ (CVe = 23.5%)

Inset in each figure represents the regressions obtained on each cultivar with the same type of equation. Models grouping all the genotypes or sub-groups of genotypes were compared with a F-test of Snedecor.

than the four other cultivars, although the soil variability was too high to find significant differences on each date. In NI plots of 1996, cv. DES had higher FTSW than the others at the beginning of the season, but it had lower values after cessation of irrigation (days 44 to 53). As previously shown with predawn leaf water potential (Wery et al., 1997), we can conclude that the five cultivars were not experiencing the same soil water deficit (characterized with FTSW) on each date of measurement.



3.4. Plant water status

Plant response to soil water deficit was analysed from the comparison of IR and NI plants for midday leaf water potential (ψ_l), relative water content (RWC), stomatal conductance (g_s) and crop water stress index (CWSI). CSWI is mainly linked to stomatal regulation, and its effect on the energy balance of the crop (Jackson, 1982). We have represented on Fig. 6 the development with time of the average values of these four plant measurements for the five cultivars. Although genotypic differences were observed for some variables on some dates of measurement, the development with time was similar for the five genotypes, and there was no interaction between genotypes and irrigation treatments (not shown).

In 1995, the IR plants maintained leaf water potential above -1.5 MPa until the cut-out stage (Fig. 6a). CWSI was maintained below 0.3 until the end of the period of irrigation (Fig. 6g). This value is generally retained as an indicator of plant stress, and used as a threshold level for irrigation management (Reginato, 1983). In 1996, IR plants clearly experienced some degree of water deficit, as shown by the reduction of ψ_l (Fig. 6b) and g_s (Fig. 6f) after day 51, that is when FTSW fell below 0.4 (Fig. 4) and when Pan evaporation was rising (Fig. 1a). Nevertheless, RWC was maintained at high values (around 80%) until day 85 (Fig. 6d). Leaf osmotic potential (not shown) decreased in a parallel manner as ψ_l, indicating a maintenance of turgor potential. This stability in RWC under conditions of reduced ψ_l is usually associated with a stability in turgor potential resulting from osmotic adjustment (Sinclair and Ludlow, 1986; Lecoeur et al., 1992). Osmotic adjustment is known to be of a great magnitude in cotton (Oosterhuis and Wullschleger, 1984; Turner et al., 1986), particularly in the case of progressive and moderate water deficits. After day 65, IR plants had a reduced g_s (Fig. 6f) and their CWSI (Fig. 6h) increased above 0.3.

In the NI plants of 1996, the cessation of irrigation (43 DAE) induced a rapid variation of the four above-mentioned variables, in comparison with IR plants. In less than 15 days, g_s dropped to 10% of its initial value (Fig. 6f) and CWSI (Fig. 6h) increased 10-fold, indicating that the plants experienced a rapid and severe water deficit. Transpiration in NI plants had almost stopped, and their canopy was slightly warmer than the air (not shown); although in IR plots, plants were at the same time 7–8°C cooler than the air, as previously observed by Jackson (1982). In 1995, the difference between NI and IR plants was less than in 1996, for the four variables (Fig. 6a,c,e,g) which is in agreement with the smaller difference observed on FTSW between IR and NI in 1995 compared to 1996 (Fig. 4).

3.5. Relationships between plant and soil water status

Although the soil water status (depth of wetting and of water extraction) and the rate of soil drying differed between experiments, irrigation treatments (Fig. 2), replications, and sometimes between cultivars (Fig. 4), the calculation of FTSW provided a way to unify the whole set of data (Fig. 7). For each plant variable (Fig. 6), we have represented the average value obtained on each combination of date × cultivar × water deficit treatment, as a function of FTSW calculated on the same day. In the case of CWSI, plant and soil measurements were not always made on the same day, and FTSW was linearly interpolated from previous and next closest values. The equation of the regression relating a plant variable to FTSW was chosen to give the lowest coefficient of variation and the lowest number of parameters. In the case of ψ_l (Fig. 7a) and g_s (Fig. 7c), both IR and NI treatments were included in the regression, as the two water regimes clearly fell in the same overall relationship. For RWC (Fig. 7b) and CWSI (Fig. 7d), we only used data from NI plots in the regression. As previously shown (Fig. 6b and d), the moderate and progressive water deficit of IR plots in 1996 has allowed some degree of osmotic adjustment to be established, resulting in a maintenance of RWC. As found by Idso et al. (1981b), negative values of CWSI (Fig. 7d) were frequently observed in IR plots. Although CWSI theoretically varies between 0 and 1, the precision on its calculation is lower in the low VPD range, resulting in a larger scatter around the CWSI = 0 value and possible negative values.

The equations found from the nonlinear fitting process are comparable to those obtained on grain legumes (Sinclair and Ludlow, 1986; Lecoeur and Sinclair, 1996), rice (Wopereis et al., 1996) or other crops (Sadras and Milroy, 1996). In cotton, Rosenthal et al. (1987) related leaf transpiration rates of pot grown plants to the transpirable soil water. Their set of data was fitted to two linear phases with a threshold value of FTSW of 0.25. Conversely, Hearn and Constable (1984) found that ψ_1 and net carbon exchange rate gradually decreased with soil water deficit, and that no clear threshold could be defined. In our case, each variable was found essentially unchanged until the soil dried to a FTSW of 0.4–0.5, but this threshold value is probably depending on plant (root distribution), soil texture, and evaporative demand (Hearn, 1994; Sadras and Milroy, 1996).

Fig. 7 provides a framework for the genotypic comparison of plant responses to drought, with separate analysis of the rate of soil dehydration (given by the rate of FTSW reduction), and the plant response to soil dehydration (given by the shape of the regression curve). The analysis of variance of plant variables conducted on each date of measurement yielded significant genotypic differences ($P = 0.05$) in the case of RWC (days 59, 62, 83, and 86 in 1996) and ψ_1 (day 39 in 1995; and days 41, 44, 65, and 86 in 1996). A number of authors observed genotypic differences between cotton genotypes for plant variables such as g_s (Leidi et al., 1993), net carbon exchange rate (Pettigrew et al., 1993; Leidi et al., 1993), canopy temperature (Hatfield et al., 1987). Nevertheless, these genotypic differences observed on a given day are difficult to interpret because they are a combination of soil water consumption (reducing FTSW) and plant response to soil dehydration (Ray et al., 1997; Wery et al., 1997). In our experiments, significant cultivar differences were observed for FTSW, on most of the days when differences for plant water status were found (see, for example, day 39 in Fig. 5a). The maintenance of a better leaf water status for some cultivars, on a given day, does not necessarily indicate a higher tolerance to soil dehydration, but may be the consequence of a lower transpiration during the previous days (Wery et al., 1997). The regressions previously established between plant variables and FTSW were recomputed per cultivar and are represented as insets on Fig. 7. No significant difference was found between the five cultivars for the relationships between ψ_1 and FTSW (Fig. 7a) or between g_s and FTSW (Fig. 7c). In the case of RWC (F-test significant at $P = 0.01$) and CWSI (F-test significant at $P = 0.05$) individual regressions of one or two of the varieties were found significantly different from the others. The susceptibility of RWC to soil dehydration (inset Fig. 7b) can be ranked in the following increasing order: STF < DES < DEL, COK, and GUA. This indicates that STF has a higher capacity of dehydration avoidance than the four other cultivars, but it is not resulting from a higher susceptibility of stomata to soil dehydration, because STF is not different from the others in the $g_s = f(\mathrm{FTSW})$ relationship (Fig. 7c). It could rather be the result of a higher capacity of osmotic adjustment of STF. DEL was significantly different from the four other cultivars in the response of CWSI to soil dehydration (Fig. 7d), but not in the $g_s = f(\mathrm{FTSW})$ relationship (Fig. 7c). It may be the consequence of a higher dehydration of the canopy, because RWC (Fig. 7b) and ψ_1 (Fig. 7a) decreased at a faster rate with FTSW for this cultivar.

4. Conclusion

Comparing several cultivars for their responses to drought under field conditions requires the quantification of the soil water deficit experienced by each cultivar, in each irrigation treatment and year (Ray et al., 1997). Our results on cotton and sunflower (Wery et al., 1997) show that it is difficult to reproduce under field conditions the same water deficit over experiments and cultivars. The fraction of transpirable soil water (FTSW), calculated from measurements of soil water content and estimation of effective rooting depth, provided an efficient way to unify two years with two irrigation treatments that led to large differences in soil hydration and water extraction by the plants. The same conclusions were drawn by Wery et al. (1997) with predawn leaf water potential which was closely related to FTSW in our experiments.

Short-term variables of plant water status (ψ_1, RWC) or plant response to water deficit (g_s, CWSI) were closely linked to FTSW over the range of cultivars and experimental conditions. Combination of field trials with greenhouse experiments (such as those of Ray and Sinclair, 1997), in genotypic comparisons, will be probably easier with this approach as we were using the same variable to characterize the soil water deficit experienced by the plant. Among the four plant variables used in our study, RWC gave the lowest coefficient of variation for the nonlinear regression and gave significant differences between genotypes in the parameters of the equation. For anisohydric species such as cotton, our results emphasize the potential of RWC (Sinclair and Ludlow, 1985; Schonfeld et al., 1988) and canopy temperature (Hatfield et al., 1987) measurements for genotypic comparison of plant response to drought under field conditions, provided they are coupled with measurements of FTSW or predawn leaf water potential.

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References

Al-Khafaf, S., Wierenga, P.J., Williams, B.C., 1978. Evaporative flux from irrigated cotton as related to leaf area index, soil water, and evaporative demand. Agron. J. 70, 912–917.

Basset, D.M., Stockton, J.R., Dickens, W.L., 1970. Root growth of cotton as measured by P^{32} uptake. Agron. J. 62, 200–203.

Blum, A., 1974. Genotypic responses in sorghum to drought stress: I. Response to soil moisture stress. Crop Sci. 14, 361–364.

Cook, C.G., El-Zik, K.M., 1993. Fruiting and lint yield of cotton cultivars under irrigated and non-irrigated conditions. Field Crops Res. 33, 411–421.

Cull, P.O., Hearn, A.B., Smith, R.C.G., 1981. Irrigation scheduling of cotton in a climate with uncertain rainfall: I. Crop water requirements and response to irrigation. Irrig. Sci. 2, 27–140.

Dancette, C., 1983. Estimation des besoins en eau des principales cultures pluviales en zone soudano-sahélienne. Agron. Trop. 38 (4), 281–293.

Dwyer, L.M., Stewart, D.W., 1984. Indicators of water stress in corn (*Zea mays* L.). Can. J. Plant Sci. 64, 537–546.

Erickson, P.I., Ketring, D.L., Stone, J.F., 1991. Response of internal tissue water balance of peanut to soil water. Agron. J. 83, 248–253.

Guo, Y., Landivar, J.A., Hengeller, J.C., Moore, J., 1994. Responses of cotton leaf water potential and transpiration to vapour pressure deficit and salinity under arid and humid climate conditions. Proc. Beltwide Cot. Prod. Conf., San Diego, CA, pp. 1301–1308.

Hatfield, J.L., Quisenberry, J.E., Dilbeck, R.E., 1987. Use of canopy temperatures to identify water conservation in cotton germplasm. Crop Sci. 27 (2), 269–273.

Hearn, A.B., 1994. The principles of cotton water relations and their application in management. In: Constable G.A., Forrester, N.W. (Eds.), Challenging the Future. Proc. World Cotton Conf.-1, Brisbane, Australia, pp. 66–92.

Hearn, A.B., Constable, G.A., 1984. Irrigation for crops in a sub-humid environment: VII. Evaluation of irrigation strategies for cotton. Irrig. Sci. 5, 75–94.

Idso, S.B., Jackson, R.D., Pinter, P.J. Jr, Reginato, R.J., Hatfield, J.L., 1981a. Normalizing the stress degree day parameter for environmental variability. Agric. Meteorol. 24, 45–55.

Idso, S.B., Reginato, R.J., Reicosky, D.C., Hatfield, J.L., 1981b. Determining soil induced water potential depressions in alfalfa by means of infrared thermometry. Agron. J. 73, 826–830.

Jackson, R.D., 1982. Canopy temperature and crop water stress. In: Hillel, D. (Ed.), Advances in Irrigation, Vol. 1. Academic Press, NY, pp. 43–85.

Lecoeur, J., Sinclair, T.R., 1996. Field pea transpiration and leaf growth in response to soil water deficits. Crop Sci. 36 (2), 331–335.

Lecoeur, J., Wery, J., Turc, O., 1992. Osmotic adjustment as a mechanism of dehydration postponement in chickpea (*Cicer arietinum* L.) leaves. Plant Soil 144, 177–189.

Leidi, E.O., López, J.M., López, M., Gutierrez, J.C., 1993. Searching for tolerance to water stress in cotton genotypes: photosynthesis, stomatal conductance and transpiration. Photosynthetica (Prague) 28 (3), 383–390.

Marini, P., Kaiser, R., Villemin, P., 1978. Etude à l'aide de P^{32} du développement racinaire du cotonnier sur deux types de sol de la plaine du Mangoky. Coton Fibres Trop. 33 (2), 291–306.

Muchow, R.C., Sinclair, T.R., 1991. Water deficit effects on maize yields under current and 'greenhouse' climates. Agron. J. 83, 1052–1059.

Munk, D.S., Grimes, D.W., Kerby, T.A., 1994. Plant responses to late season water deficits in Acala cotton cultivars. In: Constable, G.A., Forrester, N.W. (Eds.), Challenging the Future. Proc. World Cotton Conf.-1, Brisbane, Australia, pp. 14–17.

Oosterhuis, D.M., Bourland, F., Tugwell, N.P., 1992. Basis for nodes above white flower monitoring system. Ark. Farm Res. 41 (5), 3–5.

Oosterhuis, D.M., Wullschleger, S.D., 1984. Osmotic adjustment in cotton (*Gossypium hirsutum* L.) leaves and roots in response to water stress. Plant Physiol. 84, 1154–1157.

Pettigrew, W.T., Heitholt, J.J., Vaughn, K.C., 1993. Gas exchange differences and comparative anatomy among cotton leaf-type isolines. Crop Sci. 33, 1295–1299.

Ray, J.D., Sinclair, T.R., 1997. Stomatal closure of maize hybrids in response to drying soil. Crop Sci. 37, 803–807.

Ray, J.D., Samson, B.K., Sinclair, T.R., 1997. Vegetative growth and soil water extraction of two maize hybrids during water deficits. Field Crops Res. 52, 135–142.

Reginato, R.J., 1983. Field quantification of crop water stress. Trans. ASAE, Am. Soc. Agric. Eng., pp. 772–781.

Ritchie, J.T., 1981. Water dynamics in the soil–plant–atmosphere system. Plant Soil 58, 81–96.

Rosenthal, W.D., Arkin, G.F., Shouse, P.J., Jordan, W.R., 1987. Water deficit effects on transpiration and leaf growth. Agron. J. 79, 1019–1026.

Sadras, V.O., Milroy, S.P., 1996. Soil water thresholds for the responses of leaf expansion and gas exchange: a review. Field Crops Res. 47, 253–266.

SAS Institute, 1988. SAS/STAT User's Guide, Release 6.03 edn. SAS Inst., Cary, NC.

Savage, M.J., Ritchie, J.T., Bland, W.L., Dugas, W.A., 1996. Lower limit of soil water availability. Agron. J. 88, 644–651.

Schonfeld, M.A., Johnson, R.C., Carver, B.F., Mornhinweg, D.W., 1988. Water relations in winter wheat as drought resistance indicators. Crop Sci. 28, 526–531.

Silim, S.N., Saxena, M.C., 1993. Adaptation of spring sown chickpea to the Mediterranean basin: I. Response to moisture supply. Field Crops Res. 21, 121–136.

Sinclair, T.R., Ludlow, M.M., 1985. Who taught plants thermodynamics? The unfulfilled potential of plant water potential. Aust. J. Plant Physiol. 12, 213–217.

Sinclair, T.R., Ludlow, M.M., 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. Aust. J. Plant Physiol. 13, 329–341.

Tardieu, F., 1996. Drought perception by plants. Do cells of droughted plants experience water stress?. Plant Growth Regul. 20, 93–104.

Tardieu, F., Lafarge, T., Simmoneau, T., 1996. Stomatal control by fed or endogenous xylem ABA in sunflower: interpretation of correlations between leaf water potential and stomatal conductance in anisohydric species. Plant Cell Environ. 16, 75–84.

Turner, N.C., 1997. Further progress in crop water relations. Adv. Agron. 58, 293–338.

Turner, N.C., Hearn, A.B., Begg, J.E., Constable, G.A., 1986. Cotton (*Gossypium hirsutum* L.): physiological and morphological responses to water deficits and their relationship to yield. Field Crops Res. 14, 153–170.

Wery, J., Griveau, Y., Belhassen, E., Jameau, I., Seriyes, E., Tardieu, F., 1997. Analyse de la réponse de différents génotypes de tournesol au déficit hydrique. In: Riou, C. (Ed.), Compte Rendu du programme valorisation et protection de la ressource en eau, INRA, Paris.

Wopereis, M.C.S., Kropff, M.J., Maligaya, A.R., Tuong, T.P., 1996. Drought stress responses of two lowland rice cultivars to soil water status. Field Crops Res. 46, 21–39.

Wright, G.C., Smith, R.C.G., 1983. Differences between two grain sorghum genotypes in adaptation to drought stress: II. Root uptake and water use. Aust. J. Agric. Res. 34 (6), 627–636.