

ANALYSIS OF COTTON GENOTYPIC DIFFERENCES FOR PLANT RESPONSES TO DROUGHT

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Abstract

The objective of this study was to analyze, through different frameworks, the effects of a post-floral drought on growth, development and yield of cotton genotypes grown under field conditions. Three experiments were conducted under subsahelian conditions in Senegal. Five varieties were compared under different irrigation treatments differentiated after flowering. Despite large differences of soil water content between years and irrigation treatments, the fraction of transpirable soil water, FTSW, was closely related to the predawn leaf water potential measured on the same day. Genotypic differences for plant water status variables were found on some days, but they were frequently associated with genotypic differences in FTSW. The relationships between these variables and FTSW, over two years of measurements and contrasting soil water profiles, were adjusted to typical logistic functions, previously used in other species. Significant genotypic differences were found in the relationships of RWC, CWSI and ET/ET_m with FTSW. Reductions of leaf area index and intercepted radiation by soil water deficit resulted from combined effects on the rate of leaf emergence out of the shoot tip, on individual leaf area and on the duration of the period of leaf production. Despite significant differences between cultivars in the rate of development as well as in the individual leaf size, the 5 cultivars had the same LAI. Water deficit induced an earlier termination of plant development (cutout, when NAWF = 5) that reduced the effective flowering period. The effects of irrigation treatments on seed cotton yield varied from year to year, as rainfall pattern in the pre-flowering period differed. The overall variation in yield between years and experiments was accounted for by the length of the reproductive period and by the average FTSW during this period. The different frameworks of analysis of the seed cotton yield (number of bolls and average boll weight, total biomass and harvest index), allowed a common analysis of plant responses to drought as observed under the various years, irrigation conditions, and for the various genotypes. Duration of the flowering period and harvest index were the most efficient variables to explain genotypic differences in yield under the various conditions of water supply.

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, 1995). Several strategies exist for the improvement of crop production in dry areas: (1) better tactical management of water resources, and (2) adoption of better adapted varieties. Breeders currently invest little effort in understanding the physiological basis of the genotype x environment interactions (Jackson et al., 1996), 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, rate of leaf production, 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, and Lecoeur and Guilioni, 1998, 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). Differences between genotypes on a given day can rely either on their water consumption on the previous days (possibly linked to leaf area index) or on the plant susceptibility to soil dehydration.

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 analyze cotton genotypic differences in plant responses to soil water deficit (Lacape et al., 1998). FTSW was related to plant variables with different time scale and organization scale used in frameworks developed on other indeterminate species (Lacape, 1998):

- « water status framework » (Turner, 1998; Lacape et al., 1998),
- « leaf growth framework » (Lecoeur et al., 1995, on pulses),
- « reproductive development framework » (Ney et Turc, 1993, on pea),
- « yield components framework »,
- « biomass and harvest index framework » (Turner, 1998).

The results report on 3 experiments conducted under sub-sahelian conditions on five cotton (*Gossypium hirsutum* L) cultivars, grown with and without irrigation after flowering.

Materials and Methods

Experimental Site and Growth Conditions

Three 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 1994 to 1996. 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.

Air temperature, relative humidity, and class 'A' pan evaporation were measured in a weather station adjacent to the experimental field. Cotton was sown on 22 Jul. 1994, 4 Aug. 1995, and 14 Aug. 1996. 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 as to minimize damage to leaves and fruits, and weeds were controlled by hand.

Genotypes and Water Deficit Treatments

A line-source irrigation system compared 16 genotypes in 1994, of which 5 were further cultivated under two water regimes in 1995 and 1996 (Lacape, 1998). In 1994 each elementary plot was made of 3 rows of 13 m long. In 1995 and 1996 each elementary plot was 6 x 6 m. This paper reports on the results of the 5 cultivars tested during the 3 seasons. They 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 as observed in the 1994 study (Lacape, 1998). The five cultivars had similar phenology (only three days between the earliest and the latest flowering genotypes) but they covered the existing morphological variability within cultivated types.

Plants grew under near optimal water supply until the beginning of flowering, then water regimes were differentiated as an irrigated treatment (IR) and a non-irrigated treatment (NI). In 1994 the IR and NI treatments were defined from sub-plots located at distances of 0.5-3.5 m (IR treatment) and 9.5-12.5 m (NI treatment) from the sprinkler line. Irrigations on the IR plots were applied once (1994 and 1995) or twice (1996) a week to meet theoretical water requirements for a cotton crop in the region, calculated as the product of daily pan evaporation by a crop coefficient depending on phenological stage (Dancette, 1983). Irrigation was stopped on IR plots soon after the cutout phenological stage and prior to first boll split. NI plots grew under the same water supply as IR plots until the beginning of flowering (around 45 days after emergence).

After this date they received a limited amount of water from the rainfall.

Soil Water Content, Effective Rooting Depth and Calculation of FTSW

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. In 1994 soil water content was measured on part (1/3) of the plots on 3 dates: sowing, beginning of flowering and around cutout. Field calibrations relating the neutron counts to gravimetrically measured water contents were realized each year.

Effective rooting depth (ERD) was derived from neutron probe data, after comparing soil water profiles between dates of measurements (Silim and Saxena, 1993). The rate of progression of ERD varied from 18 mm d⁻¹ (in 1996) to 30 mm d⁻¹ (in 1995). ERD was calculated at each date of soil water measurement, until a maximal value (ERD_{max}). For each experiment and each plot the average ERD_{max} was close to the maximal depth of soil hydration.

The total transpirable soil water (TTSW) was estimated on each date of measurement in each elementary plot as the amount of soil water held between an upper (MAX) and a lower (MIN) 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 matrix suction limits. The upper limit of TTSW was established for the 0.3 m depth, after a heavy supply of water. MAX limit was then adjusted to the overall relationship between soil water holding capacity and soil depth. 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). As depth increases, this lower limit becomes higher than the water content at the permanent wilting point. This deviation can be accounted for by the fact that in the deeper soil layers, the access to water is reduced by the root density. 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.

Plant Water Status, Canopy Temperature and Mean Daily Evapotranspiration (ET)

Leaf relative water content (RWC), leaf water potential (ψ_l) and stomatal conductance (g_s) were measured in 1995 et 1996 on every three to seven days until the cutout stage of the crop. Measurements were made between 12:30 and 14:00 (solar time) on four (1995) and three (1996) plants per plot. Measurements were made on the uppermost (ψ_1), and on the leaf immediately below the last expanded leaf

(RWC and g.). The canopy temperature (T_c) of the center part of each plot was averaged from 4 readings made between 13:00 and 14:00 (solar time), twice a week, using a calibrated infrared radiometer. Air vapor pressure deficit (VPD) was determined at the same time using 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 ($T_c - T_a$). A crop water stress index (CWSI) was calculated following Idso et al. (1981) empirical approach, after determining the 2 limits of variation of $T_c - T_a$ against air VPD.

A simplified soil water balance model was used to calculate the evapotranspiration (ET). ET is equal to the difference between the total soil water reserve variation between 2 dates of neutron probe measurements and the amount of water received by irrigation and rain. The maximal value of ET (ET_m) could not be considered from values obtained on IR plots as these plants experienced some level of soil water deficit. ET_m was calculated as the product of pan evaporation by a crop coefficient adapted from Dancette (1983). The ratio ET/ET_m calculated during a period of maximal radiation interception was used as a measure of the relative crop transpiration.

Growth, Development and Yield

Plant height and number of main stem nodes were measured weekly throughout the season in each of the three experiments. We used the main stem (rate of node production, and variation in size of the internodes) to characterize leaf growth at the phytomer and at the plant level. Flower counts per plant (daily) and number of nodes above white flower on the main stem, NAWF, (twice a week) were used as indicators of the reproductive development of the plants. Percentage of abscission of reproductive structures was estimated on selected plants, by counting the number of harvestable bolls and the number of either aborted organs or abscission scars. Leaf area index (LAI) was measured twice a week in 1996 using a plant canopy analyzer following recommendations by Hicks and Lascano (1995). Daily fraction of intercepted radiation (Q) was then calculated using instantaneous values of intercepted radiation (Qn) following Charles-Edwards and Lawn (1984) formula: $Q = 2 * Qn / (1 + Qn)$. Total above-ground dry matter and its partitioning between vegetative and reproductive organs, were determined on a bi-weekly basis in 1995 and 1996. Final harvest index (ratio of seed cotton production to total aerial dry matter) was measured in the three experiments.

Results

Mean air temperature remained stable between 25°C and 32°C, and solar radiation fluctuated between 15 and 26 MJ m⁻² during the experiments. During the first part of the cropping season pan evaporation was 5 to 7 mm d⁻¹ and midday air VPD was 2 to 3 kPa. These variables gradually

increased to 12 mm d⁻¹ and 6 kPa respectively by harvest time.

The amount of water received by the cotton crop were brought by the rain and supplemental irrigation. Due to differences in the rainfall pattern between the 3 years, the amounts of water received and their distribution between the pre-flowering and post-flowering periods were not the same for the 3 experiments (Table 1). As an example, the total amount received by the IR plots in 1995 and 1996 was the same (618 and 603 mm) but the distribution differed between pre- (489 mm in 1995 and 293 mm 1996) and post-flowering periods (129 and 310 mm).

Soil Water Deficit

The marked difference in the seasonal pattern of water supply between 1995 and 1996 resulted in different patterns of soil water content. Compared to the measurements made at sowing, soil humectation 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.

In 1995, the lower limit of transpirable soil water (MIN) was higher than the initial soil water content at sowing, 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}), was on average 2.3 m in 1995, which is close to the rooting potential of cotton (Hearn, 1995). 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. As a consequence the maximal value of total transpirable soil water content (TTSW) was lower in 1996 (124 mm) than in 1995 (187 mm).

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 ERD, was used to quantify the soil water deficit experienced by the crop (Sinclair and Ludlow, 1986). As shown by Fig. 1, FTSW was closely related to predawn leaf water potential (predawn τ_1) which is itself linked to the soil water potential in the rooting zone (Dwyer et Stewart, 1984) and to the ABA content of the xylem sap (Tardieu et al., 1996). In plants with anisohydric behavior such as cotton, predawn τ_1 can be used to quantify the soil water deficit experienced by the crop (Guo et al., 1994). From the overall relationship between FTSW and predawn τ_1 , it can be concluded that FTSW gives, in our experiments, a fair estimate of soil water deficit experienced by the plants, despite the large differences in soil water status between the two years and the various plots of each experiment.

Pattern of Variation of FTSW During the Plant Cycle

During the pre-flowering period, irrigation and rainfall maintained FTSW between 0.6 (in 1994) and 0.8 (in 1995),

a range which is generally considered as optimum 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 even in IR plots, to reach 0.48 in 1994, 0.22 in 1995 and 0.26 in 1996 around the cutout stage. These low values of FTSW were obtained because the increase of ERD occurred in soil layers not restored to field capacity at flowering. 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; Doorenbos and Kassam, 1987). After cessation of irrigation on IR plots (around cutout) FTSW progressively dropped to near-zero values. 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. 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 1994 and 1995.

Although significant genotypic differences for FTSW were found by analysis of variance on some dates of measurement, the evolution of FTSW during the crop cycle was similar for the five cultivars, both in IR and NI plots. In 1995, cv. COK had a consistently lower FTSW in NI plots 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. As previously shown with predawn ψ_1 (Wery et al., 1997 on sunflower), we can conclude that the five cultivars were not experiencing the same soil water deficit (characterized with FTSW) on each date of measurement. FTSW provides a way of comparing genotypes that could differ in their pattern of soil water consumption (Ray et al., 1997, on maize; Wery et al., 1997, on sunflower).

« Water Status Framework » : Relationships Between Soil and Plant Water Status

In 1996, IR plants clearly experienced some degree of water deficit, as shown by the reduction of ψ_1 and g_s after FTSW fell below 0.4. Nevertheless RWC was maintained at high values (around 80%) during the same period when ψ_1 dropped to -1.8 to -2 MPa level, value generally retained as an indicator of plant stress (Grimes and Yamada, 1982). This stability in RWC under conditions of reduced ψ_1 is usually associated with a stability in turgor potential resulting from osmotic adjustment (Oosterhuis and Wullschleger, 1987; Lecoeur et al., 1992).

In the NI plants of 1996, the cessation of irrigation at the time of flowering induced a rapid variation in all of the plant variables, in comparison with IR plants. In less than 15 days, transpiration in NI plants had almost stopped and their canopy was slightly warmer than the air; and 7 to 8 °C warmer than IR plants. In 1995, the difference between NI and IR plants was lower than in 1996.

Although the soil water status (depth of humectation and depth of water extraction) and the rate of soil drying differed between experiments, irrigation treatments, replications, and sometimes between cultivars, the calculation of FTSW provided a way to unify the whole set of data. For each plant variable measured in 1995 and 1996, we have represented (Fig 2 and 3) the average value obtained on each combination of date X genotype X water deficit treatment, as a function of FTSW calculated on the same day. In the case of ψ_1 (Fig 2a) and g_s (Fig 2c), both IR and NI treatments were included in the regression, as the two water regimes clearly fell in the same overall relationship. In the case of RWC (Fig 2b), CWSI (Fig 2d) and ET/ET_m (Fig 3) the responses to FTSW differed between the IR and the NI plots. This resulted from the difference in the rate of soil dehydration between IR and NI plots.

The equations found from the non linear 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, 1995; Sadras and Milroy, 1996). Figures 2 and 3 provide 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 significant genotypic differences observed on some dates of measurements by the analysis of variance (Lacape, 1998), are difficult to interpret : the maintenance of a better leaf water status for some genotypes, 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 genotype and are represented as insets on Fig. 2 and 3. No significant difference was found between the five cultivars for the relationships between ψ_1 and FTSW (Fig 2a) or between g_s and FTSW (Fig 2c). In the case of RWC ($P < 0.01$), CWSI ($P < 0.05$) and ET/ET_m ($P < 0.05$) individual regressions of one or two of the varieties were found significantly different from the others. The susceptibility of RWC to soil dehydration (Fig 2b) can be ranked in the following increasing order: STF < DES < DEL, COK, and GUA. This higher capacity of dehydration avoidance of STF is not the

result of a higher susceptibility of stomata to soil dehydration, because STF is not different from the others in the $g_s=f(\text{FTSW})$ relationship (Fig 2c). It could rather be the result of a higher capacity of osmotic adjustment of STF (Lacape, 1998). DEL was significantly different from the four other cultivars in the responses of CWSI (Fig 2d) and ET/ET_m (Fig 3) to soil dehydration. It may be the consequence of a higher dehydration of the canopy, because RWC (Fig. 2b) and τ_1 (Fig. 2a) decreased at a faster rate with FTSW for this cultivar. This behavior of DEL cultivar could also be the result of a lower ability of soil water extraction by the roots related to characteristics like depth, root density or hydraulic resistance (Lacape, 1998).

These results emphasize the potential of RWC (Sinclair and Ludlow, 1985) and canopy temperature (Hatfield et al., 1987) measurements, as plant water stress indicators for genotypic comparison of plant response to drought under field conditions, provided they are coupled with measurements of FTSW or predawn leaf water potential.

« Leaf Growth Framework » : Main Stem Development Pattern, Leaf Area Index and its Components

All the components of the canopy leaf area index (LAI) were found susceptible to soil dehydration: - number of branches (assessed indirectly by the number of main stem nodes), - number and size of mainstem leaves. The reduction in the total number of nodes on the main stem as a result of a decreasing FTSW, can be explained by the combined effects of a reduction in the rate of node appearance out of the apical bud, and a reduction in the duration of the period of node production. Due to differences between IR and NI plants for midday canopy temperature, the development of the crop was analyzed using the sum of mean daily canopy temperatures (using a base temperature of 12°C): midday canopy temperature (T_c) replacing T_{max} in the formula : $T_{mean} = (T_{max} + T_{min})/2$.

The rate of node production was found stable during the pre-flowering period and its value was similar in the 3 years : 0.029 node/°C.d. The phyllochron (inverse of this rate) was 34.4°C.d or 2.7 days per node. After flowering, the rate of nodes production decreased in each of the irrigation treatments (IR and NI) of the 3 seasons in proportion to the average FTSW during the period (Fig 4). This rate was already reduced by 50% at a FTSW of 0.4. The duration of the period of node production was reduced because cutout (defined as the cessation of node production, and estimated as the date when NAWF reached the value of 5 nodes) occurred earlier in plants experiencing water deficit: 12 days earlier on NI than on IR plots in 1996 and 4 days earlier in 1994 and 1995.

We found significant genotypic differences in the phyllochron of well watered plants (before flowering). The 2 latest genotypes for flowering date, STF and DEL, had faster rates of node production, than the earlier and more

determinate genotypes, GUA, DES and COK. Kerby et al. (1990) found opposite results, with the earlier and more determinate cultivar having a faster rate of main stem development. The susceptibility of the rate of node production to soil dehydration differed also between the genotypes: GUA was more susceptible than the 4 others (Fig 4).

In 1996, the LAI and the fraction of radiation intercepted by the canopy, quickly dropped on NI plants after the cessation of irrigation around flowering time (Fig 5). LAI did not differ between genotypes, although differences were found in the single leaf area and rate of leaf production, because these components partially compensate for each other: varieties with faster rates of development tended to have smaller leaves (Lacape, 1998).

« Reproductive Development Framework »: Flowering Pattern, Total Number of Fruiting Sites and NAWF

Under IR conditions the total number of fruiting sites per plant was the same in each of the 3 seasons (around 220 per m²). As already noted by Hesketh et al. (1972), the rate of flowering was not reduced by water deficit. The reductions in the total number of fruiting sites under NI conditions (-13% in 1995 to -35% in 1996) or in the cumulated number of flowers (-18% in 1995 and -38% in 1996) were related to the reduction of the duration of the period of flowering by water deficit. Despite a 3 days difference between the varieties for the beginning of flowering, no genotypic difference was found for the number of fruiting sites or flowers.

The reduction of NAWF during the flowering period results from the difference between the rate of node appearance out of the apical bud and the rate of flowering on the successive first positions on fruiting branches. NAWF decreased at a faster rate under the conditions of soil water deficit than in well watered plants (Fig 6), and the decline was more important under the severe water deficit conditions of the NI plots of 1996. The NAWF value of 5, which in our case coincided with the cessation of node production (Lacape, 1998), is also used as an indicator of the opening of the last effective flower (Bourland et al., 1997). The soil water availability, assessed by an average level of FTSW, explained the variation of the duration (in canopy thermal time) of the period between the date of first flower appearance and the date of NAWF=5. The duration of this period is highly correlated with the total number of fruiting sites per m² ($r^2=0.83$). For this duration, genotypes ranked according to their degree of earliness and of determinacy: the more determinate cultivar, COK, had an earlier cutout and a shorter duration of the flowering period. These results give confirmation that NAWF can be used to estimate the date of cessation of plant development and effective flowering duration. Few measurements of NAWF during the crop cycle could be used in breeding programs to estimate the length of the reproductive period.

Seed Cotton Yield Results

Significant differences of seed cotton yield between the genotypes and an interaction between genotype and irrigation treatments were only found in 1994 (Fig 7). The higher yields obtained in this year can be explained by the higher average FTSW during the flowering period, itself linked to the higher amount of water received (Table 1). The analysis of water regime effects is complicated due to the fact that the IR and NI treatments didn't reproduce the same pattern of FTSW every year. For example, the NI treatment of 1994 gave similar average FTSW and yield as the IR treatments of 1995 and 1996 (Fig 7). For the same reasons the cultivar ranking on seed cotton yield was not the same every year.

Two variables were used to analyze the yield variation between years and water treatments: the average FTSW during the reproductive period (Fig 8a) and the duration in degree.days of this period (Fig 8b). Both variables explained the variation of the mean yields considering the 6 situations (3 years x 2 water regimes). The relationship between yield and average FTSW was the same for the 5 cultivars.

« Yield Components Framework », Number of Bolls and Average Boll Weight

This framework considers the final production per plant as the result of the setting of a number of fruits retained and of an average weight of seed cotton per boll (ABW). Under our conditions of terminal drought, both components were negatively affected by soil water deficit. The reduction in the number of harvested bolls by water deficit was a consequence of a reduction of the number of fruiting sites initiated, itself linked to the duration of the reproductive period; and of an increase in the percentage of abscised and aborted squares and young bolls (Lacape, 1998). The increase of the percentage of abscission under soil water deficit conditions could also be the result of the higher canopy temperatures (Hodges et al., 1993) of NI compared to IR plots. The variations in the different components were interpreted in relationship with the average FTSW during the flowering period. Significant genotypic differences were found for ABW (higher value for STF, and lower value for DES) and for the percentage of abscission (lower value in the case of GUA).

« Biomass and Harvest Index Framework »

From the 2 terms introduced in this model of seed cotton yield analysis (Eq. 1), biomass and harvest index (HI), the former explained the yield variations between seasons and water regimes, and the second one explained variations between genotypes. The cultivar GUA, had higher HI (based on seed cotton production) and reproductive index (based on whole reproductive dry matter) as compared to the other cultivars (Lacape, 1998). Our results suggest that HI, or any indicator of a higher ability of the genotypes to remobilize carbohydrates to the fruiting structures, could be of possible use in breeding for production under dry

conditions (Blum et al., 1983 on wheat; Meredith and Wells, 1989 on cotton).

Two approaches were used to analyze the variation of the daily weight gain: Passioura (1977) approach based on water transpired (T) and water use efficiency, (WUE): Eq 1a; and Monteith (1977) approach based on radiation interception (PARI) and radiation use efficiency (RUE): Eq. 1b.

$$\text{SC Yield} = \left[\sum_{i=\text{emergence}}^{i=\text{maturity}} (\text{Daily weight gain}) \right] * \text{HI} \quad (\text{Eq. 1})$$

$$\text{Daily weight gain} = T * \text{WUE} \quad (\text{Eq. 1a})$$

$$\text{Daily weight gain} = \text{PARI} * \text{RUE} \quad (\text{Eq. 1b})$$

Above-ground biomass accumulation of the IR plants during the period of flowering was similar in 1995 and 1996 (Fig 9a). The maximum rate of biomass accumulation was $24 \text{ g m}^{-2} \text{ d}^{-1}$. The WUE during the same period averaged $1.6 \text{ kg dry matter mm}^{-1}$ of water transpired (Lacape, 1998), and no difference was found between the varieties. The radiation utilization approach (Eq. 1b) showed that biomass accumulation was proportional to the cumulated amount of radiation intercepted (Fig 9b). On IR plants the maximum RUE was $2.33 \text{ g dry matter MJ}^{-1}$ of intercepted PAR, which is in the range of values commonly cited for C3 plants (Gosse et al., 1986). Water deficit conditions reduced both the WUE and RUE terms. Although WUE and RUE did not differ significantly between the varieties, we found some indications that these terms could be further analyzed for an utilization in breeding programs. On IR plants, RUE varied between 2.8 (DEL) and $2.1 \text{ g dry matter MJ}^{-1}$ (GUA). Specific leaf area, which had been related to WUE (Wright and Nageswara Rao, 1994, on groundnut) or carbon exchange rate (Pettigrew and Meredith, 1994, on cotton) varied significantly between the 5 cultivars (Lacape, 1998).

Conclusion

Most of the variables introduced in the different frameworks, were affected by soil water deficit (Table 2), but only some of these variables showed genotypic variation in our group of varieties (either for their level of expression under irrigated conditions, or for their response to soil water deficit). Yield differences between the varieties were small and significant only in 1 of the 3 experiments. The variables that could help in interpreting the overall better behavior of the cultivar GUA under terminal drought conditions relate to: - a better earliness in flowering, - an intermediate level of determinacy (unlike COK which was of similar earliness but very determinate), - a higher ability to allocate assimilates to the fruits (itself possibly linked to a better boll retention rate).

A number of the relationships found between plant variables and FTSW are already used in simple crop models of water consumption and yield developed for a large range of crops (for example: Sinclair, 1986 on soybean; Amir and Sinclair, 1991 on wheat). This crop modeling approach

could be useful for the interpretation of multilocational cotton variety trials, and for yield improvement under dry conditions.

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Table 1: Amounts of water received by the cotton crops in 1994 1995 and 1996.

| Period | Amount of water received (mm) | | | | | |
|-------------------------------|-------------------------------|-----|------|-----|------|-----|
| | 1994 | | 1995 | | 1996 | |
| | IR | NI | IR | NI | IR | NI |
| before sowing | 28 | 28 | 50 | 50 | 49 | 49 |
| between sowing and flowering | 373 | 373 | 439 | 439 | 244 | 244 |
| between flowering and harvest | 327 | 152 | 129 | 8 | 310 | 11 |
| Total | 728 | 553 | 618 | 497 | 603 | 304 |

Table 2: Synthetic results: Water deficit and genotype effects on the components introduced in the different frameworks of yield analysis (according to a relative scale: ++ highly marked, + marked, (+) moderate, and 0 effect not observed)

| Framework | Component | Water deficit effects | Genotype effects |
|---------------------------------|--------------------------|-----------------------|----------------------|
| « Soil and plant water status » | | ++ | (+0) ⁽ⁱ⁾ |
| « Leaf growth » | Expansion rate | ++ | (+) |
| | Dur. Expansion period | ++ | (+) |
| | Production rate | ++ | + |
| | Dur. Production period | ++ | + |
| « Reproductive development » | Flowering rate | (+) | 0 |
| | Dur. Flowering period | ++ | + |
| | Abscission and abortion | +/(+) ⁽ⁱⁱ⁾ | ++ |
| « Yield components » | Number of bolls | ++ | + |
| | Average boll weight | +/(+) ⁽ⁱⁱ⁾ | ++ |
| « Biomass ... » | Harvest Index | +/(+) ⁽ⁱⁱ⁾ | ++ |
| | Duration of cycle | ++ | + |
| « ... and radiation balance » | Intercepted PAR | ++ | 0 |
| | Radiation Use Efficiency | ++ | 0 |
| « ... and water balance » | ET | ++ | 0 |
| | Water Use Efficiency | + | (+) ⁽ⁱⁱⁱ⁾ |

(i) Genotypic differences for RWC, CWSI and mean relative transpiration (ET/ET_m), responses to FTSW; no differences for Ψ_l and g_s.
(ii) Marked effects in the case of a severe soil water deficit.
(iii) Genotypic differences for specific leaf area (characteristic related to the WUE).

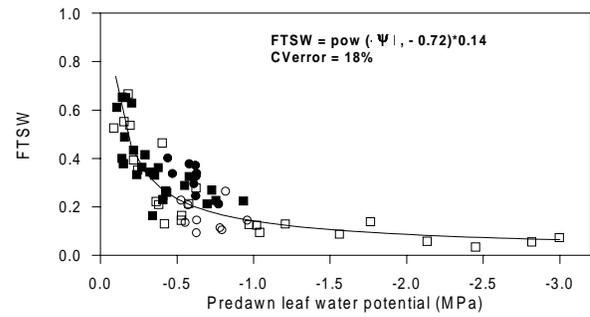


Figure 1. Relationship between FTSW and predawn leaf water potential (Ψ_l) measured on irrigated (closed symbols) and non irrigated (open symbols) cottons in 1995 (circles) and 1996 (squares). Coordinates of each point are the average of two to three plants for predawn leaf water potential and the value of FTSW for each elementary plot. $FTSW = 0.14 * (\Psi_l)^{-0.72}$, $CV_e=18\%$. (Lacape et al., 1998).

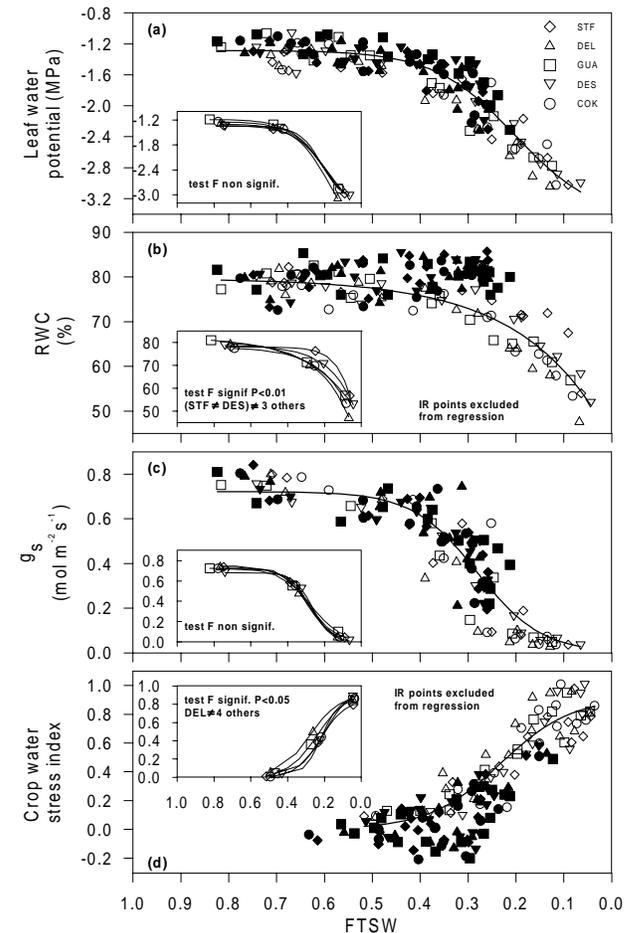


Figure 2. Relationship between FTSW and midday leaf water potential (Ψ_l , a), relative water content (RWC, b), stomatal conductance (g_s , c), and crop water stress index (CWSI, d) of irrigated (closed symbols) and non irrigated (open symbols) cottons in 1995 and 1996. Each point of Ψ_l , RWC, and g_s 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 non linear regressions:

$$\Psi_l = -3.48 + 2.20 / (1 + \exp(-(FTSW - 0.2) / 0.085)) - (CV_e = 11.0\%)$$

$$RWC = 43.46 + 36.21 * (1 - \exp(-(FTSW * 5.62))) - (CV_e = 4.4\%)$$

$$g_s = 0.72 / (1 + \exp(-(FTSW - 0.28) / 0.07)) - (CV_e = 21.6\%)$$

$$CWSI = 0.92 / (1 + \exp(-(FTSW - 0.23) / 0.07)) - (CV_e = 23.5\%)$$

Inset in each figure represents the regressions obtained on sub-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 (Lacape et al., 1998).

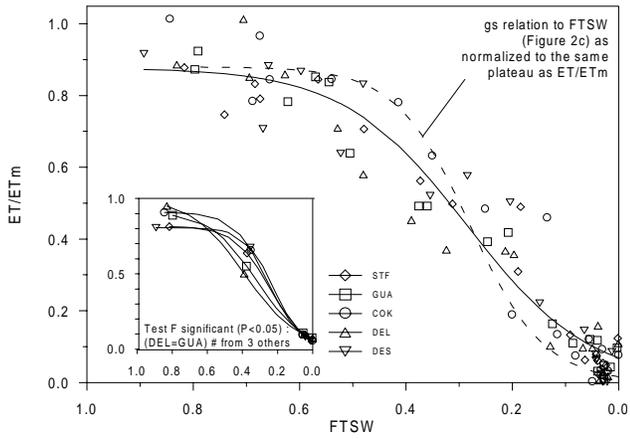


Figure 3. Relationship between FTSW and the ratio ET/ET_m calculated on NI plots. Measurements made on 6 (1995) and 13 (1996) dates. ET_m values were calculated for the same periods as ET, by multiplying the mean pan evaporation during the period by a crop coefficient adapted from Dancette (1983). The regression obtained was: $ET/ET_m = 0.88/(1 + \exp(-(FTSW - 0.29)/0.12))$, $CV_e=22\%$. Genotypes were compared (inset) using a *F* test of Snedecor (Lacape, 1998).

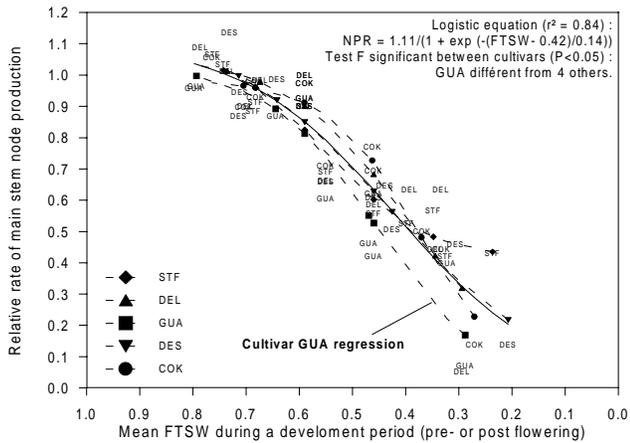


Figure 4. Relationship between FTSW and the node production rate (NPR) on the main stem during the 3 seasons. Calculations were made during 2 periods of development : pre- and post-flowering. NPR is expressed relatively to the maximal rate of IR plants in 1995 (Lacape, 1998).

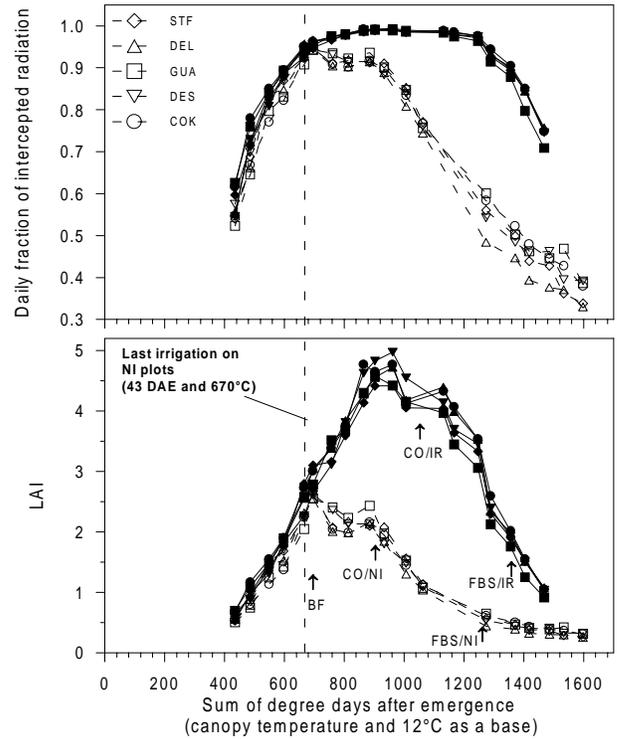


Figure 5. Pattern of variation of daily fraction of radiation (PAR) intercepted and LAI measured in 1996. Means per genotype under irrigated (solid symbols) and non irrigated (empty symbols) conditions. Dates of beginning of flowering (BF), cutout (CO), and first boll split (FBS) indicated (Lacape, 1998).

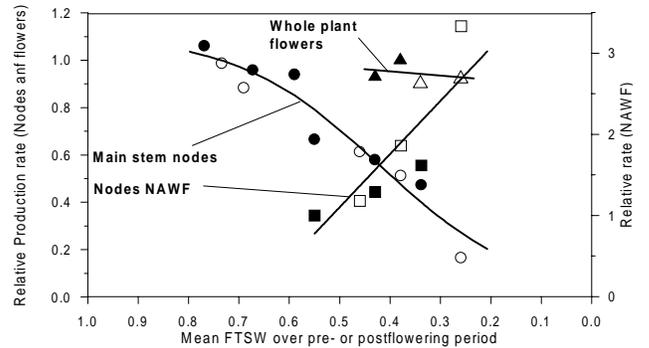


Figure 6. Relative rates of development (main stem node production, flowering per plant, and NAWF) as a function of the mean FTSW during 1 or 2 periods of development (pre- and post-flowering periods). Rates expressed relatively to a maximal value. (Lacape, 1998).

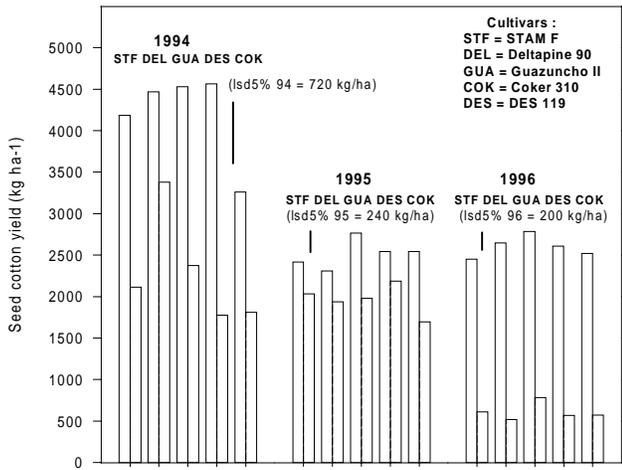


Figure 7. Seed cotton yields in the 3 experiments. Means per genotype and water regime over 3 (1994 and 1996) and 4 (1995) replicates. Irrigated (IR) treatments as gray bars, and non irrigated (NI) treatment as dashed bars. (Lacape, 1998).

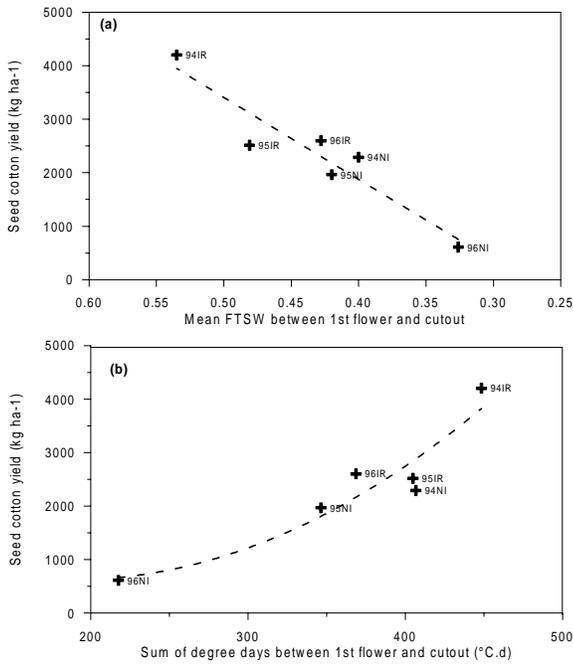


Figure 8. Seed cotton yields variations with mean FTSW during the reproductive period (a) and duration in degree.days (canopy temperature at noon as daily maximum and base temperature of 12°C) of this period (b). (Lacape, 1998).

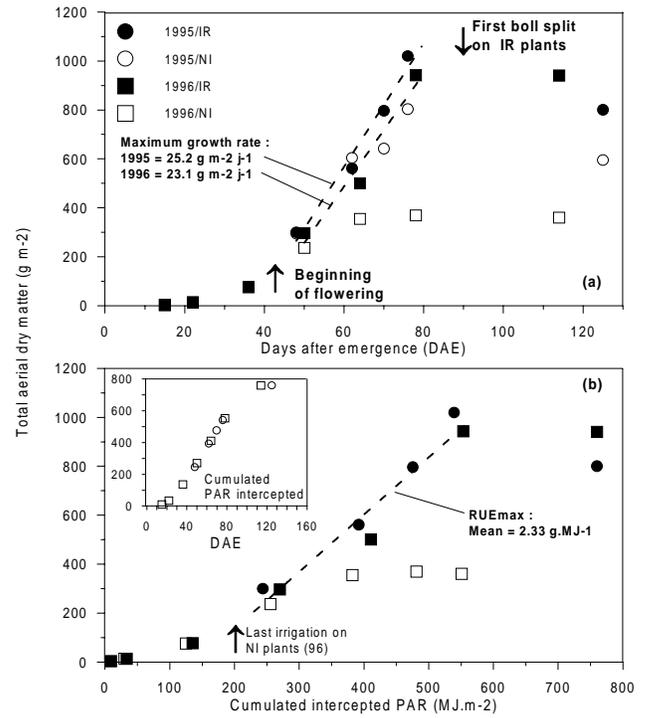


Figure 9. Pattern of variation of total aerial biomass production as a function of the number of days after emergence (a) and quantity of PAR intercepted (b). Measurements made on 30 to 40 plants of IR (solid symbols) and NI plants (empty symbols) during the 1995 (circles) and 1996 (squares) experiments. (Lacape, 1998).