Use of Model Assisted Yield Frameworks for the Analysis of Cotton Cultivar Response to Drought

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ABSTRACT

Three experiments were conducted under field conditions in Senegal to study the effects of a post-floral drought on seed-cotton yield and yield components of five cotton cultivars. The fraction of transpirable soil water (FTSW) was used to characterize the soil water deficit as experienced by the plants in each elementary plot. Two model-assisted frameworks of analysis of the seed-cotton yield were used: (1) number of bolls and average boll weight, associated with a leaf and flower development model; (2) total aerial biomass produced and harvest index, associated with a light interception model. 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 average FTSW during the reproductive period and by the duration of this period. Water deficit induced an earlier termination of plant development (cutout, when NAWF = 5) that reduced the effective flowering period and the number of fruiting sites produced. A reduction of the average boll weight was also observed under terminal drought conditions. Water deficit induced an overall reduction in leaf area index and radiation interception that largely accounted for the effects of water deficit on total aerial biomass production. 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. The two frameworks of analysis of the seed-cotton yield, and the associated phenology and growth models, allowed a common analysis of plant responses to drought as observed under the various years, irrigation conditions, and for the various genotypes.

Introduction

In most African countries cotton is grown as a rainfed crop and water deficit remains a major limitation to yield (Hearn, 1995). The adoption of better adapted cultivars is one of the strategies proposed for the improvement of crop production in dry areas. As yield performance under drought is the result of many physiological processes, breeders need alternative variables as drought-adaptive traits (Blum, 1988). Different types of analytical models have been proposed to «dissect» yield into a small number of independent physiological components.

The final seed-cotton yield can be analyzed as the product of a number of bolls and of an average weight of seed-cotton per boll (ABW).

Seed-cotton Yield per m² = Number of plants per m² x Number of bolls per plant x ABW   (Eq.1)

Number of bolls per plant = Number of flowers x (1 - rate of abscission)

Number of flowers = Flowering rate x Duration of flowering period

This yield components framework, (YCF) associates final measurements on the plant and the parameters of a simple development model based on the evolution of the number of reproductive phytomers with thermal time (Lacape, 1998).

Yield can also be analyzed as the product of above-ground biomass and harvest index (Biomass Production framework, BPF). Daily biomass production can be interpreted as the result of water (Eq. 2a) or radiation (Eq. 2b) used by the canopy.

Seed-cotton Yield per m² = ((Daily Biomass Production per m²)) x HI   (Eq.2)

Daily Biomass Production per m² = T x WUE   (Eq.2a)

Daily Biomass Production per m² = PAR_0 x RAE x RUE   (Eq.2b)

Where HI = harvest index, T = water transpired, WUE = water use efficiency, PAR_0 = incident photosynthetically active radiation, RAE = radiation absorption efficiency, RUE = radiation use efficiency

The objective of the study was to compare the efficiency of these frameworks for the analysis of seed-cotton yield variation of different genotypes under terminal drought in a set of field experiments. The second framework used equation 2b because RAE and RUE can be more easily related to morphological and

physiological characters of the plant (leaf growth and stomatal conductance).

Material and Methods

Three field experiments were carried out at the research centre, CERAAS, Bambey (14.42°N, 16.28°W) in Senegal, during the rainy seasons of 1994 to 1996. The soil was a deep sandy soil with low levels of clay + silt (12%) and organic matter (0.4%). Cultural practices insured that fertility was not a limiting factor and that weeds and insects controlled. Experiments were sown in Jul. 1994 and in Aug. 1995 and 1996 so that flowering occurred in early October, a period that coincided with the end of rains. A split-plot design with three replications in 1996 and four subsequently was used with irrigation treatments as the main plots and cultivars as sib-plots. These had three rows of 13 m in 1994, and six rows of 6 m in 1995 and 1996. Five *Gossypium hirsutum* (L.) cultivars were included: 'STAM F' (STF) from Togo, 'Guazuncho II' (GUA) from Argentina, 'Coker 310' (COK), 'Deltapine 90' (DEL), and 'DES119' (DES) from USA. They had similar phenology, only three days separating the earliest and the latest genotypes but covered existing morphological variability within cultivated types. All plots were sprinkler irrigated once or twice a week in the pre-flowering period to maintain favourable water conditions. After flowering, Irrigated plots (IR) were irrigated until cut-out and Non Irrigated (NI) plots were not.

Soil water content and FTSW. The level of soil water deficit experienced by the crop was quantified by the fraction of transpirable soil water, FTSW (Sinclair and Ludlow, 1986). Volumetric soil water content was measured once (1995) or twice (1996) a week until 2.7 m depth, using a neutron probe centred in each elementary plot. In 1994 selected plots were measured only at three stages, sowing, beginning of flowering, and cut-out. On each date of measurement, and for an estimated effective rooting depth, FTSW was calculated as the ratio of available soil water to total transpirable soil water (Lacape *et al.*, 1998). Across all the measurements, FTSW was closely related to the predawn leaf water potential and midday parameters of leaf water status measured on the same day (Lacape *et al.*, 1998). This allowed the use of the average FTSW during the effective flowering period (FTSW$_{fl}$) to quantify the soil water deficit experienced by the cotton plants in each plot.

Plant measurements. Plant measurements were designed to obtain the parameters of the two frameworks described by equations 1 and 2b. Seed-cotton yield, number of harvested bolls and average boll weight (ABW), were determined from the harvest of the inner row in 1994, and centre 9 m² plots in 1995 and 1996. Percentage of abscission of reproductive organs was estimated on selected plants, by counting the number of harvestable bolls and the number of either aborted bolls or abscission scars. Flower counts

per plant (daily) and number of nodes above white flower on the main stem, NAWF (twice a week) were used to calculate respectively the flowering rate (as a function of thermal time) and the flowering duration. The date when NAWF reached the value of 5 nodes was calculated after plotting NAWF variation with time, and used as date of last effective flower (Bourland *et al.*, 1992) for calculating the duration in thermal time of the effective flowering period.

Above-ground biomass and its partitioning between vegetative and reproductive organs, were determined on a bi-weekly basis in 1995 and 1996. Final harvest index was calculated as the ratio of seed cotton weight to total above-ground biomass. Leaf area index (LAI) was measured twice a week in 1996 using a plant canopy analyzer (Li-Cor LAI 2000). Daily RAE was calculated using midday measurements of intercepted radiation with the plant canopy analyzer (Lacape, 1998). RUE was calculated as the slope of the linear relationship between the above-ground biomass production and the cumulated radiation absorbed by the canopy at the same date (calculated with incident PAR and RAE).

Results

Water deficit experienced by the plants. Irrigation regimes and rainfall pattern in the experiments generated a variation of the level of soil water availability during the post-flowering period, assessed by FTSW$_{fl}$ (Table 1). Irrigation regimes could not be used to analyze the responses of the different genotypes, as IR and NI treatments did not have the same soil water deficit in each season.

Seed-cotton yield. Yield is always lower in the NI plots than in the IR plots (Fig. 1), but seed-cotton yields in each irrigation regime differ in the 3 experiments. These yield differences can be accounted for by the average soil water status (FTSW) in the flowering period (Fig. 2). Three contrasted situations can be distinguished based on water amounts received (Table 1) and average seed-cotton yields (Fig. 1) : the most favorable situation of IR-94, an intermediate situation observed under the 4 conditions NI-94, IR-95, NI-95, and IR-96, and lastly the most severe regime of NI-96.

The ranking of the genotypes depends on experiments and water regimes (Fig. 1). In 1994 the cultivar DEL was more productive than the 4 others under NI conditions. This performance was not confirmed in 1995 and 1996. The cultivar GUA always ranked as first or second.

Yield Components Framework (YCF). As already shown by Wells and Meredith (1984), seed-cotton yield variation mainly results from a variation of the number of harvested bolls (Fig. 3a). Nevertheless, ABW is also reduced by our terminal drought conditions. ABW is reduced by 33% under the most severe conditions of NI-96 as compared to its value under IR conditions (Fig. 3b).

The reduction of the number of harvested bolls resulted from the low number of fruiting sites initiated, itself explained by a reduction of the duration of the flowering period (earlier cut-out), and from an increase of the rate of abortion and abscission of reproductive organs (Lacape, 1998). The variation of these 2 variables was correlated with the soil water status during the flowering period (Fig. 4a and 4b). On the contrary the rate of flowering appeared stable and less affected by water deficit (Lacape, 1998) as already noted by Mc Michael and Hesketh (1982) and Guinn and Mauney (1984).

Significant differences between cultivars were observed in the case of the following variables of YCF model: - duration of the effective flowering period : higher difference between STF and COK at all soil water deficit (Fig. 4a); rate of abscission (Fig. 4b) and number of harvested bolls (Fig. 3a), with an advantage (significant in 1995) of GUA and DES cultivars (lower rate of abscission and higher number of harvested bolls); ABW (Fig. 3b), with a superiority of STF.

For the cultivar STF under IR conditions (average of the three experiments), a higher ABW (4.82 g against 4.17 g in the case of DES) and a longer period of effective flowering (32 days on average as compared to 28 days in the case of DES), did not result in a higher yield (Fig. 1), because these traits are compensated by a higher fruit shedding (63.9% against 56.9% for DES).

Biomass Production Framework (BPF). In each of the 3 seasons final aerial biomass is reduced by water deficit (Table 2). No significant varietal difference was observed in any of the irrigation regimes. Nevertheless the cultivar COK always ranked in last position for this variable (Lacape, 1998).

The measurements of radiation interception made during the crop cycle in 1996 have shown a rapid and important effect of drought conditions on LAI and intercepted radiation, RAE (Fig. 5). The difference between IR and NI treatments was significant after 6 days of drought imposition. This effect resulted from the high susceptibility of all the components of LAI to soil dehydration: rate of leaf emission by apical meristems, duration of the period of leaf emission, individual leaf size (Lacape, 1998). Despite varietal differences in some of these components, the 5 genotypes showed similar LAI (or RAE). As a consequence genotypes had also similar RUE. This parameter was reduced in the NI plants of 1996 as compared to the IR plants (0.9 g aerial dry matter MJ^{-1} of PAR for NI plants against 1.4 g MJ^{-1} for IR plants). RUE depends on photosynthesis and stomatal conductance, which had been shown to be reduced by soil dehydration below FTSW values of 0.5 (Lacape *et al.*, 1998). Water deficit also reduced the duration of crop cycle because it induces earlier cutout. This also contributed to the limitation of biomass production by reducing the quantity of absorbed radiation.

Water deficit effects on dry matter partitioning between vegetative and reproductive organs varied according to dates of measurements and experiments. In 1995 we have observed a transitory increase of the percentage of reproductive biomass (Lacape, 1998); but the final harvest index (HI) was significantly reduced under NI conditions in two of the three experiments (Table 2 and Fig. 6). In these 2 seasons (1994 and 1996), and particularly under the severe drought conditions of NI-96, the reduction of HI can be related to an increase of the rate of squares and bolls abscission (Table 2).

The cultivars ranked similarly for HI under the six situations (Fig. 6). Cultivar GUA was always superior to the others for this trait during the different in-season dry matter partitioning measurements as well as for the final HI. Meredith and Wells (1989), as well as Sequeira and El Zik (1992), had also shown some genotypic differences in HI under comparable growing conditions.

Discussion and Conclusion

The variable FTSW was efficient in analyzing the three experiments. This was possible in short term plant water status variables (Lacape *et al.*, 1998), as well as for more integrative variables of plant growth and development, and for seed-cotton yield. The variation of FTSW between experiments resulted from differences in rainfall pattern, but also from soil variability (Lacape, 1998), inherent to field conditions. The approach based on soil water deficit quantification appears essential when analyzing the responses of different genotypes to water deficit, as soil water consumption may differ between genotypes, as shown by Wery *et al.* (1997) on sunflower and by Ray *et al.* (1997) on maize.

The YCF framework has shown the importance of flowering period duration for production under dry conditions. Flowering earliness and date of cut-out conditioned this duration. Although flowering earliness remains a major adaptive trait to terminal drought conditions, the slightly earlier date of flowering initiation of COK did not confer any yield advantage under non irrigated conditions. The more « determinate » behaviour of COK, related to an earlier end of leaves and flower emission (cut-out), also limited the level of yield potential as observed under IR-94 (Fig.1). A more indeterminate habit, together with an early flowering, probably constitute favourable attributes to be introduced in cotton cultivars to be grown in drought prone areas of African countries, as these areas are also characterized by a very erratic rainfall pattern.

The BPF framework has demonstrated that all the parameters introduced in this model of biomass production need to be taken into account to explain seed-cotton yield differences between irrigation regimes. These include limitation of the radiation absorption efficiency (RAE) due to an earlier end of

LAI increase, reduction of the duration of the period of radiation interception and reduction of radiation utilization efficiency (RUE) due to stomatal closure.

Neither RAE nor RUE helped in explaining differences between cultivars under various water regimes. The fact that RUE did not differ between genotypes is partly explained by the similar maximal stomatal conductance and similar stomatal response to soil dehydration of the 5 cultivars (Lacape *et al.*, 1998). Conversely, the absence of differences in RAE was not expected as the cultivars differed in the individual leaf size (Lacape, 1998).

Results confirm that a high mobilization of carbohydrates to reproductive structures (estimated here with harvest index) is an important trait for which a margin of genetic improvement probably exists. Note that HI have not been directly used in cotton breeding (Meredith and Wells, 1989). In the case of groundnut the stability of the partitioning to reproductive structures has also been shown to be the dominant attribute of genotypes adapted to drought prone Sahelian regions (Greenberg *et al.*, 1992). The cultivar GUA that had a superior HI under the various irrigation regimes also had a higher and more stable seed-cotton yield. This advantage of cultivar GUA cannot only be related to its flowering earliness since it is also superior to DES and COK of similar earliness. It could be related to a better fruit retention rate associated with a higher susceptibility of vegetative growth (leaf production rate) to soil dehydration conditions (Lacape, 1998).

The two frameworks (YCF and BPF) would allow an analysis of varietal networks, provided water deficit experienced by each genotype in each situation is quantified. The analysis would be based on relations established between a variable quantifying the soil water deficit (mean FTSW over flowering period) and each of the parameters introduced in the equations 1 and 2. The second framework (BPF) seems to be more promising for varietal analysis since its parameters can be modeled from the knowledge of the processes of morphogenesis (in the case of RAE) and photosynthesis (in the case of RUE) utilizing dynamic models working at a daily scale. Such models have been proposed for harvest index (Spaeth and Sinclair, 1985). The BPF framework associated to dynamic models would have a better physiological relevance for the analysis of varietal networks and would allow a prediction of the behaviour of genotypes in different environments.

Acknowledgments

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Table 1. Amounts of water (mm) received by the cotton crops and average FTSW during the flowering period (FTSWfl) in the 3 experiments. Flowering period was considered between beginning of flowering and day when NAWF reached the value of 5 node.

Period	Amount of water (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
	FTSW during flowering period£					
FTSWfl	0.54	0.40	0.48	0.42	0.43	0.33

£ values in 1994 are averages of 2 dates of measurements.

Table 2 . Mean effects (average of 5 cultivars) of irrigation regimes on biomass production, harvest index and abscission percentage in the 3 experiments.

	1994		1995		1996	
	IR	NI	IR	NI	IR	NI
Total aerial biomass (g m^{-2})#	760	450	780	600	910	350
Harvest index (%)#	52.3	45.7	32.4	33.1	28.7	17.8
Abscission percentage (%)	50.4$	62.6$	63.7	64.0	56.0	72.2

Aerial biomass, and consequently harvest index, were differently measured in the 3 experiments : whole aerial dry weight basis, including in-season fallen leaves, in 1996, and partial weight in 1994 and 1995 .
$ Average of 2 cultivars.

Figure 1. Seed cotton yield in the 3 experiments. Means per genotype x water regime over 3 (1994 and 1996) and 4 (1995) replicates. Irrigated (IR) treatments as gray bars, and non irrigated (NI) treatments as dashed bars (Lacape, 1998).
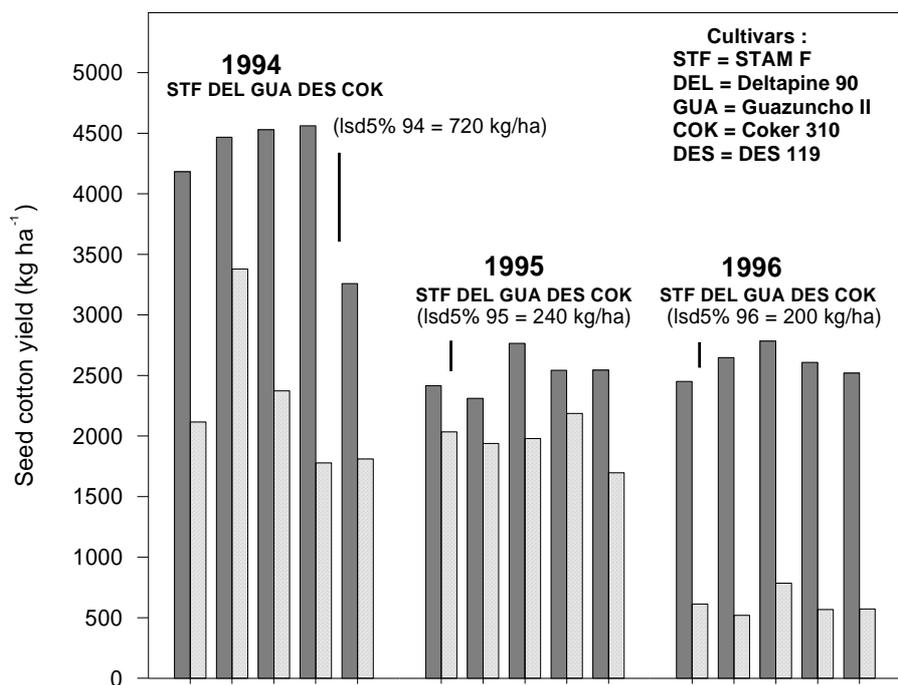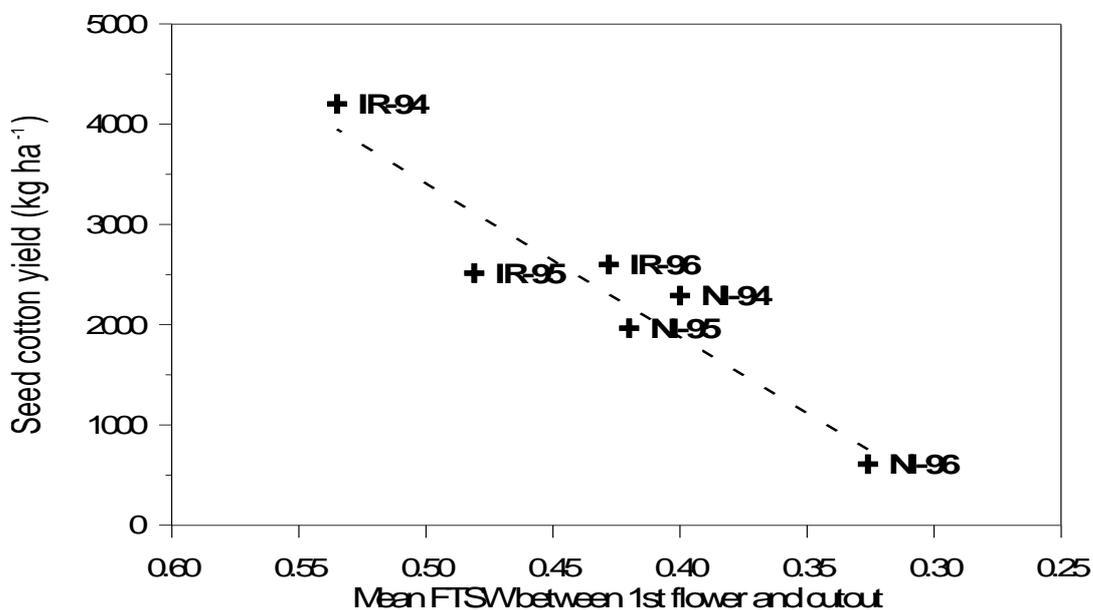

Figure 2. Relationship of seed cotton yield to mean FTSW during the flowering period : means per water regime averaged over the 5 cultivars (Lacape, 1998).

Figure 3. Relationship of seed cotton production per m² : (a) to number of harvested bolls per m², and (b) to average boll weight, ABW. Mean per water regime averaged over the 5 cultivars and mean values per genotype x water regime (Lacape, 1998).

Figure 4. Relationship of (a) the duration of the flowering period in thermal time and (b) the abscission rate, to the mean FTSW during the flowering period. Mean per water regime averaged over the 5 cultivars and mean values per genotype x water regime (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. Beginning of flowering (BF) indicated (Lacape, 1998).
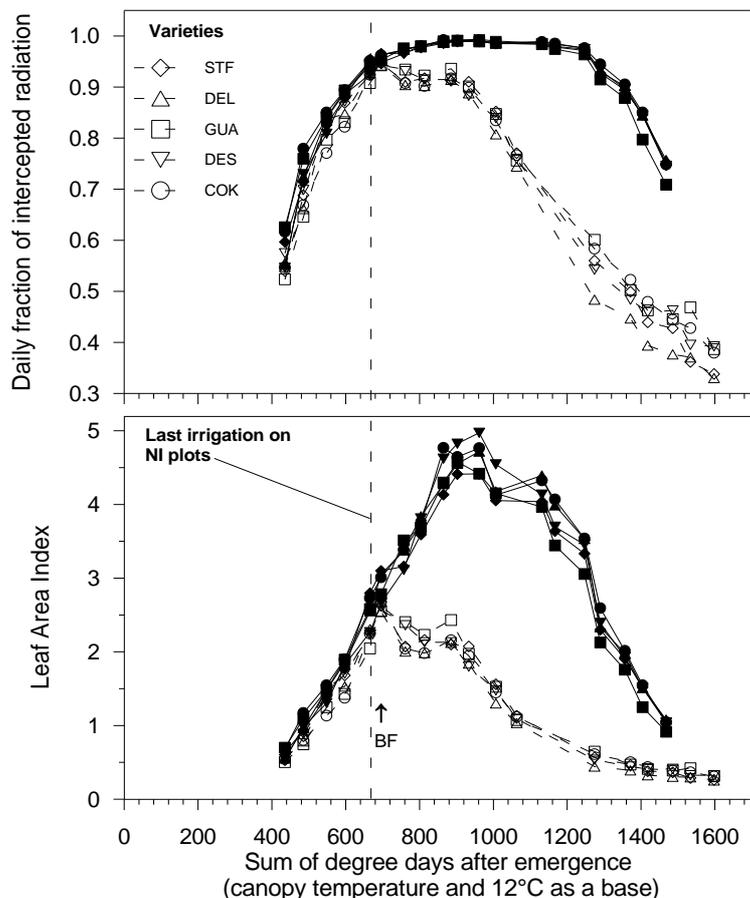
Figure 6. Harvest index in the 3 experiments. Means per genotype x water regime over 3 (1994 and 1996) and 4 (1995) replicates. Irrigated (IR) treatments as gray bars, and non irrigated (NI) treatment as dashed bars. Aerial biomass, and consequently harvest index, were differently measured in the 3 experiments : whole aerial dry weight basis in 1996, and partial weight in 1994 and 1995.