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Research

Ontogeny modifies the effects of water stress on stomatal control, leaf area duration and biomass partitioning of *Pennisetum glaucum*

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Summary

• Experiments are presented that test the relative importance, during ontogeny, of stomatal control and leaf area expansion to optimum seasonal water use in pearl millet (*Pennisetum glaucum*). These parameters play a key role in the compromise between plant growth and water saving under unpredictable conditions of semiarid environments.

• The response of growth and water use of crops to successive 15 d drought periods was measured under field conditions in Niger (West Africa).

• From emergence to anthesis, biomass partitioning to stems and panicles depended strongly on leaf area development. Water use was linearly related to green leaf area duration in well watered plots, but was reduced proportionally more than green leaf area in drought-affected plots. The relations of crop growth rate and transpiration efficiency to leaf area depended on ontogenetic changes in biomass partitioning.

• In *P. glaucum*, stomata play a dominant role in reducing crop water use under preanthesis drought, although this control becomes negligible after anthesis because of ontogenetic decline in the range of stomatal conductance. The rate of leaf senescence after anthesis is not drought-dependent.

Key words: *Pennisetum glaucum*, biomass partitioning, crop water balance, growth analysis, intermittent drought, leaf area index, ontogeny, semiarid tropics, water-use efficiency.

Introduction

For rainfed crops in drought-prone environments, rapid leaf area expansion, increased water use efficiency, and quick foliar senescence at the onset of drought are considered beneficial for total biomass production (Richards & Townley-Smith, 1987; Ludlow & Muchow, 1990). Early vigour in leaf area expansion ensures effective competition against weeds, reduces evaporation from the soil surface and allows the crop to store energy and carbohydrates for subsequent reproductive growth (Gallagher *et al.*, 1976; Pheloung & Siddique, 1991). Increased water use efficiency (WUE) has been associated with an increased ratio of carbon gain to transpiration, both of which are controlled by stomatal conductance and leaf area. However, increased WUE is not always advantageous to yield, since changes in WUE could stem from increased biomass partitioning to plant organs with no economic value (Van den Boogaard *et al.*, 1996, 1997). Accelerated leaf senescence in response to drought immediately reduces crop water requirement and hence can extend the duration of soil water availability. On the other hand, if drought is intermittent and ends with resumption of rainfall, senesced leaves cannot recover, and subsequent growth would be reduced because of decreased assimilatory surface. Maintenance of green leaf area could be advantageous in the case of temporary, intermittent drought, and would allow for a rapid recovery of assimilation rate. Green leaf area in either the pre or postanthesis period can also be critical for grain filling (Peltonen-Sainio *et al.*, 1997).

This has been observed in *Hordeum vulgare* (Van Oosterom & Acevedo, 1993), *Avena sativa* (Ehlers, 1991) and *Triticum aestivum* (Fischer & Kohn, 1966; Siddique *et al.*, 1989). However, these studies were conducted in Mediterranean or temperate climates, in which little rain falls during later stages of crop growth, and cereals must mature using stored soil moisture. The role of leaf senescence in optimizing crop growth and water use remains much less explored for crops that rely only on unpredictable rains after emergence, as is the case in much of the semiarid tropics.

For cultivated plants, adaptive morpho-physiological traits result from the ecological constraints faced by the crop, as well as from associated agronomic practices. When designing theoretical crop ideotypes, both ecological and agronomic conditions must be taken into account. Conditions found in high-input agroenvironments, such as those in most Mediterranean and temperate regions, and most agricultural research stations as well, differ strongly from those found in traditional, low-input agroenvironments, such as those in semiarid tropical regions (Donald & Hamblin, 1983; Janssens *et al.*, 1990). The latter conditions have received much less attention than the former, particularly because high-input conditions (high levels of water availability, inorganic fertilization, and plant density) are routinely used as control treatments in research stations. In the present study, an attempt was made to identify plant functional traits useful to a cereal ideotype that would be well adapted to soil water availability in low-input, semiarid agroenvironments with erratic rainfall patterns.

Pearl millet (*Pennisetum glaucum*), the staple cereal in the West African Sahel, is characterized by tall and numerous tillers capable of producing a high leaf area per plant. But under subsistence farming conditions, characterized by very few fertilizer inputs (e.g. 0.8 kg ha^{-1} y^{-1} in Niger after Mudahar, 1986), and low plant population (approx. 2–5 plants m^{-2}), leaf area indices remain quite low compared with other cereal crops, and are typically less than 1.2. Reduction in leaf area via leaf senescence or tiller mortality has been viewed as an adaptive response of pearl millet facing drought (Wallace *et al.*, 1993). A few studies have suggested that stored carbohydrates in senescing tillers are translocated to developing grains in viable tillers, which can compensate yield losses caused by water stress (Azam-Ali *et al.*, 1984; Muchow, 1989). Nonetheless, continued CO_2 assimilation by green leaves is essential for crop biomass accumulation and, consequently, grain yield. Recently, daily carbon assimilation in Sahelian pearl millet fields was found to parallel the course of LAI closely over the growing season (Levy *et al.*, 1997). Thus, leaf area appears to play a key role in conditioning drought response of the three main determinants of a cereal crop yield, namely, seasonal water use, water use efficiency, and partitioning of assimilates to grain (Passioura, 1977).

Early studies of pearl millet emphasized the role of stomata in conserving water during water deficit. In pearl millet grown on wet soil, stomata respond to changes in atmospheric vapour pressure deficit, with a response more pronounced in intermediate leaves than in upper leaves, which suggests an effect of leaf age on stomatal sensitivity to vapour pressure deficit (Squire, 1979). Sensitivity becomes reduced and is even absent in plants under dry soil conditions, although the reduction in transpiring leaf area can partially restore stomatal sensitivity to vapour pressure deficit (Black & Squire, 1979). Other studies have demonstrated the sensitivity of stomata to endogenous abscisic acid, which accumulates in the leaf in response to water stress (Henson, 1981a,b). This sensitivity declines after anthesis, such that stomata tend to remain open and thereby favour carbon assimilation during grain filling (Henson *et al.*, 1983). This last observation was made on upper leaves just beneath the panicles. Lower, older leaves were not considered. It is well established that maximum leaf conductance of pearl millet declines considerably after anthesis due to ontogenetic changes related to leaf ageing that are independent of water stress (Squire *et al.*, 1984; Do *et al.*, 1996).

Recent on-farm studies have suggested a relatively small role of stomata in regulating crop transpiration of pearl millet (Wallace *et al.*, 1993; Soegaard & Boegh, 1995). Instead, they point to leaf senescence as the main mechanism reducing crop transpiration. But agrophysiological studies have concluded that senescence was not a specific response to water deficit in pearl millet (Payne *et al.*, 1991a; Winkel *et al.*, 1997). Black & Squire (1979) have shown that stomatal regulation and leaf senescence are not mutually exclusive: stomatal conductance decreases as leaf area increases and, conversely, a reduction in transpiring area increases stomatal conductance in the remaining leaves.

Available literature, thus, suggests that stomatal sensitivity to evaporative demand is dependent upon leaf age and leaf area of the crop. This suggests that the degree to which water use is controlled by stomata and leaf area is influenced by ontogeny so as to optimize crop water use for growth. Accordingly, we propose the following hypothesis:

- During early or preflowering drought, when stomatal sensitivity is still high and reversible, water use is controlled by stomatal conductance, and green leaf area duration is relatively little affected by drought. This allows the plant to recover its assimilation capacity rapidly when drought ceases;
- During postflowering drought, when the range of stomatal response is low, plant water use is controlled via leaf senescence. Senescence will not reduce final grain production if there are sufficient carbohydrates in senescing or storage organs to be translocated to growing panicles.

To test this hypothesis, we examined the relations between green leaf area and the three components of biomass production (crop water use, water use efficiency, and partitioning of biomass to grain) of a pearl millet crop subjected to 15 d drought periods occurring prior to, during and after anthesis. We also explored how ontogenetic changes in these relations modify crop response to drought.

Table 1 Abbreviations and units of growth and water use characteristics

Abbreviation	Description	Unit
CGR	Crop growth rate	g (plant) m^{-2} (soil) d^{-1}
ET	Crop evapotranspiration	mm d^{-1}
ES	Soil evaporation	mm d^{-1}
GLAD	Green leaf area duration	days
GLAI	Green leaf area index	m^2 (leaf) m^{-2} (soil)
GLAR	Green leaf area ratio	m^2 (leaf) kg^{-1} (plant)
GLMR	Green leaf mass ratio	g (leaf) g^{-1} (plant)
HI	Harvest index	g (grain) g^{-1}(plant)
LMR	Total leaf mass ratio	g (leaf) g^{-1} (plant)
NAR	Net assimilation rate	g (plant) m^{-2} (leaf) d^{-1}
RGR	Relative growth rate	mg (plant) g^{-1} (plant) d^{-1}
SGLA	Specific green leaf area	m^2 (leaf) kg^{-1} (leaf)
SMR	Stem mass ratio	g (stem) g^{-1} (plant)
SPMR	Stem + panicle mass ratio	g (stem + panicle) g^{-1} (plant)
TR	Crop transpiration rate	mm (water) d^{-1}
TRE	Transpiration efficiency	g (plant) L^{-1}
TRL	Transpiration per green leaf area	l m^{-2} (leaf) d^{-1}

Materials and methods

Crop conditions, treatments and experimental design

The experiment was carried out in the field at the Institut des Radio-Isotopes, University of Niamey, Niger (13°29′ N, 2°10′ E) in 1993. The soil was a deep sand (93% sand in the surface 0–150 cm layer), typical of those cultivated in the Sahelian zone. In order to control crop water regime, pearl millet (*P. glaucum*, (L.) R. Br landrace Ankoutess) was grown under irrigation during the hot dry season (February to May). The crop was sown on 10 February at a spacing of one hill per square meter. Hills (or pockets) consist of holes of 5–10 cm depth made using a traditional hoe, containing a patch of 20–50 seeds and closed up immediately after sowing. Complete crop emergence occurred on 15 February and plants were thinned to a population of 3 plants m^{-2} 15 d after emergence (dae). Fertilizer applications were 30 kg ha^{-1} N, P_2O_5 and K_2O 1 d before sowing and 15 kg ha^{-1} N at 16 dae. Weeds were controlled manually. Final harvest was on 90 dae.

Water regimes consisted of four treatments: a control and three stress treatments. Plots for each water regime were sown adjacent to one another, arranged in a block design with five replications. Individual plots were 4 × 19 m (4 rows of 19 hills). The control regime (CTL) approximately simulated the average natural rainfall regime of the Tanout region, Niger (14°57′ N, 8°49′ E) where the landrace Ankoutess originates, with a gradual increase of irrigation frequency and amount until flowering, and a tapering off towards the end of the season. This water regime was determined after analysing rainfall data series for the mean length of dry spells between two successive rains and the mean daily rainfall during the rainy season. Irrigations were applied by microsprinklers at a spacing of 1 × 1 m. They took place at dusk and were the same for all treatments except stress treatments during deficit periods. In the stress treatments, irrigation was withheld: prior to flowering (from 30 to 45 dae, treatment S30); during early flowering (45–60 dae, treatment S45); or during late flowering (60–75 dae, treatment S60). During the last stress period, there was an unusually early fall of rain of 7.5 mm at 71 dae. Total water supply (irrigation + rainfall) was 380 mm in the control. Irrigation deficits relative to the control were –24% in S30, –25% in S45, and –10% in S60. During the experiment, daily mean air temperature varied between 25.5°C and 36.7°C, and daily mean incident radiation was 22 MJ m^{-2}. The daily mean vapour pressure deficit was 3.2 kPa and varied by < 10% throughout the experiment, ranging from 2.9 to 3.5 kPa in the successive time periods.

Soil water measurements

Soil water content was measured at depths of 0.10, 0.20, 0.30, 0.40, 0.60, 0.80, 1.00, 1.20, 1.40, 1.60, and 1.70 m in four of the five replicates of each irrigation treatment using a field calibrated neutron probe. Neutron probe measurements began at 9 dae and were thereafter made weekly. The amount of water stored in the soil profile was obtained by integrating water content over these depths using the trapezoid rule (Haverkamp *et al.*, 1984). Cumulative crop evapotranspiration (ET = plant transpiration + soil evaporation, see Table 1 for abbreviations and units) was obtained from the water balance equation:

$$dS = I - (ET + D) \quad \text{Eqn 1}$$

(dS, cumulative change in water stored in the 1.7 m profile; I is cumulative irrigation; D, cumulative drainage from the 1.7 m profile to deeper depths.) All terms in Eqn 1 are

relative to the first day of measurement. ET in the first days of the crop cycle was linearly interpolated assuming a zero value at crop emergence.

Plant transpiration (TR) was calculated by correcting crop evapotranspiration for evaporation from the soil surface (ES) using data collected from millet fields in Niger by Wallace *et al.* (1993) and Daamen *et al.* (1995). These authors demonstrated that ES decreases very rapidly following re-wetting of the soil surface by rain, and that most ES occurs during the first 2 d after rain. Using the data independently measured by Wallace *et al.* (1993) and Daamen *et al.* (1995) we estimated ES to be 2.5, 1.5, 0.75 and 0.5 mm d^{-1}, respectively, during the first 4 d after irrigation, and 0.25 mm d^{-1} thereafter. The same estimates were used throughout the experiment since, contrary to crops with high leaf area in temperate humid regions, crops with low leaf area in dry tropical environments have a small or even insignificant effect on ES (Daamen *et al.*, 1995).

Daily transpiration rate per unit of green leaf surface area (TRL) is largely controlled by stomatal conductance. It was calculated for specific time periods as:

$$TRL = TR/GLAD \quad \text{Eqn 2}$$

(TR and GLAD (green leaf area duration) are defined for the considered time period.)

Transpiration efficiency (TRE) for specific time periods was calculated as the ratio of the above-ground dry matter increase to TR. As atmospheric vapour pressure deficit remained in a narrow range throughout the experiment, TRL and TRE values among successive time periods were compared without normalization with respect to vapour pressure deficit.

Biomass measurements and derived data

Above-ground biomass was sampled at 15 d intervals beginning 30 dae for the control plants, and from the end of the deficit periods for the stress treatments. Plant growth before the deficit periods was assumed identical to that of the control plants. At any one harvest, two plants were harvested from each of the four replicate plots in which soil moisture was monitored (i.e. 8 plants for each treatment), and separated into stems, green leaves, senescent leaves, and panicles, and dried at 80°C for 3 d. At final harvest, dry matter was measured on four plants from each plot (i.e. 16 plants for each treatment), panicles were threshed, and grain mass was determined. Except for GLAI (see Eqn 4), all growth characteristics over successive time periods were calculated using the classical interval method (Radford, 1967; Evans, 1972) and, thus, refer to the mid-point of each time period. Biomass growth and green leaf area expansion were assumed to be linear between two successive harvests. The relative growth rate (RGR) was divided into a physiological component, net assimilation rate (NAR), and three morphological components, green leaf area ratio (GLAR), green leaf mass ratio (GLMR), and specific green leaf area (SGLA):

$$RGR = NAR \times GLAR = NAR \times GLMR \times SGLA \quad \text{Eqn 3}$$

The green leaf area index (GLAI) was derived from the green leaf dry mass using the following relation:

$$GLAI = (133.6\ GLDM + 22.69)\ CD \quad \text{Eqn 4}$$

(GLDM, green leaf dry mass per plant (g per plant); CD, planting density (3 plants m^{-2})). Payne *et al.* (1991c) demonstrated that this linear model gives accurate estimations for big individual leaves or whole plant leaf area in pearl millet, independent of harvest date, nutrient stress and water stress.

Statistics

Treatment means were separated using two-sample *t*-tests for simple comparisons, or Tukey's tests after one-way analysis of variance for multiple comparisons (in the text, differences are indicated with an * if significant at $P < 0.05$, and with ^{ns} if not statistically significant). Relations between the variables over the 0–60 dae period were tested with linear regression equations, using values for all individual plots in the control treatment ($n = 12$). As relations between TRE or CGR and GLAI were exponential, regression was calculated on log-transformed data. Departure from the fitted model in the stress treatments was evaluated using the 95% prediction intervals.

Results

Field water balance and crop water use

Mean water content at 1.7 m was approx. 0.06 $m^3\ m^{-3}$ for all of the irrigation treatments throughout the experiment. Hydraulic conductivity at this water content is sufficiently low to assume that D was negligible (Payne *et al.*, 1991b). The remaining terms of Eqn 1 are summarized in Fig. 1 and Table 2. Soil water reserves at the onset of drought in S30, S45, and S60 were only sparingly available, and decreased rapidly as they were used to maintain ET at a reduced rate (Fig. 1b). Data suggest that, by harvest, average soil water content was *c.* 0.03 $m^3\ m^{-3}$, which is the approximate water content of these soils at –1500 kPa (i.e. the matric potential associated with permanent wilting).

Table 3 gives the mean daily rates of ET, TR and TRL for successive time periods during the crop growth cycle. TR of control plots during the first 30 d period was 2.5 mm d^{-1}, corresponding to 53% of total ET and to a TRL value near 13.8 l $m^{-2}\ d^{-1}$. TRL was maximal during this stage of continuous emergence and expansion of new leaf tissue. In the next period (30–45 dae), TR of the control increased to 4.6 mm d^{-1} (i.e. 75% of total ET), while TRL decreased to 6.4 l $m^{-2}\ d^{-1}$. For stressed plants during this period, TR and TRL were significantly reduced by 51% and 41%, respectively, compared with plants in the control treatment.

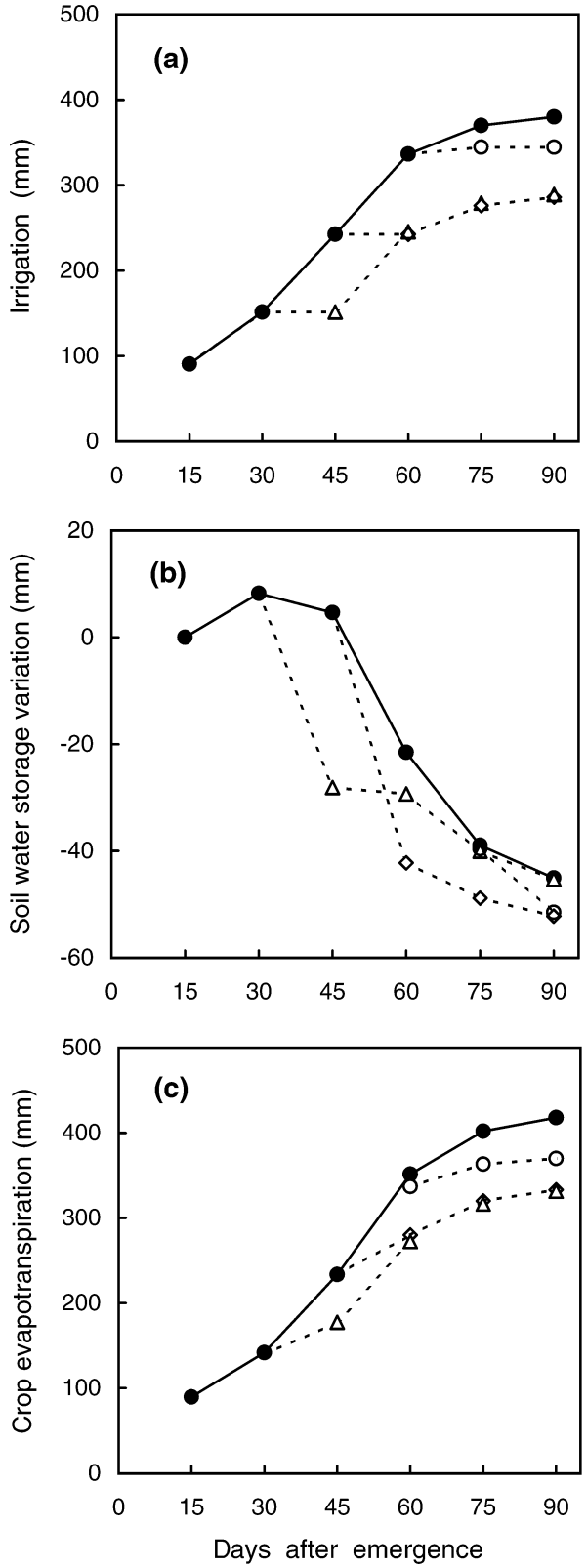

Fig. 1 Cumulative data for *Pennisetum glaucum* on (a) crop irrigation (b) variation in soil water storage and (c) crop evapotranspiration in the control (closed circles), S30 (triangles), S45 (squares) and S60 (open circles) treatments.

During the next 15 d period (45–60 dae), TR of control plants reached 6.2 mm d^{-1} (78% of ET), and TRL continued to decrease by 20%* compared to the previous period. Re-irrigation allowed plants of S30 treatment to return to TRL values comparable to those of the control. However, ET and TR remained significantly lower for S30 plants compared with those of the control treatment (–20%* and –24%*, respectively). This was due to reduced leaf area per plant (Table 3). The amount of irrigation withheld during the 15 d drought period for treatment S45 was roughly equivalent to that withheld for the S30 treatment (94 and 91 mm, respectively). In fact, ET, TR and TRL for treatment S45 were reduced against the control in the same proportions as those observed during drought in treatment S30, despite the fact that drought affected plants at different stages of development.

During the 60–75 dae period, ET, TR and TRL of control plants decreased sharply compared with the previous period (Table 3). Furthermore, the contribution of TR in ET decreased from 78 to 65%. During this period, TR and TRL were similar for all treatments, suggesting near total recovery for the previously stressed S30 and S45 treatments, and a negligible effect of the late drought treatment (S60). However, growth and water use data during this period were highly variable, possibly due to rapid changes in water availability and plant metabolism due to senescence and panicle filling. Statistically, ET was least for treatment S60, mainly due to reduced ES. The situation was essentially the same for the last period of the crop growth cycle (75–90 dae), with still lower values of ET, TR and TRL.

Over the entire crop growth cycle, cumulative ET and TR were similarly reduced in treatments S30 and S45 (–20%* for ET and –24%* for TR), and only marginally reduced in treatment S60 (–12%* for ET, –10%^{ns} for TR) (Table 2). These reductions were closely proportionate to the irrigation deficit of the different treatments (–25% in S30 and S45, –10% in S60). The estimated cumulative ES reached 142 mm in the control, and about 120 mm in stressed treatments.

Crop growth, water use efficiency, and allocation of biomass

In an earlier paper, Winkel *et al.* (1997) reported effects of the stress treatments on phenology, shoot growth, and grain yield using data from all five blocks of this experiment. In this paper, crop growth and yield data are only taken from the four blocks in which soil water measurements were made. Final grain yield in the control treatment was 77 g m^{-2}. Compared with the control, yield was reduced by 53%* in S30, 65%* in S45, and remained statistically unchanged in S60 (Table 2). Total above-ground biomass, which was 454 g m^{-2} in the control, was reduced proportionally by 38%^{ns} in S30 and 48%* in S45, and remained statistically unchanged in S60. Harvest index varied from 0.17 in the control, to 0.08* in

Table 2 Treatment means for cumulative crop water use and growth characteristics at final harvest

Water regime	Irrigation (mm)	ET (mm)	ES (mm)	TR (mm)	TRE (g mm^{-1})	GLAD (d)	HI (g g^{-1})	Grain yield (g m^{-2})	Total yield (g m^{-2})
CTL	380	418a	142	276a	1.7ab	55a	0.17a	77a	454ac
S30	289	331c	123	208b	1.3ab	55a	0.08b	23b	279bc
S45	286	333c	122	211b	1.1b	53a	0.11ab	27b	238b
S60	345	365b	116	249a	2.0a	58a	0.18a	9a	496a

ET, crop evapotranspiration; CTL, control regime; ES, soil evaporation; TR, crop transpiration; TRE, transpiration efficiency; GLAD, green leaf area duration; HI, harvest index. Values followed by different letters are statistically different at $P < 0.05$.

Table 3 Treatment means for daily crop water use and growth characteristics in different time periods

Period	Treatment	ET (mm)	TR (mm)	TRL	TRE	SPMR	GLMR	GLAR	GLAI	SGLA	CGR	RGR	NAR
0–30 dae	CTL	4.7	2.5	13.8	0.6	0.16	0.84	39.0	0.21	41.2	1.5	105	7.2
30–45 dae	CTL	6.1a	4.6a	6.4a	1.7a	0.42a	0.58a	7.9a	0.74a	13.5a	7.7a	38a	10.6a
	S30	2.5b	2.2b	3.7b	1.6a	0.36b	0.64b	8.6a	0.60b	13.6a	3.4b	24b	6.0b
45–60 dae	CTL	7.9a	6.2a	5.1a	4.2a	0.62a	0.34a	4.6a	1.23a	13.4a	26.3a	36a	21.7a
	S30	6.3b	4.7b	4.4a	2.5b	0.46b	0.49b	6.6b	1.07ab	13.5a	12.0b	30a	11.2b
	S45	3.1c	2.8c	2.9b	1.9b	0.53b	0.38a	5.2a	0.97b	13.5a	5.2c	11b	5.4b
60–75 dae	CTL	3.4a	2.2a	2.3a	−2.4a	0.70a	0.14a	1.9a	0.98ab	13.5a	−5.6a	−6a	−5.7a
	S30	2.9a	1.8a	1.6a	−1.5a	0.55b	0.34b	4.5b	1.14ab	13.4a	−1.8a	−3a	−1.8a
	S45	2.7ab	1.5a	1.8a	−0.6a	0.57bc	0.27bc	3.6ab	0.83b	13.5a	−1.1a	−2a	−1.2a
	S60	1.8b	1.5a	1.4a	5.1a	0.68ac	0.19ac	2.6a	1.18a	13.4a	−7.9a	−9a	−7.6a
75–90 dae	CTL	1.1a	0.3a	1.0a	−75.8a	0.68a	0.05a	0.7a	0.31a	14.2a	−1.1a	1a	−8.6a
	S30	1.0a	0.3a	0.6a	7.9a	0.58b	0.15b	2.0b	0.48a	14.4a	2.0a	3a	4.4a
	S45	0.9ab	0.1a	0.2a	1.2a	0.58b	0.14b	1.9b	0.41a	15.1a	1.1a	2a	3.1a
	S60	0.4b	0.2a	0.4a	124.1a	0.67a	0.10ab	1.4ab	0.50a	14.3a	3.2a	5a	4.1a

CTL, control regime; ET, crop evapotranspiration; dae, days after emergence; TR, crop transpiration rate; TRL, transpiration per green leaf; TRE, transpiration efficiency; SPMR, stem + panicle mass ratio; GLMR, green leaf mass ratio; GLAR, green leaf area ratio; GLAI, green leaf area index; SGLA, specific green leaf area; CGR, crop growth rate; RGR, relative growth rate; NAR, net assimilation rate. For a given time period, values followed by different letters are statistically different at $P < 0.05$.

S30, 0.11^{ns} in S45, and 0.18^{ns} in S60. Hence, under our experimental conditions, crop production was most affected by water deficit prior to or at early flowering (respectively, S30 and S45), while postflowering stress (S60) had no significant effect.

Table 3 gives information on mean crop growth and water use characteristics for successive time periods in the four treatments. CGR in the control increased continuously from emergence to early flowering. Thereafter, CGR became nil or negative, indicating net loss of above-ground biomass. During the 30–45 dae period, the increase in CGR was the result of the rapid increase in GLAI, as NAR remained nearly the same. In the next period, the increase in CGR was due to increases in both GLAI and NAR. Despite the dry period, CGR in S30 also increased continuously from emergence to early flowering, but at lower rates than in the control, due to lower GLAI and NAR values. Compared with the control, CGR of S30 was reduced by 55%* during the stress period. Even during the next 15 d following reirrigation, CGR of S30 was 54%* less than that of the control. Water stress during 45–60 dae (S45) had the most severe impact on CGR, reducing it by 80%* compared with control treatment. This reduction was due to low values for GLAI and NAR occurring simultaneously. After anthesis (60 dae), CGR, NAR and GLAI decreased sharply, and there were no longer any differences between control, stressed or reirrigated treatments.

RGR of control plants was maximal during the first 30 d, decreased to a plateau until 60 dae, and became nil or negative thereafter. Early and mid-season drought significantly decreased RGR compared with the control by 37%* in S30 and 68%* in S45. This decrease in RGR could be entirely attributed to lower NAR, as GLAR, GLMR and SGLA in S30 and S45 remained similar to the control during stress. Thereafter, in reirrigated S30 plants, the significantly higher GLAR (+44%* relative to the control) partly compensated for the low NAR value (still −48%* relative to the control), and RGR recovered almost completely (−16% relative to the control). Increased values of GLAR in stressed and recovering plants were due mainly to increased GLMR, as

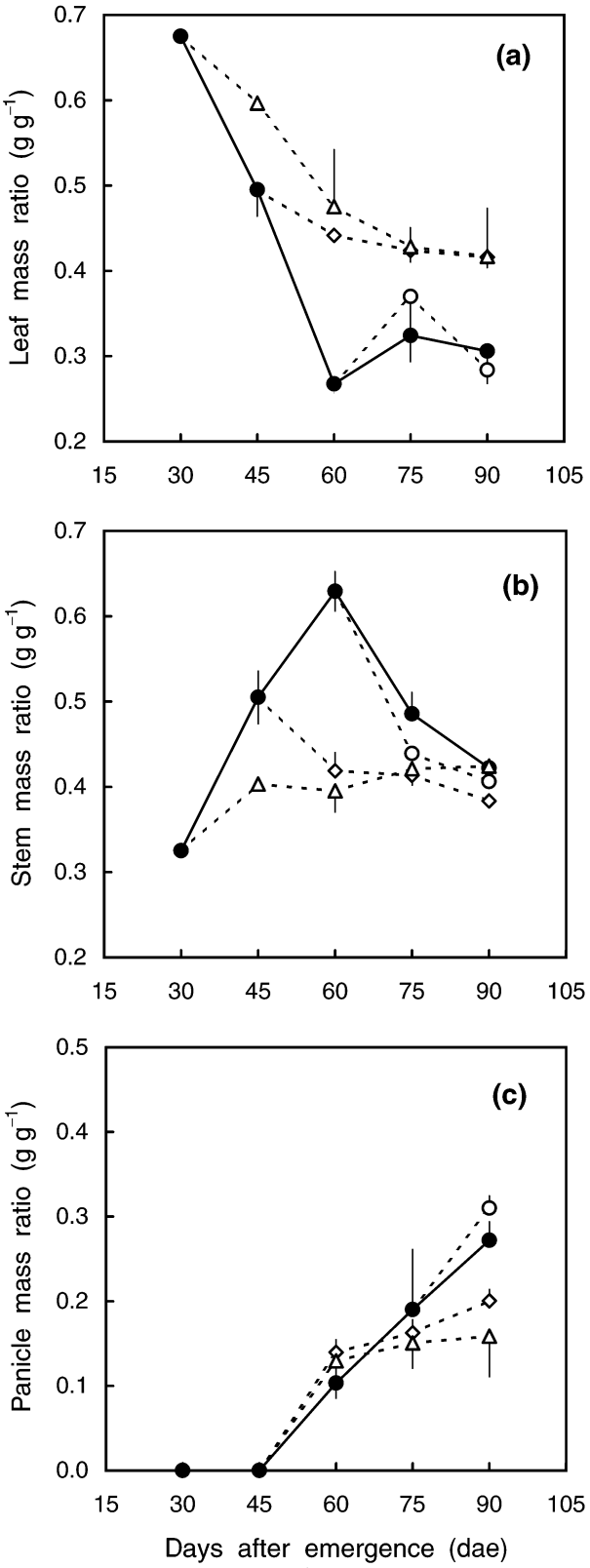

Fig. 2 Seasonal variations in (a) leaf (b) stem and (c) panicle mass ratios in the four treatments for *Pennisetum glaucum*. Crop evapotranspiration in the control (solid circles), S30 (triangles), S45 (triangles) and S60 (open circles) treatments (means ± SE).

SGLA did not vary between treatments from 30 to 90 dae. After 60 dae, RGR of stressed or reirrigated plants did not differ from those of the control.

The allocation of above-ground biomass among different organs in the control varied according to the phenological development of the crop (Fig. 2). At 30 dae, shoots were composed mostly of leaves. More and more dry matter was partitioned to stems from 30 dae onwards, and to panicles from 45 dae onwards. During the 45–60 dae period, biomass was allocated to rapidly growing stems and emerging panicles, and less so to leaf expansion. Accordingly, during this period, LMR decreased to 0.27 and SMR increased to 0.63. From 60 to 90 dae, LMR and total standing biomass remained approximately constant or even declined for control plants, while PMR increased, apparently at the expense of stem biomass. This constitues circumstantial evidence of translocation of stored assimilates to panicles. Early and mid-season water stress (S30 and S45) immediately reduced SMR, which levered off at a value of about 0.40 from the end of the stress period to the final harvest. Compared with the control, partitioning of biomass to panicles remained unaffected by water stress until 60 dae (PMR approx. 0.12 in all treatments). But after 60 dae, PMR increased for control plants, whereas it did not for S30 and S45 plants. There was no effect of stress during the 60–75 dae period (S60) on PMR.

GLAI in control plots was 0.21 during the 0–30 dae period, and increased by three-fold during the following 15 d (Table 3). Water stress during this period of rapid leaf expansion reduced GLAI by 19%* in S30 compared with control plants. During the 45–60 dae period, GLAI reached 1.23 in the control treatment, and was reduced by 21%* in the stress treatment (S45). At this time, in the re-irrigated S30 treatment, GLAI was no longer significantly different from control plants (–13%). During the next period (60–75 dae), leaf senescence of control plants progressed rapidly, such that GLAI values of stress treatments were within 20% of those of the control. The acceleration of leaf senescence towards the end of the crop cycle rapidly decreased GLAI to values near 0.45 in the three stress treatments, and to 0.3 in the control. Over the entire 0–90 dae period (Table 2), GLAD was 55 d for the control, with negligible effects due to water stress (+1% in S30, –3% in S45, +6% in S60).

TRE of control plants increased from emergence to early flowering due to a continuous increase in growth rate and decrease in transpiration per unit leaf area (Table 3). Under early drought (treatment S30), the decrease in growth was proportionate to that of transpiration rate, and, thus, TRE remained similar to that of the control. During the next period (45–60 dae), TRE was significantly reduced in S30 and S45. In re-irrigated S30, the decrease in TRE could be attributed to the resumption of high TRL and GLAI values, while NAR remained significantly lower than that of the control. In S45, crop growth was much more reduced than transpiration, leading to decreased values of TRE. After 60 dae, when growth

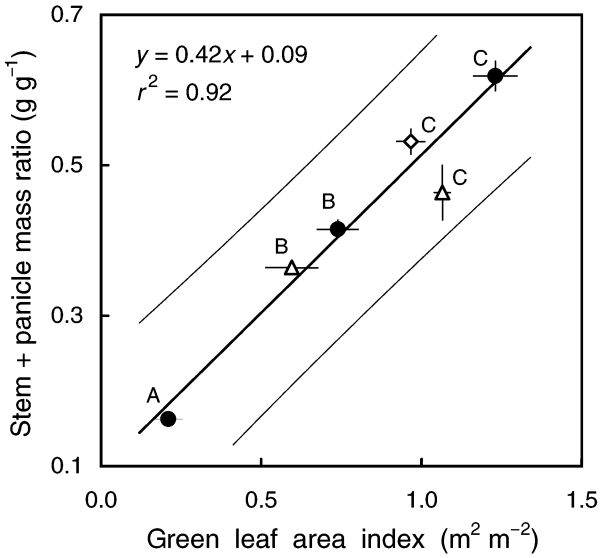

Fig. 3 Relation between mean values of stem + panicle mass ratio and green leaf area index at three time periods (A: 0–30 dae, B: 30–45 dae, C: 45–60 dae) in the control (solid circles), S30 (triangles) and S45 (triangles) treatments (means ± SE) in *Pennisetum glaucum*. Regression was calculated for the individual control plots (n = 12). Thin lines show the 95% prediction interval.

became nil or negative, TRE in all treatments decreased to values not statistically different from zero. Over the entire crop cycle (Table 2), TRE in the stressed treatments was not statistically changed compared to the control.

Relationships of crop water use and growth to green leaf area and biomass allocation

Contrary to postanthesis water deficit (S60) which had virtually no impact on plant growth and water use, preanthesis stress (S30 and S45) had a negative effect on biomass allocation and green leaf area. These two components fitted the same linear relation in the control, S30 and S45 treatments from 0 to 60 dae, corresponding roughly from emergence to flowering (Fig. 3). Thus, up until anthesis, the allocation of biomass to storage organs (stems and panicles) appeared to be tightly dependent on green leaf area (i.e. on the morphological component related to the plant's ability to produce new assimilates). This relation was independent of crop phenological stage and water regime. Due to the linearity between biomass allocation and green leaf area until anthesis, the different relationships of crop growth and water use with GLAI and SPMR were quite similar (e.g. Figures 4c and 5). Thus, to simplify the presentation in the following, the emphasis will be put on the relations with GLAI.

During the first 60 d of the growth cycle, in well-watered treatments (control or reirrigated S30), crop water use in terms of ET and TR remained linearly related to GLAI (Fig. 4a,b). However, under conditions of water stress (S30 and S45), ET and TR were proportionally reduced much more than GLAI, and data points deviated from this linear relation. This suggests that, at least until flowering, reduction in green leaf area was not the only factor, or even the most influential one, limiting crop water use under drought.

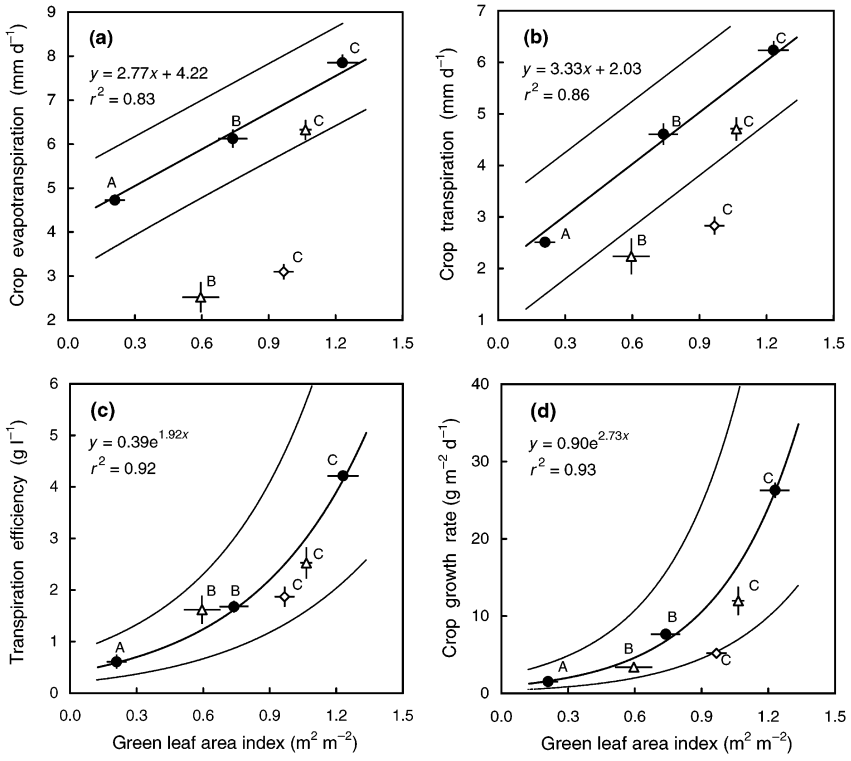

Fig. 4 Relations of (a) crop evapotranspiration (b) crop transpiration (c) transpiration efficiency, and (d) crop growth rate with mean values of green leaf area index at three time periods (A: 0–30 dae, B: 30–45 dae, C: 45–60 dae) in the control (solid circles), S30 (triangles) and S45 (triangles) treatments (means ± SE) in *Pennisetum glaucum*. Regression was calculated for the individual control plots (n = 12). Thin lines show the 95% prediction interval.

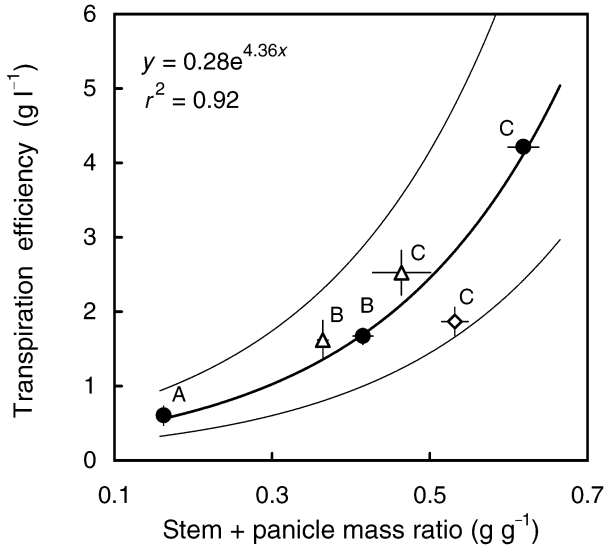

Fig. 5 Relation between transpiration efficiency and mean values of stem + panicle mass ratio at three time periods (A: 0–30 dae, B: 30–45 dae, C: 45–60 dae) in the control (solid circles), S30 (triangles) and S45 (triangles) treatments (means ± SE) in *Pennisetum glaucum*. Regression was calculated for the individual control plots (n = 12). Thin lines show the 95% prediction interval.

Both CGR and TRE of control treatments increased exponentially with GLAI over the 0–60 dae period (Fig. 4c,d). Neither the S30 nor the S45 stressed treatments departed significantly from these relations. Therefore, in contrast to crop water use, the relation of CGR and TRE to GLAI appeared independent of water regime, and instead dependent on changes in biomass allocation related to ontogeny.

Discussion

Control of crop water use vs plant response to drought

Because ET was generally equal to or greater than irrigation during the entire growing cycle, we can conclude that water supply was the limiting factor to crop growth in all treatments, including the control (De Wit, 1958). The linear relation between ET and GLAI (Fig. 4a) suggests that soil evaporation was little affected by crop development, as already reported by Daamen *et al.* (1995) and Pilbeam *et al.* (1995) in sparse crops. Cumulative ES values for our experiment are in accordance with estimates of 35% of total rainfall given by Wallace *et al.* (1993). Thus, hydrological conditions in this experiment generally mimicked those found during the growing season in relatively dry regions of the northern Sahel, from which the landrace Ankoutess originates. This is true even for the control treatment which simulates the average rainfall pattern in northern Sahel but would appear stressed late in the season when compared with conventional experiments with full irrigation up until crop maturity. In an agroecological perspective, analysing crop responses to drought will be more relevant if the control refers to the average rainfall pattern under which the plants have been selected since centuries rather than an arbitrary and high watering level, unrealistic for a dryland agricultural system.

Drought leads to physiological stress that causes plants to decrease crop water use by reduction in the stomatal conductance and/or the green leaf area. Ontogeny modifies the response of crop growth and water use to drought throughout the growing season, with periods of maximal TR and CGR being generally the most sensitive to water stress. In well-watered pearl millet, stomatal conductance remains high until anthesis, and thereafter decreases rapidly (Squire *et al.*, 1984; Do *et al.*, 1996). Similarly, our data show a 50% decrease in TRL in well-watered plants from the 45–60 to the 60–75 dae period (Table 3). Furthermore, GLAI in drought-affected treatments was reduced but always less so than crop water use or TRL, implying significant control on TR by stomata until anthesis. Thus, until flowering, the regulation of crop water use appears to result from a potentially broad and reversible stomatal response. This would appear to be a better adaptation to intermittent drought spells than an immediate delay in leaf growth or, a fortiori, the permanent senescence and shedding of leaves. This is in contrast to recent works suggesting relatively weak influence of stomata on crop transpiration in pearl millet (Wallace *et al.*, 1990, 1993; Soegaard & Boegh, 1995). Several causes can be invoked for this difference. Those experiments were conducted on-farm under rainfed conditions and without control of plant density. Plant populations were much more heterogeneous in these experiments, leading to potential problems in leaf area sampling. Both Soegaard and Boegh (1995) and Wallace *et al.* (1993) mention that LAI was over-estimated in their studies. More importantly, crops in their studies were apparently not exposed to drought during preanthesis growth stages. Consequently, stomatal control would have played a relatively minor role in regulating crop water use compared to leaf senescence.

Consequences of drought on plant growth and grain yield

Even though GLAI and TR values for treatments S30 and S45 were similar to those of the control after flowering, panicle filling was severely reduced in these treatments (Table 2). Furthermore, grain yield of the control treatment, in which water availability decreased gradually during panicle filling, was similar to that of treatment S60, in which water availability was suppressed over most of this period. This suggests that, under Sahelian rainfall conditions, panicle filling does not depend solely on crop water use or green leaf area after flowering. These conditions contrast those of

temperate cereals grown on stored water (e.g. Passioura, 1976) or of pearl millet abundantly irrigated until crop maturity (Bidinger *et al.,* 1987; Mahalakshmi *et al.*, 1987, 1991).

What does this say of the role of postanthesis maintenance of GLAI in determining grain yield? In treatments S30 and S45, GLAI values were similar to those of the control from 60 to 90 dae due to a higher partitioning to green leaves (see GLAR and GLMR in Table 3). Thus, leaf production was less affected by drought than stems and panicles were. This was related to the fact that postanthesis senescence of tillers was retarded in plants stressed before anthesis (Winkel *et al.*, 1997). Delayed leaf senescence may have been due to increased leaf N content due to limited panicle sink size (e.g. Fischer, 1973; Biswas & Mandal, 1987; Jordan, 1993). For crops such as pearl millet with high tillering capacity, prolonged green leaf duration following early drought could limit yield loss by sustaining leaf assimilation in recovering plants. Moreover, maintenance of GLAI after anthesis could help pearl millet to take advantage of an unusually long rainy season, as may occur in the highly variable climate of the Sahel (Le Barbé & Lebel, 1997; Sivakumar & Salaam, 1999). It may also facilitate common practice of Sahelian farmers to making successive harvests in the same field. Both situations offer opportunity for main stems on late plants or tillers on early plants to grow and produce panicles which otherwise would remain undeveloped. Under such conditions of unpredictable rain and traditional, low-input farming, extended tillering associated with leaf area maintenance and large interindividual variability in the flowering period are valuable traits for a cereal ideotype (Janssens *et al.*, 1990; Renno & Winkel, 1996; De Rouw & Winkel, 1998).

Considering the positive relationship between green leaf area and grain filling found in many cereal species, and since critical phases for grain yield of pearl millet occur before or at early flowering, maintenance of GLAI at these stages should be crucial in the case of water deficit. In this study, GLAI reduction was significant but limited (about −20%) during the drying phases of treatments S30 and S45, while TR decreased by about 50% in both treatments. This has two implications. First, as was already mentioned, stomatal control appears to be important in restricting crop water use under preflowering drought. Second, the major yield reduction caused by preflowering drought appears to be related to factors or processes other than GLAI. Grain yield also depends on developmental processes such as meristem differentiation, meiosis or pollination, which are not directly related to the plant leaf area. In sorghum, Amzallag (1999) showed that the plant sensitivity to environmental stresses depends on the hormonal metabolism integrating the different meristems within the whole organism. This functional integration of the various meristems depends on the timing of morphogenesis, which could explain the irreparable damage on final grain production caused by environmental stress during earlier phases of development.

Seasonal changes in water use efficiency were related to phenological changes in biomass allocation (Fig. 5). The same was found for pearl millet cultivated in Sahelian farmers' fields, where water use efficiency was maximum at the heading stage, during the final stage of leaf area growth (Friborg *et al.*, 1997). TRE values of 4.2 mg g^{-1} found in control plots during the 45–60 dae period compare well with the estimates of 3–4.7 mg g^{-1} by Azam-Ali *et al.* (1984) for low density pearl millet fields before flowering. In fact, TRE and CGR would be expected to increase with SPMR from 0 to 60 dae, as respiration and transpiration rates are lower in stems and panicles than they are in leaves. This positive effect of the change in biomass allocation added to the increase in GLAI, which explains the exponential increase of TRE and CGR with GLAI over the 0–60 dae period (Fig. 4c,d). Ehlers (1991), working with oats, proposed that during early growth stages when GLAI is still low a great proportion of solar radiation reaches the soil surface between plants, thus generating sensible heat that enhances the transpiration without contributing to photosynthesis. The same should have occurred in our experiment, as solar radiation was high and GLAI was less than 1.0 over most of the crop cycle (periods A and B in Fig. 4). Although radiation interception increases from emergence to flowering, in low density pearl millet fields, it reaches a maximum of only 50% at anthesis (Azam-Ali *et al.*, 1984; Bégué *et al.*, 1991). Daily sensible heat flux was found to be nearly 66% of the evapotranspiration flux and 40% of the net radiation in a pearl millet field with dry soil and LAI about 0.3 (Soegaard & Boegh, 1995).

Water deficit affected water use efficiency through changes in biomass allocation as well as through instantaneous changes in transpiration and assimilation. Its impact depends on the stage of development and involved indirect effects. Early water deficit (S30) did not immediately induce significant modifications in biomass allocation nor in TRE, though values of plant water use and growth (TR, TRL, NAR, RGR and CGR) were severely reduced. But S30 retained significant after-effects of earlier water deficit on plant growth, biomass allocation and water use efficiency, even after TRL had recovered normal values upon reirrigation. This demonstrates the irreparable effects of preanthesis drought and the inability of late tillers to effectively compensate for this damage when water supply becomes progressively limited after flowering. A detailed analysis of flowering in the present experiment (De Rouw & Winkel, 1998) showed that only 16% of plants in the S30 treatment were early enough to delay flowering and to produce eared tillers after irrigation had resumed. This was insufficient to compensate for the 31% of plants made totally sterile because of drought. Mid-season water deficit (S45) induced immediate modifications in biomass allocation and water use efficiency, as well as reductions in all other crop growth and water use characteristics. Its impact on the pattern of biomass allocation was also lasting as shown by the values of SPMR, GLMR or GLAR after 60 dae, after TR and TRL recovered

values similar to the control. Late water deficit (S60) reduced crop water use (ET) during stress, but this was mainly attributable to lower ES, and had no impact on any plant growth or water use characteristic.

Conclusion

Our initial hypothesis was only partially validated because, contrary to what was expected, a reduction in green leaf area of the crop occurred in the case of preanthesis drought and not for postanthesis drought. In this latter period, soil water resources decreased rapidly irrespective of water regime, and leaf senescence affected all treatments. In fact, leaf senescence after anthesis was delayed in previously drought-stressed treatments compared with the control, but without apparent benefit for grain yield. Before anthesis, leaf area reduction caused by drought was significant (−20% compared with the control) but was always less than the reduction in transpiration per unit leaf area (−40% compared with the control). This supports the hypothesis of stomatal control as the dominant cause of reduction in crop evapotranspiration during preanthesis drought. Stomatal control kept the same relative value after anthesis (compare S60 with the control) but it became negligible in absolute terms because of the ontogenetic decline in maximum stomatal conductance following anthesis. This ontogenetic effect cancelled the potential advantage of stomatal regulation and, combined to irreparable damage of drought on meristems, explains the poor recovery of the crop after preanthesis droughts.

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