Journal of
Experimental
Botany

# Effect of the timing of water deficit on growth, phenology and yield of pearl millet (*Pennisetum glaucum* (L.) R. Br.) grown in Sahelian conditions

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## Abstract

Several studies conducted under high input conditions have indicated little susceptibility of pearl millet to water deficit untill early grain filling, because the losses in main shoot production were fully compensated by increased tiller fertility. The present study assessed the impact of water deficits at three development stages: prior to flowering (S30), at the beginning of flowering (S45), and at the end of flowering (S60) in pearl millet grown in experimental conditions similar to Sahelian farming conditions. It included a control irrigation treatment simulating the natural distribution of rainfall throughout the cropping season. Both biomass production and grain yield were severely reduced by S30 and S45, while S60 had no effect. In S30 and S45, the flowering of tillers was delayed or totally inhibited. In both of these treatments, the low number of productive tillers did not compensate for damage to panicle initiation and flowering of the main shoot. All treatments maintained green leaves on the main shoot during the grain filling period, and in S30 leaf growth recovered from mid-season drought. These results illustrate how pearl millet mostly escapes drought by matching its phenology to the mean rainfall distribution in the Sahel. In the case of mid-season drought, some late productive tillers and the maintenance of green leaf biomass of the main shoots limited, but did not overcome, the yield losses. This study stresses the importance of agro-ecological conditions in control treatments, particularly the water regime and crop density, when assessing crop drought resistance.

## Introduction

The usual effects of drought on the development of a plant are a lowered production of biomass and/or a change in the distribution of this biomass among the different organs. The drought resistance of a cultivated plant reflects its capacity to limit the impact on the economic yield of these changes in biomass production and distribution. This capacity will depend on the development phase affected by water deficit, as well as on the intensity and the length of the drought. In Sahelian climates, where agrosystems are based essentially on pearl millet (*Pennisetum glaucum* (L.) R. Br.), the risks of drought can be classed into two types according to their impact on pearl millet cultivation.

(1) Droughts at the beginning or end of the cropping season, frequent and often long, but to which peasant farmers respond by successive re-sowing (in the case of early droughts) or by the choice of short-season cultivars tolerant of post-floral water deficits (in the case of late droughts);

(2) Intermediate droughts, less frequent and often brief (about 10 d), but very unpredictable and without any practical remedies. They affect development stages such as initiation of panicles, earing, or flowering which, in cereals, are generally sensitive to water deficits. The variability of these droughts in time and space complicates the characterization of drought-resistant varieties.

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It is in relation to these climatic risks that the most sensitive phases of plant growth must be identified. Knowing the components of final production deployed in each of these phases, one can better analyse the adaptation characteristics of the plant and, hence, define more efficiently the objectives of improvement of drought resistance (Janssens *et al.*, 1990; Sedgley and Belford, 1991).

Few studies on the adaptive strategies of pearl millet have used the integrated approach necessary to bring out the optimal combinations of phenological and morpho-physiological traits developed at different levels of biological organization (Winkel and Do, 1992). However, a number of indices suggest that the adaptation of pearl millet to drought relies on morphological and phenological traits rather than on physiological attributes like osmotic adjustment or tissue elasticity (Do *et al.*, 1994). In previous studies, it was reported that the period of grain filling is the most sensitive to water deficit, mainly because at earlier stages, the losses on the main shoot were compensated by an increase in the production of later tillers (Mahalakshmi and Bidinger, 1986; Bidinger *et al.*, 1987; Mahalakshmi *et al.*, 1987). This implies that abundant tillering and asynchronous development of shoots permit certain panicles to escape the effects of drought occurring during the course of the growing season. However, the vegetative development of pearl millet and, consequently, its possible adjustment to water stress, are very much influenced by experimental conditions, in particular, the timing and intensity of water deficit (Mahalakshmi *et al.*, 1987), the soil fertility and the planting density (Azam-Ali *et al.*, 1984; Carberry *et al.*, 1985). In most of the published works, the control plants were irrigated up to harvest, and the population densities and the soil fertility levels were very high (commonly 10 plants $m^{-2}$ sown in rows, 80 to 120 kg nitrogen per hectare). In these conditions, the stressed plants survived up to 50 consecutive days of drought, and the grain production by plants stressed during 28 d reached 3000 kg $ha^{-1}$. In Sahelian regions, droughts usually last 10–15 d between tillering and early grain filling (Sivakumar, 1992), pearl millet is always sown in a hill (a group of several seeds planted in one hole), recommended cultivation density is one hill per square metre with three plants per hill (INRAN, 1987), and practically no inputs are used. Grain yields in farming conditions are between 400 and 600 kg $ha^{-1}$ (Anand Kumar, 1989; World Resources Institute, 1992). These low-input conditions contrast strongly with those normally found on research stations. However, the identification of the characteristics of drought adaptation should be based on an experimental method that reproduces as closely as possible the vegetative development of pearl millet observed in traditional farming conditions. This approach is difficult because of the necessity of controlling certain environ-

mental factors and, in particular, the water regime. Due to the unpredictability of the rains in the normal growing season, drought experiments are usually conducted on irrigated plots during the dry season. The study presented here analyses the effects on the growth and flowering of pearl millet of drought periods of 15 d at different stages of development. This study was carried out in the Sahelian region, during the dry season, using an irrigation regime which simulated the natural rainfall. Population density and soil fertility were close to traditional farming conditions. Its particular objectives were (i) to identify the development stages most sensitive to drought, (ii) to evaluate the ability of tillers to compensate for losses in production on the main shoot in cases of pre-flowering stress; and (iii) to discuss the adaptive value of certain morpho–phenological traits in relation to local drought conditions.

## Materials and methods

The experiment was carried out in the field at the Institut des Radio-Isotopes, University of Niamey (Niger). The soil was a deep sandy soil (93% sand in the 0–150 cm layer), typical of those cultivated in the Sahelian zone. Pearl millet (*Pennisetum glaucum* (L.) R. Br., landrace Ankoutess) was grown during the hot dry season (February to May). It was assumed that traits of drought resistance would be expressed more strongly in this landrace than in any other, as it originates in the region of Tanout (14°57′N, 8°49′E) whose annual precipitation (223 mm) is among the lowest, and frequency of the dry spells among the highest, in the agricultural zone of the Sahel (Sivakumar, 1991). As Ankoutess flowers in about 60 d, it is considered as insensitive to daylength (Pearson, 1984; Clément, 1985). Mean air temperature varied between 25.5 °C and 36.7 °C, mean daily incident radiation was 22 MJ $m^{-2}$ and mean daily vapour pressure deficit was 3.2 kPa (Fig. 1). A rain of 7.5 mm occurred 71 d after emergence (DAE). The crop was sown on 10 February at a spacing of one hill per square metre. Complete crop emergence occurred on 15 February and plants were thinned to a population of 3 plants $m^{-2}$ at 15 DAE. Fertilizer applications were 3 g $m^{-2}$ N, $P_2O_5$ and $K_2O$ one day before sowing and 1.5 g $m^{-2}$ N at 16 DAE. Weeds were controlled manually. Final harvest was at 90 DAE.

Water regimes consisted of four treatments, a control irrigated throughout the study, and three stress treatments in which irrigation was withheld prior to flowering (from 30–45 DAE, treatment S30), during early flowering (45–60 DAE, treatment S45) and late flowering (60–75 DAE, treatment S60). Irrigation was applied by microsprinklers at a spacing of 1 × 1 m. Water applications were the same for all treatments except during the deficit periods. The control regime approximately simulated the natural rainfall regime of the region of Tanout, with a gradual increase of irrigation frequency and amount until flowering, and a tapering off towards the end of the season (Fig. 1). 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. Due to technical constraints, irrigations higher than 17 mm were split over two consecutive days.

Plots for each water regime were sown adjacent to one another, arranged in a block design with five replications.
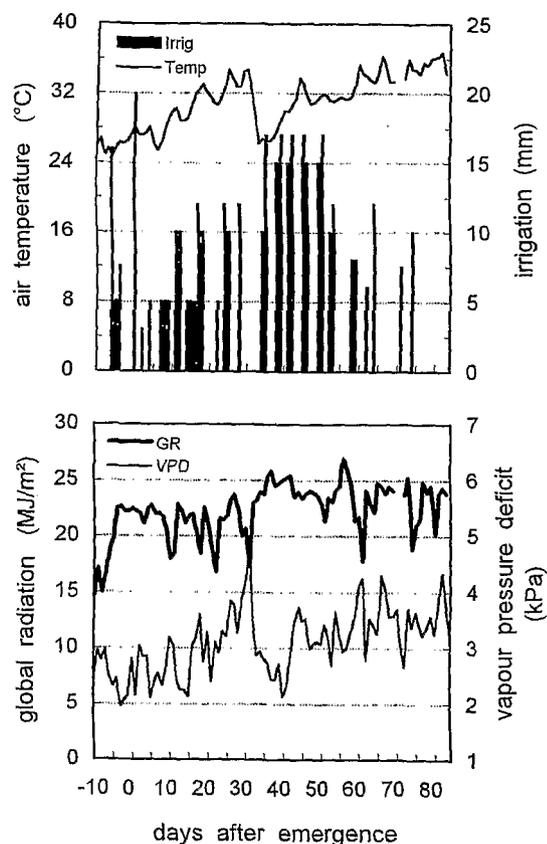
**Fig. 1.** Daily mean air temperature, irrigation, global radiation and vapour pressure deficit during the experiment (first day after emergence was 15 February).

Individual plots were 20 × 5 m (4 rows of 19 hills). Only the two central rows were sampled. Phenology was monitored every 2–3 d on four plants in each plot by recording the number of panicles at the stages of female flowering and grain maturity. Above-ground dry matter was sampled at 15 d intervals from 30 DAE on in the control plots and from the end of the deficit periods in the stress treatments (the growth of the plants before the deficit periods was assumed identical to that of control plants). Two plants in each plot (i.e. 10 plants for each treatment) were harvested, 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 in each plot ($n = 20$ for each treatment), panicles were threshed and grain number and weight were determined. The statistical significance of the differences between the control and the stress treatments was analysed by $t$-tests with a 0.05 probability level (in the text, differences are shown with an*, if statistically significant, and [ns] if not statistically significant).

## Results

### Final production and yield components

The final production of above-ground biomass and its allocation among the different organs of the plant are given in Table 1. The grain yield of the control treatment was 23 g plant$^{-1}$ (i.e. 690 kg ha$^{-1}$). This falls in the higher range of yields observed generally in the traditional Sahelian farming environment (400–600 kg ha$^{-1}$). The S60 treatment had a grain yield equivalent to that of the control (26 g plant$^{-1}$). The difference, which is statistically not significant, results essentially from a higher number of eared tillers in S60. In contrast, the total production of above-ground biomass was reduced by 39%* in S30 and 44%* in S45. Grain yield for both treatments was reduced by 65%*. Thus, water deficits during the 30–45 and 45–60 DAE periods were the most detrimental for crop growth. Even though their impact on final grain production was identical, their effect on the different yield components varied.

The number of fertile panicles on the main shoots was affected in the same way by both treatments (−44%* in S30, −41%* in S45), but the number of panicles on the tillers was only affected by S45 (−69%* as opposed to −28%[ns] in S30). The number of grains per panicle on the main shoots was significantly reduced by S30 only (−44%*). On the tillers, S30 reduced the number of grains per panicle though not significantly (−29%[ns]) and S45 had no effect. The single-grain mass on the main shoots was lower than that of the control for S30 (−23%*) and S60 (−15%*). On the tillers, the single-grain mass was also lower than that of the control for S45 (−26%[ns]), but was 18%[ns] higher for S30.

The drought in the 30–45 DAE period reduced panicle emergence on the main shoots, grain formation on the main shoots and the tillers, and grain filling on the main shoots. The tillers contributed to 42% of the final grain mass. Their grains, which probably formed after irrigation was resumed, were filled to the same extent as those of the control tillers. However, this recovery was not sufficient to compensate for grain loss on the main shoots. The drought during the 45–60 DAE period reduced the emergence of panicles irrespective of their location (main shoot or tiller), and to a lesser extent the number of grains on the main shoots. The grain number on the tillers was not affected, but these tillers were too few in number and their grains too small to compensate for losses on the main shoots. The tillers supplied 18% of the final grain mass. The late drought (60–75 DAE) did not lead to any significant loss in yield. The small loss observed in the single-grain mass had no effect on the total production of seeds as it was compensated for by a higher number of eared tillers, but differences were statistically not significant.

### Vegetative development

*Stems and tillering.* For all water regimes, the relative distribution of final biomass of stems was similar in main shoots and tillers (respectively 48% and 52% on average) and represented about 40% of the total above-ground biomass of the plants (Table 1). Compared with the

**Table 1.** *Treatment means for above-ground biomass and grain yield components at final harvest (n=20 in each treatment)*

|  |  | Control | S30 | S45 | S60 |
|---|---|---|---|---|---|
| Total biomass | Main shoot | 67 a | 34 b | 36 b | 67 a |
| (g plant$^{-1}$) | Tillers | 77 ab | 54 bc | 44 c | 90 a |
|  | Whole plant | 144 a | 88 b | 80 b | 157 a |
| Stem | Main shoot | 31 a | 18 b | 16 b | 29 a |
| (g plant$^{-1}$) | Tillers | 31 ab | 20 bc | 16 c | 35 a |
|  | Whole plant | 62 a | 38 b | 32 b | 64 a |
| Leaves | Main shoot | 8 a | 7 a | 7 a | 7 a |
| (g plant$^{-1}$) | Tillers | 37 a | 27 b | 26 b | 40 a |
|  | Whole plant | 45 ab | 34 bc | 33 c | 47 a |
| Grain yield | Main shoot | 18 a | 5 b | 7 b | 18 a |
| (g plant$^{-1}$) | Tillers | 5 a | 3 a | 1 a | 8 a |
|  | Whole plant | 23 a | 8 b | 8 b | 26 a |
| Panicle number | Main shoot | 0.9 a | 0.5 b | 0.6 b | 1.0 a |
| (no. plant$^{-1}$) | Tillers | 0.7 a | 0.5 ab | 0.2 b | 0.9 a |
|  | Whole plant | 1.6 ac | 1.0 ab | 0.8 b | 1.9 c |
| Grain number | Main shoot | 2402 ac | 1343 b | 1733 ab | 2755 c |
| (no. panicle$^{-1}$) | Tillers | 1485 a | 1051 a | 1481 a | 1829 a |
|  | Whole plant | 2192 a | 1060 b | 1743 ab | 2295 a |
| Single-grain mass | Main shoot | 7.2 a | 5.6 b | 6.7 ab | 6.1 b |
| (mg grain$^{-1}$) | Tillers | 4.9 a | 5.7 a | 3.6 a | 4.6 a |
|  | Whole plant | 6.8 a | 5.4 b | 6.3 ab | 5.4 b |

Value followed by the same letter within a given line are not significantly different ($P<0.05$).

control, the S30 and the S45 treatments greatly reduced the growth of the stems of the main shoots ($-44\%*$ for S30, $-49\%*$ for S45). However, S30 did not affect the tillers in a significant way ($-29\%^{ns}$) while S45 reduced stem biomass by 50%*. These losses were due only to a slowing of the growth of these stems and not to a reduction of their number, which was identical in the four treatments since tillering was practically complete at 30 DAE (9 tillers plant$^{-1}$ on average, SE=0.7).

Figure 2 shows that water deficit slowed the resumption of the growth of stems after re-irrigation (in the case of S30) or stopped their growth at the level attained before the drought (in the case of S45), and thus prevented high growth of the stems observed on the control plants between 45 and 60 DAE. This gain in stem biomass on the control plants was not sustained: it was followed between 60 and 75 DAE by a loss of biomass, which was not significant for main shoots ($-17\%$), but attained $-54\%*$ on the tillers.

*Leaves and senescence.* Table 1 shows that final leaf production was less affected by drought than stems and panicles were. The S30 and S45 treatments led to a small decrease in total leaf biomass, which was statistically significant for S45 ($-25\%$). There was no effect in S60. On the main shoots, where leaf biomass never constituted more than a quarter of total leaf biomass, the final leaf production was the same for all water regimes. On the tillers, leaf biomass was reduced by $-26\%*$ in the S30 and $-29\%*$ in the S45 treatments.

The impact of water treatments on green leaf biomass was more apparent than on total leaf biomass (Fig. 3). With control plants, green leaf biomass attained its max-

imum at 45 DAE. There was a continued high production of green leaf biomass between 45 and 60 DAE, but the senescence cancelled its effects. Senescence after 60 DAE affected the green leaf biomass on tillers more severely than on main shoots. The percentages of senescence were similar for both main shoots and tillers at 60 DAE (about 42%), but 15 d later they reached 71% on the tillers and only 54% on the main shoots (Table 2). Furthermore, the senescence of the main shoots and their green leaf biomass, which was maintained at 6 g plant$^{-1}$ practically until the end of the growing season, showed little sensitivity to the phases of water deficit (Table 2; Fig. 3).

On the tillers, by contrast, S30 and S45 caused significant reductions of green leaf biomass by the end of the dry period ($-34\%$ for S30, $-49\%$ for S45) (Fig. 3). In both cases, reduction of the green leaf biomass of the tillers did not result from an increase in the leaf senescence (Table 2). For S30, tiller senescence at 60 and 75 DAE was even significantly lower than that of the control plants. Taking place only at the beginning of the normal period of rapid leaf expansion, S30 immediately slowed the growth of foliage. In the second half of the growth

**Table 2.** *Percentage of leaf senescence at 60 and 75 DAE*

|  | Main shoot | | Tillers | | Whole plant | |
|---|---|---|---|---|---|---|
|  | 60 DAE | 75 DAE | 60 DAE | 75 DAE | 60 DAE | 75 DAE |
| Control | 43 a | 54 a | 41 a | 71 a | 42 a | 67 a |
| S30 | 24 b | 44 a | 20 b | 41 b | 21 b | 44 b |
| S45 | 36 ab | 41 a | 44 a | 61 ab | 42 a | 53 ab |
| S60 | — | 45 a | — | 47 b | — | 51 ab |

Values followed by the same letter within a given column are not significantly different ($P<0.05$).
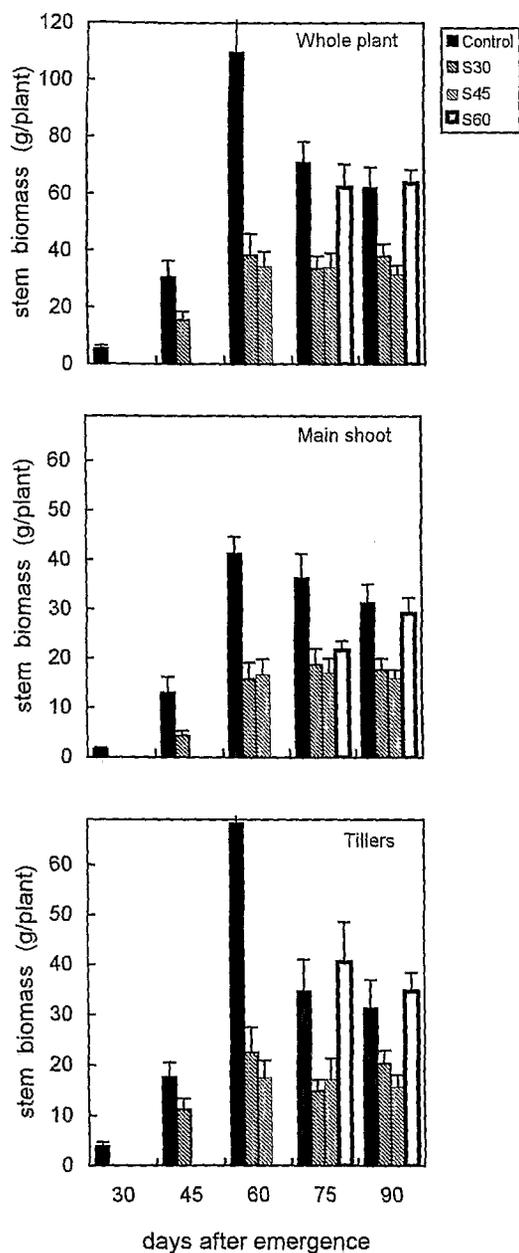
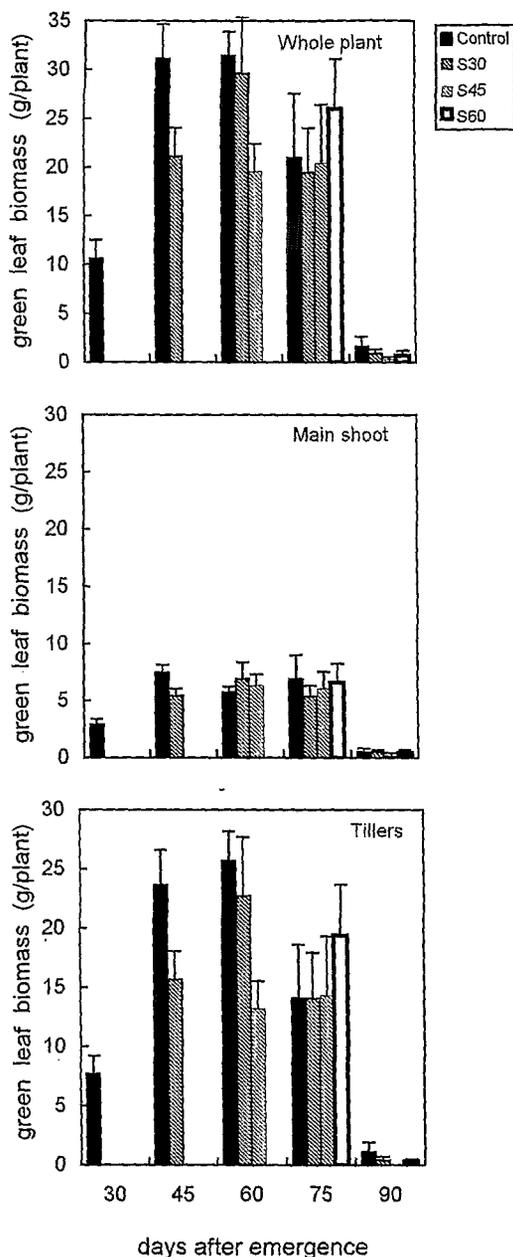Fig. 2. Seasonal variations in stem biomass (vertical bars show 1 SE).



Fig. 3. Seasonal variations in green leaf biomass (vertical bars show 1 SE).

phase of leaves (45–60 DAE), 15 d of re-irrigation permitted the plants of the S30 treatment to recover to the same level of green biomass as the control plants, without showing as high a percentage of senescence. For S45, senescence at the end of the stress phase (60 DAE) was not different from that which began to affect the controls in the same period (42% on the whole plant). But the drought had practically stopped leaf growth at the level reached at 45 DAE (35 g plant$^{-1}$ at 60 DAE in S45 compared with 31 g plant$^{-1}$ at 45 DAE for the controls). The re-irrigation after 60 DAE was insufficient and too late for a resumption of leaf growth in the S45 treatment.

## Reproductive development

*Flowering.* Figure 4 presents for the four treatments the cumulative evolution of the flowering of panicles expressed in relation to the final number of panicles in the control treatment (1.6 panicles plant$^{-1}$ = 100% flowering). On control plants, flowering started at 40 DAE on the main shoots, and 10 d later on the tillers. Then, the flowering of panicles of the main shoots and the tillers was rapid and practically complete in both cases at 65 DAE. The tillers comprised finally 38% of the flowered panicles on the plant.
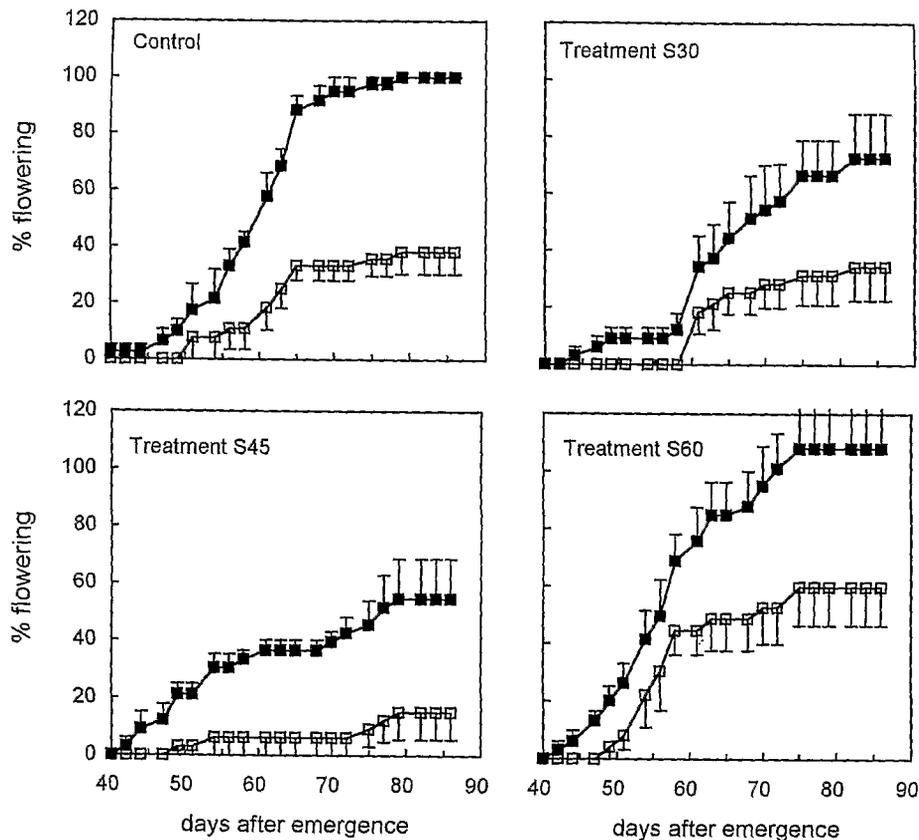
**Fig. 4.** Cumulative percentage of flowered panicles per plant in relation to the final number of panicles in control plants (100%=1.6 panicles plant$^{-1}$; (■): whole plant, (□): tillers; vertical bars show 1 SE).

The S30 treatment greatly inhibited flowering of the early main shoots, but did not prevent the flowering of the late main shoots and only slowed down the flowering of the tillers by 10 d. The final flowering of the tillers was comparable to that of the controls, but the flowering of the whole plant attained only 73% of that observed in the absence of water deficit. Thus, even though it was not affected by the stress applied during the initiation of the panicles, the flowering of the tillers was not able to compensate for the losses brought about on the first main shoots. The S45 treatment did not compromise the flowering of the early main shoots, but it inhibited almost totally that of the tillers which normally flower around 50 DAE and that of the late main shoots. Although flowering slightly resumed on main shoots and tillers after 75 DAE, the total number of flowered panicles was 42% less than that of control plants. The S60 treatment, affecting only the end of the rapid flowering phase of the panicles and appearing after a period of high watering, had no significant effect on the floral development of the plants.

*Filling of the panicles.* For the control plants, panicle biomass was negligible up to 45 DAE, then increased very rapidly in the following 15 d on the main shoots as on the tillers (Fig. 5). In this period, the establishment of

sterile support structures (rachis, peduncules), represents a large part of the growth of the panicles. After 60 DAE, the main part of the growth of the panicles is due to grain filling. In the control and S60 treatments, the growth of the panicles had by then practically ceased on the tillers whereas it continued on the main shoots. The growth of the panicles on the main shoots between 60 and 75 DAE coincided with leaf senescence and loss of stem biomass in tillers (Figs 2, 3), while green leaf mass of the main shoots was maintained.

In spite of re-irrigation between 45 and 60 DAE, S30 initially retarded panicle growth of the main shoots. This suggests that the initiation of the support structures and of the spikelets within the meristems was damaged irreversibly by this pre-flowering stress. Even though late tillers had well-filled grains (Table 1; Fig. 4), the very slow growth of the panicles up to the end of the growing season did not permit compensation for this very early damage. A lasting effect of S30 is also indicated by the difference between the number of flowered panicles and that of fertile panicles (Fig. 4; Table 1): 14% of the flowered panicles remained barren, probably because of pollination or fertilization failure, or subsequent grain abortion. S45 had the same result on the production of panicles, with 18% of the flowered panicles remaining sterile.
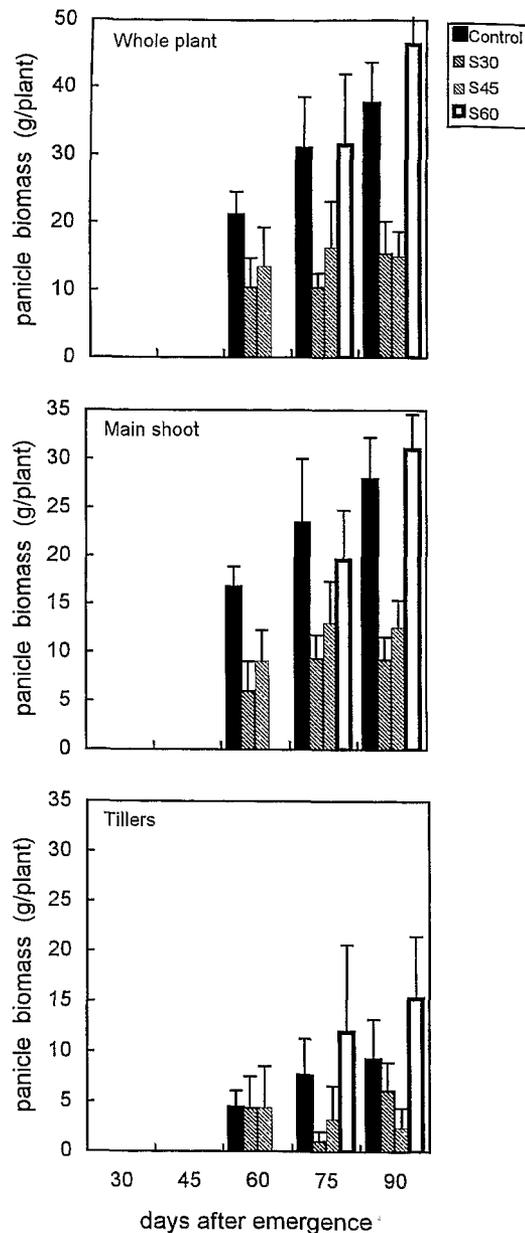
Fig. 5. Seasonal variations in panicle biomass (vertical bars show 1 SE).

## Discussion

*Drought susceptibility and development stage*

Of the three drought periods studied, the two immediately prior to and after the beginning of the flowering of the first panicles (S30 and S45) had similarly severe effects, whereas the third (S60), which occurred at the end of the flowering period, had no effect on the final production. It should be noted that the yield of the control was comparable to the best on-farm yields in the Sahel. Since the irrigation schedule simulated approximately the natural decrease of rainfall towards the end of the growing season, the water deficit in S60 was only 13% (29 mm)

relative to the control. In this situation no difference in the yield was observed between S60 and the control. The innocuousness of this late drought and the gravity of the deficits occurring before mid-flowering constitute an important difference when compared with previously reported results. Several studies indicated that, in pearl millet, the susceptibility to drought stress is low up to the time of flowering of the main shoot, but increases sharply afterwards (Mahalakshmi and Bidinger, 1985*b*, 1986; Bidinger *et al.*, 1987; Mahalakshmi *et al.*, 1987). Where such is the case, tolerance to mid-season stress could result from an escape strategy based on highly asynchronous tiller development. It should be noted that in those experiments (most of them conducted in India), the control treatment was irrigated at field capacity from crop emergence up until crop maturity, and drought stress treatments were imposed by withholding irrigation during selected periods. In such conditions, soil water storage in the heavier soils of India may have been sufficient to sustain early 'stressed' plants until irrigation resumed. In the Sahel, however, rains set in gradually, then become progressively less frequent after flowering (Sivakumar, 1992), and soils have very low holding capacity. The experimental conditions were closer to this situation and, thus, the results are more appropriate to Sahelian agriculture.

### Drought and panicle development

The droughts occurring immediately prior to or after the beginning of flowering did not modify the timing of the reproductive switch and in both cases the flowering began on the first main shoots around 42 DAE. It was afterwards slowed greatly by the drought. The pre-floral stress (S30) delayed by 10 d the start of tiller flowering, but afterwards they developed normally. Mahalakshmi and Bidinger (1985*a*) made the same observation. In contrast, the stress in the early flowering phase (S45) did not delay the start of the tiller flowering, but it inhibited almost immediately their subsequent development, which led to their almost complete elimination. Mahalakshmi and Bidinger (1985*b*) also observed the virtual elimination of the eared tillers caused by a water stress beginning in the pre-floral phase, but following 10 d after the mid-flowering stage. In all cases where the drought ends before flowering (corresponding to S30 in this study), these authors point out an increase in the tiller fertility on the stressed plants. This increase is the basis for the compensation of the yield losses on the main shoots due to drought, a compensation which renders the production of plants deprived of irrigation between 20 and 48 DAE equal or superior to that of the control plants (Mahalakshmi and Bidinger, 1986). In contrast, these data show that panicle and grain abortion caused by drought during panicle initiation and early flowering was not reversible.

## Conservation of leaves facing stress

At the whole plant level, the reduction in leaf biomass was clearly less than that of the stems or the panicles. Moreover, this loss was sustained only by the tillers: in spite of the severity of the S30 and S45 stresses, the leaf biomass on the main shoots was the same in the four treatments and, whatever the water regime, the biomass of the green leaves stayed more or less the same from 45–75 DAE. The photosynthetic organs thus had been less affected by the drought than the structural and storage organs. The maintenance of leaves on the main shoots whatever the water regime, can be associated with the fact that they serve as source for the most advanced panicles, which are priority carbon sinks. It has been suggested that, on eared shoots, the sink strength would stimulate photosynthesis and nitrogen metabolism and delay senescence in the underlying leaves (Henson *et al.*, 1983; Henson and Mahalakshmi, 1985; Biswas and Mandal, 1987). The stability in green leaf biomass of eared shoots seems well-suited to intermediate water stress, as it could allow rapid recovering in assimilate production when the rains return (Ludlow and Muchow, 1988). On the tillers, the panicles are less advanced and constitute less important carbon sinks. In this case, the stress immediately limited the growth of leaves and, therefore, the transpiration surface. When the stress was relieved relatively early by high re-irrigation (S30), leaf growth recovered on tillers.

In these cultivation conditions, senescence did not appear to be a specific response to intermediate water deficits. Payne *et al.* (1991) concluded the same in a growth analysis study of pearl millet. On the control plants, senescence was already severe at 60 DAE, in conjunction with the reduction of irrigation. The same phenomenon appears in nature where the length of the dry periods in the region of Tanout increases considerably from the 50th day after sowing (Sivakumar, 1991). The leaf senescence which affected essentially the tillers accompanied the important loss of their stem biomass and coincided with the rapid growth of the panicles of the main shoots on the control plants.

## Strategy of pearl millet facing water stress

The hypothesis that high asynchrony of tiller development and delay in flowering provide individual pearl millet plants with an effective mechanism to escape mid-season stress is an attractive one. In some experiments, it has been found that tiller compensation could make the yield of plants lacking irrigation for 28 d during panicle development higher than that of well-watered plants (Mahalakshmi and Bidinger, 1986). The present study shows that, for a landrace in cultivation conditions close to those of Sahelian farmers, the number of productive tillers and the number of grains on their panicles were

not sufficient to compensate the damage of water stress to the main shoot of an individual plant. Yet, in the case of early relief of drought, it was clear that good grain filling in productive tillers, supported by the recovery of leaf growth, contributed to limit the yield losses of the main shoot. Stability in leaf biomass on eared shoots and important losses in stem biomass could also help sustain the panicle growth. But the capacity of leaves to generate assimilates, as well as that of stems to remobilize pre-anthesis carbohydrate, cannot be accurately evaluated without considering the capacity of sinks to store them (Evans, 1993). These results indicate that under Sahelian conditions the sink demand of panicles was irreversibly damaged by mid-season drought.

On the whole, the strategy of pearl millet facing intermediate drought seems to be similar to that of most cereal plants. The development of the main panicle coincides with a period of increasing probability of rain, thus reducing the high risks associated with drought events occurring prior to or at the beginning of flowering (Sivakumar, 1992). Thereafter, the flowering phase corresponds to the onset of rains beneficial to the grain maturation (Hall *et al.*, 1979). Hence, as Fisher and Maurer (1978) concluded for other cereals, phenological escape by matching the crop phenology to the expected rainfall distribution remains in pearl millet the major trait of adaptation in drought-prone environments. Drought escape related to asynchrony of shoots could be more important at the agrosystem level than at the plant level. In fact, at the agrosystem level, genotypic diversity of the landraces and environmental heterogeneity result in high inter-individual variability of plant growth and development which confers adaptability to drought on the crop (Brouwer *et al.*, 1993; Renno and Winkel, 1996).

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