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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

2 Several studies conducted under high input conditions have indicated little susceptibility of
pearl millet to water deficit until early grain filling, because the losses in main shoot
4 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
6 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
8 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,
10 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
12 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
14 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
16 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
18 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
20 resistance.

22 Key words: drought resistance strategy, experimental conditions, main shoots, tillers,
Pennisetum glaucum.

24

Introduction

26 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.

28 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
30 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
32 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:

34 - 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
36 by the choice of short-season cultivars tolerant of post-floral water deficits (in the case of late droughts);

38 - intermediate droughts, less frequent and often brief (about 10 days) but very unpredictable and without any practical remedies. They affect development stages such
40 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
42 characterization of drought resistant varieties.

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

48 Few studies on the adaptive strategies of pearl millet have used the integrated approach necessary to bring out the optimal combinations of phenological and
50 morphophysiological traits developed at different levels of biological organisation (Winkel and Do, 1992). However, a number of indices suggest that the adaptation of pearl millet to
52 drought relies on morphological and phenological traits rather than on physiological attributes like osmotic adjustment or tissue elasticity (Do, 1994). In previous studies, it

54 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
56 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
58 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
60 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
62 (Mahalakshmi *et al.*, 1988), 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
64 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
66 conditions, the stressed plants survived up to 50 consecutive days of drought, and the
grain production by plants stressed during 28 days reached 3000 kg per hectare. In
68 Sahelian regions, droughts usually last 10-15 days between tillering and early grain filling
(Sivakumar, 1992), pearl millet is always sown in a hill (a group of several seeds planted
70 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
72 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
74 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
76 vegetative development of pearl millet observed in traditional farming conditions. This
approach is difficult because of the necessity of controlling certain environmental factors,
78 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
80 dry season. The study presented here analyses the effects on the growth and flowering of
pearl millet of drought periods of 15 days at different stages of development. This study
82 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
84 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
86 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
88 conditions.

90 **Material and methods**

The experiment was carried out in the field at the Institut des Radio-Isotopes, University of
92 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.,
94 landrace Ankoutess) was grown during the hot dry season (February to May). We assume
that traits of drought resistance would be expressed more strongly in this landrace than in
96 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
98 highest, in the agricultural zone of the Sahel (Sivakumar, 1991). As Ankoutess flowers in
about 60 days, it is considered as insensitive to daylength (Pearson, 1984; Clément,
100 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
102 rain of 7.5 mm occurred 71 days after emergence (DAE). The crop was sown on 10
February at a spacing of one hill per square metre. Complete crop emergence occurred
104 on 15 February and plants were thinned to a population of three plants m⁻² at 15 DAE.
Fertilizer applications were 3 g m⁻² N, P₂O₅ and K₂O one day before sowing and 1.5 g m⁻²
106 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,
108 and three stress treatments in which irrigation was withheld prior to flowering (from 30 to
45 DAE, treatment S30), during early flowering (45 to 60 DAE, treatment S45) and late
110 flowering (60 to 75 DAE, treatment S60). Irrigation was applied by microsprinklers at a
spacing of 1 x 1 metre. Water applications were the same for all treatments except during

112 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
114 flowering, and a tapering off towards the end of the season (Fig. 1). This water regime
was determined after analyzing rainfall data series for the mean length of dry spells
116 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.

118 Plots for each water regime were sown adjacent to one another, arranged in a block
design with five replications. Individual plots were 20 x 5 m (4 rows of 19 hills). Only the
120 two central rows were sampled. Phenology was monitored every two or three days on four
plants in each plot by recording the number of panicles at the stages of female flowering
122 and grain maturity. Above-ground dry matter was sampled at 15 days intervals from 30
DAE on in the control plots and from the end of the deficit periods in the stress treatments
124 (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,
126 separated into stems, green leaves, senescent leaves, and panicles, and dried at 80°C for
three days. At final harvest, dry matter was measured on four plants in each plot ($n = 20$
128 for each treatment), panicles were threshed and grain number and weight were
determined. The statistical significance of the differences between the control and the
130 stress treatments was analyzed 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
132 significant).

134 **Results**

Final production and yield components

136 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
138 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
140 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.
142 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
144 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
146 different yield components varied.

The number of fertile panicles on the main shoots was affected in the same way by
148 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
150 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
152 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
154 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,
156 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
158 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
160 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
162 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
164 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-
166 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.

168

Vegetative Development

170 *Stems and tillering*

For all water regimes, the relative distribution of final biomass of stems was similar in main
172 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 control, the
174 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 (-
176 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
178 identical in the four treatments since tillering was practically complete at 30 DAE (9 tillers
plant⁻¹ on average, SE = 0.7).

180 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
182 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
184 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.

186 *Leaves and senescence*

Table 1 shows that final leaf production was less affected by drought than stems and
188 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
190 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
192 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
194 total leaf biomass (Fig.3). With control plants, green leaf biomass attained its maximum at
45 DAE. There was a continued high production of green leaf biomass between 45 and 60
196 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

198 senescence were similar for both main shoots and tillers at 60 DAE (about 42%), but 15
days later they reached 71% on the tillers and only 54% on the main shoots (Table 2).
200 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
202 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
204 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
206 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
208 period of rapid leaf expansion, S30 immediately slowed the growth of foliage. In the
second half of the growth phase of leaves (45-60 DAE), 15 days of re-irrigation permitted
210 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,
212 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
214 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
216 DAE was insufficient and too late for a resumption of leaf growth in the S45 treatment.

218 ***Reproductive development***

Flowering

220 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
222 panicles plant⁻¹ = 100% flowering). On control plants, flowering started at 40 DAE on the
main shoots, and 10 days later on the tillers. Then, the flowering of panicles of the main
224 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.

226 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
228 tillers by 10 days. 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
230 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
232 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
234 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
236 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
238 watering, had no significant effect on the floral development of the plants.

240 *Filling of the panicles*

For the control plants, panicle biomass was negligible up to 45 DAE, then increased very
242 rapidly in the following 15 days on the main shoots as on the tillers (Fig.5). In this period,
the establishment of sterile support structures (rachis, peduncules), represents a large
244 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
246 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
248 with leaf senescence and loss of stem biomass in tillers (Figs 2, 3), while green leaf mass
of the main shoots was maintained.

250 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
252 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
254 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
256 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,
258 or subsequent grain abortion. S45 had the same result on the production of panicles, with
18% of the flowered panicles remaining sterile.

260

Discussion

262 ***Drought susceptibility and development stage***

Of the three drought periods studied, the two immediately prior to and after the beginning
264 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
266 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
268 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
270 was observed between S60 and the control. The innocuity of this late drought and the
gravity of the deficits occurring before mid-flowering constitute an important difference
272 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
274 shoot, but increases sharply afterwards (Mahalakshmi and Bidinger, 1985b, 1986;
Bidinger *et al.*, 1987; Mahalakshmi *et al.*, 1987). Where such is the case, tolerance to mid-
276 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
278 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
280 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
282 Sahel, however, rains set in gradually, then become progressively less frequent after
flowering (Sivakumar, 1992), and soils have very low holding capacity. Our experimental

284 conditions are closer to this situation and, thus, our results are more appropriate to
Sahelian agriculture.

286

Drought and panicle development

288 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
290 first main shoots around 42 DAE. It was afterwards slowed greatly by the drought. The
pre-floral stress (S30) delayed by 10 days the start of tiller flowering, but afterwards they
292 developed normally. Mahalakshmi and Bidinger (1985a) made the same observation. In
contrast, the stress in the early flowering phase (S45) did not delay the start of the tiller
294 flowering, but it inhibited almost immediately their subsequent development, which led to
their almost complete elimination. Mahalakshmi and Bidinger (1985b) also observed the
296 virtual elimination of the eared tillers caused by a water stress beginning in the pre-floral
phase but following 10 days after the mid-flowering stage. In all cases where the drought
298 ends before flowering (corresponding to S30 in our study), these authors point out an
increase in the tiller fertility on the stressed plants. This increase is the basis for the
300 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
302 equal or superior to that of the control plants (Mahalakshmi and Bidinger, 1986). In
contrast, our data show that panicle and grain abortion caused by drought during panicle
304 initiation and early flowering was irremediable.

306 ***Conservation of leaves facing stress***

At the whole plant level, the reduction in leaf biomass was clearly less than that of the
308 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
310 in the four treatments and, whatever the water regime, the biomass of the green leaves
stayed more or less the same from 45 to 75 DAE. The photosynthetic organs thus had
312 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

314 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
316 stimulate photosynthesis and nitrogen metabolism and delay senescence in the
underlying leaves (Henson *et al.*, 1983; Henson and Mahalakshmi, 1985; Biswas and
318 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
320 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
322 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.

324 In our 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
326 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
328 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
330 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.

332

Strategy of pearl millet facing water stress

334 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
336 an attractive one. In some experiments, it has been found that tiller compensation could
make the yield of plants lacking irrigation for 28 days during panicle development higher
338 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
340 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
342 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
344 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
346 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,
348 1993). Our results indicate that under Sahelian conditions the sink demand of panicles
was irreversibly damaged by mid-season drought.

350 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
352 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).
354 Thereafter, the flowering phase corresponds to the rarefaction of rains, beneficial to the
grain maturation (Hall *et al.* 1979). Hence, as Fisher and Maurer (1978) concluded for
356 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
358 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
360 diversity of the landraces and environmental heterogeneity result in high interindividual
variability of plant growth and development which confers adaptability to drought on the
362 crop (Brouwer *et al.*, 1993; Renno and Winkel, 1996).

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environment*. Oxford, UK: Oxford University Press.

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TABLES

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

442

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

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

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TABLE 2. Percentage of leaf senescence at 60 and 75 DAE

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

Values followed by the same letter within a given column are not significantly different ($P < 0.05$)

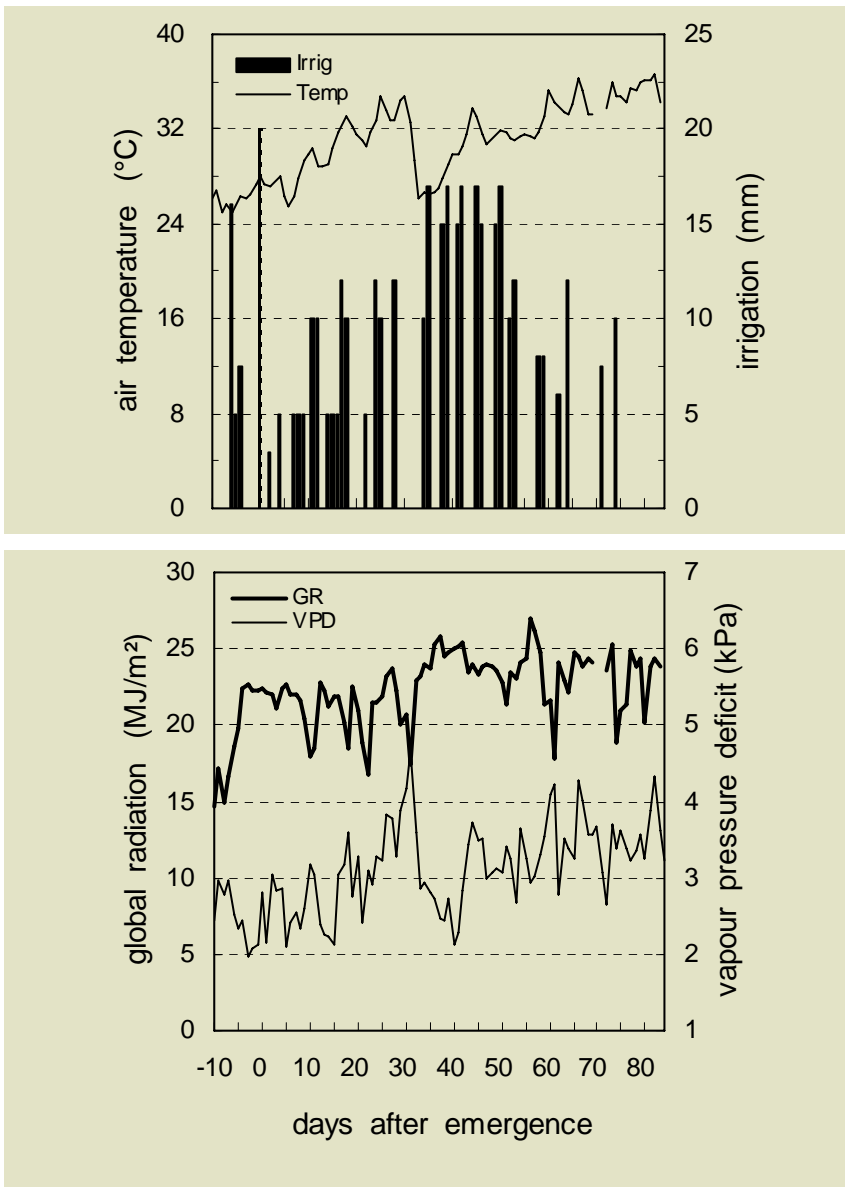
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FIGURES

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Figure 1. Daily mean air temperature, irrigation, global radiation and vapour pressure deficit during the experiment (first day after emergence was 15 February).

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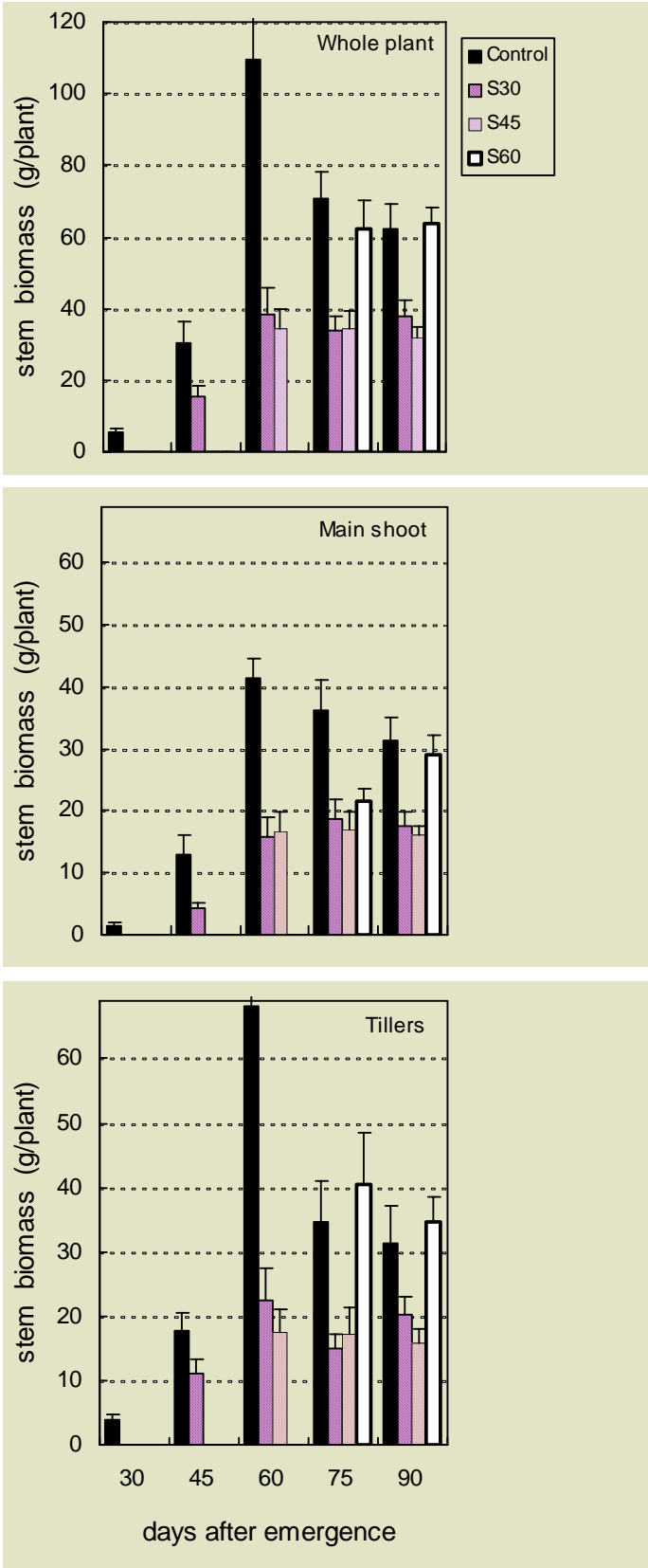


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Figure 2. Seasonal variations in stem biomass (vertical bars show one standard-error).

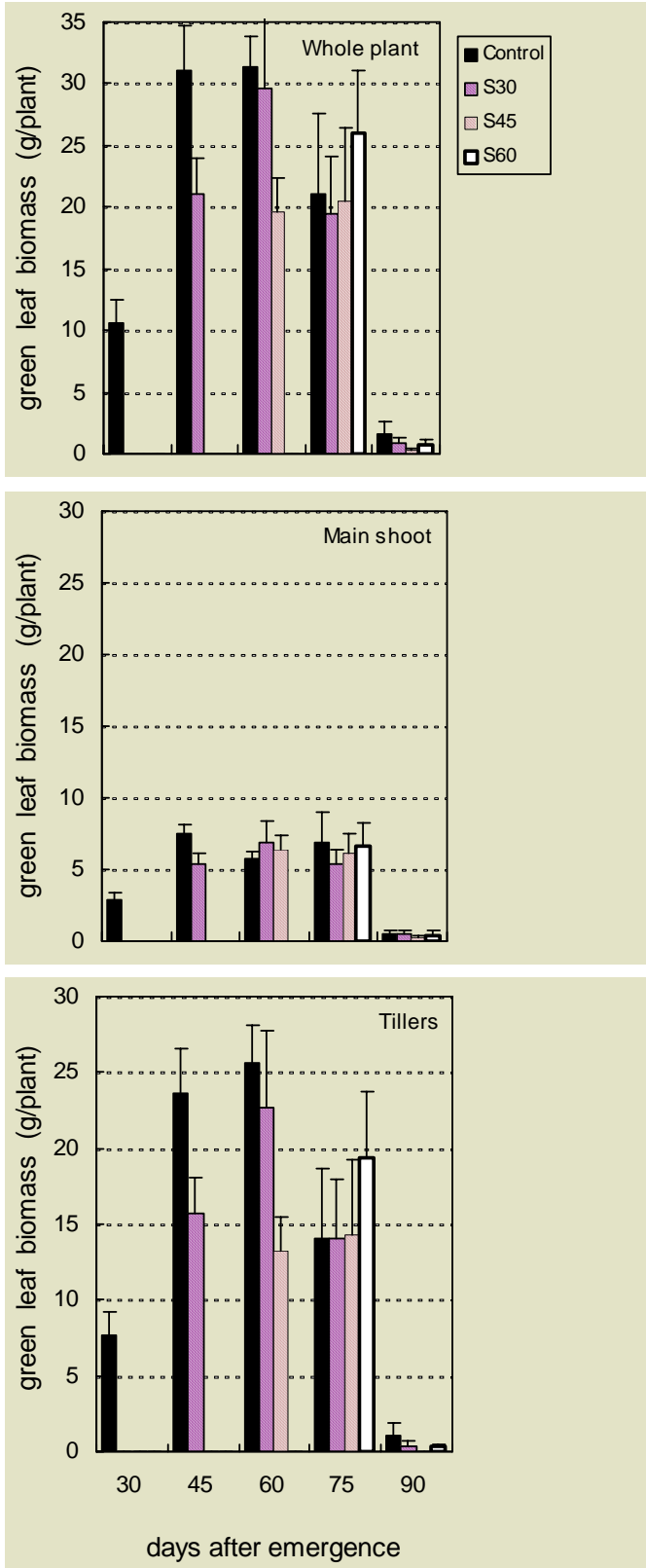
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Figure 3. Seasonal variations in green leaf biomass (vertical bars show one standard-error).

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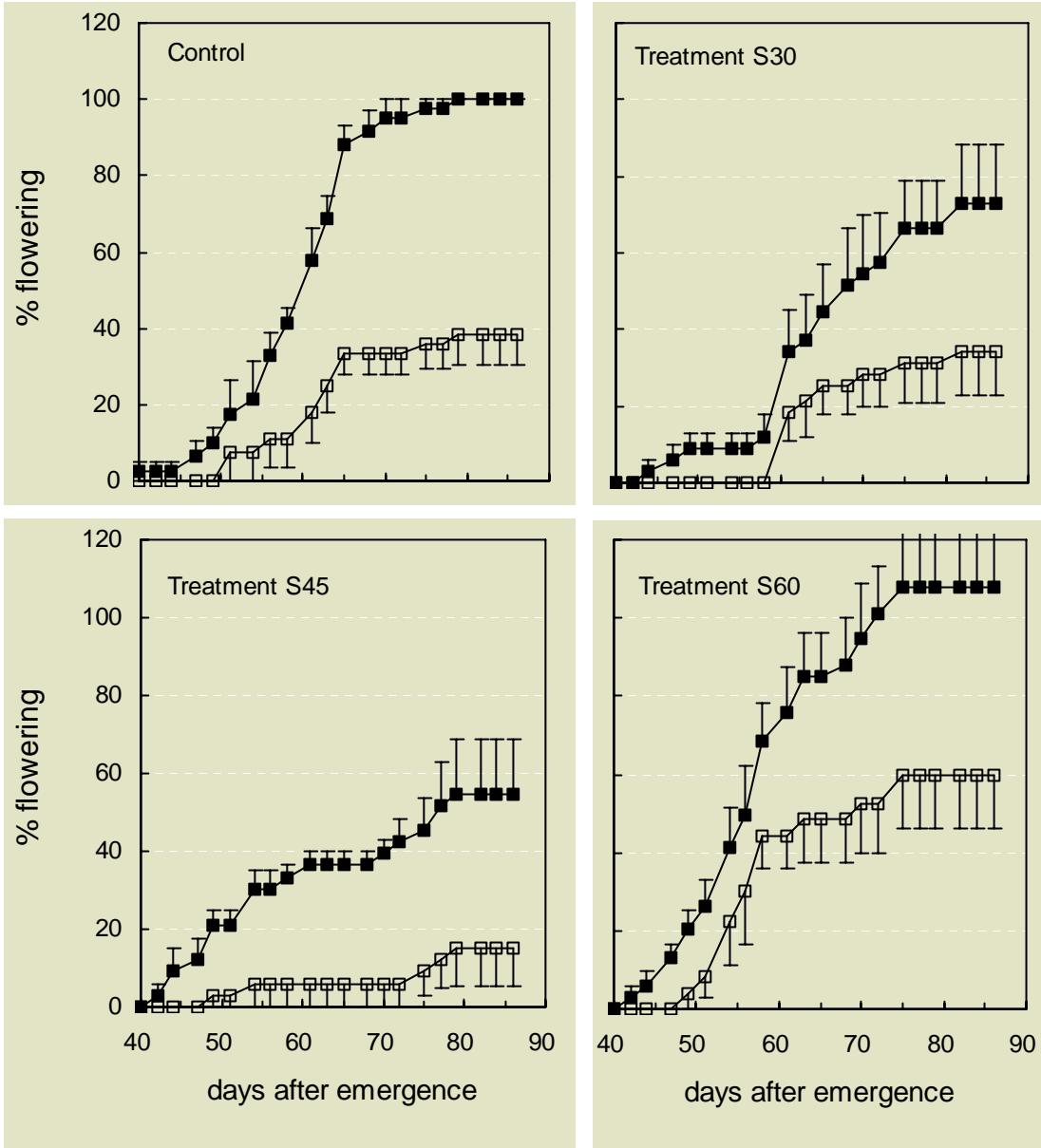


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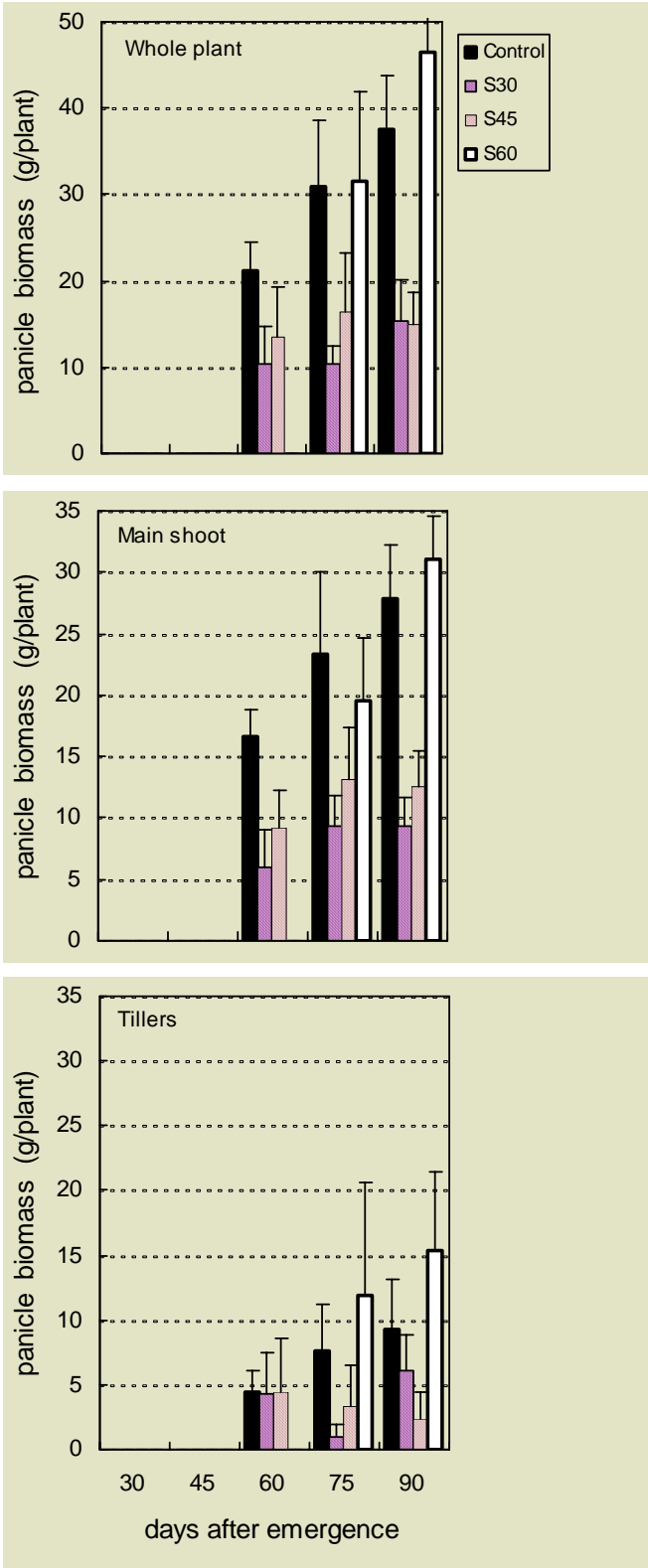
Figure 4. Cumulative percentage of flowered panicles per plant in relation to the final number of panicles in control plants (100% = 1.6 panicles plant⁻¹ ; ■ : whole plant, □ : tillers; vertical bars show one standard-error).

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470 **Figure 5. Seasonal variations in panicle biomass (vertical bars show one standard-**
472 **error).**



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