CSIRO Publishing

Australian Journal of Agricultural Research

VOLUME 52, 2001

A journal for the publication of original contributions towards the understanding of an agricultural system

All enquiries and manuscripts should be directed to:

Australian Journal of Agricultural Research
CSIRO Publishing
PO Box 1139 (150 Oxford St)
Collingwood, Vic. 3066, Australia

Telephone: +61 3 9662 7628
Fax: +61 3 9662 7611
Email: ajar@publish.csiro.au

Published by CSIRO Publishing
for CSIRO and the Australian Academy of Science

www.publish.csiro.au/journals/ajar

Aust. J. Agric. Res., 2001, **52**, 801-808

Timing and height of defoliation affect vegetative growth and floral development in grain sorghum

S. E. Ockerby[AB], *D. J. Midmore*[A], *and D. F. Yule*[C]

[A]Plant Sciences Group, Central Queensland University, Rockhampton, Qld 4702, Australia.
[B]Queensland Department of Primary Industries, PO Box 1054, Mareeba, Qld 4880, Australia.
[C]Queensland Department of Natural Resources, 80 Meiers Rd, Indooroopilly, Qld 4068, Australia.

Abstract. In earlier work, we found that the near complete defoliation of grain sorghum [*Sorghum bicolor* (L.) Moench] seedlings delayed panicle initiation and anthesis. Several aspects of the required defoliation remain unclear, however, including which parts of the seedling's foliage need to be removed, the timing of defoliation, and what effects differing defoliation treatments have on the morphology of plants that re-form after defoliation is terminated. To answer these questions, sorghum plants (cv. Boomer) grown under natural (*c.* 11.5 h) or extended (14 h) photoperiods were defoliated during the vegetative development phase. Treatments removed the fully exposed leaf-blade and/or the partially exposed and still expanding leaves and were varied by commencing and ceasing defoliation at different times, by cutting the plants at different heights, and by leaving some green leaf area on the plant. All defoliation treatments, except the one in which only the fully exposed leaf-blade was removed, resulted in delays in panicle initiation and anthesis. Defoliation treatments terminating on the same date, yet commencing between the second and fifth leaf stages, the latter just prior to panicle initiation in control plants, gave the same delay to panicle initiation. Serial defoliation at 3–4-day intervals maintained the plants in a vegetative state. Subsequent plant development and growth were associated with the morphology of plants when defoliation was terminated, thus were influenced by the height at which defoliation was performed. Plants defoliated above the first ligule took longer to initiate reproductive development and re-formed bigger plants than did those defoliated above the second ligule. Defoliation did not always reduce the plant biomass at anthesis compared with that of control plants. We interpret these responses as evidence that the signal to initiate reproductive development in sorghum originates in the partially exposed expanding leaves and possibly the leaf primordia, and that removal of those leaves resets the plant's developmental program to an earlier phase. For farmers of rain-fed crops this is an exciting result, since it now seems likely that post-sowing management, via defoliation, can be developed to control flowering time and adjust the yield potential of crops in line with the amount of in-crop rain.

Additional keywords: flowering, leaf development, panicle initiation, phenology, plant architecture.

Introduction

In previous work, we found that the delay in anthesis associated with the defoliation of sorghum seedlings was caused by a delay in floral induction marked by panicle initiation (PI; Ockerby *et al*. 2001). Defoliation also resulted in change, usually a reduction, in the number of leaves, green leaf area, and dry weight of plants at anthesis. Responses to different defoliation treatments varied in terms of both the length of delay in PI and the architecture of plants that re-formed after defoliation was terminated. In particular, there appeared to be different effects associated with removal of fully exposed green leaves and those leaves that were immature and still expanding.

Investigations analogous to our current study in unravelling the roles of exposed and expanding leaves and leaf primordia in floral induction in sorghum have been done in excised and cultured maize shoot meristems (Irish and Nelson 1988, 1991; Irish and Jegla 1997). Excised meristems with 4–6 leaf primordia were found to be determined for floral development, but those with fewer leaf primordia were reset and, before tassel initiation, re-formed a full complement of vegetative nodes. Thus, the presence of the 4–6 youngest leaf primordia was sufficient to provide a signal that conditioned the meristem to form an inflorescence. Moreover, phase change (Poethig 1990) was reversed by meristem culture; maize shoot meristems that were reset by culture first formed leaves with juvenile traits and later resumed adult development. Despite the few extra (<4) nodes, the later developing portions of culture-derived shoots were identical in leaf number and morphology to the

 10.1071/AR00092 0004-9409/01/080801

Table 1. Mean monthly maximum and minimum temperatures (°C), solar radiation (MJ/m^2.day) and photoperiod (h), and total rainfall (mm)

Month	Days after sowing	Maximum temp.	Minimum temp.	Solar radiation	Photoperiod	Rainfall
May	1–21	25.68	16.57	17.05	11.5	6.6
June	22–51	23.57	15.4	14.81	11.3	2.6
July	52–82	22.69	12.43	16.11	11.4	36.4
Aug.	83–113	23.07	13.57	18.12	11.7	12.6
Sept.	114–144	26.15	14.91	22.5	12.2	8.4
Oct.	145–175	29.01	17.8	25.32	12.7	7
Nov.	176–198	28.83	19.53	19.91	13.1	88.4

adult region of normal maize plants (Irish and Karlen 1998). If such responses occur in intact plants, as our earlier experiments (Ockerby *et al*. 2001) implied, then defoliation treatments that affect different parts of the seedling's canopy may impact on the length of the delay, and the vegetative architecture and yield potential of the plant that re-forms after defoliation ceases.

We sought and found answers to the questions of precisely when defoliation should be applied and to which parts of seedling did defoliation prevent the change from vegetative to reproductive development. With this information, it is now feasible to develop post-sowing management for sorghum that will assist farmers to avoid water stress in their crops at anthesis. Based on how much water is in the soil and the probability of in-crop rain, plants that have yet to initiate panicles can be defoliated to delay panicle initiation so as to permit a balanced use of water between vegetative and reproductive growth.

Materials and methods

A field experiment was conducted during 1999 at Walkamin Research Station, Queensland Department of Primary Industries (17° 08′S, 145° 26′E, altitude 591 m) in north Queensland, Australia. The soil was a Euchrozem, a deep red, pedal, uniform clay soil with neutral reaction trend formed on basalt, and classified as Uf6.31 after Northcote (1979). Maximum and minimum temperatures, solar radiation, and rainfall were recorded daily during the experiment (Table 1).

Experimental design and treatments

The experiment was a split-plot design with 2 main-plot treatments and 2 replications, laid out in a randomised complete block design. The main plots were either natural (*c*. 11.5 h) or extended (14 h) photoperiod. Within each main plot, the treatment structure was a random design. The treatments applied to the subplots were the following 9 levels of defoliation (using scissors):

T1, no defoliation (control);

T2–T5, twice-weekly defoliation removing all leaf (fully exposed and partially exposed leaf blades and sheaths) from the plant at a height just above the second leaf ligule (T2–T5 commenced when the second, third, fourth, or fifth ligule, respectively, was first visible, and ceased when PI was recorded in control plants);

T6, as for treatment 2 but defoliation continued for 14 days after PI in control plants;

T7, as for treatment 2 but defoliation was performed just above the first ligule;

T8, twice-weekly defoliation, removing only fully exposed leaf-blades (T8 commenced when the second ligule was first visible and ceased at PI in control plants);

T9, twice only defoliation, removing only the exposed portion of leaf-blades above the third and sixth leaves, respectively (T9 was imposed when the ligules of the third and sixth leaves were first visible).

There was minimal (<10 mm) stem elongation before PI in all treatments, so defoliation did not remove the shoot apical meristem or the leaf primordia or the immature leaves <20 mm in length.

Photoperiod treatment details

The photoperiod extension treatment was imposed by suspending twenty-four 100-watt incandescent bulbs 1.2 m above the ground in each main plot covering an area of 20 m by 4.5 m, providing 60–600 lux and 2–12 $\mu mol/m^2$.s of PAR at canopy level. Lamps were programmed to turn on before dusk and off at 1900 hours and on at 0500 hours and off after dawn. Natural photoperiod is shown in Table 1.

Cultural practice

Field plots were marked and the soil was cultivated to a depth of 0.15 m on 1 May 1999. A basal fertiliser containing (g/m^2) 3 P, 4.1 K, 3.3 S, and 0.6 Zn, and prilled urea with 14.7 N, was applied and mixed with the cultivated soil. On 10 May, 2 or 3 sorghum [*Sorghum bicolor* (L.) Moench cv. Boomer] seeds were sown by hand in a 0.175-m square pattern in plots 1.8 m long and 1.2 m wide, and the outermost rows were designated as guard area. An unplanted area 0.2 m wide separated the plots. The plots were irrigated twice-weekly using sprinklers. Seedlings emerged between 16 and 18 May and were thinned to one plant with 2 fully exposed leaves per grid position on 21 May. When PI was recorded in each subplot, plants were again removed so that the distance between the remaining plants was at least 0.35 m. Thus , the plants in each subplot experienced similar competition from neighbouring plants during the reproductive development and grain growth phases.

The experiment was hand-weeded and insecticides were sprayed as required. At the soft dough stage of grain-filling, one randomly selected sorghum head in each subplot was covered with a brown paper bag to minimise grain losses due to birds.

Measurements

Panicle initiation

One plant was sampled twice-weekly from each subplot until spikelets were visible on the inflorescence. The mainstem of plants was cut at ground level, wrapped in plastic, and stored on ice. In the laboratory, fully exposed leaf blades (ligule emerged from the whorl)

Table 2. Impact of defoliation treatments (*per se*) on the green leaf area (cm^2/plant), plant dry weight (g/plant), youngest fully exposed leaf number, and total leaf number of plants at 3 days after defoliation treatments were terminated
In the case of T9 defoliation had ceased for 11 days

Defoliation treatment (n = 4)	Start	Finish	Periodicity	Green leaf area	Plant dry weight	Youngest fully exposed leaf number	Total leaf number
1. Control	—	—	0	199.5	1.220	6.75	13.25
2. All leaves above 2nd ligule	2nd leaf stage	PI in control	Twice weekly	4.6	0.053	6.00	12.50
3. All leaves above 2nd ligule	3rd leaf stage	”	”	4.8	0.072	6.50	12.75
4. All leaves above 2nd ligule	4th leaf stage	”	”	4.0	0.069	6.25	12.50
5. All leaves above 2nd ligule	5th leaf stage	”	”	3.4	0.075	6.25	13.00
6. All leaves above 2nd ligule	2nd leaf stage	PI plus 14 days	”	5.1	0.062	6.00	12.25
7. All leaves above 1st ligule	”	PI in control	”	0.7	0.025	6.00	11.00
8. Fully exposed leaf-blade	”	”	”	37.2	0.295	7.00	13.75
9. Expanding leaves above whorl	3rd and 6th leaf stages	11 days before PI in control	Twice	33.8	0.193	6.75	14.00
s.e.d.				4.9	0.045	0.22	0.507
l.s.d. (P = 0.05)				10.3	0.096	0.47	1.07

and sheaths were peeled off, and the length and area (Paton Electronic Planimeter) of each blade were measured. Expanding leaves that were partly or wholly immature (i.e. not green) and leaf primordia (<2 mm) were removed with a scalpel under a dissecting microscope, and the numbers of fully exposed leaves, expanding leaves, and leaf primordia were recorded. The development stage of the shoot apical meristem was scored after Moncur (1981), from 1 (vegetative with only leaf primordia) through to 7 (spikelets on the inflorescence). Panicle initiation was deemed to have occurred when primary branches were observed as swellings at the base of the meristem (Stage 3). All meristems with spikelets were scored as 7 irrespective of subsequent floral development. The period from sowing to PI was the vegetative development period, and from sowing to anthesis was the vegetative growth period.

Anthesis

The date when anthers were visible in 50% florets on the panicle of a single plant (randomly selected in each subplot at PI) was recorded as the time of anthesis. The plant was then sampled. The numbers of senesced and green leaves were recorded and the area of each green leaf blade was measured. Leaf blade and stem plus leaf sheath samples were then dried at 70°C until a constant weight was recorded. The primary branches on the mainstem panicle were counted. The period from PI to anthesis was defined as the reproductive period.

Maturity

A single plant in each plot was sampled when the grain had turned brown. Leaf, stem plus sheath and the panicle were dried at 70°C until a constant weight was recorded. The panicle was threshed, and grain dry weight and weight per kernel were recorded.

Results

Photoperiod treatment

There were no significant (P > 0.05) differences between the timings of PI and anthesis under natural (77.2 and 124.9 days, respectively) and extended (79.2 and 126 days, respectively) photoperiod treatments. There were no significant interactions between photoperiod and defoliation treatments.

Plant status in defoliation treatments at PI in the control

Three days after either PI was achieved in control plants or defoliation treatments were terminated, defoliation (*per se*) significantly (P < 0.05) reduced the green leaf area (GLA) and the dry weight of plants in comparison with the control plants (Table 2). The dry weight of plants in T2–T7 was negligible. Removing only the fully exposed leaf-blade or twice only defoliation at the 3rd and 6th leaf stages gave smaller reductions than removal of leaves above the 1st or 2nd leaf ligule. Plants in the fully exposed leaf-blade defoliation treatment were larger because leaf sheaths and the immature leaf-blade wholly within the whorl were not removed. Plants in the 3rd and 6th leaf stage defoliation treatment were larger partly because defoliation was terminated 11 days before PI in control plants and partly because the 1st, 2nd, 3rd, and 6th leaves, and the basal sections of the 4th, 5th, and 7th leaf-blades were not removed. The removal of exposed and expanding leaves above the 1st or 2nd ligule slowed the rate of leaf emergence (fewer fully exposed leaves) compared with the control, but only leaf removal above the 1st ligule slowed leaf initiation (fewer total leaves i.e. primordia, immature, expanding, and exposed) (Table 2).

Defoliation treatments

Altering the commencement of defoliation

Treatments T2–T5, in which defoliation above the second ligule commenced when the second–fifth ligule was first visible, respectively, all delayed PI by 26–34 days and anthesis by 21 days compared with the control (T1) (Table 3). Thus the period of vegetative development was longer than in the control. The time from the end of defoliation to anthesis in these treatments, however, was

Table 3. Effects of defoliation treatments on the duration (days) of development and growth phases in sorghum: from sowing to panicle initiation (PI), from sowing to anthesis, from the end of defoliation to anthesis, reproductive development, and sowing to maturity
Means within parameters followed by the same letter are not significantly different at $P = 0.05$

Defoliation treatment ($n = 4$)	Start	Finish	Periodicity	Sowing to PI	Sowing to anthesis	End of defoliation to anthesis[A]	Reproductive development period[B]	Sowing to maturity
1. Control	—	—	0	51a	106a	106e	55e	162a
2. All leaves above 2nd ligule	2nd leaf stage	PI in control	Twice weekly	77c	127d	77b	50d	174b
3. All leaves above 2nd ligule	3rd leaf stage	”	”	82d	129d	79bc	47cd	191c
4. All leaves above 2nd ligule	4th leaf stage	”	”	77c	127d	77b	50d	182bc
5. All leaves above 2nd ligule	5th leaf stage	”	”	85d	128d	78b	43bc	182bc
6. All leaves above 2nd ligule	2nd leaf stage	PI plus 14 days	”	109f	148f	81c	39ab	189c
7. All leaves above 1st ligule	”	PI in control	”	102e	137e	87d	35a	189c
8. Fully exposed leaf-blade	”	”	”	53a	110b	60a	57e	162a
9. Expanding leaves above whorl	3rd and 6th leaf stages	11 days before PI in control	Twice	68b	117c	78b	49d	162a
s.e.d.				2.3	1.2	1.2	2.2	5.0
l.s.d. ($P = 0.05$)				4.9	2.5	2.5	4.6	10

[A]For control plants from sowing to anthesis.
[B]Reproductive development period from PI to anthesis.

about 28 days shorter than the vegetative growth period in control plants. Because plant dry weight was negligible in T2–T5 when defoliation ceased, most vegetative growth in these treatments occurred during this latter period. The reproductive periods were also shortened by 5–12 days. Defoliation treatments increased the total leaf number; however, the green leaf number, green leaf area, plant dry weight, and number of panicle branches at anthesis were all reduced (Table 4). Plant parameters at anthesis did not differ significantly between defoliation treatments T2–T5.

Continuing defoliation for 14 days

Continuing defoliation for 14 days (T6) after it ceased in T2 increased the delay in PI by 32 days and anthesis by 21 days beyond those of T2. The time from the end of defoliation to anthesis lengthened; however, the reproductive period shortened (Table 3). Compared with T2, continued defoliation increased leaf number, green leaf number, and area and total dry weight at anthesis, such that with respect to the latter parameters plants in T6 were no different from those in the control (T1) (Table 4).

Height of defoliation

Lowering the height of defoliation from above the second ligule (T2) to above the first ligule (T7) delayed PI by an extra 25 days and anthesis by 10 days compared with control plants (T1). This led to a longer period from the end of defoliation to anthesis in T7 compared with T2, although it was shorter than the vegetative growth period in the control. The duration of the reproductive period was very short (Table 3). Defoliation at the lower height increased total and green leaf number, green leaf area, plant dry weight, and

Table 4. Effects of defoliation treatments on the total leaf number, green leaf number, green leaf area (cm^2/plant), plant dry weight (g/plant), and branch number on the panicle of sorghum at anthesis
Means within parameters followed by the same letter are not significantly different at $P = 0.05$

Defoliation treatment ($n = 4$)	Start	Finish	Periodicity	Total leaf number	Green leaf number	Green leaf area	Plant dry weight	Branch no. on panicle
1. Control		—	0	12.75a	9.5d	1106d	33.0de	46.3b
2. All leaves above 2nd ligule	2nd leaf stage	PI in control	Twice weekly	15b	7.75b	603b	20.3b	36.8a
3. All leaves above 2nd ligule	3rd leaf stage	”	”	15b	7.75b	618b	19.5ab	34.8a
4. All leaves above 2nd ligule	4th leaf stage	”	”	15.75bc	8.25bc	694b	22.9b	36.5a
5. All leaves above 2nd ligule	5th leaf stage	”	”	15.75bc	7.5b	653b	23.3b	36.8a
6. All leaves above 2nd ligule	2nd leaf stage	PI plus 14 days	”	17.75d	9.0bcd	1213d	37.4e	39.8a
7. All leaves above 1st ligule	”	PI in control	”	18.25d	10d	895c	28.1cd	45.5b
8. Fully exposed leaf-blade	”	”	”	12.5a	5.5a	473a	15a	36.3a
9. Expanding leaves above whorl	3rd and 6th leaf stages	11 days before PI in control	Twice	14.75b	8.5bc	920c	28c	51.0b
s.e.d.				0.55	0.64	59	2.4	2.8
l.s.d. ($P = 0.05$)				1.15	1.35	124	4.9	5.9

Table 5. Effects of defoliation treatments on the plant dry weight (g/plant), grain dry weight (g/plant), and kernel dry weight (mg) of sorghum at maturity

Means within parameters followed by the same letter are not significantly different at $P = 0.05$

Defoliation treatment ($n = 4$)	Start	Finish	Periodicity	Plant dry weight	Grain dry weight	Kernel dry weight
1. Control	—	—	0	85.7	43.1	33.02
2. All leaves above 2nd ligule	2nd leaf stage	PI in control	Twice-weekly	61.2	32.3	28.26
3. All leaves above 2nd ligule	3rd leaf stage	”	”	75.9	34	27.1
4. All leaves above 2nd ligule	4th leaf stage	”	”	88.9	47	30.17
5. All leaves above 2nd ligule	5th leaf stage	”	”	83.9	36	29.36
6. All leaves above 2nd ligule	2nd leaf stage	PI plus 14 days	”	83.5	36.3	26.94
7. All leaves above 1st ligule	”	PI in control	”	96.7	44.4	29.69
8. Fully exposed leaf blade	”	”	”	56.9	28.7	28.93
9. Expanding leaves above whorl	3rd and 6th leaf stages	11 days before PI in control	Twice	73	37.3	28.85
s.e.d.				14.7	5.23	2.83
l.s.d. ($P = 0.05$)				n.s.	$P = 0.058$	n.s.

n.s., not significant.

number of panicle branches at anthesis above those of T2, and only green leaf area was less than the control (Table 4).

Defoliation of fully exposed leaf-blade

Twice-weekly defoliation of the fully exposed leaf-blade (T8) had no effect on the timing of PI, but delayed anthesis briefly (Table 3). The total number of leaves was not affected but there were fewer green leaves, and reductions in green leaf area, plant dry weight, and the number of panicle branches at anthesis compared with control plants (T1) (Table 4).

Defoliation of partially exposed leaf-blades above the third and sixth ligules

The delay in T9 was 17 days for PI and 11 days for anthesis compared with control plants (T1) (Table 3). Although PI occurred earlier in T9 than in T2–T5, the period from the end of defoliation to PI was of the same duration in these treatments, perhaps because defoliation in T9 was terminated 11 days before PI in the control plants. The reproductive period of T9 was also of the same duration as those in T2–T5. Defoliation in T9 increased the total leaf number compared with the control (T1) (Table 4). Compared with T2–T5, leaving 4 entire and some partial leaves on the plant at the termination of defoliation lessened the reductions in green leaf area and total dry weight at anthesis. The number of panicle branches was the same as in the control.

Defoliation treatment effects at maturity

Defoliation treatments that caused large delays in anthesis also delayed maturity, though to a lesser extent (Table 3). The growth parameters of plants in the defoliation treatments were not significantly ($P > 0.05$) different from those in the control (Table 5) except for the removal of fully exposed leaf-blades (T8), which reduced ($P = 0.058$) the grain dry weight.

Defoliation treatment effects on the length of fully expanded leaves

At the time when spikelets were first visible on the inflorescence, control plants (T1) had produced 8 fully exposed leaves and the length of each successive leaf increased in a linear trend (Fig. 1). For defoliation treatments, the measurements were made on those entire leaves that grew after defoliation was terminated; older leaves were removed in the defoliation treatments. Except for the 2 uppermost leaves, the lengths of successive leaves in defoliation treatments increased in the same linear trend as control plants. At the time when spikelets were first visible, there were fewer fully exposed leaves in defoliation treatments (only 4 in T2 and T6, and 7 in T7), and compared with the control, the older leaves were longer, particularly in T2.

Defoliation treatment effects on green leaf area (GLA) profiles at anthesis

In Figure 2 the GLA profiles of defoliated plants at anthesis are compared with control plants (T1). The flag leaf and the 3 leaves immediately below it comprised about 75% of the total GLA in all treatments. These leaves were generally reduced in area by defoliation above the second ligule (T2), or by defoliation of the fully exposed leaf-blade (T8). Only in the continued defoliation treatment (T6) were the flag leaf and the leaf immediately below it larger than those in the control. All defoliation treatments reduced the area of lower leaves, but again, T2 and T8 had the greatest effects.

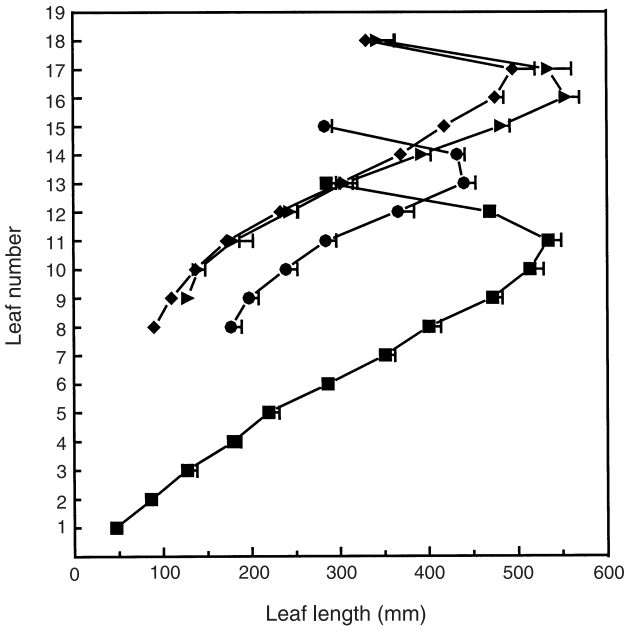

Fig. 1. Effects of defoliation treatments on the length of fully expanded, entire leaves on sorghum plants measured either when spikelets were first visible on the inflorescence or at anthesis. Defoliation treatments (n = 4) were: ■ T1, control; ● T2, 2nd ligule at 2nd leaf stage; ▲ T6, 2nd ligule plus 14 days; and ◆ T7, 1st ligule at 2nd leaf stage. Bars indicate the s.e.m.

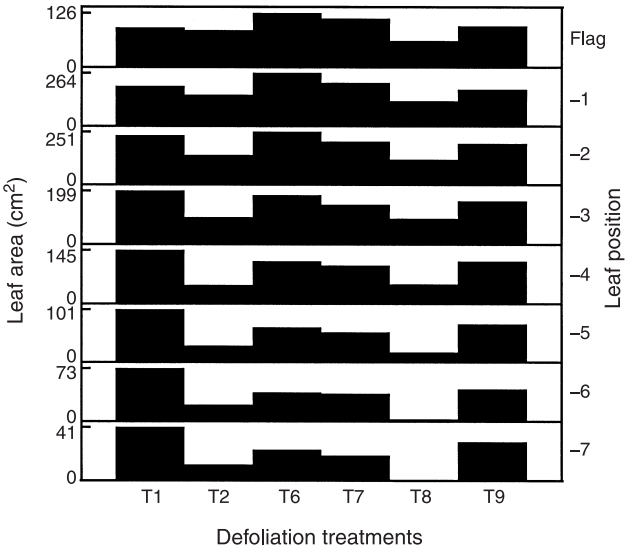

Fig. 2. Area of individual green leaves of sorghum plants at anthesis subjected to defoliation treatments. Defoliation treatments (n = 4) were: T1, control; T2, 2nd ligule at 2nd leaf stage; T6, 2nd ligule plus 14 days; T7, 1st ligule at 2nd leaf stage; T8, fully exposed leaf blade; and T9, expanding leaves above whorl at 3rd and 6th leaf stages. Leaf position (–1) indicates the leaf immediately below the flag leaf. The l.s.d. (P = 0.05) for Flag to Flag–7 leaves, respectively, were 28, 41, 37, 35, 31, 23, 12, and 4 cm^2.

Discussion

In this experiment we found that delays in PI (Ockerby *et al.* 2001) and anthesis (Vanderlip *et al.* 1977; Trybom *et al.* 1978) in sorghum associated with defoliation were responsive to the timing of the defoliation and the parts of the seedling's foliage that were removed. To invoke a delay in PI, defoliation was necessary only at the fifth leaf stage (T5), shortly before PI in control plants. Removal of only the fully exposed leaf-blade (T8) gave no delay but removal of immature and partially exposed leaves at progressively lower ligules increased the delay. Defoliation treatments also affected the morphology of the plant that re-formed after defoliation was terminated. Removal of only the exposed leaf-blade caused the biggest decrease in plant size at anthesis because PI was not delayed and no extra leaves were initiated to compensate for those removed by defoliation. Plants that re-formed in either the continued defoliation or defoliation above the first ligule treatments most resembled control plants at anthesis. The delay in floral induction (Table 3) and the size of the plant that re-formed at anthesis (Table 4) in defoliation treatments were strongly and negatively associated with the size of the plant when defoliation was terminated (Table 2).

We believe that defoliation-induced delays in PI are analogous to the findings of Irish and Nelson (1988, 1991) and Irish and Jegla (1997) in excised maize meristems. They learned that vegetative development, and the likelihood of onset of floral initiation, was regulated by the presence of 4–6 leaf primordia on excised meristems, but with fewer primordia the plant was 'reset' and regenerated a full complement of juvenile and adult leaves. In our experiments, when only fully exposed leaf-blade was removed (T8) and expanding and immature leaves and leaf primordia were not treated, there was no delay in PI nor was there an increase in total leaf number. Thus, we may conclude that the fully exposed leaf-blade played no direct role in signaling the meristem to change from vegetative to floral development. This result is contrary to the accepted role of leaves in photoperiodic plants to provide information to the meristem that evokes flowering. Sorghum is widely regarded to be a short day plant but the photoperiod extension treatment in our experiment failed to delay PI.

Because defoliation of only the fully exposed leaf-blade did not delay PI, but the defoliation of immature and partially exposed leaves did, it seems likely that the latter components of the seedling's foliage could be the source of the signal to evoke floral development. The comparison of defoliation either above the second ligule (T2) or above the first ligule (T7) lends support to this hypothesis. Although PI and anthesis were delayed in both treatments compared with the control, the plants in each treatment appeared to be reset to different ontogenological times. At the time when defoliation was terminated in T2, cutting at the height of the

second ligule left more green leaf-blade (by leaving the second leaf attached) and, to a greater extent, more unexposed and immature leaf within the whorl of the plant than in T7. The larger plant at the termination of defoliation in T2 may have reduced the delay to PI by hastening the attainment of a state of reproductive competence or ripeness to flower (Hopkinson and Ison 1982; Atherton *et al*. 1998).

Evidence to affirm the importance of the size of the immature leaves in regulating the onset of PI also comes from the common responses noted in defoliation treatments T2–T5. Although defoliation in these treatments commenced when the second–fifth ligule, respectively, was first exposed it was terminated at the same time in all treatments when PI was recorded in control plants. In all these treatments the plants were morphologically similar when defoliation was terminated (Table 2) and thus, perhaps consequently, the ensuing periods until PI or anthesis were of similar duration.

Continuing the defoliation treatment in T6 compared with T2 disproportionately lengthened the delay in PI and anthesis. It seems likely that the defoliation was performed so frequently and continued for so long that it imposed some physiological stress, akin to shock, that the plants took some time to recover from. The leaf initiation rate in T6 did not increase after defoliation was terminated, although it did in all other treatments (S. E. Ockerby, D. J. Midmore, D. F. Yule unpublished data), and we observed that the growth of new leaves between defoliation events slowed as the treatment period lengthened. The delay in PI and the production of 2 more leaves in T6 compared with T2 indicates that the shoot apical meristem continued to initiate leaf primordia for as long as PI was delayed.

The first-formed leaves after defoliation treatments were terminated were shorter than the leaves at the same node in the control plants and generally of a similar length to the juvenile leaves of control plants (Fig. 1). The effects were most noticeable in the treatment defoliated at the height of the first ligule (T7) and the plants at anthesis in that treatment most resembled non-defoliated sorghum plants at anthesis in terms of leaf length, green leaf area, and green leaf number. Cultured shoots derived from excised shoot apical meristems of maize with 3 or fewer leaf primordia re-formed a complete complement of vegetative nodes and initiated leaves with the juvenile trait of epicuticular wax (Irish and Nelson 1988). Irish and Karlen (1998) showed that juvenile patterns of differentiation in maize shoots including leaf length were the result of signaling throughout the plant and not of the chronological age of the node or meristem. Because all defoliation treatments in our experiments showed the same trend in leaf blade length, despite expression at different nodal positions, we concur with this result and suggest that signaling for juvenile traits was related to the size of the plant after defoliation was terminated.

Kaitaniemi *et al*. (1999) derived functions for architectural changes during sorghum morphogenesis. By digitising the vegetative structures in growing plants, they showed that the relationship between the lengths of successive fully expanded leaves within a plant was nearly constant for all plants, and the lengths of existing leaf blades were accurate predictors of the lengths of up to 6 subsequently formed blades. Our data suggest that leaf lengths may, to a large extent, be conditioned by the size (source strength?) of the previous leaf. Our data support the conclusion that leaf development is a size-dependent process (Lawson and Poethig 1995).

The delays in PI and anthesis in the current experiment were much longer than those in our earlier field study of sorghum defoliation (Ockerby *et al*. 2001). The maximum delay in PI in this experiment was 56 days in T6 compared with 19 days in the earlier experiment in a treatment equivalent to T2. The difference may reflect the cooler temperatures and slower rates of development in this experiment, because it was conducted during winter and the earlier experiment during summer. Also, different timings of termination of defoliation treatments resulted in different green leaf area profiles at anthesis. These results, taken collectively, suggest that defoliation may invoke a wider range than first thought in delays in the onset of reproductive development and in the growth and yield potential of the re-formed plant.

Defoliation of the fully exposed leaf-blade of sorghum (T8) reduced the area of each leaf (Fig. 1) and the green leaf area and dry weight of the plant at anthesis. Plant growth after anthesis in T8 was about half of the level in the control and grain dry weight was marginally lower ($P = 0.058$) than in the control and T7. The plant and grain dry weights of T8 were both approximately 66% of control plants. The lesser grain dry weight in T8 was not associated with weight per kernel, but with fewer branches on the panicle. Although the reproductive development periods in both treatments were of similar duration, slower growth before anthesis in T8 probably reduced branch number. We had expected that defoliation of the fully exposed leaf blade would severely limit grain dry weight, but this did not happen. We suggest that the grain dry weight in this experiment was generally too small to expose large differences between treatments. When treatment yields were recalculated on an area basis, at a plant population of 56 700/ha, the crop's grain yield was only 2.5 t/ha. Had the yield potential in the experiment been greater, plants in T8, because of their lesser dry weight and green leaf area at anthesis, may not have been able to capitalise on it. All other defoliation treatments produced plants at maturity that were not significantly different from control plants, and we conclude that the extra vegetative development and growth of the defoliated plants gained from resetting the ontogenological time adequately compensated for lost leaf area caused by defoliation, *per se*. These latter results

conflict with those in our earlier study (Ockerby *et al*. 2001) that indicate the grain yields of plants defoliated above the third or second ligule were only 68% of the control plants. The plants in the earlier study experienced shorter delays in PI and produced only 2 more leaves than the control plants. Different growth may have been caused by different environmental conditions in defoliated treatments compared with controls in that study. The yield benefits associated with defoliation treatments to control flowering time now need to be demonstrated in rain-fed sorghum crops.

The extent of defoliation also affected the morphology of the plant at anthesis. Earlier we showed (Ockerby *et al*. 2001) that defoliation of field-grown sorghum above the second ligule delayed PI and a bigger plant was re-formed than if defoliation was performed above the third ligule. The trend continued in the current experiment with plants defoliated above the first ligule having more leaves, green leaf area, and dry weight at anthesis than those plants defoliated above the second ligule, and similar green leaf area and plant dry weight to the control plants. Continued defoliation in T6 increased the area of the 2 uppermost leaves on the plant and those leaves contribute significantly (45%) to canopy photosynthesis during grain filling (Fischer *et al*. 1976).

Although this experiment was done under well-watered conditions, these findings have important implications for the post-sowing management of crops in water-limited environments. Farmers may sow crops on early-season rains then use defoliation to delay the onset of reproductive development, terminating defoliation only after soil water is replenished by a major rainfall event. Because defoliated plants will reach panicle initiation and anthesis in fewer days compared with crops sown after the rainfall, less soil water may be depleted by evapotranspiration before anthesis, giving a lower likelihood of water stress at anthesis and crop failure in the defoliated crop. The crop that was planted early and not defoliated may have already failed, having flowered during a period of plant water stress. By applying the final defoliation at different heights (ligules) the subsequent growth and yield potential of the crop may be adjusted in accordance with the amount of soil water and rainfall predictions.

Acknowledgments

We thank Laurie Punter for technical assistance and Ken Cotterill for literature searches. The Grains Research and Development Corporation supported this project.

References

Atherton JG, Yeh DM, Craigon J, Tucker GA (1998) Leaf initiation and shoot apical diameter in relation to phase transition in cineraria. *Journal of Horticultural Science and Biotechnology* **73**, 45–51.

Fischer KS, Wilson GL, Duthie I (1976) Studies of grain production in *Sorghum bicolor* (L. Moench). VII Contribution of plant parts to canopy photosynthesis and grain yield in field stations. *Australian Journal of Agricultural Research* **27**, 235–242.

Hopkinson JM, Ison RL (1982) Investigations of ripeness to flower in tobacco. *Field Crops Research* **5**, 335–348.

Irish EE, Nelson TM (1988) Development of maize plants from cultured shoot apices. *Planta* **175**, 9–12.

Irish EE, Nelson TM (1991) Vegetative to floral conversion occurs in multiple steps in maize tassel development. *Development* **112**, 891–898.

Irish EE, Jegla D (1997) Regulation of extent of vegetative development of the maize shoot meristem. *The Plant Journal* **11**, 63–71.

Irish EE, Karlen S (1998) Restoration of juvenility in maize shoots by meristem culture. *International Journal of Plant Science* **159**, 695–701.

Kaitaniemi P, Room PM, Hanan JS (1999) Architecture and morphogenesis of grain sorghum, *Sorghum bicolor* (L.) Moench. *Field Crops Research* **61**, 51–60.

Lawson EJR, Poethig RS (1995) Shoot development in plants: time for a change. *Trends in Genetics* **11**, 263–268.

Moncur MW (1981) 'Floral initiation in field crops.' (CSIRO: Melbourne)

Northcote KH (1979) 'A factual key to the recognition of Australian soils.' 4th edn. (Rellim Technical Publications: Glenside, S. Aust.)

Ockerby SE, Midmore DJ, Yule DF (2001) Leaf modification delays panicle initiation and anthesis in grain sorghum. *Australian Journal of Agricultural Research* **52**, 127–135.

Poethig RS (1990) Phase change and the regulation of shoot morphogenesis in plants. *Science* **250**, 923–930.

Trybom JC, Vanderlip RL, Moore WA (1978) Delaying flowering of grain sorghum lines for hybrid seed production. *Crop Science* **18**, 712–714.

Vanderlip RL, Ball JD, Banks PJ, Reece FN, Clark SJ (1977) Flaming grain sorghum to delay flowering. *Crop Science* **17**, 902–905.

Manuscript received 14 June 2000, accepted 20 April 2001