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Leaf modification delays panicle initiation and anthesis in grain sorghum

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Abstract. Water stress at anthesis is the major cause of yield reduction or crop failure in grain sorghum [*Sorghum bicolor* (L.) Moench] in central Queensland. Rainfall is difficult to predict and it is impractical to substantially alter the timing and amount of water stored in the soil, so we focussed on whether crop ontogeny could be managed, ultimately giving farmers some capability to align anthesis with in-crop rain. It is widely considered that a signal, transported from the leaf to the shoot apical meristem, is integral to the onset of panicle initiation and reproductive development. We hypothesised that modifying the leaves may interrupt the signal and cause a delay in the onset of reproductive development. Delays in sorghum anthesis associated with leaf modification treatments applied before panicle initiation were found to be a consequence of delays in panicle initiation. The longest delays in panicle initiation were obtained by twice-weekly defoliation above the second ligule (15–45 days); delays were shorter when plants were defoliated above the third ligule (10–41 days) or when only the fully exposed leaves were removed (0–13 days), depending on genotype. Although panicle initiation was delayed, leaf initiation continued, so extra leaves were produced. Defoliation of fully irrigated plants, however, generally reduced green leaf area, plant dry weight at anthesis, and grain yield, all by 30–50%. The application of ethephon also delayed anthesis, and changed the pattern but not the area of leaf produced, and did not alter grain yield. In rain-fed agriculture, where grain yields are frequently <50% of irrigated controls, delaying panicle initiation by 2 weeks may provide a better rainfall environment during which anthesis and grain-filling will occur. Reductions in green leaf area, although reducing yield potential, may promote a more balanced use of water between vegetative and grain growth. There was sufficient evidence to indicate that defoliation before panicle initiation could provide simple post-sowing management to achieve this scenario.

Additional keywords: defoliation, flowering, grain yield, phenology, photoperiod, water use efficiency.

Introduction

In determinate rain-fed crops, water stress at anthesis reduces yield disproportionally below that supported by the total amount of water available for crop growth. Crops affected by water stress at anthesis may grow a large vegetative biomass but produce little or no grain. The problem occurs frequently in summer-cropping environments in Australia, and is endemic in large areas of central Queensland where the shallow soils have a limited soil water storage. Invariably, stored rain that falls before sowing is used by evapotranspiration during vegetative crop growth, and is depleted before anthesis. Unless rain falls after sowing, fertility and grain growth are constrained by water stress. Our interest is in delaying, and ultimately controlling, the timing of panicle initiation and anthesis in sorghum to align the latter with availability of soil water.

Sorghum ontogeny is under genetic and environmental controls. Sorghum is a quantitative short-day plant, and its developmental pattern can be reasonably predicted as functions of photoperiod and temperature (Hammer *et al.* 1989; Ellis *et al.* 1997). Sorghum is a determinate plant, such that development at the apical meristem undergoes transition from the adult vegetative phase to the reproductive phase (Poethig 1990); after panicle initiation no more leaves can be initiated on the mainstem.

Defoliation of maize at the 5-leaf stage has been used to assess yield losses associated with hail damage (Crookston and Hicks 1978, 1988). Results varied—yield advantages (48%) occurred when yields (4.83 t/ha) and the end-of-season available water were low, but yield declined (8%) in high-yielding (9.31 t/ha) environments. At defoliation, the terminal growing point had differentiated into primordial

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tassel tissue, and while leaves 1–8 were mostly or partly severed, leaves 9–18 had not expanded to the height of the cut. Yield advantages were hypothesised to be due to the reduction in early vegetative growth and an associated stimulation of embryonic ear growth. Shapiro *et al.* (1986) showed that complete defoliation of irrigated maize prior to the 7-leaf stage had no effect on grain yield, but yield declined linearly with defoliation at later leaf stages. Early defoliation of sweet corn increased harvest index as a function of reduced plant stover and not an increase in ear weight (Crockett and Crookston 1981).

In earlier studies, sorghum seedlings have been successfully treated before the panicle differentiation stage with flaming (Vanderlip *et al.* 1977), and flaming, clipping and contact herbicide (Trybom *et al.* 1978) to align the flowering of parental lines in hybrid seed production; delays of up to 8 days were achieved. Similar treatments have produced flowering delays in maize (Green 1949; Dungan and Gausman 1951). While attempting to simulate armyworm damage in maize, Brown and Mohamed (1972) found a delay in tasseling when plants were cut off at ground level. They noted that because the growing point of the plant was below ground level a considerable number of new leaves grew out of the stump, although only 50% of the normal crop yield was realised. Vasilas and Seif (1985) found that early defoliation often increased maize yields by decreasing transpiration or delaying flowering until irrigation water was applied. In sorghum, we postulate that defoliation, or changes in the growth of leaves, and therefore the removal of, or changes in, the signal that evokes floral development, will result in a delay in timing of panicle initiation and, consequently, anthesis. Treatments should also produce a change in the ontogenological amount and timing of green leaf area.

Materials and methods

Two glasshouse experiments and one field experiment were conducted between 1997 and 1999 at Mareeba and at the nearby 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). Mean monthly values of maximum and minimum temperature and relative humidity, solar radiation, and rainfall recorded daily throughout the experiments, and associated photoperiods are shown in Table 1.

Cultural practice

Expts 1 and 2 were conducted in a glasshouse. Plants were grown in 4.5-L black plastic pots that contained 5.2 kg of air-dried surface soil (0– 0.1 m) which had been crushed to pass through a 0.2-cm sieve. Prior to potting, 24 g of slow-release fertiliser with 16% N, 4% P, and 8% K was mixed into the soil in each pot. Subsequently, pots were fertilised with 100 mL water containing 0.16 g soluble fertiliser with 23% N, 4% P, 18% K, and micronutrients at 20, 38, 68, 85, and 104 days after sowing (DAS) in Expt 1, and 0, 7, 35, 50, 83, and 107 DAS in Expt 2.

In Expt 1, 6 seeds per pot were sown on 23 September 1997. Fifty percent of seedlings had emerged on 27 September; these were thinned to 4 evenly developed plants on 3 October.

Table 1. Mean monthly maximum and minimum temperatures (°C), maximum and minimum relative humidity (%), solar radiation (MJ/m^2.day), photoperiod (h), and total rainfall (mm) during the three experiments

Month	Days after sowing	Max. temp.	Min. temp.	Max. relative humidity	Min. relative humidity	Solar radiation	Photoperiod	Rainfall
				Expt 1, glasshouse 1997–98				
Sept.	1–7	33.1	17.9	76.5	38.6	n.a.	12.4	–
Oct.	8–39	32.6	19.0	77.0	40.6	n.a.	12.7	–
Nov.	40–69	34.9	21.5	80.4	43.0	9.4	13.1	–
Dec.	70–100	35.1	23.5	85.3	48.4	10.3	13.3	–
Jan.	101–131	35.1	24.2	90.1	55.1	11.1	13.2	–
Feb.	132–147	36.8	23.2	84.4	46.0	13.4	13.0	–
				Expt 2, glasshouse 1998				
Dec.	1–27	34.8	23.5	85.4	49.0	10.0	13.3	–
Jan.	28–59	35.1	24.2	90.1	55.1	11.1	13.2	–
Feb.	60–87	36.4	23.6	87.0	49.1	11.9	12.9	–
Mar.	88–118	34.8	23.0	88.1	51.0	10.1	12.4	–
Apr.	119–148	33.2	21.4	87.0	50.4	6.9	11.9	–
				Expt 3, field 1998				
Oct.	1–16	29.9	19.7	n.a.	n.a.	20.2	12.8	76
Nov.	17–46	29.5	19.6			21.2	13.1	130
Dec.	47–78	30.3	19.7			23.2	13.3	87
Jan.	79–110	29.9	20.9			20.1	13.2	275
Feb.	111–129	29.3	20.8			17.9	12.9	396
Mar.	129–141	28.5	21.0			16.4	12.6	58

n.a., not applicable.

In Expt 2, 6 seeds were sown on 4 December 1997. Fifty percent of seedlings had emerged on 7 December, and these were thinned to 4 evenly developed plants on 12 December. In both experiments, plants were subsequently removed for dissection to determine the timing of panicle initiation (PI), after which only 1 plant was left per pot.

Expt 3 was done in the field. Plots were marked and the soil was cultivated to a depth of 0.15 m on 7 October 1998. A basal fertiliser containing (kg/ha) 49 P, 24 K, 22 S, and 9 Zn, and prilled urea at 180 N, were applied and mixed with the cultivated soil. On 16 October, 2 or 3 seeds were sown by hand on a 9 by 11 grid with seeds spaced 0.1 m apart; the outermost rows were designated as guard area. An unplanted area ranging from 0.3 to 1.2 m separated the plots. Plots were irrigated daily using overhead sprinklers. Fifty percent of seedlings had emerged on 23 October and these were thinned to 1 evenly developed plant in each position on 2 November.

Plots were hand-weeded, and insecticides were sprayed as required. At the soft dough stage of grain-filling, the sorghum heads designated for sampling at maturity were covered with a brown paper bag, and plots were covered with netting to minimise losses due to birds.

Experimental designs and treatments

The experiments investigated the ontogeny and growth of sorghum [*Sorghum bicolor* (L.) Moench] genotypes in response to a range of physical (defoliation using scissors), physiological (photoperiod and water stress), and hormonal (growth retardant) treatments. We expected that these treatments may affect the flowering signal, produced in leaves, that initiates panicle development at the shoot apical meristem.

Expt 1 used a randomised complete block design with 3 replications. The treatments (1 pot per treatment) were arranged as a 2×2×5 complete factorial and consisted of 2 irrigation treatments, fully irrigated or water stressed from 13 to 43 DAS; 2 sorghum genotypes, cvv. Buster or QL24; and 5 plant modification treatments:

(1) no modification, control;
(2) defoliation of all leaf above the third leaf ligule at 26 DAS (4th exposed leaf stage);
(3) ethephon 0.5% to runoff at 17 DAS;
(4) photoperiod extension to 15 h from 15 DAS until PI in the control;
(5) mainstem removal below the apical meristem at PI at 45 DAS.

Expt 2 used a randomised complete block design with 4 replications. The treatments (1 pot per treatment) imposed on sorghum (cv. Buster) were arranged as a 3×5 complete factorial and consisted of 3 levels of water stress:

(1) nil;
(2) stress from the appearance of the fourth leaf until 10 days after PI in the control at 39 DAS;
(3) stress from 10 days after PI in the control until 48 DAS;

and 5 levels of plant modification:

(1) no modification, control;
(2) once-only defoliation of all leaf above the second leaf ligule at18 DAS;
(3) weekly defoliation of all leaf above second leaf ligule at 18–37 DAS;
(4) mainstem removal below the apical meristem after PI in the control at 43 DAS;
(5) mainstem removal at 5 cm height after anthesis in the control at 69 DAS.

Expt 3 used a split-plot design with 2 replications, with main plots laid out in a randomised complete block design. The main plots were either natural (Table 1) or extended (15 h) photoperiod. Within each main plot, the subplot treatment structure was a 3×5 factorial design. The subplot treatments were 3 levels of genotype: Buster, Boomer, or QL24; and 5 levels of leaf modification:

(1) no modification, control;
(2) twice weekly defoliation of all leaf above the second leaf ligule;
(3) twice weekly defoliation of all leaf above the third leaf ligule;
(4) twice weekly defoliation of all fully exposed leaf blades;
(5) twice weekly application of ethephon 0.5% to runoff.

Modification treatments commenced on 16 October (18 DAS) and were applied to each genotype until PI was recorded in control plants of that genotype.

Treatment details

Photoperiod extension

The photoperiod extension treatment in Expt 1 was imposed by transferring treatment pots from the experimental benches to a separate, screened part of the glasshouse, where a bank of two 36 W cool white fluorescent tubes and five 60 W incandescent bulbs suspended 1 m above the plant canopy provided 12–20 μmol/m^2.s PAR. The pots were transferred at about 1800 hours and again at about 0700 hours. The dark period extended from 2000 to 0500 hours. Natural photoperiod ranged from 12.6 h at the start of the experiment to 13.2 h at the time when QL24 had likely attained PI.

The photoperiod extension treatment in Expt 3 was imposed by suspending twelve 100 W incandescent bulbs 1.2 m above the ground covering an area of 10 m by 4.5 m providing 60–600 lux and 2–12 μmol/m^2.s of PAR. The dark period extended from 2000 to 0500 hours. Natural photoperiod ranged from 12.8 h at the start of the experiment to 13.2 h at the time when the last treatment attained PI.

Irrigation

In Expts 1 and 2, water was applied to each pot through a surface drip-irrigation system delivering water at approximately 40 mL/min. Irrigation was controlled automatically by a solenoid system triggered to switch on when the water potential of 'Watermark 200–253' sensor, placed horizontally in the soil, 50 mm above and central to the base of one pot in each treatment, reached 0.8 bars, and switch off when water potential was 0.33 bars. Drainage from the bottom of the pot occurred before the irrigation event ceased.

Pots subjected to water stress treatments were removed from the drip-irrigation system and watered strategically to ensure plant survival. The water stress treatment in Expt 1 commenced on 6 October and ceased on 6 November. These pots were watered 4 times on 10, 20, and 28 October and 3 November by adding water by weight until the gravimetric water content (θg) was 0.158 g/cm^3; θg was 0.281 g/cm^3 for pots at the drained upper limit. Water stress treatment pots in Expt 2 were given 80 mL of water, usually on a daily schedule if plants showed visual symptoms of water stress; the water was sufficient for plants to recover from stress symptoms for several hours.

Measurements

Panicle initiation

To determine the timing of PI and the number of leaf primordia, the mainstem of treatment plants was cut at ground level, wrapped in plastic, and stored on ice. Fully exposed leaf blades and sheaths were peeled off, and the area of the blade was measured. Unexpanded leaves and leaf primordia were removed with a scalpel under a dissecting microscope. The number of leaves and leaf primordia was recorded for each sample in each treatment. The developmental stage of the apical meristem was scored after Moncur (1981): 1, vegetative with only leaf primordia visible; 7, spikelets visible on the inflorescence. Panicle initiation was deemed to have occurred when primary branches were observed as swellings at the base of the apical meristem (Stage 3). All meristems with spikelet differentiation were scored as 7 irrespective of subsequent floral development.

In Expt 1, samples were taken strategically, during a period from 19 October to 19 December, to determine whether treatments caused a delay in the onset of PI. There were too few plants to do replicated sampling of all treatments at the same time.

Having established in Expt 1 that some treatments did delay PI, samples of all treatments in Expt 2 were taken on 2 occasions, 3 and 12 January, so that differences between treatments could be statistically tested, and an initial assessment of the length of the delay could be made. Plants in Expt 3 were sampled twice-weekly from each treatment until spikelets were visible on the inflorescence, with the aim to precisely quantify the delay associated with treatments.

Anthesis

Plants were inspected thrice-weekly, and the time of anthesis was recorded when the panicles on 50% of plants had visible anthers in 50% of florets. A single plant per treatment was sampled, and the area of each leaf blade was recorded. Samples were then dried at 70°C until a constant weight. In Expt 3 the primary branches on the mainstem panicle were counted.

Maturity

Plants were grown to maturity only in Expt 3. A single plant per treatment was sampled when the grain had turned brown; however, only Buster and Boomer were taken since modified plants of QL24 were affected by disease. Leaf, stem plus sheath, and panicle were dried at 70°C until a constant weight. The panicle was threshed and grain dry weight recorded.

Results

Crop duration

Timing of panicle initiation

Expt 1. Sampling for PI was difficult because we had only *a priori* knowledge of the timing, and only a few plants to dissect. Panicle initiation was first observed in the control plants of the genotype Buster on 30 October (37 DAS), at which time samples of QL24 were vegetative. On 31 October (38 DAS), a fully replicated sample of irrigation and modification treatments of Buster showed that, with the exception of the treatment combining water stress with photoperiod extension, all plants had attained PI. The genotype QL24 continued to develop vegetatively in all treatments until 18 November (56 DAS) after which time no more plants were available to sample.

Expt 2. On 3 January (29 DAS), control plants had attained PI, whereas plants treated with early water stress, and/or single or weekly defoliation, continued to develop

Table 2. Water stress and defoliation treatment effects on panicle development stage in sorghum (Expt 2)

The developmental stage of the apical meristem was scored after Moncur (1981): 1, vegetative with only leaf primordia visible; 7, fully differentiated with spikelets visible on the inflorescence

Water stress treatment	Modification treatment: Control	Defoliated once	Defoliated weekly
	29 Days after sowing		
None	5.0	1.3	1.0
Early stress	2.7	1.0	1.0
Late stress	5.9	2.5	1.0
l.s.d. ($P = 0.05$) for the interaction = 1.73			
	40 Days after sowing		
	6.8	6.2	1.0
l.s.d. ($P = 0.05$) = 0.36			

Table 3. Interactions between genotype and modification treatments on the duration from sowing to panicle initiation (PI) and anthesis, total leaf number, green leaf area, dry weight, and the number of primary branches on the panicle at anthesis, and the grain dry weight at maturity in sorghum in Expt 3

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

Modification treatment	Genotype: Buster	Boomer	QL24
	Duration from sowing to PI (days)		
Control	32.7a	35.2ab	60.7g
Defoliation at 2nd ligule	47.5e	54.5f	105.0k
Defoliation at 3rd ligule	42.0d	47.5e	102.0j
Defoliation of exposed leaf	32.7a	38.7c	73.5h
Ethephon	37.0bc	44.0d	81.0i
	Duration from sowing to anthesis (days)		
Control	62.5a	70.25cd	102.8i
Defoliation at 2nd ligule	76.5f	84.0h	148.0m
Defoliation at 3rd ligule	71.3de	80.5g	143.3l
Defoliation of exposed leaf	63.8a	74.5ef	113.8j
Ethephon	67.5bc	74.6f	123.8k
	Total leaf number		
Control	14.25a	15.5ab	24.0f
Defoliation at 2nd ligule	15.25ab	17.75d	26.75g
Defoliation at 3rd ligule	15.0ab	17.25cd	27.0g
Defoliation of exposed leaf	15.75abc	16.0bc	25.5fg
Ethephon	16.0bc	19.5e	32.25h
	Green leaf area at anthesis (cm^2/plant)		
Control	1963bc	2942d	6644g
Defoliation at 2nd ligule	1668b	2066c	5320f
Defoliation at 3rd ligule	1234a	2068c	4207e
Defoliation of exposed leaf	1590ab	2800d	6624g
Ethephon	1978bc	3164d	5584f
	Plant dry weight at anthesis (g/plant)		
Control	54.3abc	59.3bc	200.4g
Defoliation at 2nd ligule	27.9a	36.3abc	104.4e
Defoliation at 3rd ligule	27.9a	30.9ab	92.8de
Defoliation of exposed leaf	46.2abc	66.8cd	175.0g
Ethephon	52.9abc	54.2bc	137.2f
	Number of primary branches on panicle		
Control	45.0abc	67.8fg	61.5efg
Defoliation at 2nd ligule	42.8ab	54.0cde	62.5efg
Defoliation at 3rd ligule	40.2a	58.5def	62.8efg
Defoliation of exposed leaf	51.8bcd	64.8f	78.3h
Ethephon	47.0abc	70.8gh	65.0fg
	Grain dry weight (g/plant)		
Control	74.8	82.7	–
Defoliation at 2nd ligule	47.5	54.8	–
Defoliation at 3rd ligule	43.7	58.9	–
Defoliation of exposed leaf	65.2	80.7	–
Ethephon	72.3	76.8	–

vegetatively at the apical meristem (Table 2). On 13 January (40 DAS), only plants with defoliation at weekly intervals remained in the vegetative state. On 30 January, the mean stage of apical meristem development for the weekly defoliation treatment ranged from 3 for the no water stress treatment to 5 for the early water stress treatment.

Expt 3. The duration from sowing to PI was the same for control plants of the genotypes Buster and Boomer, but longer for QL24 (Table 3). The defoliation of fully exposed leaf blades did not delay PI in Buster, but other subplot treatments did. All subplot treatments delayed PI in Boomer and QL24, and delays were longer than when apparent in Buster. In all genotypes, PI was delayed more by defoliating above the second leaf ligule than defoliating above the third leaf ligule. Photoperiod extension did not change the timing of PI.

Sowing to anthesis

Expt 1. Genotype, water stress, and photoperiod extension treatments that delayed PI also delayed anthesis (Table 4). Anthesis of the primary tillers that developed after removal of the mainstem at PI was also delayed. There were no interactions between genotype, water stress, and modification treatments.

Expt 2. Anthesis was delayed only by weekly defoliation (Table 4); the length of the delay was similar to the delay in PI for this treatment (Table 2). Mainstem removal at PI or anthesis resulted, of course, in later anthesis of the primary tillers. The tillers of plants with mainstems removed just after PI (in the control plants) took a further 63 days to reach anthesis, whereas those with the mainstems removed just after anthesis took a further 56 days to reach anthesis.

Expt 3. The duration from sowing to anthesis of control plants of Buster was shorter than for Boomer, which in turn was shorter than for QL24 (Table 3). The twice-weekly defoliation of fully exposed leaf blades did not delay anthesis in Buster, but all other modification treatments did. All modification treatments delayed anthesis in Boomer and QL24, but whereas the delays were similar in Buster and Boomer, they were significantly longer in QL24. As for PI, anthesis in all genotypes was delayed more by defoliating above the second ligule than defoliating above the third ligule. Photoperiod extension did not affect the timing of anthesis.

Sowing to maturity

Expt 3. The control plants of QL24 matured at 140 DAS. It was difficult to determine maturity in modified plants of QL24 because of crop disease. In an analysis of the other genotypes, maturity was earlier in Buster (109 DAS) than Boomer (114 DAS; l.s.d. $P = 0.05$, 2.15), and defoliation at the second or third ligule delayed maturity by 7–9 days (l.s.d. $P = 0.05$, 3.4); neither defoliation of the fully exposed leaves nor ethephon altered the date of maturity.

Table 4. Duration from sowing to anthesis (days) for modification, genotype, and water stress treatments in two glasshouse experiments

Data for mainstem removal treatments refer to the primary tiller

Treatment	Duration from sowing to anthesis	
	Expt 1	Expt 2
Modification		
Control	104.7	68.8
Defoliation once at 4th leaf	108.7	64.7
Defoliation weekly at 4th leaf	–	80.9
Mainstem removal at PI	151.7	106.5
Mainstem removal at anthesis	–	112.7
Ethephon	98.3	–
Photoperiod extension	113.7	–
l.s.d. ($P = 0.05$)	6.9	10.5
Genotype		
Buster	87.0	86.6
QL24	143.9	–
l.s.d. ($P = 0.05$)	4.3	
Water stress		
Control	111.5	85.3
Early	119.4	83.6
Late	–	91.1
l.s.d. ($P = 0.05$)	4.3	n.s.

n.s., not significantly different ($P = 0.05$)

Total leaf number

Water stress did not affect total leaf number in either Expt 1 or Expt 2.

Expt 1

Buster produced fewer leaves than did QL24 (13.4 *v.* 28.1; l.s.d. $P = 0.05$, 2.1). For modification treatments, leaf number (mean over 2 genotypes) increased only when the mainstem was removed at PI compared with the unmodified control (27.7 *v.* 18.3; l.s.d. $P = 0.05$, 3.3), thus the primary tiller produced 9 leaves.

Expt 2

Leaf number was affected by modification treatments. Compared with the control which produced 12 leaves, leaf number was reduced by once-only defoliation (10.7) and weekly defoliation (9.8, l.s.d. $P = 0.05$, 0.8). More leaves were produced by the primary tiller of plants with the mainstem removed at PI (13.5), but the primary tiller of plants with the mainstem removed at anthesis produced the same number of leaves as the control. The total number of leaves on plants with the mainstem removed at either PI or anthesis was obviously greater than in the control.

Expt 3

Plants defoliated at the second or third ligule produced more leaves than the control treatment in both Boomer and QL24, but not Buster (Table 3). Defoliation of the fully

Table 5. Interaction between modification and genotype (Buster and QL24) treatments on the log-transformed means of green leaf area (cm^2/plant) and plant dry weight (g/plant) of sorghum at anthesis in Expt 1

Means within parameters followed by the same letter are not significantly different at $P = 0.05$. DAS, days after sowing; PI, panicle initiation

Modification treatment	Green leaf area		Plant dry weight	
	Buster	QL24	Buster	QL24
Control	7.03b	8.77d	2.84b	4.70cd
Defoliation once at 26 DAS	6.53a	8.71d	2.26a	4.68cd
Ethephon at 17 DAS	7.24bc	8.54d	3.04bc	4.42c
Photoperiod extension at 15 DAS	7.49c	8.80d	3.34c	4.93d
Mainstem removal at PI, 45 DAS	7.46c	8.55d	3.31c	4.39c

exposed leaves had no effect, but ethephon produced many more leaves in all genotypes.

Green leaf area (GLA) and number at anthesis

Expt 1

At anthesis, QL24 had 4 times as much GLA as Buster (6098 *v*. 1378 cm^2/plant; l.s.d. $P = 0.05$, 1145). The analysis of log-transformed means showed a significant interaction between genotype and modification treatments. Whereas modification had no effect on the GLA of QL24, defoliation reduced, and photoperiod extension and mainstem removal at anthesis increased, the GLA of Buster at anthesis (Table 5), the latter due to an increase in the number of tillers (data not reported).

Expt 2

The GLA of Buster was reduced by early water stress compared with the control (1365 *v*. 1815 cm^2/plant; l.s.d. $P = 0.05$, 295) but was not affected by late stress (1550). Leaf modification also affected GLA; compared with the control (1671 cm^2/plant), GLA was reduced by defoliation once (843) or at weekly intervals (764; l.s.d. $P = 0.05$, 381). The GLA of tillers that grew after mainstem removal at PI was increased (3036) due to a greater tiller number; but the GLA of tillers with mainstem removal after anthesis (1569) was comparable to the control.

Expt 3

On average the GLA at anthesis was smallest for Buster (1687 cm^2/plant) and smaller for Boomer (2608) than QL24 (5676; l.s.d. $P = 0.05$, 454). The GLA was affected also by modification treatment; compared with the control (3849 cm^2/plant), GLA was reduced by defoliation above the third ligule (2503) or second ligule (3018), but not changed by defoliation of the fully exposed leaf (3671) or ethephon treatment (3575; l.s.d. $P = 0.05$, 586). The combination of genotype and modification treatments showed 2 interesting results (Table 3); for Buster and QL24 the reduction in GLA was not as great when defoliation was above the second compared with the third ligule, and defoliated plants of one genotype (Boomer) produced the same GLA as control plants of another (Buster). At anthesis, the average size of green leaves on the control plants was 311 cm^2. Leaf size was smaller for plants defoliated above the third ligule (255; l.s.d. $P = 0.05$, 34) or second ligule (272), and for those treated with ethephon (270), but larger for plants with defoliation of the fully exposed leaves (360). The number of green leaves at anthesis was greater in the control plants (11.6) than in plants defoliated above the third ligule (9.2; l.s.d. $P = 0.05$, 0.8) or second ligule (10.4), and those with defoliation of the fully exposed leaves (9.4), but less than in those treated with ethephon (12.8).

Above-ground dry weight at anthesis

Expt 1

The analysis of log-transformed means showed a significant interaction between genotype and modification treatments, but no effect of the water stress treatment. Modification treatment had small effects on the dry weight of QL24 plants at anthesis; however, in line with GLA, the dry weight of Buster was reduced by defoliation and increased by photoperiod extension or mainstem removal after anthesis (Table 5).

Expt 2

The plant dry weight at anthesis was reduced by both early (22.2 g/plant) and late (24.1) water stress compared with the control (29.6; l.s.d. $P = 0.05$, 5.2). Modification also had an effect; compared with the control (26.4 g/plant), plant dry weight was reduced by defoliation once (13.1) or at weekly intervals (13.0), increased by mainstem removal at PI (49.4), and not changed by mainstem removal at anthesis (24.2; l.s.d. $P = 0.05$, 6.7).

Expt 3

As for GLA, the interaction between genotype and modification treatments for plant dry weight at anthesis was statistically significant (Table 3) but this was due to the heaviness of QL24 (142 g/plant) relative to Buster (41.8) and Boomer (49.5; l.s.d. $P = 0.05$, 12.7). Despite lacking statisti-

cal significance within the genotypes Buster and Boomer, the main effect of leaf modification treatments was similar across all genotypes; compared with the control (104.7 g/plant), plant dry weight was reduced by defoliation above the third ligule (50.5) or second ligule (56.2), and by ethephon (81.4), but not changed by defoliation of fully exposed leaves (96.0; l.s.d. $P = 0.05$, 16.5).

Primary branches on the panicle

Expt 3

The effects of leaf modification treatments varied for different genotypes (Table 3). In Buster and QL24, defoliation of the fully exposed leaves increased the number of primary branches on the panicle, whereas in Boomer, primary branch number decreased only in response to defoliation at the third ligule.

Grain dry weight

Expt 3

The mean grain dry weight of Buster (60.7 g/plant) was less than that of Boomer (70.8; l.s.d. $P = 0.05$, 9.6). Both genotypes responded similarly to modification and the interaction was not significant (Table 3). Defoliation at the second or third ligule reduced grain yield by 27 g/plant (l.s.d. $P = 0.05$, 15), but defoliation of the fully exposed leaves or ethephon had no effect.

Discussion

The results confirmed that anthesis in sorghum is delayed by a range of leaf modification treatments including clipping (Vanderlip *et al.* 1977) and water stress (Craufurd *et al.* 1993). Delays in anthesis were associated with delays, of similar duration, in the onset of reproductive development marked by PI.

Treatments that extended the period of vegetative development or leaf initiation in the field in Expt 3 increased the total leaf number. Defoliation treatments in the glasshouse, however, although delaying PI, reduced total leaf number. Genotypic effects may explain this anomaly since the earliest genotype Buster was used mostly in the glasshouse and its leaf number did not respond to modification treatment in the field. Pao and Morgan (1986) found that the floral initiation-delaying effect of sorghum maturity gene Ma_1 in the absence of Ma_2 was less strongly expressed in the growth room than in the field, possibly an effect of temperature. We also suspect that cutting height may have been important, since glasshouse plants had longer leaf sheaths than plants in the field (solar radiation in the glasshouse was 50% of that outside), so the absolute height of cutting was higher. Cutting at a higher level in glasshouse plants had the effect of removing less of the expanding leaf initial tissue contained in the whorl.

Twice-weekly defoliation of all fully exposed leaves of Buster failed to invoke a delay in the onset of PI. In the two later genotypes, Boomer and QL24, the delay due to this treatment was evident but it was much shorter than if the plants were defoliated at the height of the third ligule. These comparisons indicate that the fully exposed leaves alone do not produce the signal to the plant to begin reproductive development. Rather, we believe that the expanding leaves may be the source of the signal, and that fully exposed leaves may be necessary to the plant to attain a state of competence for reproductive development. Hopkinson and Ison (1982) likewise concluded that the expanded leaves of seedbed or stressed tobacco plants were unable to invoke floral initiation.

In all genotypes in Expt 3, the delay in PI was greater with defoliation at the height of the second than the third ligule. The treatments differed in that the second ligule treatment removed both the third exposed leaf and a greater proportion of the expanding leaf in the whorl. Either this suppressed to a greater extent the signal to invoke reproductive development than in plants defoliated above the third ligule, and/or it slowed the rate of plant regrowth and delayed the time at which the plant was competent to initiate a panicle.

Ethephon delayed PI and anthesis and increased the total leaf number in all genotypes in Expt 3. Our reason for including this treatment was that ethephon applied to corn, through the release of ethylene (Warner and Leopold 1969), reduces leaf size and enhances leaf carbon exchange rate (Kasele *et al.* 1995) and increases grain yield when water supply is limiting (d'Andria *et al.* 1997). Ethephon reduced leaf area in QL24, but for Buster and Boomer the leaf area at anthesis was unchanged. There was one more green leaf in ethephon-treated plants of all genotypes at anthesis, compared with control plants, and the average size of green leaves was smaller. We conjecture that a link exists between ethylene-induced changes in cell division and elongation within leaves (Burg *et al.* 1971) and processes controlling the change from vegetative to reproductive development. Reducing the eventual size of specific leaves by ethephon may in effect be analogous to limiting the amount (or rate) of expansion in leaves during vegetative development.

We can conclude, in accordance with our hypothesis, that specific modifications to expanding leaves delay the production of the signal that invokes developmental change (PI) at the apical meristem. Also clear is the fact that serial modification will maintain the meristem in a vegetative state, and while this is done, leaf initiation will continue, so extra leaves are produced. It seems likely that leaf modification prevents the plant from achieving the state of competence that is necessary to switch to reproductive development. Expanding and fully exposed leaves have different impacts on the production of the signal.

Delays in PI and anthesis induced by defoliation at the second ligule were not of long duration in the context of a cropping season, but demonstrate the potential for post-sowing management of crop development. In Boomer, leaf

modification needed to be applied before 35 DAS and this delayed flowering by 14 days. Since sorghum is a determinate species, defoliation after PI would not greatly affect anthesis date, but would reduce GLA and crop growth rate. Under the irrigated experimental conditions, defoliation increased total leaf number but reduced by 30–50% the GLA and dry weight at anthesis, and grain dry weight. This large yield penalty in response to defoliation reflects the reduction in leaf area and crop growth rate before anthesis. The effects of defoliation were not always negative, however, since defoliation above the third leaf ligule in Buster and QL24 increased the number of primary branches on the panicle (Table 3). Reproductive development may have been promoted in lieu of vegetative growth as suggested by Crookston and Hicks (1978, 1988), who recorded yield increases in defoliated, water-stressed maize crops.

Sorghum is sensitive to water stress; grain yield may decline by 41–45% in response to moisture deficits gradually intensifying throughout the season (Garrity *et al.* 1982). Craufurd and Peacock (1993) reported that drought between booting and flowering reduced sorghum yield by 87%, but the same stress on vegetative plants had no effect. In rain-fed systems in central Queensland, crops are frequently planted on a near-full profile of soil water but this water is mostly depleted before anthesis; in-crop rainfall is imperative to high yields. Sorghum crops yield only 1.5 t/ha on average, significantly less than the 6 t/ha yield of irrigated crops (Wade and Douglas 1990). Crop modification to delay PI, as found in these experiments, may present a way of avoiding drought at anthesis. It may be possible to plant crops on small falls of early-season rain and, through leaf modification, maintain them in a vegetative developmental state until the more reliable mid-season rain falls. Our experiments showed that the vegetative growth period of Boomer sown on these later rains might be as long as 70 days. For Boomer planted earlier, however, and defoliated at the second ligule until mid-season rain falls, the effective vegetative growth period (from rain until anthesis) may be only 50 days. We contend that this reduction of 20 days in vegetative growth will reduce water use during vegetative growth, and increase the amount of water available at anthesis and during grain filling, so increase actual grain yield. Potential grain yield may decrease because of defoliation, *per se*, but the ability of the plant to realise that potential is boosted because water is available at anthesis and during grain-filling. Similar benefits were reported for wheat in response to leaf area reduction by leaf cutting (Richards 1983). Further, because the duration and grain yield responses of genotypes of differing maturity responded similarly to defoliation, the use of a later maturing, higher yielding genotype may increase the flexibility of crop management.

Mainstem removal (below the apical meristem) at PI, or at anthesis, obviously transposed the yield-determining growth phases of tillers to a later time; in a rain-fed situation this would also mean a different growth environment associated with water, temperature, and radiation. Mainstem removal also reduced the effective vegetative period, particularly in Expt 1, so the water used for evaporation and transpiration during this period would have decreased, and more water would have been available for transpiration at anthesis and during grain-filling.

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