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The Effect of Changes of Assimilate Supply around Flowering on Grain Sink Size and Yield of Maize (*Zea mays* L.) Cultivars of Tropical and Temperate Adaptation

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Abstract

Two maize (*Zea mays* L.) cultivars of temperate and one of tropical adaptation were grown in a subtropical (27°S.) environment under favourable conditions of plant population density, water and nutrient supply. The radiation incident to the plant during the period from flag leaf to 10 days after flowering was varied from the control by either shading or temporarily restraining leaves of neighbouring plants. The effects of these changes in assimilate supply, and of the presence of the male inflorescence, on the immediate dry weight of various plant parts and grain sink size, and consequential on dry matter production and grain yield was investigated. The radiation treatments effected small but significant changes in crop growth rate. Shading reduced the dry weight of the ear, and husk of the female inflorescence and male inflorescence (tassel). There were increases due to enhanced radiation. While removal of tassels also enhanced the dry weight of the female inflorescence, there was no evidence that the male inflorescence was a preferred sink for assimilates during this stage of growth.

In the temperate cultivars, grain number m^{-2} was associated with ear dry weight at 10 days after anthesis ($r = 0.95^{**}$). However, only in the tropical cultivar did the larger grain sink result in an increase in grain yield. Shading reduced grain yield in all cultivars probably because of a reduction in the supply of labile assimilates for grain filling.

Introduction

The relationship between assimilate supply (source), distribution of dry matter to the grain and the storage capacity represented by number and upper size limits of grains, has been studied in a number of cereals including maize (Tollenaar 1977) to determine the limitation to grain yield. In general, grain yields of maize cultivars adapted to tropical environments are low and are limited by the grain sink capacity (Goldsworthy 1974) and differ from higher yielding cultivars of temperate adaptation which are source limited (Tollenaar 1977). In the tropical cultivars, assimilates in excess of those required for grain are stored in the stem and other plant parts, so that harvest index (ratio of grain weight to total shoot dry weight) is low and ranges from 0.3 to 0.4 (Goldsworthy *et al.* 1974). This contrasts with a value of 0.55 reported for temperately adapted germplasm (Daynard *et al.* 1969).

Tollenaar (1977), in a review of the control of yield development in maize, concluded that the amount of radiation intercepted and therefore the photosynthate produced by the plant during flowering is the dominant factor determining final kernel number. However, not only is the rate of crop dry matter production important for grain sink development, but so also is the amount of assimilate allocated to the developing female inflorescence. This latter will be influenced by competition between various sinks, including the stem (Johnson *et al.* 1986), the male inflorescence (Mostut and Marais 1982) and the female inflorescence which are active at this time.

A few studies (Early *et al.* 1967; Prine 1971) have examined the effect of a considerable reduction in assimilate supply around flowering on grain sink development in temperately adapted

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maize cultivars. However, it is not feasible to extrapolate from these findings, to predict the probable effect of a small increase in crop growth rate at this stage on the size of the grain sink and the consequential effect on grain yield. This information would be of particular interest for the improvement of tropically adapted maize genotypes whose grain yield appears to be limited by the grain sink capacity. Also studies in maize have shown that the demand for assimilates by the grain sink influences photosynthesis (Moss 1962) and may delay foliar senescence (Tollenaar and Daynard 1982). Thus understanding the effects of changing the grain sink capacity, brought about by small changes in assimilate supply during the period around flowering, on source supply during grain filling, might also be relevant to the improvement of genotypes whose grain yield is source limited.

This study was conducted to examine the direct effects of small changes (a decrease and an increase) in dry weight production during the period from flag leaf to 10 days following flowering on the size of the female inflorescence and subsequent effects on the size of the grain sink and its influence on the amount of assimilate produced during the post-treatment period (grain filling) and hence grain yield in maize cultivars of tropical and temperate adaptation. Since the effect of changes in dry weight depend on the allocation of dry matter to plant parts, including the male and female inflorescence, the effect of physically removing the male inflorescence (de-tasseling) at the beginning of the treatment period was also examined.

Materials and Methods

The three maize hybrids chosen for the study were: XL81 and XL94 which are early and late maturing single cross hybrids respectively, developed from germplasm of temperate adaptation and commonly grown in subtropical and temperate areas in Australia; and Pioneer 6181, a hybrid of germplasm more suited to maize production in tropical regions because it is tolerant to diseases specific to the lowland tropics. For most tropical maize the cultivars quantitative effects of daylength are evident at photoperiods longer than 14.5 h day^{-1}, the maximum daylength at latitudes of 30° or less from the equator (Francis 1972; Fischer and Palmer 1984). They were sown on the 20 October 1984 at Redland Bay (South-east Queensland), which is located at latitude 27° 31′ S. and longitude 153° 19′ E. at 95 m elevation. The soil is a deep, friable, well-aerated red loam with a clay content of 60%, 15% silt and 25% sand, and a pH of 5.5–6.2. Total rainfall received during the experimental period was 920 mm, and this was supplemented with irrigation to maintain adequate soil moisture for maximum plant growth. The mean weekly maximum and minimum temperatures ranged from 24.4 to 31.4°C and from 17° to 21.4°C respectively. Shortwave radiation for the same period ranged from 16 to 34 MJ m^{-2} day^{-1}, with the highest radiation flux densities occurring during the period from 45 to 70 days after emergence. There was a declining trend in radiation during the later period of grain filling.

The experimental site was fertilized with a basal dressing of 40 kg N, 40 kg P and 40 kg K ha^{-1} prior to sowing and with 90 kg N ha^{-1} applied as side dressings in equal amounts on days 14 and 42 after emergence. The crop was maintained free of weeds (by hand weeding), and insect pests were controlled when necessary.

The trial was a randomized complete block design with three replications. The treatments consisted of the three cultivars which were exposed to three different radiation environments during the period from flag leaf emergence to 10 days following anthesis. Within these plots alternate plants were detasseled to provide treatments of with (+) and without (−) tassel. These treatments were arranged in a split-split plot with cultivars as main plots, radiation as subplots and tassel presence as sub-subplots.

The radiation treatments consisted of ambient radiation flux (control), enhanced radiation to some parts of the canopy brought about by physically confining the leaves of plants from neighbouring rows, and reduced radiation by the placement of a Sarlon shade cloth (80% transmission of photosynthetically active radiation (PAR)) above and on the sides (except on the South) of the plant canopy. The enhanced and reduced radiation treatments were terminated 10 days after anthesis by respectively removing the restraining wires so that the leaves of neighbouring plants resumed their pre-treatment spatial arrangements, and by removing the shade. Within each subplot the tassels of alternate plants were carefully removed by hand between 8 and 5 days prior to anthesis. This treatment resulted in a small increase in the radiation flux above the leaf canopy in all treatments.

Each experimental subplot consisted of 6, 8 and 9 rows for control, enhanced and reduced radiation treatments respectively, each of 10 m length and 0.75 m between rows. Seeds were sown by hand at the rate of 4 per hill with a distance of 0.25 m between hills. At 14 days, plants were thinned, leaving one plant per hill to attain a plant population density of 52 000 plants ha^{-1}.

Harvests for the determination of dry matter yield of plant parts were made at flag leaf, 10 (A10) and 30 (A30) days after anthesis and at maturity (defined by the formation of a black layer at the base of the grain). All harvests were made from the two central rows in the control and reduced radiation treatments and from the three central alternate rows in the enhanced radiation treatment, leaving sufficient plants at the end and between harvest areas to avoid edge effects. The area harvested at flag leaf was 1.5 m^2, while that for the other harvests was 3.0 m^2 for the control and 4.5 m^2 for the enhanced radiation treatment. These harvests consisted of an equal number of tasseled and detasseled plants.

The harvested plants were separated into stem and leaf sheath, leaf lamina, male inflorescence (tassel), ear (central axis with its floral structures) and husks (modified leaves and peduncle) of the female inflorescence and grain (when appropriate), dried at 70°C in a forced-draught dehydrator for 72 h, and weighed. For the last two harvests, the mean size of grains was determined from the dry weight of 200 randomly selected kernels.

During the period of the radiation treatments the amount of PAR intercepted by the canopy of the control and shaded treatments was determined from measurements of the photon flux above and at the base of the canopy taken between 1100 and 1400 hours at intervals of 5 days and from the accumulated radiation flux for the site.

Results

10 Days after anthesis

Flag leaf and anthesis occurred on 53, 60 and 61 and 61, 69 and 70 days after emergence in XL81, XL94 and Pioneer 6181 respectively. Thus the duration of the radiation treatments which extended for another 10 days following anthesis was 18 days in all cultivars. The mean daily shortwave solar radiation was 29.3 MJ m^{-2} day^{-1} during the treatment period for XL81 and 28.9 MJ m^{-2} day^{-1} for XL94 and Pioneer 6181.

Table 1. The effect of varying radiation during the period from flag leaf to 10 days after anthesis on crop dry weight and its distribution to various plant parts at 10 days after anthesis in a tropically (Pioneer 6181) and temperately (XL81 and 94) adapted maize cultivars

Cultivar	Radiation treatment	Dry weight (g m^{-2}) of: Total	Stem and leaf sheath	Leaf lamina	Female inflorescence Ear[A]	Husk[A]	Male inflorescence
P.6181	C[B]	1084	560	296	48	142	44.4
	R	1002	543	273	39	115	32.2
	E	1190	542	332	99	172	45.0
XL81	C	988	521	189	110	149	19.2
	R	846	446	170	95	120	15.6
	E	1064	550	198	126	168	21.8
Xl94	C	1206	666	267	107	141	24.6
	R	973	545	251	63	95	19.4
	E	1337	661	281	137	233	25.2
l.s.d. (P = 0.05)							
Cultivar		N.S.	N.S.	62	—	N.S.	7.0
Radiation		106	N.S.	23	—	48	6.0
Cultivar × radiation		N.S.	N.S.	N.S.	19	N.S.	N.S.

[A]Ear represents the central axis and reproductive organs; husk represents modified leaves and peduncle.
[B]C, control; R, reduced radiation; E, enhanced radiation.

The dry matter yields at the commencement (flag leaf) of the radiation treatments were 403, 638 and 545 g m^{-2} for XL81, XL94 and Pioneer 6181 respectively. At 10 days after anthesis there was a significant effect of the radiation treatments on dry matter yield, the effects being similar for each cultivar (Table 1). There was a 21% decrease and a 14% increase over the control crop in the reduced and enhanced radiation treatments respectively, and the average crop growth rates during the treatment period were 30.8, 24.1 and 35.0 g m^{-2} day^{-1} for the control, reduced and enhanced radiation treatments respectively.

The radiation treatments had a significant effect on the dry weights of all plant parts except the stem, and there was no increase in tassel weight in the enhanced radiation treatment. Shading reduced the dry weight of the leaf lamina, ear, husk and tassel by 8, 22, 24 and 24% respectively, while there was a respective increase of 8, 41, 29 and 4% due to additional exposure. The response of the cultivars was somewhat similar, although there was a significant interaction of the radiation and cultivar treatments on ear dry weight due to a large increase in XL94. Although not significant, there was a larger increase in leaf lamina weight in Pioneer 6181 than in the other two cultivars.

There were also differences among the cultivars in leaf, ear and tassel dry weights in the control treatment (Table 1). The earlier flowering cultivar (XL81) had less leaf lamina weight than the other two cultivars, while Pioneer 6181 had the smallest and largest ear and tassel dry weight respectively.

There was no significant interaction between the cultivar and the tassel treatments. Tassel removal increased total dry weight at 10 days after anthesis, which was associated with an increase in ear and husk dry weight (Table 2). There was a tendency (7% level of significance) for an interaction between the effects of the tassel and radiation treatments on total dry weight with the largest increase in the ear and husk dry weights under the increased radiation treatment.

Table 2. The effect of the presence of tassels on the dry weight, at 10 days after anthesis, of various plants parts of maize cultivars exposed to different radiation environments during the period from flag leaf to 10 days after anthesis
(Data are the means for three maize cultivars)

Radiation environment	Presence of tassels	Dry weight (g m^{-2}) of: Total	Female inflorescence Ear	Husk
Control	+	1068	76	129
	–	1088	98	159
Reduced	+	904	56	94
	–	959	77	126
Enhanced	+	1031	86	134
	–	1273	155	237
	l.s.d. (P = 0.05)			
	Radiation	89	—	—
	Tassel	106	—	—
	Radiation × tassel	N.S.	20	82

Black Layer (Maturity)

There was a significant effect due to the interaction of the cultivar and radiation treatments on grain yield. This response is shown in Fig. 1 in which the radiation treatments are quantified by their effect on dry matter production during the treatment period. The lower radiation treatment significantly reduced the grain yield of Pioneer 6181, XL81 and XL94 by 9.2, 9.5 and 11.9% respectively. However, the enhanced radiation environment significantly affected the grain yield only of Pioneer 6181 by increasing it by 29%. Grain yields of XL81 and XL94 were similar and significantly higher than that of Pioneer 6181 at all radiation treatments.

Table 3. The effect of the presence of tassels on grain yield and its components for maize cultivars exposed to different radiation environments during the period from flag leaf to 10 days after anthesis

Radiation environment	Presence of tassels	Grain yield ($g\ m^{-2}$)	Grain No. m^{-2}	$10^3 \times$ Grain size (g)
Control	+	738	2622	278
	–	757	2701	280
Reduced	+	673	2454	275
	–	668	2580	258
Enhanced	+	773	2761	277
	–	806	2991	269
	l.s.d. (P = 0.05)			
	Radiation	N.S.	—	N.S.
	Tassel	N.S.	—	N.S.
	Radiation × tassel	N.S.	178	N.S.

There was a significant effect of the interaction of cultivar and radiation treatments on the components of grain yield, grain number m^{-2} and grain size (Figs 1*b* and 1*c* respectively). The lower grain yield in the reduced radiation treatment was associated with a significant redution in mean grain size in all cultivars, with only a small, non-significant reduction in grain number. Enhanced radiation increased grain number m^{-2} in Pioneer 6181 and XL81, but in the latter, this was associated with a significant reduction in grain size. The lower grain yield of Pioneer 6181 in all radiation environments was associated with fewer grains m^{-2} and to a lesser extent, smaller grains. Mean grain size of XL94 was significantly larger than than those of the other two cultivars.

The presence of the tassel had no significant effect on grain yield (Table 3). There was, however, an increase in grain number m^{-2} in response to detasseling in the enhanced radiation treatment, and this was due particularly to the response of Pioneer 6181 (data not shown (Table 3).

Although there was a significant effect of cultivar and radiation treatments on total dry matter at maturity (black layer formation), there was no significant effect of the radiation treatments on dry matter increase during either the early or later part of the grain filling period, and the effects on total dry matter at maturity were similar to those recorded at the end of the radiation treatment period. There were, however, differences among the cultivars, with a greater increase in dry weight during the final stage of grain filling in XL94 (Table 4).

Harvest index, measured as the ratio of grain to total dry matter yield, was influenced by the interaction of the radiation and cultivar treatments (Table 4). In Pioneer 6181, the enhanced radiation treatment increased the harvest index, while in XL81 shading resulted in a lower value. Harvest indices differed among the cultivars in the control treatments with values of 0.38, 0.52 and 0.45 for Pioneer 6181, XL81 and XL94 respectively. There were also differences in the proportion of the dry weight increase measured from 10 days after anthesis to maturity which was allocated to the grain. During the period between 10 and 30 days after anthesis, the increase in grain weight in Pioneer 6181 was similar to the change in total dry weight, except in the enhanced radiation treatment where there was a tendency for the grain dry weight increase to exceed current assimilate supply. In the other two cultivars, the increase in grain weight was much larger than the change in crop dry weight. During the later stage of grain filling, when there was only a small increase in crop dry weight in Pioneer 6181 and XL81, the increase in grain dry matter in the control and enhanced radiation treatments exceeded the change in crop dry weight in these two cultivars. In XL94, the grain weight increase during this period was less than the change in crop dry weight, the more so in the reduced radiation treatment.

Tassel removal had no signficant effect on either total dry matter production or harvest index (data not shown).

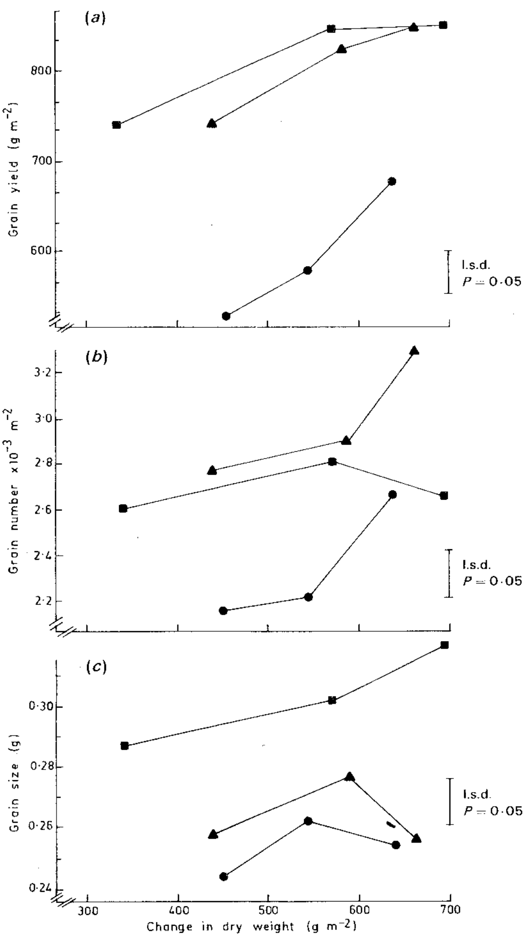

Fig. 1. Grain yield (*a*), grains m^{-2} (*b*), and grain size (*c*) of three maize cultivars (● Pioneer 6181, ▲ XL81, and ■ XL94) associated with changes in dry weight from flag leaf to 10 days after anthesis as a result of different radiation environments.

Discussion

The manipulation of the radiation environment of the plant effected small but significant changes in crop growth rate during the period from flag to 10 days after anthesis. This was associated with variation in the dry weight of the male and female inflorescences, indicating that these organs are important sinks for assimilates during this particular stage of growth. Removal of the male inflorescence resulted in an increase (25.3, 35.3 and 78.2% in the control, reduced and enhanced radiation treatment respectively) in the weight of the female inflorescence, suggesting competition between them for assimilates. There was, however, no evidence from the effect of the reduced radiation treatment on their dry weight that either one of these inflorescences was the dominant sink. The reduction in dry weight was somewhat similar (24.4 and 23.8% for the female and male inflorescence respectively) in both. Nevertheless, the proportion of the total dry weight as male or female inflorescence at 10 days after anthesis, did differ among the cultivars, with the tropical hybrid (Pioneer 6181) having a smaller and larger percentage as ear and tassel respectively.

The response in grains m^{-2} to tassel removal in Pioneer 6181 in the study here in supportive of the findings of Fischer *et al.* (1987), which show that selection for smaller tassels in tropical-

Table 4. The effect of different radiation environments during the period from flag leaf to 10 days following anthesis (A10), on final (B.L.; black layer formation) dry matter yield and harvest index and on dry matter production and its allocation to grain dry weight during the early (A10–A30; from 10 to 30 days after anthesis) and later (A30–B.L.) stages of grain filling in three maize cultivars

Cultivar	Radiation treatment	Total dry weight (g m^{-2})	Harvest index	Change in dry weight (g m^{-2} during:		Allocation of dry weight to grain during:	
				A_{10}–A_{30}	A_{30}–B.L.	A_{10}–A_{30}	A_{30}–B.L.
Pioneer 6181	C[A]	1528	0.38	466	52	1.07	1.57
	R	1458	0.37	457	50	1.06	1.10
	E	1632	0.42	518	52	1.21	1.13
XL81	C	1587	0.52	520	61	1.36	1.93
	R	1573	0.46	515	133	1.22	0.71
	E	1629	0.54	540	36	1.36	4.02
XL94	C	1889	0.45	542	202	1.34	0.61
	R	1712	0.44	571	176	1.23	0.30
	E	1931	0.44	537	168	1.36	0.71
l.s.d. (P = 0.05)							
Cultivar		240	N.S.	N.S.	123	0.26	0.62
Radiation		95	N.S.	N.S.	N.S.	N.S.	0.45
Cultivar × Radiation		N.S.	0.03	N.S.	N.S.	N.S.	N.S.

[A]C, control; R, reduced radiation; E, enhanced radiation.

ly adapted maize, which is characterized by a large male inflorescence, increases the grain number m^{-2} and grain yield.

in XL81 and Pioneer 6181, the number of grain m^{-2} was correlated with ear dry weight at 10 days after anthesis (grain number m^{-2} = 1823 + 11.1 g m^{-2} of ear dry weight; r = 0.95**). Thus the changes in ear dry weight as a result of current assimilate supply influenced this component of grain sink size. In Pioneer 6181, the increased grain sink capacity resulted in an increase in grain yield and harvest index. This tropical cultivar had fewer grains m^{-2} and a lower harvest index than the temperate materials, and it would appear that grain yield of this cultivar is limited by the grain storage capacity. Other workers (Yamaghuchi 1974; Goldsworthy *et al.* 1974) have concluded that the development of an adequate grain sink is the limiting process for grain yield in other tropically adapted cultivars, although this condition may be ameliorated through selection for a reduction in the size of the stem (Johnson *et al.* 1986) and leaf and tassel (Fischer *et al.* 1987).

In XL81, even though there was an increase in grain number m^{-2} owing to the enhanced assimilate supply, mean grain size was reduced and grain yield was similar to the control. In this cultivar, as in Pioneer 6181, the increase in potential grain sink capacity via increased numbers of grain did not influence the supply of assimilates during the grain filling period (source) which appears to be the limiting factor for grain yield in XL81. Thus there is no evidence from this study that small changes in the grain sink capacity which might influence the demand for grain filling assimilates (Tollenaar and Daynard 1984), influences their supply, and this differs from the effects of a catastrophic reduction in grain sink as reported by Moss (1962).

The cultivar XL94 responded differently to the others to the radiation treatments. The increase in ear dry weight at 10 days after anthesis was associated with large changes in the number of fully developed ears per plant (3.0 and 1.8 ears $plant^{-1}$ for enhanced radiation and control treatments respectively; data not shown) evident 10 days after anthesis, but at maturity there was an average of 1.20 and 1.15 ears per plant, respectively. It is likely that, whereas in the other two cultivars there was no effect of the enhanced radiation on the number of ears and grain number m^{-2} increased, in XL94 the higher initial number of ears may have resulted in inter-ear competition, such that the number of grains on the surviving ears was reduced. Thus, although prolificacy has been advocated as a useful trait for selection in maize (Motto and Moll 1983), there may be some conditions where it can decrease the grain sink capacity.

In all cultivars grain size decreased under the lower radiation treatment. In this treatment the increase in grain weight during the period from 10 days after anthesis to black layer exceeded the change in dry weight during the same period in Pioneer 6181 and XL81. Thus in these two cultivars there was some contribution to grain yield of materials produced prior to 10 days after anthesis. Other studies (Palmer *et al* 1973; Edmeades *et al.* 1979) have shown that during the lag phase of grain growth (the period immediately following fertilization and prior to rapid and linear grain filling) there is temporary storage of assimilates in the female inflorescence (husk) which are later retranslocated for the filling of the grain. It is likely that the shading treatment which reduced husk dry weight at 10 days after anthesis. Other studies (Palmer *et al.* 1973; Edmeades *et al.* 1979) have shown that during the lag phase of growth (the period immediately following fertilization and prior to rapid and linear grain filling) there is temporary storage of assimilates in the female inflorescence (husk) which are later retranslocated for the filling of the grain. It is likely that the shading treatment which reduced husk dry weight at 10 days after anthesis limited the amount of such labile assimilates and hence the size of the grain. However, there is some evidence that the reduced radiation during the early stage of grain development may have reduced their potential for grain storage and hence the smaller grain size. In the final stage of grain filling there was a significant reduction in the proportion of the dry matter increase allocated to grain in this treatment.

The tropical cultivar differed in the amount of assimilates produced during the grain filling period, it being lower in Pioneer 6181 than for the other two cultivars. While there is no evidence (as presented earlier) that grain yield in the tropical material was limited by the supply of grain filling assimilates, nevertheless high potential grain yield depends on large amounts of dry matter production during the grain filling period. It would appear that, although an immediate yield improvement would result from an increase in the grain sink capacity in the tropical material, further enhancement would require an increase in the amount of dry matter produced during grain filling. The duration from flowering to black layer was similar in XL94 and Pioneer 6181. However, changes in leaf area index due to leaf senescence and hence radiation intercepted during the grain filling period were not recorded, and it is therefore not known if the cultivars differed in the efficiency of converting incident radiation into dry matter. During the period between flag leaf emergence to 10 days after anthesis when the amount of PAR intercepted by the crop was measured (and was greater than 95% of the PAR flux and similar in all cultivars), efficiency of dry matter production was 1.98, 2.24 and 2.14 g MJ^{-1} (PAR) for Pioneer 6181, XL81 and XL94 respectively. Thus there may be also an opportunity to increase the rate of dry matter production in the tropical material.

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