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Does Maintaining Green Leaf Area in Sorghum Improve Yield under Drought? II. Dry Matter Production and Yield

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ABSTRACT

Retention of green leaf area at maturity (GLAM), known as stay-green, is used as an indicator of postanthesis drought resistance in sorghum [*Sorghum bicolor* (L.) Moench] breeding programs in the USA and Australia. The critical issue is whether maintaining green leaves under postanthesis drought increases grain yield in stay-green compared with senescent hybrids. Field studies were undertaken in northeastern Australia on a cracking and self-mulching gray clay. Nine closely related hybrids varying in rate of leaf senescence were grown under two water-limiting regimes, post-flowering water deficit and terminal (pre- and postflowering) water deficit, and a fully irrigated control. Under terminal water deficit, grain yield was correlated positively with GLAM ($r = 0.75^{**}$) and negatively with rate of leaf senescence ($r = -0.74^{**}$). Grain yield also increased by ≈ 0.35 Mg ha⁻¹ for every day that onset of leaf senescence was delayed beyond 76 DAE in the water-limited treatments. Stay-green hybrids produced 47% more postanthesis biomass than their senescent counterparts (920 vs. 624 g m⁻²) under the terminal water deficit regime. No differences in grain yield were found among eight of the nine hybrids under fully irrigated conditions, suggesting that the stay-green trait did not constrain yield in the well-watered control. The results indicate that sorghum hybrids possessing the stay-green trait have a significant yield advantage under postanthesis drought compared with hybrids not possessing this trait.

WATER DEFICIT is the major constraint to rainfed sorghum production worldwide. Drought can occur before and after flowering, and resistance to water deficit at both of these stages has been reported in sorghum (Rosenow et al., 1996). Resistance to postanthesis drought is important in Australia's northern grain belt, since crops generally grow into water deficit (Chapman et al., 2000). Symptoms of susceptibility to postanthesis drought include premature leaf and stem senescence, charcoal rot [*Macrophomina phaseolina* (Tassi) Goidanich], fusarium stalk rot (*Fusarium moniliforme* J. Sheld.), lodging, and reduced seed size. Expression of postanthesis drought symptoms is heightened when crop growth is favorable prior to flowering and is followed by severe water deficit, particularly in the latter half of grain filling. Chapman et al. (2000) reported a

high frequency of this water limitation in Australian sorghum-growing environments.

A mechanism of resistance, known as stay-green (Rosenow, 1977), is indicated by maintenance of green stems and upper leaves when water is limiting during grain filling. Green leaf area at maturity is used as an indicator of postanthesis drought resistance in sorghum breeding programs in the USA (Rosenow et al., 1983) and Australia (Henzell et al., 1992). Green leaf area at maturity and its components have been found to vary with both water regime and genotype (Borrell et al., 2000). The critical issue is whether retention of green leaf area under postanthesis drought actually increases grain yield in stay-green compared with senescent hybrids. Positive associations between green leaf area duration and grain yield have been observed in a range of cereals, including wheat, *Triticum aestivum* L. (Evans et al., 1975); maize, *Zea mays* L. (Tollenaar and Daynard, 1978; Wolfe et al., 1988); oat, *Avena sativa* L. (Helsel and Frey, 1978); and sorghum (Henzell et al., 1992).

There is limited understanding of the physiological processes underlying the stay-green trait, including the basis of genetic variation. According to Bonhert et al. (1995), mechanisms by which plants adapt to abiotic stresses need to be quantified at a physiological, molecular, and genetic level, and future research must be directed at functional characterization and biochemical integration of molecular and genetic data. Sorghum genotypes with the stay-green trait continue to fill their grain normally under drought (Rosenow and Clark, 1981) and exhibit increased resistance to charcoal rot (Rosenow, 1984) and lodging (Henzell et al., 1984; Woodfin et al., 1988). Stay-green genotypes also contain more cytokinins (McBee, 1984) and basal stem sugars (Duncan, 1984) than do senescent genotypes. Increased accumulation of soluble sugars in stay-green types is associated with greater functional leaf area during grain filling, thereby reducing their dependence on stored assimilates from the stem to fill grain (Duncan et al., 1981; McBee et al., 1983). Higher concentration of stem sugars improves the digestible energy content of the straw,

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Abbreviations: AGDM, aboveground dry mass; CGR, crop growth rate; DAE, days after emergence; GLAM, green leaf area at maturity; ND, no water deficit treatment; PFD, postflowering water deficit treatment; TD, terminal water deficit. *, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

making stay-green a valuable trait for both grain and fodder production in dual purpose sorghums (Van Oostrom et al., 1996). If photosynthesis is maintained for longer than normal in stay-green types, they may yield more in crops for which carbohydrate is a main harvest component (Thomas and Smart, 1993).

Initially, stay-green was selected under water-limited conditions to reduce lodging, since live plants have stronger stems. However, previous research has found that such selection may reduce yield potential, as sorghum plants with a high grain sink/source ratio are more likely to senesce when water is limiting (Henzell and Gillieron, 1973; Rosenow et al., 1983). The need existed, therefore, to clarify the association between rate of leaf senescence and grain yield in water-limited environments. To address this issue, Henzell et al. (1992) carried out preliminary studies using visual ratings of leaf senescence. More detailed experiments on these associations are reported here.

Our study had three main objectives. First, we examined grain yield and its components in nine closely related hybrids varying in stay-green grown under three water regimes. Second, we determined the association between rate of leaf senescence and yield in these hybrids under water-limiting conditions. Third, we examined the partitioning of biomass among stem, leaf, and panicle components in these hybrids under postanthesis water deficit, including the reliance of yield on stem reserves. Water and genotype effects on leaf area production and senescence were examined in the first paper of this series (Borrell et al., 2000).

MATERIALS AND METHODS

General

Details on the experiment site, treatments, agronomy and leaf observations are given in the first paper in this series (Borrell et al., 2000). Soil type is a cracking and self-mulching gray clay with abundant CaCO_3 concretions and a high montmorillonite clay content (McKeown, 1978). Briefly, the experiment design was a split plot with three replicates in which three irrigation treatments were applied to main plots (6 by 31.5 m) and nine hybrids varying in rate of leaf senescence were allocated to subplots (3.5 by 6 m) (Exp. 1). All plots were hand-sown under plastic covers on 15 Dec. 1994 and emerged 18 Dec. 1994. The water regime treatments were no deficit (ND), postflowering deficit (PFD), and terminal (pre- and postflowering) deficit (TD). No irrigation was applied to TD plots; plants in this treatment should have relied solely on stored soil water except that an additional 80 mm of water entered the profile through the plastic in a series of rainfall events near anthesis. The magnitude of water entry under the plastic was determined by the neutron scattering technique using a neutron probe (Model 503R, CPN Corp., Martinez, CA) and there were no significant differences ($P > 0.05$) among plots in water entry. The nine hybrids examined were from crosses of three females varying in the B35 source of stay-green (AQL39, senescent; AQL41, intermediate; A35, stay-green) and three males similarly varying in the KS19 source of stay-green (R69264, senescent; RQL36, intermediate; RQL12, stay-green).

The nine hybrids were also examined under rainfed conditions at Hermitage Research Station (Exp. 2) on the same

soil type as Exp. 1. The experiment design was a randomized block design with four replicates and nine hybrids. Plot size was 6 by 1.42 m. The experiment site was fertilized prior to sowing with 100 kg N ha^{-1} as urea. No irrigation was applied. All plots were sown on 24 Nov. 1994 in rows 0.71 m apart and subsequently thinned to a population of 100 000 plants ha^{-1} . Totals of 123 and 148 mm of rain were recorded during the pre- and postanthesis periods, with the largest fall (68 mm) occurring 22 d after anthesis. A 6- m^2 area (4.25 by 1.42 m) was machine harvested at maturity. Grain was dried in a forced draft oven at 80°C for 48 h before weighing.

Harvests

In Exp. 1, a single row of length 1 m was cut from one of the three center rows of each plot at 30, 46, 59 (anthesis + 3d), 87, and 114 d after emergence (DAE). At least 0.5-m intervals of crop were left between sampling areas within a row and no adjacent areas were sampled. Harvests at 30, 59, and 114 DAE corresponded with the phenological stages of panicle differentiation, anthesis, and physiological maturity. To determine the timing of panicle differentiation, two plants per plot were sampled twice weekly from 21 DAE onwards. Preliminary stem dissection studies found that panicle differentiation, defined as the rapid elongation of the rachis and the accompanying development of the upper primary and secondary branches (Moncur, 1981), corresponded with a panicle length of ≈ 2 mm. Hence panicle differentiation was defined as the time when the panicle had attained a length of 2 mm. Anthesis was defined as the time when 50% of the anthers had extruded from 50% of 10 tagged panicles in each plot. Physiological maturity was defined as the time at which basal grains in 50% of the tagged panicles attained black layer. Each sample was dried in a forced draft oven at 80°C for 48 h before weighing. All samples at 59 and 114 DAE, and also TD samples at 87 DAE, were divided into mainstem and tiller components, then further partitioned into green leaf, senesced leaf, stem (including leaf sheaths), and panicle. Plant number, culm number, panicle number, aboveground dry mass (AGDM), grain yield, 1000-grain weight, and stem length were determined at maturity (11 Apr. 1995) for all plots. Stem length was defined as the distance from the base of the stem to the top of the peduncle (characterized by the first branch of the panicle).

The following parameters were calculated on a plot basis. Harvest index was derived by dividing grain yield by aboveground dry mass. Grain number per panicle was calculated by dividing grain yield by the product of panicle number and mass per grain. Seasonal average crop growth rate was determined by dividing AGDM by the number of days from emergence to physiological maturity (black layer). Average grain growth rate was calculated by dividing grain yield by the number of days from anthesis to physiological maturity. Stem reserves are defined as the difference in stem dry mass between anthesis and maturity harvests.

Statistical Analyses

Data were analyzed by standard analysis of variance, and pairwise comparisons of means were performed using the protected LSD procedure at $P = 0.05$ (Carmer and Swanson, 1973). Within each water treatment, correlations ($n = 9$) were calculated between grain yield and the following parameters: AGDM, harvest index, grain size, grain number per square meter, average crop growth rate, average grain growth rate, duration of grain growth, relative rate of leaf senescence (Borrell et al., 2000), GLAM, stem length, and stem reserves mobi-

lized for grain filling. Correlations were also calculated between green leaf dry mass at maturity and panicle dry mass at maturity.

RESULTS AND DISCUSSION

Dry Matter Production

Genotype and water regime did not interact significantly for biomass production at either panicle initiation or anthesis. At panicle initiation (30 DAE), AGDM was not affected by water regime (Fig. 1). However, AGDM differed ($P < 0.01$) among genotypes, increasing from 150 g m^{-2} (AQL39/RQL36) to 224 g m^{-2} (AQL39/R69264). By the anthesis harvest (59 DAE), AGDM was similar in all genotypes, although variation ($P < 0.01$) was observed among water regimes, with AGDM being greater ($P < 0.01$) in ND and PFD ($\approx 938 \text{ g m}^{-2}$) compared with TD (828 g m^{-2}).

A genotype \times water regime interaction ($P < 0.055$) was observed for biomass at maturity (Fig. 1). In the five senescent hybrids (AQL39/R69264, AQL41/R69264, A35/R69264, AQL39/RQL36, AQL41/RQL36; open symbols), biomass production was almost 30% less under TD compared with ND. Yet in the four stay-green hybrids (A35/RQL36, AQL39/RQL12, AQL41/RQL12, A35/RQL12; closed symbols), AGDM was only 13% less under TD compared with ND. For example, when AQL39, AQL41, and A35 were crossed with RQL36, AGDM in the senescent hybrid (AQL39/RQL36) decreased from 2029 g m^{-2} (ND) to 1299 g m^{-2} (TD), yet the decline was much less in the stay-green hybrid (A35/RQL36), decreasing from 2204 g m^{-2} (ND) to 1827 g m^{-2} (TD).

Post-anthesis biomass production was 44% higher ($P < 0.001$) for hybrids grown under ND compared with TD ($1089 \text{ vs. } 756 \text{ g m}^{-2}$). Genotypic variation was also significant ($P = 0.05$), although the interaction between genotype and water regime was not. Under terminal water deficit, postanthesis biomass production in the stay-green hybrid A35/RQL12 was twice that of the senescent hybrid AQL39/R69264 ($1029 \text{ vs. } 537 \text{ g m}^{-2}$). Overall, stay-green hybrids produced 47% more biomass between anthesis and maturity compared with their senescent counterparts ($920 \text{ vs. } 624 \text{ g m}^{-2}$) under water-limited conditions (TD).

Rate of Crop Growth

There was no significant genotype \times water regime interaction for crop growth rate (CGR). Averaged across hybrids, CGR between emergence and maturity harvest (114 DAE) increased ($P < 0.01$) with water regime: 14.4 (TD), 16.6 (PFD), and 17.9 (ND) $\text{g m}^{-2} \text{ d}^{-1}$. Averaged across water regimes, genotypic variation in CGR for the same period was also significant ($P < 0.01$), ranging from $14.6 \text{ g m}^{-2} \text{ d}^{-1}$ (AQL39/RQL36) to $18.1 \text{ g m}^{-2} \text{ d}^{-1}$ (A35/RQL36). Since differences in phenology among genotypes were relatively small (Borrell et al., 2000), variation in biomass production was largely due to variation in CGR.

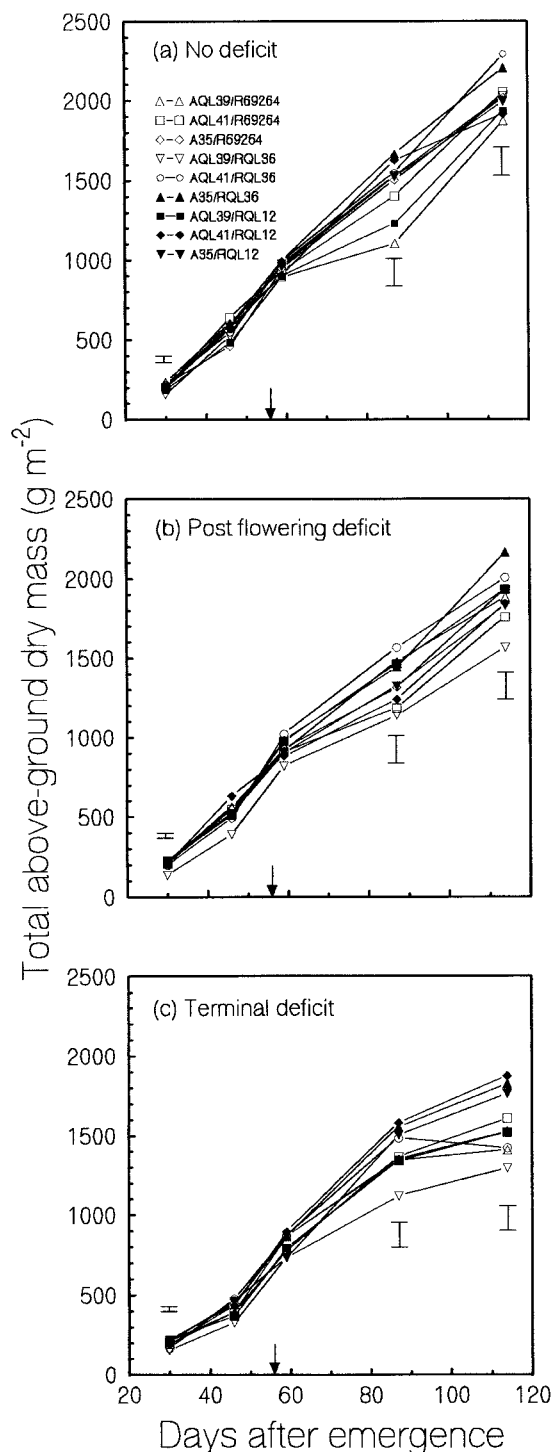


Fig. 1. Temporal pattern of aboveground dry matter production for nine sorghum hybrids grown under three water regimes: (a) no water deficit, (b) postflowering water deficit, and (c) terminal water deficit. Anthesis at Day 56 is marked with an arrow. Vertical bars denote LSD ($P = 0.05$).

Partitioning of Biomass among Organs under Water-Limited Conditions

The impact of rate of leaf senescence on biomass partitioning among the leaf, stem, and panicle was examined in the TD treatment, since severity of drought was greater in this treatment than in PFD. To demonstrate

the effects of the B35 and KS19 sources of stay-green on biomass partitioning, two examples will be discussed. First, three females varying in rate of leaf senescence (AQL39, senescent; AQL41, intermediate; A35, stay-green) will be examined in crosses with a common male (RQL36, intermediate) to highlight the impact of the B35 source of stay-green on biomass partitioning. The effects of this source of stay-green on biomass partitioning will also be examined in crosses with R69264 (senescent) and RQL12 (stay-green) males. Second, three males similarly varying (R69264, senescent; RQL36, intermediate; RQL12, stay-green) will be examined in crosses with a common female (AQL41, intermediate) to highlight the impact of the KS19 source of stay-green on biomass partitioning. The effects of this source of stay-green on biomass partitioning will also be examined in crosses with AQL39 (senescent) and A35 (stay-green) females.

Example 1 (B35 Source of Stay-Green)

During the first half of the grain-filling period, green leaf dry mass remained relatively constant in AQL39/RQL36 (senescent) and AQL41/RQL36 (intermediate), yet increased in A35/RQL36 (stay-green) such that by mid grain filling, green leaf dry mass in the stay-green hybrid (295 g m⁻²) was greater ($P < 0.05$) than in the

senescent (195 g m⁻²) and intermediate (232 g m⁻²) hybrids (Fig. 2a). While green leaf dry mass declined in all hybrids during late grain filling, the differences observed at mid grain filling were maintained through to maturity, resulting in more ($P < 0.05$) green leaf dry mass at maturity in the stay-green hybrid (131 g m⁻²) than in the intermediate (58 g m⁻²) and senescent (72 g m⁻²) hybrids. However, there was no difference in dead leaf dry mass among these genotypes (Fig. 2b).

Interestingly, stem dry mass remained relatively constant (≈ 400 g m⁻²) throughout the grain-filling period in the stay-green hybrid, but declined in the intermediate hybrid from ≈ 400 to 300 g m⁻² during the second half of the grain-filling period, such that stem dry mass was significantly lower ($P < 0.01$) at maturity in the intermediate hybrid (Fig. 2c). Stem dry mass in the senescent hybrid was low (≈ 270 g m⁻²) throughout the grain-filling period.

During the first half of the grain-filling period, the accumulation of biomass in the panicle was similar in the stay-green and intermediate hybrids and less in the senescent hybrid, although these differences were not significant (Fig. 2d). However, during the second half of the grain-filling period, panicle dry mass increased by 204, 114, and 376 g m⁻² in the senescent, intermediate, and stay-green hybrids, respectively, resulting in almost

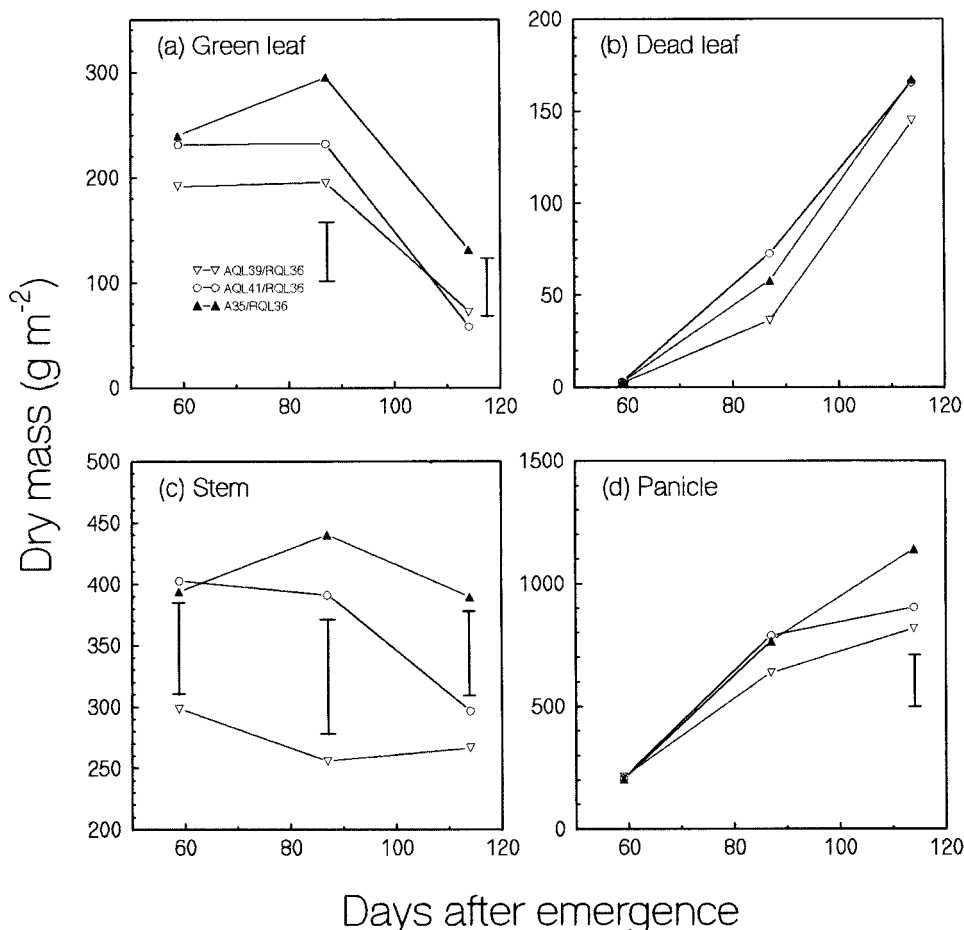


Fig. 2. The effects of the A35 source of stay-green on biomass partitioning among various plant components in crosses with RQL36: (a) green leaf, (b) dead leaf, (c) stem, and (d) panicle. Vertical bars denote LSD ($P = 0.05$).

30% more ($P < 0.05$) panicle dry mass in the stay-green than in the senescent hybrid.

There were no differences at maturity in green leaf dry mass and panicle yield among the same three females (AQL39, AQL41, and A35) when crossed with R69264 (senescent male, data not shown). However, when crossed with RQL12 (stay-green), green leaf dry mass and panicle dry mass at maturity were highly correlated ($r = 0.86^{***}$, $n = 9$) in these females. Genotypic differences in biomass partitioning were similar to those reported for crosses with RQL36, with green leaf dry mass at maturity and final panicle yield greater ($P < 0.05$) in the stay-green and intermediate hybrids compared with the senescent hybrid. Stem dry mass declined in the first half of the grain-filling period in the senescent hybrid, but remained consistently high in the stay-green and intermediate hybrids throughout the grain-filling period.

Example 2 (KS19 Source of Stay-Green)

During the first half of the grain-filling period, green leaf dry mass remained relatively constant in AQL41/R69264 (senescent) and AQL41/RQL36 (intermediate), but increased in AQL41/RQL12 (stay-green) so that by mid grain filling, green leaf dry mass in the stay-green hybrid (263 g m^{-2}) was greater ($P < 0.05$) than in the senescent hybrid (198 g m^{-2}) (Fig. 3a). During late grain

filling, green leaf dry mass declined faster in the senescent and intermediate hybrids compared with the stay-green hybrid, resulting in greater ($P < 0.05$) green leaf dry mass at maturity in the stay-green hybrid (167 g m^{-2}) than in the senescent and intermediate hybrids ($\approx 56 \text{ g m}^{-2}$). Conversely, dead leaf dry mass at maturity was greater ($P < 0.01$) in the senescent and intermediate hybrids ($\approx 170 \text{ g m}^{-2}$) than in the stay-green hybrid (89 g m^{-2}) (Fig. 3b).

Throughout the grain filling period, stem dry mass remained relatively constant and high in the stay-green hybrid ($\approx 400 \text{ g m}^{-2}$) and relatively constant and low in the senescent hybrid ($\approx 320 \text{ g m}^{-2}$) (Fig. 3c). The intermediate hybrid (AQL41/RQL36) is the same as that used in the first example and, as explained above, its stem dry mass declined during the second half of the grain-filling period. Green leaf dry mass at maturity was correlated ($r = 0.77^{**}$, $n = 9$) with final panicle dry mass, resulting in greater grain yield in the stay-green (1027 g m^{-2}) than intermediate (756 g m^{-2}) hybrid (Fig. 3d).

There were no differences at maturity in green leaf dry mass and panicle yield among the same three males (R69264, RQL36, and RQL12) when crossed with AQL39 (senescent female, data not shown). However, when crossed with A35 (stay-green), green leaf dry mass and panicle dry mass at maturity were highly correlated

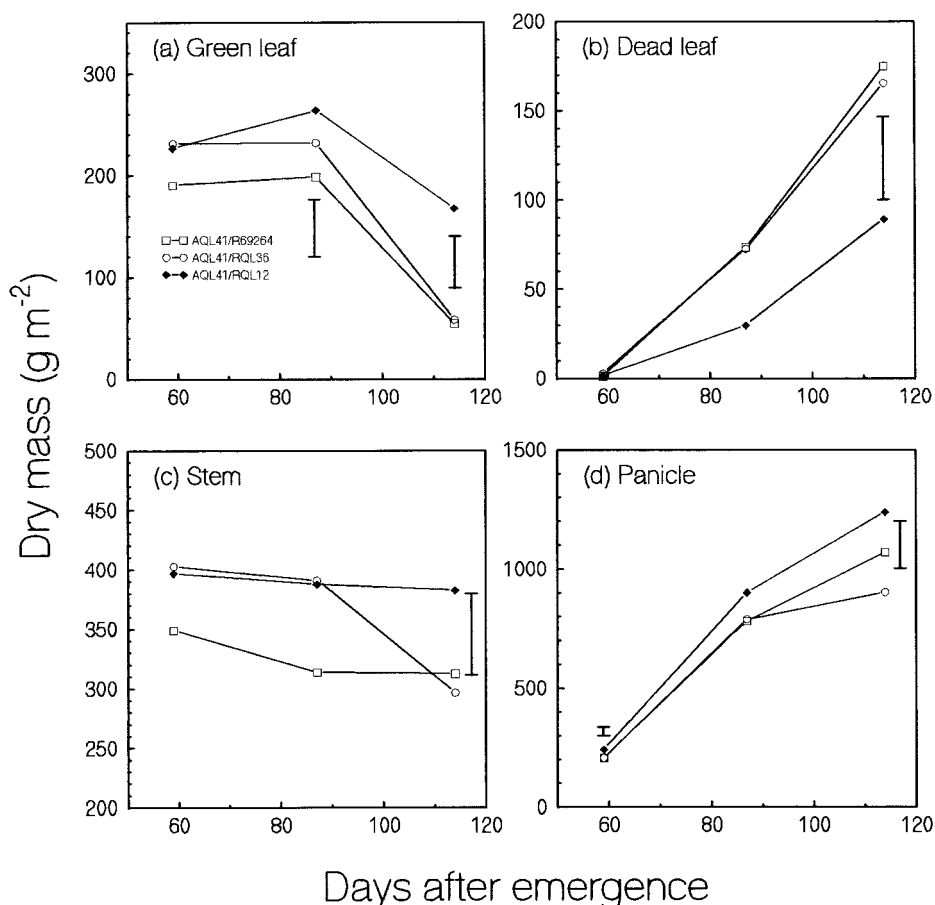


Fig. 3. The effects of the RQL12 source of stay-green on biomass partitioning among various plant components in crosses with AQL41: (a) green leaf, (b) dead leaf, (c) stem, and (d) panicle. Vertical bars denote LSD ($P = 0.05$).

($r = 0.96^{***}$, $n = 9$) in these males. Genotypic differences in biomass partitioning were similar to those reported for crosses with AQL41, with green leaf dry mass at maturity and final panicle yield greater ($P < 0.05$) in the stay-green and intermediate hybrids compared with the senescent hybrid. Stem dry mass declined throughout the grain-filling period in the senescent hybrid, remained consistently high in the intermediate hybrid, and increased throughout the grain filling period in the stay-green hybrid, such that final stem dry masses in the stay-green and intermediate hybrids were greater ($P < 0.05$) than in the senescent hybrid (data not shown).

In both examples, most (>80%) of the increase in panicle growth during the second half of the grain-filling period in the intermediate hybrid could be accounted for by reserves mobilized from the stem, assuming 100% conversion efficiency. However, since stem mass remained relatively constant during the grain-filling period in the stay-green and senescent hybrids, it is likely that panicle growth was largely dependent on photo assimilation rather than stem reserves in these hybrids. When crossed with RQL36, greater grain yield in the stay-green (A35/RQL36) than senescent (AQL39/RQL36) hybrid (933 vs. 669 g m⁻²) was probably associated with maintenance of photosynthetic capability in the stay-green hybrid, evidenced by more GLAM in the stay-green (17 459 cm² m⁻²) than senescent (9575 cm² m⁻²) hybrid. Similarly, when crossed with AQL41, the greater grain yield in the stay-green hybrid (AQL41/RQL12) was associated with the retention of more green leaves during the latter half of grain filling. Overall, rates of crop growth during the latter half of the grain-filling period in the stay-green hybrids (9.4 g m⁻² d⁻¹) were twice that of the senescent hybrids (4.6 g m⁻² d⁻¹) under TD, providing evidence of continued photosynthetic activity in stay-green types.

More direct evidence of extended photosynthetic capability in stay-green compared with senescent sorghums is provided by De Villiers et al. (1993). Western analysis of proteins extracted from leaves found a high degree of stability of chloroplast-associated proteins in two stay-green genotypes (Q101 and ICSV 745) compared with a senescent genotype (R16). Q101, like RQL12, is a QDPI line derived from KS19, which in turn was derived from the cross between Combine Kafir 60 and Short Kaura, the latter being from Nigeria. Delayed degradation of these proteins is correlated with the delayed onset of senescence in the stay-green genotypes. Indeed in Q101, the chloroplast proteins LHCP2, OEC33, and Rubisco were retained until late in senescence, indicating that photosynthesis may be maintained for longer during senescence in this genotype.

Many earlier studies have reported an association between stay-green and lodging resistance (Henzell et al., 1984; Rosenow, 1984; Woodfin et al., 1988). The positive correlation ($r = 0.71^*$, $n = 9$) reported in our study between rate of leaf senescence and magnitude of stem reserves mobilized under TD (Table 1) suggests that stay-green hybrids are less reliant on nonstructural stem carbohydrate to fill their grain than are senescent

hybrids, thereby enhancing stem strength and possibly reducing lodging.

It has also been observed that stay-green genotypes produce significantly higher levels of sucrose, glucose, fructose, and starch within the plant, particularly in the stem, compared with senescent genotypes (McBee and Miller, 1982; McBee et al., 1983; McBee, 1984). This factor has been associated with increased yields in the stay-green genotypes, but the reason for this has not been clear (McBee et al., 1983). The current study does provide an explanation. Retention of the uppermost green leaves in stay-green hybrids during the latter half of the grain-filling period enables these types to continue assimilating C and complete grain filling, as evidenced by the positive correlation ($r = 0.75^{**}$, $n = 9$) between GLAM and grain yield (Table 1). Various workers (Stickler and Pauli, 1961; Goldsworthy, 1970; Fischer and Wilson, 1971) have shown the upper leaves contribute significantly to grain yield. In fact, Fischer and Wilson (1971) reported that assimilation by the panicle and upper four leaves accounted for 93% of grain yield. In our study, it is likely that stem masses remained high in stay-green hybrids because sink demand was largely met by current photo-assimilation, thereby minimizing the demand for nonstructural carbohydrate from the stem.

Is the under-utilization of stem and leaf reserves by stay-green hybrids a cost associated with this trait? As senescence is a mobilization function and a high harvest index is desirable in seed crops, domestication and varietal improvement have selected for efficient recovery of nutrients from expendable, short-lifespan foliage (Thomas, 1992). Increased yield in stay-green hybrids is dependent on the supply of photo assimilate from green leaves exceeding the supply of preanthesis stem and leaf reserves in senescent and intermediate hybrids. In the current studies, grain yield in stay-green hybrids was greater than that in senescent hybrids by up to 25% in Exp. 1 and 50% in Exp. 2, suggesting that there was no cost associated with nonsenescence.

Partitioning of Growth to Yield

Grain Yield

Genotype and water regime interacted significantly ($P < 0.055$) for yield (Table 2). Grain yield declined with increasing water deficit in the five senescent hybrids (AQL39/R69264, AQL41/R69264, A35/R69264, AQL39/RQL36, AQL41/RQL36) but was maintained under increasing water deficit in the four stay-green hybrids (A35/RQL36, AQL39/RQL12, AQL41/RQL12, A35/RQL12). For example, in AQL39/RQL36 (senescent), yield declined from 991 g m⁻² under ND to 669 g m⁻² under TD. In contrast, AQL41/RQL12 (stay-green) maintained yield at ≈ 1000 g m⁻² across all water regimes. Hence, grain yield under the fully irrigated control was not correlated with yield under terminal water deficit.

No variation in grain yield was observed among eight of nine hybrids under ND (the exception being AQL41/RQL36, which was greater than AQL39/R69264, AQL39/RQL36, AQL39/RQL12, AQL41/RQL12, and

Table 1. Correlation matrices for a range of yield determinants grown under three levels of water supply in Exp. 1 ($n = 9$).‡

	Yield	AGDM	HI	Grain size	Grain number m^{-2}	Grain growth rate	Duration of grain growth	Rel. rate of senescence	GLAM	Stem reserves
No water deficit										
Yield	1.00									
AGDM‡	0.90***	1.00								
HI	0.49	0.06	1.00							
Grain size	0.06	-0.23	0.61	1.00						
Grain number/ m^2	0.77**	0.87***	0.01	-0.59†	1.00					
Grain growth rate	0.95***	0.95***	0.26	-0.08	0.81**	1.00				
Duration of grain growth	0.29	-0.04	0.73*	0.42	-0.01	-0.04	1.00			
Rel. rate of senescence	-0.14	-0.11	-0.06	0.22	-0.23	-0.23	0.23	1.00		
GLAM	0.57†	0.78**	-0.28	-0.72*	0.92***	0.66*	-0.20	-0.31	1.00	
Stem reserves	-0.31	-0.58†	0.47	0.64*	-0.64*	-0.51	0.53†	0.62*	-0.79**	1.00
Postflowering water deficit										
Yield	1.00									
AGDM	0.74**	1.00								
HI	0.64*	0.11	1.00							
Grain size	0.42	0.21	0.82**	1.00						
Grain number/ m^2	0.79**	0.69*	0.12	-0.21	1.00					
Grain growth rate	0.92***	0.85***	0.38	0.26	0.83**	1.00				
Duration of grain growth	0.41	-0.11	0.74**	0.46	0.11	0.02	1.00			
Rel. rate of senescence	0.48	0.09	0.17	-0.30	0.70*	0.38	0.36	1.00		
GLAM	-0.30	0.25	-0.50	-0.22	-0.15	-0.13	-0.47	-0.63*	1.00	
Stem reserves	0.10	-0.28	0.62*	0.46	-0.23	-0.17	0.63*	-0.22	-0.15	1.00
Terminal water deficit										
Yield	1.00									
AGDM	0.97***	1.00								
HI	0.39	0.15	1.00							
Grain size	0.46	0.39	0.46	1.00						
Grain number/ m^2	0.79**	0.80**	0.15	-0.18	1.00					
Grain growth rate	0.90***	0.94***	0.08	0.20	0.85***	1.00				
Duration of grain growth	0.70*	0.56	0.73*	0.70*	0.31	0.32	1.00			
Rel. rate of senescence	-0.74**	-0.77**	-0.06	-0.33	-0.57†	-0.85***	-0.20	1.00		
GLAM	0.75**	0.82**	-0.09	0.34	0.57†	0.90***	0.15	-0.96***	1.00	
Stem reserves	-0.58†	-0.68*	0.26	0.18	-0.76**	-0.74**	-0.02	0.71*	-0.71*	1.00

†, *, **, *** Significant at the 0.1, 0.05, 0.01, and 0.001 levels of probability, respectively.

‡ AGDM, aboveground dry matter; GLAM, green leaf area at maturity; HI, harvest index.

A35/RQL12), suggesting that in well-watered conditions there was no yield cost associated with the stay-green trait.

Grain yield under ND was highly correlated with AGDM ($r = 0.90***$, $n = 9$), but not with harvest index, indicating that production of biomass per se was more important in yield attainment than partitioning of biomass to yield (Table 1). It is not surprising then, that grain yield under ND was also highly correlated with rate of crop growth ($r = 0.82**$, $n = 9$) and stem length ($r = 0.81**$, $n = 9$) (data not shown). Of the components of yield, grain number per square meter was correlated with grain yield ($r = 0.77**$, $n = 9$), but grain size was not (Table 1). Furthermore, grain yield was not correlated with any of the components of GLAM (total plant leaf area, onset and rate of leaf senescence; data not shown). Total plant leaf area was, however, negatively correlated ($r = -0.65*$, $n = 9$) with onset of leaf senescence, indicating that leaves began to die earlier in those hybrids with a greater initial benchmark of green leaf area around anthesis.

Grain yield was not significantly less under PFD (1007 $g m^{-2}$) compared with ND (1030 $g m^{-2}$). Since PFD plots were irrigated until just prior to anthesis, water did not limit growth until late in the grain filling period. Relative rate of leaf senescence was greater under PFD compared with ND (1.13 vs. 0.32 percentage loss leaf area index d^{-1}), resulting in less than half the GLAM

under PFD (17 600 $cm^2 m^{-2}$) compared with ND (39 200 $cm^2 m^{-2}$). Relative rate of leaf senescence was not correlated with yield, AGDM or harvest index (Table 1) because the onset of rapid senescence occurred too late in the grain-filling period to greatly affect yield (Fig. 4). Rate of leaf senescence, however, when calculated from the slope of the broken-stick function, was positively correlated ($r = 0.68*$, $n = 9$) with grain yield. In this case, it is possible that grain yield determined the rate of

Table 2. Grain yield in nine sorghum hybrids grown under three levels of water supply in Exp. 1.

Female parents	Male parents		
	R69264	RQL36	RQL12
$g m^{-2}$			
No water deficit			
AQL39	969	991	942
AQL41	1097	1193	969
A35	1029	1071	1007
Postflowering water deficit			
AQL39	996	792	986
AQL41	1104	1073	991
A35	1081	1103	940
Terminal water deficit			
AQL39	753	669	827
AQL41	896	756	1027
A35	844	933	936
LSD (0.05) = 174 (when comparing means within the same water regime)			
LSD (0.05) = 171 (when comparing means among water regimes)			

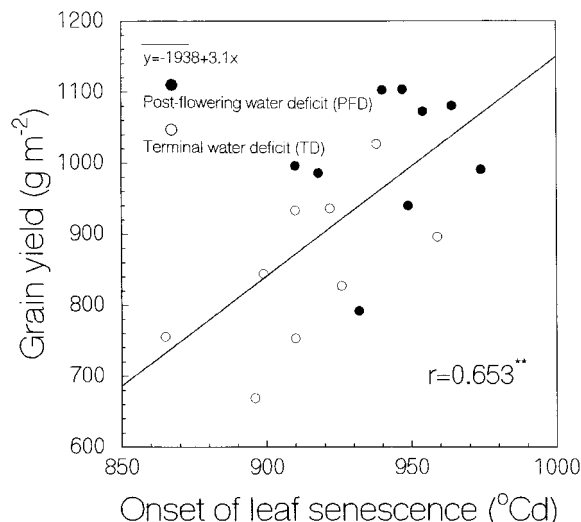


Fig. 4. The relationship between onset of leaf senescence and grain yield for sorghum hybrids grown under postflowering water deficit and terminal water deficit.

senescence, and not vice versa, since high yield potential had already been set before rapid senescence commenced (Fig. 4), and leaves senesced in response to sink demand.

Yields were still relatively high within the TD treatment, primarily due to infiltration of ≈ 80 mm of water under the plastic during a large rainfall event near anthesis. Despite this water entry, plants grown under TD encountered severe water stress during the second half of the grain-filling period, resulting in yields ranging from 669 g m^{-2} (AQL39/RQL36, senescent) to 1027 g m^{-2} (AQL41/RQL12, stay-green). That hybrids grown under PFD and TD displayed similar leaf senescence patterns (Borrell et al., 2000) despite PFD hybrids yielding more than TD hybrids (Table 2) appears anomalous. A closer examination of the senesced plant leaf area functions for PFD and TD (Borrell et al., 2000) reveals that onset of senescence was delayed ($P < 0.1$) and rate of senescence was greater ($P < 0.001$) in hybrids grown under PFD compared with TD. Of these components of senescence, onset was more important than rate in explaining yield variation across these treatments. A combined analysis of PFD and TD data found that grain yield was correlated with onset of leaf senescence ($r = 0.653^{**}$, $n = 18$, Fig. 4), but not with rate. This relationship shows that grain yield increased by $\approx 0.35 \text{ Mg ha}^{-1}$ for every day (or $3.1 \text{ g m}^{-2} \text{ }^{\circ}\text{C d}^{-1}$) that onset of senescence was delayed beyond 76 DAE ($866 \text{ }^{\circ}\text{C d}$). The extent to which delayed onset of leaf senescence affects grain yield will depend on the timing and severity of drought. Hence in Exp. 1, the greater yield in PFD than TD hybrids (1007 vs. 849 g m^{-2}) is explained largely by the delayed onset of senescence in PFD compared with TD hybrids (943 vs. $914 \text{ }^{\circ}\text{C d}$). Within TD, grain yield was correlated with onset of leaf senescence ($r = 0.615^{*}$, $n = 9$), but not with rate ($r = -0.345$, $n = 9$). Yield was negatively correlated with relative rate of leaf senescence ($r = -0.74^{**}$, $n = 9$), equating to a yield decline of $\approx 30 \text{ g m}^{-2}$ for each 0.1% increase in the relative rate

Table 3. Average grain yield of hybrids formed with three female and three male parents varying in rate of senescence grown under terminal water deficit (Exp. 1) and rainfed conditions (Exp. 2).

	Grain yield (terminal deficit)	Grain yield (rainfed)
	g m ⁻²	
Female parents		
AQL39	750	339
AQL41	893	549
A35	904	626
LSD ($P = 0.05$)	114	79
Male parents		
R69264	831	488
RQL36	786	484
RQL12	930	543
LSD ($P = 0.05$)	114	NS

of leaf senescence per day ($y = 1211 - 294x$). In this case, it is possible that rate of leaf senescence determined grain yield, and not vice versa, since onset of senescence commenced early enough for rate of senescence to affect yield.

The correlation between yield and onset of leaf senescence across the two water-limiting regimes (Fig. 4) has implications for plant breeders who visually rate stay-green at maturity only. For example, a subset of hybrids may receive the same stay-green rating at maturity, yet large variation in yield may also be observed within this subset due to differences in the onset of leaf senescence among hybrids. Therefore some means of rapidly assessing the onset of leaf senescence may be useful in screening hybrids for stay-green. Ultimately, selection for the stay-green phenotype based on molecular markers associated with delayed onset of leaf senescence should be worthwhile.

Although differential expression of stay-green is generally observed in sorghum crops yielding $< 4 \text{ Mg ha}^{-1}$ under postanthesis drought, this trait can still confer a significant advantage at higher yield levels. The critical issue is the timing and severity of drought in relation to crop growth and water supply, rather than yield potential per se. Yield under TD was greater ($P < 0.05$) in A35 hybrids (904 g m^{-2}) and AQL41 hybrids (893 g m^{-2}) than in AQL39 hybrids (750 g m^{-2}) (Table 3). Yield was also greater ($P < 0.05$) in RQL12 hybrids (930 g m^{-2}) than in R69264 hybrids (831 g m^{-2}) and RQL36 hybrids (786 g m^{-2}) under TD conditions.

In the complementary rainfed study (Exp. 2), grain yields were much lower ($3\text{--}6 \text{ Mg ha}^{-1}$, Tables 3 and 4), but yield trends among genotypes were similar for plants grown under TD in Exp. 1. Plots were irrigated prior to sowing in Exp. 1, yet Exp. 2 was not irrigated and

Table 4. Grain yield of nine sorghum hybrids grown under rainfed conditions (Exp. 2).

Female parents	Male parents			Mean
	R69264	RQL36	RQL12	
g m ⁻²				
AQL39	303	323	390	339
AQL41	567	504	577	549
A35	594	623	661	626
Mean	488	483	543	
LSD (0.05) = 137 LSD (0.01) = 185				

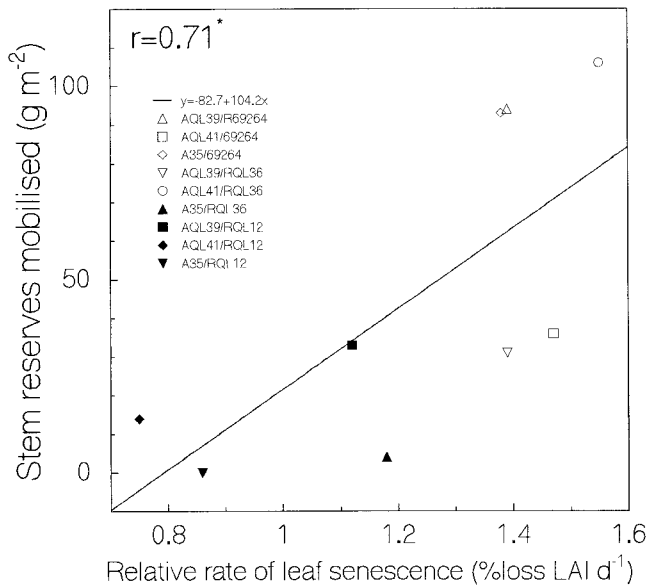


Fig. 5. The relationship between relative rate of leaf senescence and stem reserves mobilised for nine sorghum hybrids grown under terminal water deficit.

grain yield relied largely on in-crop rainfall. Furthermore, the heavy rainfall in February coincided with anthesis in Exp. 1 and with mid grain filling in Exp. 2, thereby substantially enhancing grain growth in Exp. 1, yet having less impact on yield in Exp. 2. Grain yield ranged ($P < 0.01$) from 303 g m^{-2} (AQL39/R69264, highly senescent) to 661 g m^{-2} (A35/RQL12, highly stay-green). Yield of A35 hybrids (626 g m^{-2}) was greater than for AQL39 hybrids (339 g m^{-2}) and AQL41 hybrids (549 g m^{-2}). No differences in grain yield were observed among the male parents (Table 3).

Thomas and Smart (1993) suggested that plants exhibiting Type A stay-green (delayed onset of senescence) and Type B stay-green (reduced rate of senescence) might be expected to show a higher yield in crops for which carbohydrate is a major component of the harvest, since these stay-green types continue to photosynthesise for longer than normal. Borrell et al. (2000) found the KS19 source of stay-green displays both Types A and B, although the B35 source of stay-green displays only Type B behavior; that is, the onset of leaf senescence is delayed compared with the normal type although the rate of leaf senescence is not different. Our study

supports the above hypothesis of Thomas and Smart (1993), since grain yield variation among hybrids under TD was correlated with green leaf area at maturity ($r = 0.75^{**}$) and relative rate of leaf senescence ($r = -0.74^{**}$) (Table 1). These outcomes agree with earlier work by Henzell et al. (1992) which found a significant negative correlation between visual leaf senescence ratings and yield in 76 grain sorghum hybrids grown under water-limited conditions in central Queensland.

Harvest Index

There was no genotype \times water regime interaction for harvest index. Harvest index was greater ($P < 0.05$) for plants grown under PFD (0.54) and TD (0.53) compared with those grown under ND (0.51). Genotypic variation in harvest index was highly significant ($P < 0.01$), ranging from 0.50 (AQL39/RQL36 and A35/RQL36) to 0.55 (AQL41/R69264).

Under TD, the relative rate of leaf senescence was correlated with AGDM ($r = -0.77^{***}$), but not with harvest index (Table 1), suggesting the association between high grain sink/source ratio and senescence under water-limited conditions reported by Henzell and Gillieron (1973), Duncan et al. (1981), Rosenow et al. (1983), and Tangpremsri (1989) can be broken. Indeed, AQL41/RQL12 attained a high grain yield under terminal deficit by combining a low rate of leaf senescence with a high harvest index. This outcome is encouraging, and allays concerns expressed by some plant breeders that selection for stay-green may result in developing hybrids with small panicles. The observation that in dioecious plants such as *Spinacia* and *Cannabis*, the leaves of the two sexes senesce simultaneously during the reproductive phase despite the difference in sink load between seedless males and fruit-bearing females, provides further evidence that retention of leaf greenness is not solely dependent on sink demand (Thomas, 1992).

Contribution of Stem Reserves to Grain Yield

The contribution of stem reserves (defined as the difference in stem dry mass between anthesis and maturity harvests) to grain yield was affected by water regime and hybrid. There are a number of weaknesses inherent to the method of determining C reserves by dry weight analysis (Borrell et al., 1989). First, no allowance is made

Table 5. Grain yield, grain number per square meter, mass per grain, and duration and rate of grain growth for nine sorghum hybrids averaged across three water regimes in Exp. 1.

Hybrid	Grain yield	Grain number	Mass per grain	Duration of grain growth	Rate of grain growth
	g m^{-2}	m^{-2}	mg	d	$\text{g m}^{-2} \text{d}^{-1}$
AQL39/R69264	906	31 331	29.1	55.8	16.3
AQL41/R69264	1032	38 232	27.0	59.2	17.5
A35/R69264	985	32 986	30.0	59.6	16.5
AQL39/RQL36	817	33 538	24.4	54.2	15.0
AQL41/RQL36	1007	38 070	26.4	55.9	17.9
A35/RQL36	1035	38 816	26.8	55.8	18.6
AQL39/RQL12	918	36 155	25.4	54.1	17.0
AQL41/RQL12	996	34 428	28.9	57.7	17.3
A35/RQL12	961	34 446	27.9	55.9	17.2
LSD ($P = 0.05$)	100	3 899	1.4	2.5	1.9

for any decline in stem mass due to respiration; second, there is no estimate of the allocation of the dry matter transfer to any other organs; third, maximum stem mass may be attained after anthesis; and fourth, it is possible to vary the apparent contribution of stem reserves to grain by varying grain yield. Nonetheless, dry matter analysis of the stem and grain does provide an estimate of the contribution of stem reserves to grain yield.

Between anthesis and maturity, stem dry mass increased ($P < 0.05$) by an average of 36 g m^{-2} across all hybrids under fully irrigated conditions, and therefore stem reserves did not contribute to yield under ND. Under PFD, biomass accumulation in the stem during the grain-filling period varied among hybrids, increasing in four and decreasing in five hybrids. For the latter hybrids, the estimated contribution of stem reserves to grain yield ranged from 7 g m^{-2} (A35/RQL12) to 22 g

m^{-2} (A35/R69264). Under PFD, relative rate of leaf senescence (percentage loss leaf area index d^{-1} , Borrell et al., 2000) was not correlated with the magnitude of stem reserves mobilized (Table 1).

However, under TD all hybrids except A35/RQL12 mobilized some stem reserves during grain filling. In absolute terms, the estimated contribution of stem reserves to grain yield under TD was small, varying from zero in A35/RQL12 to about 100 g m^{-2} (15% of grain yield) in AQL39/R69264 and AQL41/RQL36. Under TD, relative rate of leaf senescence was positively correlated ($r = 0.71^*$, $n = 9$) with the magnitude of stem reserves mobilized (Fig. 5), indicating that stay-green hybrids (filled symbols) do not deplete stem reserves to fill grain to the same extent as senescent hybrids (open symbols), and suggests that they may be more resistant to lodging.

Components of Yield

There was no significant genotype \times water regime interaction for grain number per square meter. Grain numbers were lower ($P < 0.01$) under TD (30 720) compared with ND and PFD (37640), and ranged among genotypes from 31 330 (AQL39/R69264) to 38 820 (A35/RQL36) (Table 5). Genotype and water regime interacted ($P < 0.1$) for panicle number per square meter (data not shown). For example, the number of panicles declined from 21 m^{-2} (ND) to 14 m^{-2} (TD) in AQL39/RQL36 (senescent), yet remained at $\approx 19 \text{ m}^{-2}$ across all water regimes in A35/RQL36 (stay-green), suggesting that tiller survival may be enhanced by stay-green in some genetic backgrounds. No genotype \times water regime interaction was observed for grain number per panicle, with a value of ≈ 2000 across all water regimes (data not shown). However, genotypes varied ($P < 0.01$) in this parameter, ranging from 1660 (AQL39/R69264) to 2246 (A35/RQL12).

No significant genotype \times water regime interaction was observed for grain size. Averaged across hybrids, grain size was unaffected by water regime, maintaining a value of $\approx 27 \text{ mg}$ across all treatments. Averaged across water regimes, genotypic variation was significant ($P < 0.01$), ranging from 24.4 mg (AQL39/RQL36) to 30.0 mg (A35/R69264) (Table 5). Overall, grain yield was correlated ($P < 0.01$) with grain number per square meter in all water regimes, but was not correlated with grain size in any water regime (Table 1). Furthermore, grain growth rates were simply a function of grain numbers, since grain growth rate was correlated with grain number per square meter in ND ($r = 0.81^{**}$, $n = 9$), PFD ($r = 0.83^{**}$, $n = 9$) and TD ($r = 0.85^{***}$, $n = 9$), but was not correlated with grain size in any water regime.

Duration and Rate of Grain Growth

Genotype and water regime did not significantly interact for duration of grain growth (anthesis to physiological maturity). The length of the grain-filling period was $\approx 56 \text{ d}$ for all water regimes. However, considerable genotypic variation was observed ($P < 0.01$), ranging from 54 d (AQL39/RQL36 and AQL39/RQL12) to 60 d

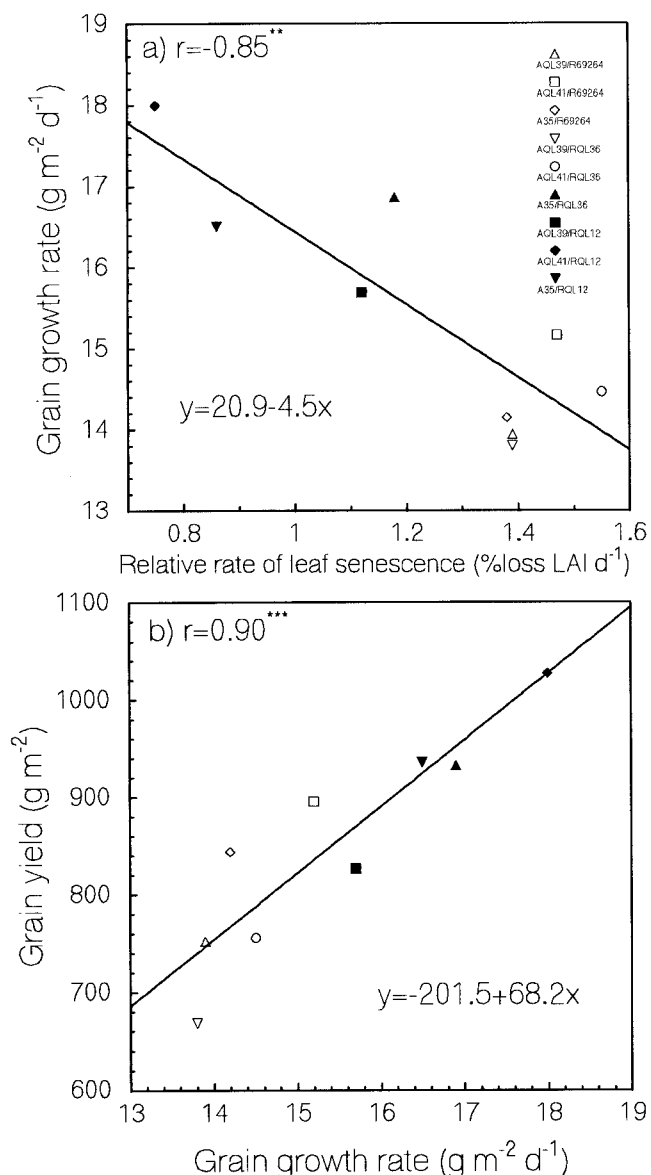


Fig. 6. The relationships between (a) relative rate of leaf senescence and grain growth rate and (b) grain growth rate and grain yield for nine sorghum hybrids grown under terminal water deficit.

(A35/R69264) (Table 5). Short grain-filling periods in AQL39/RQL36 and AQL39/RQL12 were primarily associated with late flowering and early maturity, respectively (Borrell et al., 2000).

There was no significant genotype \times water regime interaction for rate of grain growth. Average rate of grain growth was higher ($P < 0.01$) under ND ($18.1 \text{ g m}^{-2} \text{ d}^{-1}$) compared with TD ($15.4 \text{ g m}^{-2} \text{ d}^{-1}$). Genotypic variation was also observed, ranging ($P < 0.05$) from $15.0 \text{ g m}^{-2} \text{ d}^{-1}$ (AQL39/RQL36) to $18.6 \text{ g m}^{-2} \text{ d}^{-1}$ (A35/RQL36) (Table 5).

Since the stay-green trait extends green leaf area duration in the latter half of grain filling, it might be expected that the length of the grain-filling period be increased accordingly, but the duration of grain filling was not correlated with relative rate of leaf senescence under TD. Rather, relative rate of leaf senescence was correlated with grain growth rate ($r = -0.85^{***}$) and, in turn, grain growth rate was correlated with grain yield ($r = 0.90^{***}$, Fig. 6). Therefore rate, and not duration of grain growth, was the more important factor in yield determination under TD.

CONCLUSIONS

Postanthesis biomass production was 44% higher for hybrids grown under fully irrigated conditions compared with terminal water deficit ($1089 \text{ vs. } 756 \text{ g m}^{-2}$). Under terminal water deficit, grain yield was correlated positively with GLAM and negatively with rate of leaf senescence. Importantly, harvest index was not correlated with rate of leaf senescence, allaying concerns expressed by some plant breeders that selection for stay-green may result in developing hybrids with small panicles. Grain yield also increased by $\approx 0.35 \text{ Mg ha}^{-1}$ for every day that onset of leaf senescence was delayed beyond 76 DAE under water-limited conditions. Stay-green hybrids produced 47% more biomass between anthesis and maturity than their senescent counterparts ($920 \text{ vs. } 624 \text{ g m}^{-2}$) under water-limited conditions, suggesting that sorghum hybrids possessing the stay-green trait have a significant yield advantage under postanthesis drought.

No variation in grain yield was observed among eight of nine hybrids in the fully irrigated control, suggesting that there was no yield cost associated with the stay-green trait under well-watered conditions. Grain yields under ND and TD were not significantly correlated. This study also provides evidence that stay-green may contribute to lodging resistance. A positive correlation was observed between rate of leaf senescence and magnitude of stem reserves mobilized, suggesting that stay-green hybrids are less reliant on nonstructural stem carbohydrate to fill their grain than are senescent hybrids. This may result in stronger stems and less lodging.

Overall, stay-green hybrids yielded more than senescent hybrids under postanthesis drought, yet there was no yield cost associated with this trait under well-watered conditions. Therefore, growing stay-green hybrids should benefit sorghum producers in drier years through

increased yield and lodging resistance, without imposing a yield cost in wetter years.

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