

GENOTYPIC VARIATION FOR RATE AND ONSET OF LEAF SENESCENCE IN GRAIN SORGHUM

A.K. Borrell, A.C.L. Douglas and R.G. Henzell

Hermitage Research Station, Queensland Department of Primary Industries, Warwick, QLD 4370

Abstract

When water is limiting during grain filling, genotypic variation for stay-green has been observed in grain sorghum hybrids. Green leaf area at maturity (GLAM) is an excellent indicator of stay-green. The key components determining GLAM are: 1) total plant leaf area (TPLA), 2) duration of leaf senescence, and 3) rate of leaf senescence. Duration of leaf senescence is a function of the timing of the onset of senescence and the timing of physiological maturity. A field study at Hermitage Research Station (28°10'S, 152°02'E) in south-eastern Queensland, Australia, was conducted in 1995 to assess genotypic variation in the above three components. Nine hybrids were examined from crosses of three females varying in rate of leaf senescence (AQL39, senescent; AQL41, intermediate; A35, stay-green) and three males similarly varying (R69264, senescent; RQL36, intermediate; RQL12, stay-green), enabling a comparison of the A35 and RQL12 sources of stay-green. Genotypic variation was found for TPLA, onset of leaf senescence, duration of leaf senescence and rate of leaf senescence. The mechanism of leaf area maintenance also varied between the A35 and RQL12 sources of stay-green.

Key words: Sorghum bicolor, stay-green, drought-resistance traits.

Rainfed sorghum production in northern Australia is limited primarily by drought, particularly during grain filling (1). Hybrids with the stay-green drought-resistance trait have an advantage under water-limited conditions because they maintain more photosynthetically active leaves in the upper canopy compared with hybrids without this trait (2). Recent studies in grain sorghum in northern Australia (3, 4) have found significant negative correlations between leaf senescence and grain yield under drought.

Key components determining stay-green are:

- total plant leaf area (TPLA);
- duration of leaf senescence; and,
- rate of leaf senescence.

Maximum green leaf area occurs about 10 days before anthesis. Duration of leaf senescence is a function of the timing of the onset of senescence and the timing of physiological maturity. Timing of the onset of leaf senescence during the grain filling period is determined by the severity of water deficit. Delayed onset of leaf senescence and a slower rate of leaf senescence were used by Thomas and Smart (5) to categorise two separate types of functional stay-green. In a study of the inheritance of stay-green and its components in a nine-parent complete diallel, Van Oosterom *et al.* (6) reported that inheritance of the onset of senescence was additive, whereas the inheritance of the rate of senescence was completely dominant for a slow rate.

To improve yield under drought, knowledge of the extent of genotypic variation in the above three components is required. In particular, higher maximum green leaf area, delayed onset of leaf senescence, and reduced rate of leaf senescence are all pathways to increased green leaf area at maturity. Coefficients for these parameters are also required to modify leaf senescence routines in the APSIM-SORG simulation model. Subsequently, the model will be used to assess the value of the stay-green drought resistance trait in a range of target environments throughout the northern grain belt, extending from northern New South Wales to Central Queensland.

The aim of this study was to determine the extent of genotypic variation in TPLA, duration of leaf senescence, and rate of leaf senescence in nine hybrids varying in green leaf area retention under drought.

Materials and methods

A field study was undertaken at Hermitage Research Station (28°10'S, 152°02'E) in the sorghum cropping zone of southern Queensland, Australia, on a cracking and self-mulching black clay (Elphinstone depositional). The experimental design was a split plot with three replicates. Three water regimes (no deficit, post-flowering deficit and terminal deficit) were applied to main plots and nine hybrids varying in rate of leaf senescence were allocated to sub-plots. Data will be presented only for the terminal deficit treatment which was not irrigated and depended solely on stored soil water. It was in this treatment that stay-green was best expressed. Main plots were 6 x 31.5 m with a 2.8 m buffer zone between them, and sub-plots were 6 x 3.5 m (5 rows). Replicates were separated by a 4 m roadway and a 4 m cropped buffer zone.

Ridges of height 0.2 m were established 0.7 m apart parallel to the direction of slope and replicates were covered with black plastic at ground level to exclude rainfall and prevent evaporation losses. Seeds were sown manually through cross-cuts spaced at 0.1 m intervals in the plastic along the crest of the ridges on 15 December 1994. All plots were watered after sowing to assist germination and plants emerged on 18 December. Following establishment, seedlings were thinned to one per hole to give a population of 14 plants/m².

Nine hybrids were examined from crosses of three females varying in rate of leaf senescence (AQL39, senescent; AQL41, intermediate; A35, stay-green) and three males similarly varying (R69264, senescent; RQL36, intermediate; RQL12, stay-green).

Early in crop growth, ten representative plants were tagged from the centre of row one in each plot. Production of leaves on both main and tiller culms was measured on four tagged plants by identifying and marking a known leaf number early in crop growth and then recording the number of fully expanded and senesced leaves at weekly intervals (7). In addition, the green area of all fully expanded leaves on both main and tiller culms was measured on two tagged plants at each of three harvest times corresponding to the expansion of the 6th, 12th and flag leaves. The number of leaves senesced on each tagged plant, together with the known area of those leaves, was used to calculate total senesced plant leaf area (SPLA).

Broken-stick functions were fitted to the individual plot data for TPLA and SPLA. Maximum green leaf area per plant was derived from the asymptote of the TPLA function. Onset of leaf senescence was estimated as the time at which the linear phase of the SPLA function commenced *ie.* the intersection of the lag and linear phases of the broken-stick function. Rate of leaf senescence was determined by the slope of the linear phase of the SPLA function.

Green leaf area at maturity (GLAM) can be described mathematically as follows:

$$\text{GLAM} = \text{TPLA} - (\text{Duration}_{\text{sen}} \times \text{Rate}_{\text{sen}})$$

where:

TPLA = total plant leaf area (asymptote attained about 10 days before anthesis) (cm²/plant);

Duration_{sen} = duration of leaf senescence (°C.day);

Rate_{sen} = rate of leaf senescence (cm²/plant/°C.day).

Duration of leaf senescence is defined as the number of days from the onset of senescence to physiological maturity *ie.* black layer appearance.

Grain dry mass was determined at physiological maturity (11 April, 1995) for all sub-plots. Green leaf area at maturity was determined for all sub-plots with an electronic planimeter (Delta-T image analysis system) and data were analysed by standard analysis of variance and pairwise comparisons of means were performed using the protected *t*-test procedure at the 5% level. A correlation was calculated between grain yield and GLAM.

Results

GLAM was correlated ($r^2 = 0.56$) with grain yield in this study. Of the female parents, GLAM was higher ($P < 0.05$) in A35 (stay-green) compared with AQL41 (intermediate) and AQL39 (senescent) (Table 1). Of the male parents, GLAM was highest ($P < 0.05$) in RQL12 (stay-green), least in R69264 (senescent) and intermediate in RQL36 (Table 2).

Interestingly, the mechanism of leaf area maintenance varied with the source of stay-green. To demonstrate the effects of the A35 and RQL12 sources of stay-green on the components of GLAM, two comparisons were made. Firstly, three females varying in rate of leaf senescence (AQL39, senescent; AQL41, intermediate; A35, stay-green) were examined in three male backgrounds (R69264, senescent; RQL36, intermediate; RQL12, stay-green). Mean values were compared. Secondly, the same three males were examined over the same three females, and means compared.

Table 1. Green leaf area at maturity and its components for RQL12, A35 and R69264 hybrids grown under terminal deficit in the 1995 season.

Source	TPLA (cm ² /plant)	Onset of leaf senescence (°C.day)	Duration of leaf senescence (°C.day)	Rate of leaf senescence (cm ² /plant/°C.day)	GLAM (cm ² /plant)
QL39 (senescent)	3018	911	253	7.17	822
QL41 (intermediate)	2990	921	270	7.87	667
A35 (stay-green)	3488	910	284	7.56	1213
R69264 (senescent)	3038	923	289	8.53	508
RQL36 (intermediate)	3479	890	286	8.18	888
RQL12 (stay-green)	2978	929	251	5.90	1305
L.S.D. (0.05)	134	22	25	1.14	187

A35 hybrids (stay-green) attained higher ($P < 0.05$) TPLA compared with AQL39 (senescent) and AQL41 (intermediate) hybrids (Table 1). Variation in onset of leaf senescence among the female parents was not significant ($P < 0.05$). Surprisingly, duration of leaf senescence was longest ($P < 0.05$) in A35 (stay-green), least in AQL39 (senescent), and intermediate in AQL41. No significant differences in rate of leaf senescence were observed among the female parents. Therefore, the main reason for higher GLAM in A35 hybrids compared with AQL39 and AQL41 hybrids was increased TPLA.

TPLA in RQL12 (stay-green) and R69264 (senescent) hybrids was less ($P < 0.05$) than in RQL36 (intermediate) hybrids (Table 2). Onset of leaf senescence was delayed ($P < 0.05$) in RQL12 (stay-green) and R69264 (senescent) hybrids compared with RQL36 (intermediate) hybrids. Duration of leaf senescence was less in RQL12 (stay-green) hybrids than in RQL36 (intermediate) hybrids. Rate of leaf senescence was less ($P < 0.05$) in RQL12 (stay-green) hybrids compared with R69264 (senescent) and RQL36 (intermediate) hybrids. Therefore, higher GLAM in RQL12 hybrids than in R69264 and RQL36 hybrids was primarily due to delayed onset and reduced rate of leaf senescence.

Discussion

This study has found genotypic variation in GLAM and its components: TPLA, duration of leaf senescence and rate of leaf senescence. Significantly, it highlights differences in the modes of operation of the A35 and RQL12 sources of stay-green. That such differences exist in these mechanisms should not be surprising, since the A35 and RQL12 germplasm is derived from sorghum lines native to Ethiopia and Nigeria, respectively. A35 is derived from durra landraces in Ethiopia, while RQL12 is derived from KS19, which in turn was derived from the cross between Combine Kafir 60 and Short Kaura, the latter being from Nigeria.

According to the classification of stay-green by Thomas and Smart (5), the RQL12 source of stay-green displayed both Types A and B. Compared with the normal type, Types A and B are functionally stay-green and may arise after alteration of genes involved, respectively, in the timing of the initiation of senescence (delayed onset) and the regulation of its rate of progress (reduced rate). In addition, we

found TPLA to be low in RQL12 hybrids. Van Oosterom *et al.* (6), in a diallel analysis of the stay-green trait and its components in sorghum, also reported that two QDPI lines derived from KS19 (Q101 and Q102) displayed delayed onset of leaf senescence, reduced rate of leaf senescence, and low TPLA. On the other hand, the A35 source of stay-green displayed neither Type A nor B behaviour in the three backgrounds examined. However, TPLA was higher in A35 hybrids, and this advantage was maintained to maturity.

Thomas and Smart (5) suggested that plants exhibiting Types A and B stay-green 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. The current study supports this hypothesis, since GLAM was positively correlated with grain yield.

Coefficients for GLAM and its components will be used to modify the leaf senescence routines in the APSIM-SORG simulation model. These coefficients, together with an understanding of the functional basis of physiological responses, will be used to simulate the stay-green drought-resistance trait. Subsequently, the model will be used to assess the value of stay-green in a wide range of target environments throughout the northern grain belt.

Conclusion

Grain yield in sorghum was correlated with green leaf area at maturity under post-anthesis drought. Hybrids containing the A35 and RQL12 sources of stay-green retained significantly more green leaf area at maturity compared with intermediate (AQL41 and RQL36) and senescent (AQL39 and R69264) hybrids. However, the mechanism of leaf area maintenance varied with the source of stay-green. Using the stay-green classification system of Thomas and Smart (5), RQL12 hybrids displayed Types A and B behaviour (*ie.* delayed onset and reduced rate of leaf senescence), while A35 hybrids displayed neither Type A nor B behaviour. Higher GLAM in A35 (stay-green) hybrids compared with AQL39 (senescent) and AQL41 (intermediate) hybrids was due to increased TPLA prior to anthesis, and this advantage was maintained to maturity.

Acknowledgments

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