Theor Appl Genet (2000) 100:1225–1232 

**Y.Z. Tao · R.G. Henzell · D.R. Jordan · D.G. Butler**
**A.M. Kelly · C.L. McIntyre**

# Identification of genomic regions associated with stay green in sorghum by testing RILs in multiple environments

Received: 22 March 1999 / Accepted: 11 November 1999

**Abstract** Stay green is an important drought resistance trait for sorghum production. QTLs for this trait with consistent effects across a set of environments would increase the efficiency of selection because of its relatively low heritability. One hundred and sixty recombinant inbreds, derived from a cross between QL39 and QL41, were used as a segregating population for genome mapping and stay green evaluation. Phenotypic data were collected in replicated field trials from five sites and in three growing seasons, and analysed by fitting appropriate models to account for spatial variability and to describe the genotype by environment interaction. Interval mapping and non-parametric mapping identified three regions, each in a separate linkage group, associated with stay green in more than one trial, and two regions in single trial. The regions on linkage groups B and I were both consistently identified from three trials. The multiple environment testing was very helpful for correctly identifying QTLs associated with the trait. The utilisation of molecular markers for stay green in sorghum breeding is also discussed.

**Key words** Sorghum · Genome mapping · Stay green · Marker-assisted selection · Multi-environment testing

Communicated by J.W. Snape

Y.Z. Tao (✉) · D.R. Jordan · C.L. McIntyre
CSIRO Tropical Agriculture, 306 Carmody Rd, St. Lucia, QLD 4067, Australia
e-mail: yvezhi-tao@tag.csiro.au
Fax: +61 7 3214 2881

R.G. Henzell
QDPI Hermitage Research Station, Warwick, QLD 4370, Australia

D.G. Butler · A.M. Kelly
QDPI Toowoomba, QLD 4350, Australia

## Introduction

Even though sorghum is a perennial plant, it will, in general, die as a result of drought stress during grain filling (Stout and Simpson 1978; Rosenow and Clark 1981). The stay green trait, which by definition, results in plants remaining relatively alive under these conditions, is proving a valuable drought resistance mechanism (Rosenow 1983). Plants with this trait continue to fill their grains normally under limited water conditions (Rosenow and Clark 1981; Duncan et al. 1981), and its direct contribution to grain yield has become increasingly evident (Henzell 1992; Borrell and Douglas 1997). Stay green is also associated with resistance to charcoal rot (Rosenow 1983; Duncan 1984) and lodging (Woodfin et al. 1988), and has been used as a selection index for charcoal rot resistance. However, Tenkouano et al. (1993) have suggested that the two traits are under separate genetic control exhibiting dissimilar segregation patterns.

For the last two decades, sorghum breeders have used stay green for indirect selection for drought resistance, although the physiological mechanism and genetic control of this trait are not well understood. Van Oosterom et al. (1996) conducted a complete nine-parent diallel to describe: (1) stay green as post-flowering green leaf area duration and its components: green leaf area at flowering, timing for onset of senescence, and senescence rate; and (2) the expression of heterosis for stay green in terms of heterosis for its components. The results showed that in spite of significant genotype-environment interactions for the component traits, the expression of heterosis for non-senescence was stable across experiments.

Inheritance studies of the stay green trait in B35, an important stay green source line which has been widely used in sorghum drought resistance breeding, indicate that it is influenced by a major gene that exhibits varied levels of dominant gene action depending on the environment in which the evaluations are made (Tenkouano et al. 1993; Walulu et al. 1994). More recently, a RI pop-

ulation, with B35 as one of the parents, was characterised under multiple drought and non-drought conditions for the inheritance of traits associated with post-flowering drought resistance (Tuinstra et al. 1996, 1997, 1998). Stay green was found to be associated with several genomic regions in an RAPD-based genetic map.

Grain sorghum is grown mostly under rainfed conditions in Australia. Consequently, yield is limited by water supply and periods of drought stress can occur at any stage of development, but most likely post-flowering (Cooper and Chapman 1996). Selection for stay green has been conducted in multi-environment tests for developing superior drought resistant genotypes in Australian sorghum breeding programs (Henzell et al. 1997). However, as stay green is expressed only in those tests in which terminal stress occurred, neither the efficiency nor the reliability of selection is high when only conventional breeding approaches are used for selection of this trait. Marker-assisted selection for stay green will greatly increase the efficiency of selection for the trait (McIntyre et al. 1997). The work reported here was aimed at identifying QTLs for stay green with consistent effects across a set of environments. In this paper, we present the results of the detection of genomic regions with major effects on stay green in sorghum through testing a recombinant inbred population in multiple environments.

## Materials and methods

### Genetic stock

One hundred and sixty random recombinant inbred lines (RILs) were developed from the cross QL39/QL41, with 152 lines retained for analysis once those with poor seed set were discarded. The parental lines and RILs were developed by the Queensland Department of Primary Industries (Henzell 1992; Henzell et al. 1994). QL41 is a stay green line derived from the cross QL33/B35. QL39 is a midge-resistant line but is senescent. Lines derived from QL41 crossed with QL39 and QL38 (another key sorghum midge-resistant line) comprise a large part of the female stay green and midge-resistant gene pool in the QDPI and Australian seed industry breeding programs (Henzell et al. 1997).

### Field trials and phenotypic data collection

Field trials in this series of experiments were conducted across seven sites and three growing seasons, 1994–95, 1995–96 and 1996–97 (Tao et al. 1999). Phenotypic data for stay green was taken from five of the trials in which sufficient water stress was observed. These were Hermitage-G, Biloela-2, Dalby, Hermitage-E and Bongeen, and coded as HG-95, BI-96, DA-96, HE-96 and BO-97. The trials were planted as two replicates of an alpha design with five plots per block, and 36, 30, 33 blocks in 1994–95, 1995–96 and 1996–97 respectively. The plots were double-row (5.5 m×0.7 m), organised in a two-dimensional array of up to ten columns and 60 rows, where the direction of rows was across the narrowest dimension of the plots. For each plot, stay green was visually scored 2 weeks before harvesting, based on a 1–9 rating system, where a rating of 1 indicates no senescence and 9 indicates complete plant death.

### Statistical analysis

The model for the data combined across all trials, $\mathbf{y}^{(n\times 1)}$ is

$$\mathbf{y}=\mathbf{X}\tau+\mathbf{Z}\mathbf{u}+\mathbf{e},$$

where $\boldsymbol{\tau}^{t(t\times 1)}$ is a vector of fixed site effects, $\mathbf{u}^{(b\times 1)}$ is a vector of random genotype effects, $\boldsymbol{X}^{(n\times t)}$ and $\boldsymbol{Z}^{(n\times b)}$ are the associated design matrices, and $\boldsymbol{e}$ is the vector of residuals. The joint distribution of the random components is assumed to be normally distributed, with mean zero and variance matrix

$$\sigma^2\begin{bmatrix}\boldsymbol{G}(\gamma) & \mathbf{0}\\ \mathbf{0} & \boldsymbol{R}(\phi)\end{bmatrix},$$

where γ and ϕ are vectors of variance parameters. The distribution of the complete data $\boldsymbol{y}$ is then

$$\mathbf{y}\sim\mathbf{N}[\mathbf{X}\tau,\sigma^2(\mathbf{Z}\mathbf{G}\mathbf{Z}'+\mathbf{R}\mathbf{I}].$$

In the analysis of multi-environment trials there are many forms for the matrices **R** and **G** as given by Cullis et al. (1998). These matrices reflect the spatial covariance of plot errors from each trial and the variance structure of the genetic factors in the model respectively. Selection of an appropriate model for a spatial trend in the trials followed the method of Gilmour et al. (1997), who assessed the sample variograms and tested REML (Patterson and Thompson 1971) log-likelihood ratios. The data were analysed using ASREML (Gilmour et al. 1995). Best linear unbiassed predictions (BLUPs) and standard errors were obtained for the genotype by environment interaction effects. Overall genotype effects were estimated using the approach of Smith et al. (1998).

### Map construction

A genetic linkage map was previously developed on the same RIL population (Tao et al. 1998). An additional 118 markers, including 17 SSR and 101 RFLP markers, were identified and mapped onto the map in this study. The RFLP and SSR methods and procedures for map construction are as described previously (Tao et al. 1998).

### QTL analysis

MapQTL (Van Ooijen and Maliepaard 1996) was used for QTL analysis in this study. Both non-parametric mapping and interval mapping were conducted separately on each phenotypic data set to identify genomic regions associated with stay green. For the non-parametric mapping method, the rank sum test of Kruskal-Wallis was conducted. A stringent significant level of 0.005, as suggested by the authors of the program, was applied to identify the loci with genetic effects on stay green. For interval mapping, a LOD threshold of 2.4 was used to claim the presence of a putative QTL in a given genomic region. This threshold level corresponds to a test of presence of a QTL at the 0.05 level of significance according to the ”sparse-map” case (Lander and Botstein 1989; Van Ooijen 1992).

## Results

### Linkage map

In our previous report (Tao et al. 1998), using the same RI population, a total of 155 RFLP, eight SSR and three simply inherited morphological trait loci were mapped onto 21 linkage groups. In this study, the additional 118 markers were mapped and resulted in a total of 311 loci, including 281 RFLP, 25 SSR and five morphological loci on the map. RFLP markers include cereals anchors, maize, sorghum, and sugarcane probes. SSR markers

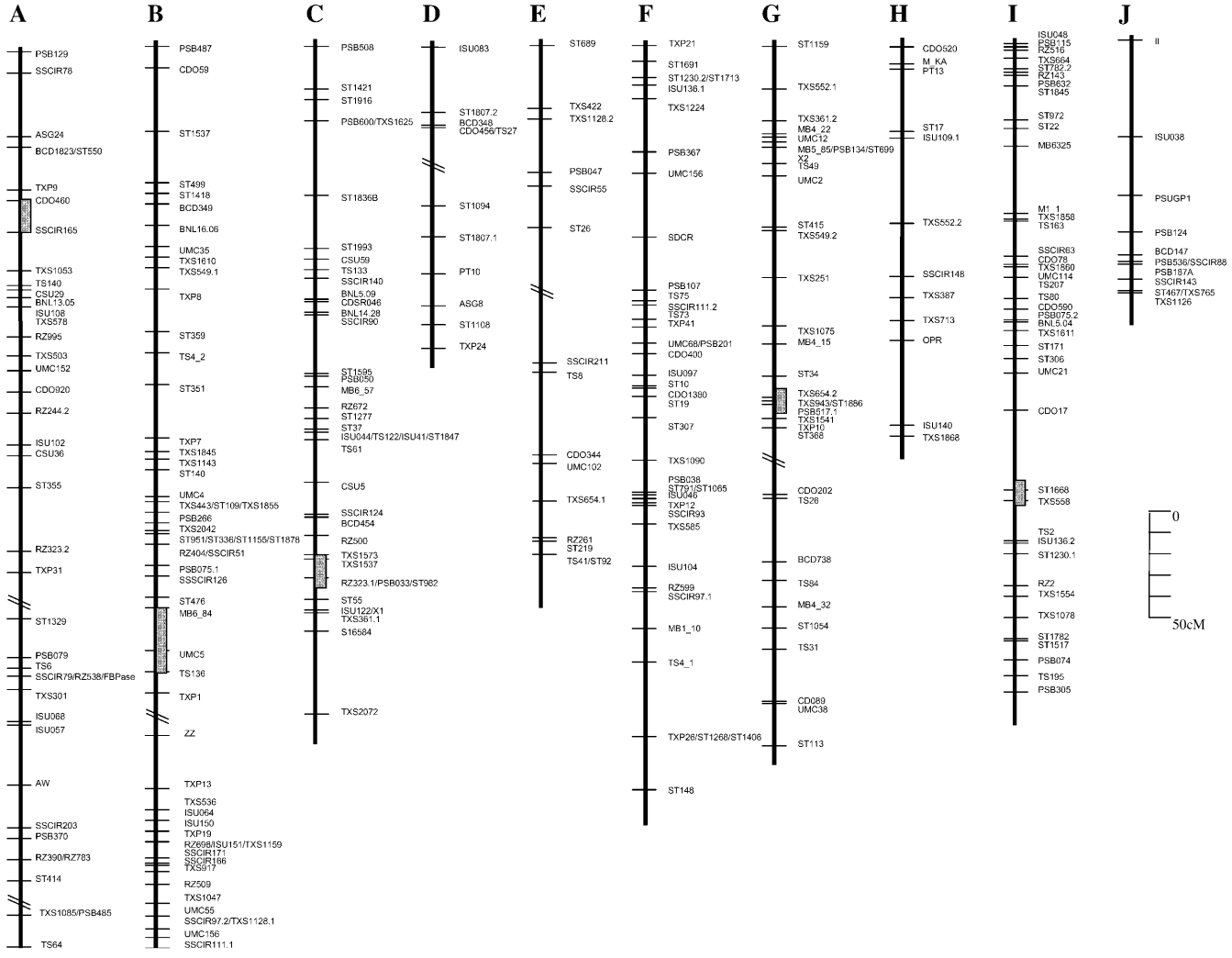


**Fig. 1** Sorghum genetic map of the recombinant inbred population derived from the cross QL39×QL41. Regions associated with stay green are indicated in the *blocked bars*

were all generated from sorghum SSR primers (Tao et al. 1998). Morphological markers included awn (*AW*), mesocarp thickness (*Z*), pericarp colour intensified gene (*I*), seedling colour (*SDCR*), and organophosphate insecticide reaction (*OPR*), respectively.

In most cases, the outcome of this new mapping was very consistent with the previous results in terms of both genetic distance and the order of loci. Some linkage groups previously mapped were joined together, thus the number of linkage groups was reduced from 21 to 14. Another three new linkage groups with two or three loci and one new group with six loci were also formed. By using reference markers from other published sorghum maps, ten linkage groups were formed and named in terms of the same designations as listed in the maps of Chittenden et al. (1994) and Lin et al. (1995) (Fig. 1, Table 1). Previously mis-labelled probes in three cases were also found and corresponding loci names were thus corrected in the present map.

## Phenotypic data for stay green

The phenotypic data for stay green were collected from all trials and the range of stay green ratings varied from trial to trial. At DA-96, the stay green rating ranged from 5.4 to 8.4, while at trial HE-96 the stay green scored from 2.6 to 7.2. The range of stay green scores at the other three trials were between the DA-96 and HE-96 trials, from 4.2 to 8.3 at BI-96, from 2.9 to 6.7 at BO-97, and from 3.7 to 6.1 at HG-95 respectively. In general, the stay green rating for QL41 was lower than the QL39, although the differences between these two lines were smaller in the trials DA-96 and HE-96 (Fig. 2).

## G×E interaction

The aim of the multi-environment trial analysis was to obtain the most precise estimates of genotype performance to include in the subsequent mapping procedure. The model for genotype by environment interaction estimated a separate genetic variance for each site, and allowed genetic correlations to vary between pairs of sites (Table 2), following the factor analytic approach of

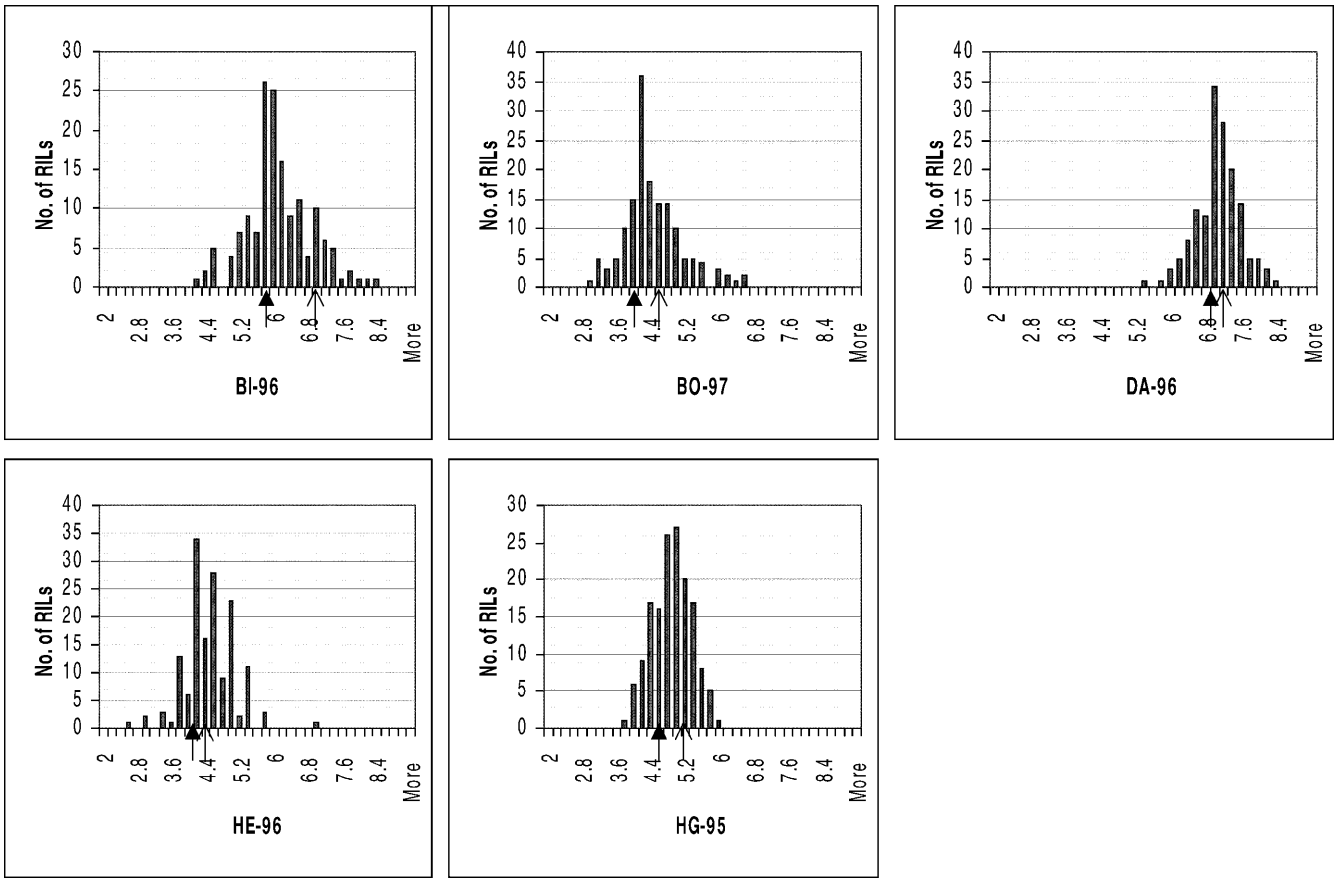


**Fig. 2** Histograms illustrating the frequency of stay green scores for the 160 RILs in the data of five individual field trials: BI96, BO97, DA96, HE-96 and HG-95. Stay green scores for QL39 and QL41 are indicated with *open and solid arrows* respectively

**Table 1** Relationships between sorghum genetic maps developed by different groups

| Present map | Previous map, Tao et al. 1999 | Chittenden et al. 1994, Lin et al. 1995 | Pereria et al. 1994, Dufour et al. 1997, Bovin et al. 1999 | Xu et al. 1994 |
|---|---|---|---|---|
| A | 4+16, 13+14 | A | G | C |
| B | 5, 6 | B | F | G, H |
| C | 3 | C | C | J, A |
| D | 21 | D | B | E |
| E | 10, 11+17 | E | I | B |
| F | 2 | F | D | I |
| G | 8+12, 15+20 | G | E | F |
| H | 7+18+19 | H | J | D, M |
| I | 1 | I | H | B |
| J | 9 | J | A | D, M |

**Table 2** Parameter estimates from the model fitted to the genotype by environment interaction for stay green data across five sites in Queensland

| Site | Error variance | Genetic variance | Genetic correlation | | | |
|---|---|---|---|---|---|---|
| | | | hg95 | bi96 | da96 | he96 |
| hg95 | 0.4033 | 0.3111 | | | | |
| bi96 | 0.8071 | 0.8005 | 0.65 | | | |
| da96 | 0.6421 | 0.3891 | 0.45 | 0.69 | | |
| he96 | 0.2595 | 0.4954 | 0.27 | 0.42 | 0.29 | |
| bo97 | 0.3819 | 0.6265 | 0.52 | 0.80 | 0.56 | 0.34 |

Smith et al. (1998). In addition, the model allowed for heterogeneous error variances at each site, and an autoregressive component for the two-dimensional spatial structure was required at three of the five sites (Table 2). Although staygreen was measured as a rating, the residual plots did not appear to violate the normality assumption.

The estimates for genetic correlation between pairs of sites, which range from 0.29 to 0.80, indicate a significant level of genotype by environment interaction. An overall genetic effect estimated from this model may not

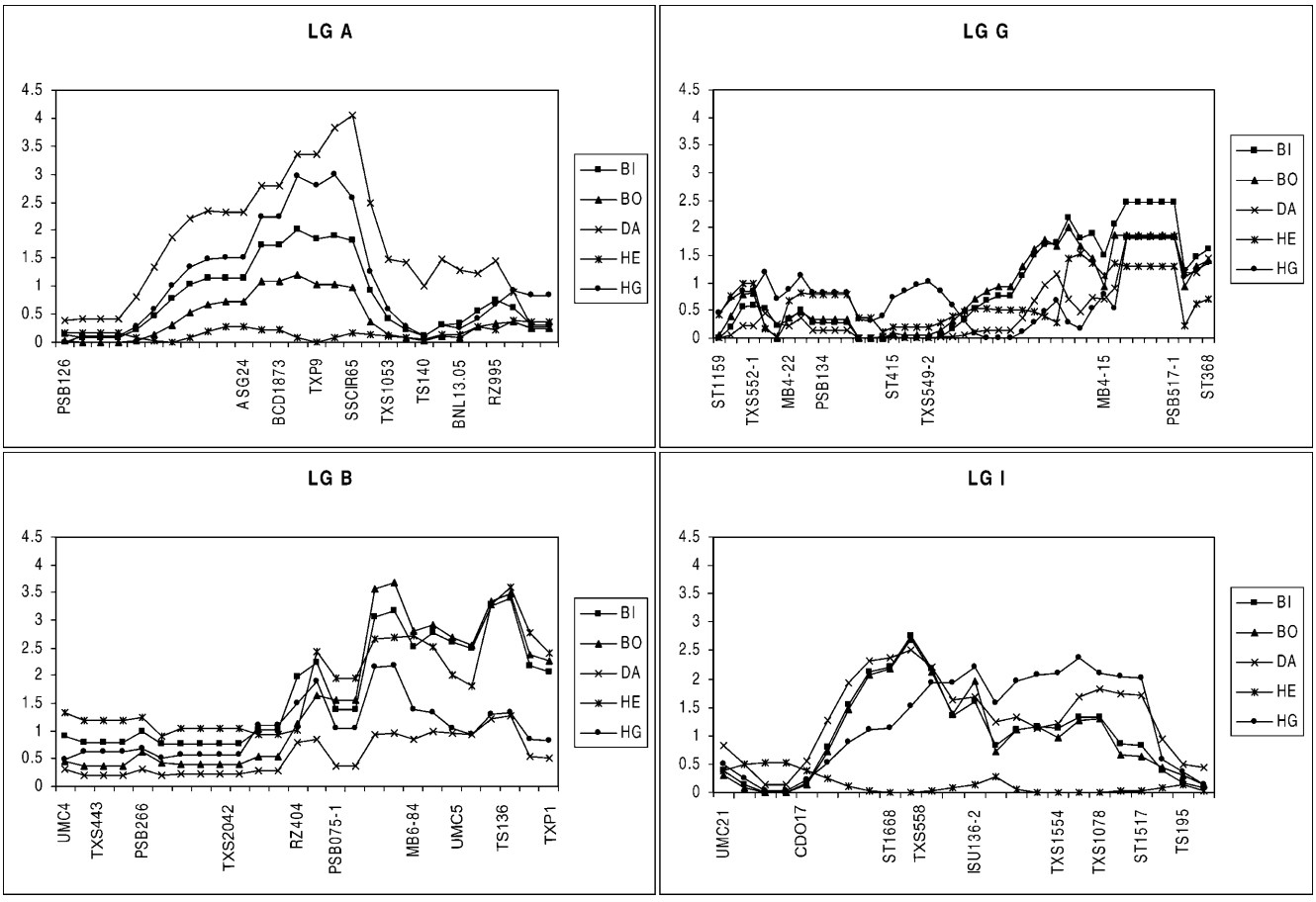


**Fig. 3** LOD-likelihood plots of linkage groups A, B, G and I for stay green

provide an adequate representation of stay green at any one particular site due to the high level of genotype by environment interaction. Consequently, QTLs were mapped to each trial individually.

## QTLs associated with stay green

Interval QTL mapping was performed with MAPQTL for the data sets from each individual site. Genetic regions with a LOD score greater than the threshold of 2.4 were then identified as QTLs associated with stay green. In BI-96, three QTLs associated with stay green were found and are located on LG B, LG G and LG I. They accounted for 14.1%, 10.9% and 11.2% of the variation respectively. In BO-97, two QTLs were identified, and are located on LG B and LG I, accounting for 14.0% and 10.7% of the variation respectively. In DA-96, two QTLs associated with stay green were found and are located on LG A and LG I, accounting for 15.3% and 10.3% of the variation respectively. In HE-96, only one QTLs was identified and was located on LG B, accounting for 14.5% of the variation. In HG-95, two QTLs were identified and are located on LG A and LG C, accounting for 15.1%, and 13.1% of the variation respectively (Table 3).

The QTL region on linkage group B was consistently identified from three trials, BI-96, BO-97 and HE-96, and the region on linkage I was also identified from three trials, BI-96, BO-97 and DA-96. However, the region of linkage group G was only supported by trial BI-96. The region of LG A was identified from two trials, DA-96 and HG-95 (Fig. 3) and the region of LG C was identified only in HG-95 (data not shown).

For the non-parametric mapping method, the Kruskal-Wallis test (the non-parametric equivalent of one-way analysis of variance) was conducted for each trial and a significance level of 0.005 was applied to identify the loci with genetic effects on stay green. In agreement with the results from interval mapping, the loci with the highest level of significance identified are in the same regions of linkage groups A, B, C, G and I. These loci are CDO460 and SSCIR165 in LG A, MB6–84 and TS136 in LG B, TXS1537 and ST982 in LG C, TXS654 and TXS943 in LG G, and ST1668 and TXS558 in LG I respectively (Table 3).

For the loci in regions of linkage groups B, G and I, the phenotypic means of lines with the QL39 genotype was greater than the phenotypic means of lines with the QL41 genotype. This suggests that these regions, associated with stay green, were inherited from QL41. However, for the loci in the regions of linkage group A and C,

**Table 3** Locations and effects of QTLs affecting stay green detected from both non-parametric mapping, indicated by significance level, and interval mapping, indicated by LOD score and the percentage of variation explained

| Interval | LG | Significant level[a]/LOD score (% variation explained) | | | | |
|---|---|---|---|---|---|---|
| | | BI-96 | BO-97 | DA-96 | HE-96 | HG-95 |
| CDO460 | | | | ******* | | ****** |
| | A | | | 3.88 | | 3.13 |
| SSCIR165 | | | | (15.3%) ******* | | (15.1%) ***** |
| MB6-84 | | ***** | ***** | | ****** | |
| | B | 3.39 | 3.47 | | 3.71 | |
| TS136 | | (14.1%) ****** | (14.0%) ***** | | (14.5%) ******* | |
| TXS1537 | | | | | | ****** |
| | C | | | | | 3.08 |
| ST982 | | | | | | (13.1%) ****** |
| TXS654 | | **** | | | | |
| | G | 2.46 | | | | |
| TXS943 | | (10.9%) **** | | | | |
| ST1668 | | **** | ***** | ***** | | |
| | I | 2.76 | 2.70 | 2.5 | | |
| TXS558 | | (11.2%) **** | (10.7%) ****** | (10.3%) **** | | |

[a] Significance levels: ***: 0.01; ****: 0.005; *****: 0.001; ******: 0.0005

the phenotypic means of lines with the QL39 genotype was less than the phenotypic means of lines with the QL41 genotype (data not shown). This implies that the significant stay green regions on linkage group A were derived from the senescent parent QL39.

## Discussion

### Relationships of different sorghum maps

A number of sorghum genetic maps have been established since the beginning of the 90s and some of these maps have been used for identifying QTLs for different traits in sorghum. Aligning these maps is obviously important in allowing researchers to share information, but this has been difficult. Previous attempts resulted in only one-half of the linkage groups being unambiguously aligned with other sorghum maps. The reasons for this include the large number (21) of linkage groups, the lack of sufficient common loci and the frequent inconsistency in probe location (Tao et al. 1998).

Current attempts to align at least some of the sorghum maps have been much more successful. This has resulted from placing more markers on the map, reducing the number of linkage groups, and having more common loci. For example there are 37, 31, and 31 common loci between the current map and the maps of Xu et al. (1994), Lin et al. (1995) and Bovin et al. (1999) respectively. The designations for linkage groups as given in the maps of Lin et al. (1995) and Chittenden et al. (1994) were used in this map. Corresponding designations used in maps developed from other groups are shown in Table 1.

### Regions for stay green

The QTL region on linkage group B was consistently identified from three trials, BI-96, BO-97 and HE-96. The region on linkage group I was confirmed by three trials, BI-96, BO-97 and DA-96. That these regions do contain genes for stay green is also strongly supported by data from the pedigree-analysis study. This study showed that both regions were derived from B35 (D. Jordan, unpublished), the source of stay green in QL41, which in turn is the source of stay green in the RILs used in this study. The significance of these regions is enhanced by the fact that they have been retained through four generations of crossing and phenotypic selection for stay green (amongst other traits) in the QDPI breeding program (D. Jordan, unpublished). This is consistent with the successful use of QL41 as a source of stay green in Australian sorghum breeding programs.

The region of LG A identified from two trials, DA-96 and HG-95, is very different from the regions mentioned above because the significant genetic effect for stay green was actually derived from the senescent parent QL39. It is possible that this region is a real QTL for stay green, but apparently not being expressed in QL39 and having a different mechanism for stay green. It is also possible that this region is linked with another trait(s) that influences the expression of stay green in some environments. This hypothesis will be explored in a subsequent paper.

Seven genomic regions were found associated with stay green from combined data analysis in a RI population derived from TX7078/B35 (Tuinstra et al. 1997). However, only two of these regions with the highest levels of significance were consistent across the two envi-

ronments in their study. It is difficult to align the regions identified in the present study and in that of Tuinstra et al. at this time because of the lack of common loci between the two maps. Different marker systems were used for mapping, mainly RAPDs for their study and RFLPs and SSRs for the current study.

### Marker-assisted selection for stay green

The success of marker-assisted selection is influenced by the consistency of the expression of the genes linked to the markers across environments within the target environment. It is desirable then to use multi-environment testing to determine the phenotype of traits such as stay green for which expression varies amongst environments (Kang 1998). It is also important that the multi-environments employed for phenotype testing actually sample the target environment. The environments in the five trials used in this study were representative of the most common stress environment encountered by sorghum in Australia. The consistency across the majority of these environments, and of the association of the regions on linkage groups B and I with the expression of stay green, provides added confidence in their real value for marker-assisted selection in Australia.

It worth noting that there was a relatively small difference in stay green between the two parents of the segregating population used in this study (Fig. 2), which is not an ideal case for any genetic mapping. However, the identification of several genomic regions in this population indicated strongly the power of the approach of detecting QTLs by the application of molecular markers on RILs through multi-environment testing. Most mapping populations are actually similar to the population used in this investigation, because it is common to make crosses between two inbreds which differ not only in the trait of interest but which also segregate for other traits that contribute to performance. Basically these populations are the ones that are currently available and useful in plant breeding programs and therefore contribute to the utility of the identified markers.

**Acknowledgments** We thank Messrs. Darell Fletcher and Tony McCosker for growing the field tests and Miss Mikigo Miyaki for her technical assistance for genome mapping. This research is funded by GRDC.

## References

Boivin K, Deu M, Rami JF, Trouche G, Hamon P (1999) Towards a saturated sorghum map using RFLP and AFLP markers. Theor Appl Genet 98:320–328

Borrell AK, Douglas AC (1997) Maintaining green leaf area in grain sorghum increased nitrogen uptake under post-anthesis drought. Int Sorghum Millets Newslett 38:89–92

Chittenden LM, Schertz KF, Lin YR, Wing RA, Paterson AH (1994) A detailed RFLP map of *Sorghum bicolor*×*S. propinquum*, suitable for high-density mapping, suggests ancestral duplication of *Sorghum* chromosomes or chromosomal segments. Theor Appl Genet 87:925–933

Cooper M, Chapman SC (1996) Breeding sorghum for target environments in Australia. In: Foale MA, Henzell RG, Kneipp J (eds) Proc 3rd Australian Sorghum Conf, Tamworth, 20–22 Feb 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No 93, pp 173–188

Cullis BR, Gogel BJ, Verbyla AP, Thompson R (1998) Spatial analysis of multi-environment early generation variety trials. Biometrics 54:1–18

Dufour P, Deu M, Grivert L, D'Hont A, Paulet F, Bouet A, Lanaud C, Glaszmann JC, Hamon P (1997) Construction of a composite sorghum genome map and comparison with sugarcane a related complex polyploid. Theor Appl Genet 94:409–418

Duncan RR (1984) The association of plant senescence with root and stalk diseases in sorghum. In: Mughogho LK (ed) Sorghum root and stalk rots, a critical review. ICRISAT, Patancheru, AP, India, pp 99–110

Duncan RR, Bockholt AJ, Miller FR (1981) Descriptive comparison of senescent and nonsenescent sorghum genotypes. Agron J 73:849–853

Gilmour AR, Thompson R, Cullis BR (1995) Average information REML: an efficient algorithm for variance parameter estimation in linear mixed models. Biometrics 51:1440–1450

Gilmour AR, Cullis BR, Verbyla AP (1997) Accounting for natural and extraneous variation in the analysis of field experiments. J Agric, Biol Environ Statistics 2:269–293

Henzell, RG (1992) Grain sorghum breeding in Australia: current status and future prospects. In: Foale MA, Henzell RG, Vance PN (eds) Proc 2nd Australian Sorghum Conf, Gatton, 4–6 Feb 1992. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No 68, pp 70–82

Henzell RG, Franzmann BA, Brengman RL (1994) Sorghum midge resistance research in Australia. Internatl Sorghum Millets Newslett 35: 41–47

Henzell RG, Hammar GL, Borrell AK, McIntyre CL (1997) Research on drought resistance in grain sorghum in Australia. Int Sorghum Millets Newslett 38:1–9

Kang MS (1998) Using genotype by environment interaction for crop cultivar development. Adv Agron 62:199–253

Lander ES, Botstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–199

Lin YR, Schertz KF, Paterson AH (1995) Comparative analysis of QTLs affecting plant height and maturity across the Poacea, in reference to an interspecific sorghum population. Genetics 141: 391–411

McIntyre CL, Tao YZ, Jordan DR, Henzell RG (1997) Application of molecular markers to sorghum breeding in Australia. Int Sorghum Millets Newslett 38:11–15

Patterson HD, Thompson R (1971) Recovery of interblock information when block sizes are unequal. Biometrika 58:545–554

Pereria MG, Lee M, Bramel-Cox P, Woodman W, Doebley J, Whitkus R (1994) Construction of an RFLP map in sorghum and comparative mapping in maize. Genome 37:236–243

Rosenow DT (1983) Breeding for resistance to root and stalk rots in Texas. In: Mughogho LK (ed) Sorghum root and stalk rots, a critical review. ICRISAT, Patancheru, AP, India, pp 209–217

Rosenow DT, Clark LE (1981) Drought tolerance in sorghum. In: Loden HD, Wilkinson D (eds) Proc. 36th Annu Corn and Sorghum Industry Research Conf, Chicago, pp 18–31

Smith AB, Cullis BR, Gilmour AR, Thompson R (1998) Multiplicative models for interaction in spatial mixed model analyses of multi-environment trial data. Proc IBC98 Int Biometrics Conf, Cape Town, South Africa, 13–18 Dec 1998, pp 91

Stout DG, Simpson GM (1978) Drought resistance of sorghum bicolor. I. Drought avoidance mechanisms related to leaf and water status. Can J Plant Sci 58:213–224

Tao YZ, Jordan DR, Henzell RG, McIntyre CL (1998) Construction of a genetic map in a sorghum RIL population using probes from different sources and its alignment with other sorghum maps. Aust J Agric Res 49:729–736

Tao YZ, Henzell RG, Jordan DR, Butler DG, Kelly AM, McIntyre CL (1999) Identification of QTLs for traits in sorghum by test-

ing RILs in multiple environments. In: Langridge P, Barr A, Auricht G, Collins G, Granger A, Handford D, Paull J (eds) Proc 11th Aust Plant Breed Conf pp 79–80

Tenkouano A, Miller FR, Frederiksen RA, Rosnow DT (1993) Genetics of nonsenescence and charcoal rot resistance in sorghum. Theor Appl Genet 85:644–648

Tuinstra MR, Grote E M, Goldsbrough PB, Ejeta G (1996) Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. Crop Sci 36:1337–1344

Tuinstra MR, Grote E M, Goldsbrough PB, Ejeta G (1997) Genetic analysis of post-flowering drought tolerance and components of grain development in *Sorghum bicolor* (L.) Moench. Mol Breed 3:439–448

Tuinstra MR, Grote E M, Goldsbrough PB, Ejeta G (1998) Evaluation of near-isogenic sorghum lines contrasting for QTL markers associated with drought tolerance. Crop Sci 38: 835–842

Van Ooijen JM, Maliepaard C (1996) MapQTL (tm) version 3.0 softwear for the calculation of QTL positions on genetic maps. CPRO-DLO, Wageningen, The Netherlands

Van Ooijen JW (1992) Accuracy of mapping quantitative trait loci in autogramous species. Theor Appl Genet 84:803–811

Van Oosterom EJ, Jayachandran R, Bidinger FR (1996) Diallel analysis of the stay green trait and its components in sorghum. Crop Sci 36:549–555

Walulu RS, Rosenow DT, Wester DB, Nguyen HT (1994) Inheritance of the stay green trait in sorghum. Crop Sci 34:790–972

Woodfin CA, Rosenow DT, Clark LE (1988) Association between the stay green trait and lodging resistance in sorghum. In: Agronomy abstracts, ASA, Madison, Wisconsin, P102

Xu GW, Magill CW, Schertz KF, Hart GE (1994) A RFLP linkage map of S*orghum bicolor* (l.) Moench. Theor Appl Genet 89: 139–145