Theor Appl Genet (2002) 104:1373–1378
DOI 10.1007/s00122-002-0923-3

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# Genetic mapping of QTLs associated with greenbug resistance and tolerance in *Sorghum bicolor*

Received: 28 July 2001 / Accepted: 23 August 2001 / Published online: 27 April 2002


**Abstract** Ninety three recombinant inbreds of *Sorghum bicolor* (L. Moench) were derived from a cross between two sorghum lines GBIK and Redlan. This population was used to identify quantitative trait loci (QTLs) for resistance and tolerance to greenbug (*Schizaphids graminum* Rondani) Biotypes I and K. One hundred and thirteen loci (38 SSRs and 75 RAPDs) were mapped in 12 linkage groups covering 1,530 cM. In general, nine QTLs were detected affecting both resistance and tolerance to greenbug (GB) Biotypes I and K. The phenotypic variance explained by each QTL ranged from 5.6% to 38.4%. Four SSRs and one RAPD marker were associated with the expression of all resistance and tolerance traits. These markers appear to be linked to biotype nonspecific resistance and tolerance genes. Four additional markers were associated with biotype-specific resistance or tolerance traits. The detection of more than one locus for each biotype supports the hypothesis that several regions, which represent different genes, control the expression of resistance and tolerance to greenbug in sorghum. The results can be used for marker-assisted selection and the breeding of greenbug-tolerant sorghum cultivars.

**Keywords** RAPDs · Simple sequence repeats · (SSRs) · *Schizaphids graminum* · *Sorghum bicolor* · SPAD

Communicated by H.F. Linskens

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## Introduction

Sorghum (*Sorghum bicolor* L. Moench) is a species of main economic importance among the cereal crops cultivated in countries with tropical climates and also has growing importance in temperate regions. It is an important crop in Kansas, USA, with over 6.4 million tons of grain sorghum produced in 2000. The sorghum crop is host to several important insect pests including the greenbug (*Schizaphids graminum* Rondani), which can cause severe crop damage and economic loss. Although genetic sources of resistance have been developed to minimize greenbug damage, new greenbug biotypes have appeared every few years to overcome these sources of resistance. Biotype C was first reported by Harvey and Hackerott (1969) and Biotypes I and K have been identified in recent years (Harvey et al. 1991, 1997). This pest can damage all growth-stages of the sorghum plant, but damage to young plants can be particularly severe. When greenbugs feed on sorghum, damage can be seen as chlorosis and the formation of red spots. Plant damage, apparently, is caused by a toxin or elicitor injected by feeding greenbugs (Ma et al. 1999). This damage to tissue, especially on chlorophyll, can now be quantified by non-destructive methods. The SPAD chlorophyll meter has been used as measures of tolerance to aphid stress (Girma et al. 1998).

Several linkage maps of *S. bicolor* using RFLP markers have been constructed (Hulbert et al. 1990; Binelli et al. 1992; Whitkus et al. 1992; Berhan et al. 1993; Chittenden et al. 1994; Pereira et al. 1994; Ragab et al. 1994; Xu et al. 1994; Dufour et al. 1996, 1997; Peng et al. 1999; Subudhi et al. 2000; Ventelon et al. 2001. Only a small number of SSR primer sets have been developed for sorghum, and linkage-map locations have been published for sorghum SSR loci (Taramino et al. 1997; Tao et al. 1998, 2000; Kong et al. 2000).

The use of molecular markers and QTL mapping may provide a methodology to more-effectively utilize favorable genes for greenbug resistance in sorghum. The use of Quantitative Trait Locus (QTL) mapping to identify

quantitative disease resistance genes in plants is discussed in detail elsewhere (Young 1996). The use of recombinant inbred (RI) lines has many advantages over $F_2$ or backcross populations for QTL studies (Burr and Burr 1991). Progress has been made in mapping agriculturally important genes with molecular markers, which form the foundation for marker-aided selection (MAS). The use of MAS can expedite difficult screening procedures such as testing for disease or insect resistance. Our approach to the localization of genes for host-plant resistance and tolerance to the greenbug *S. graminum* Biotypes I and K in sorghum is based on SSR and RAPD mapping in a recombinant inbred population.

## Materials and methods

The genetic association of polymorphic DNA with greenbug Biotypes I and K caused by *S. graminum* (Rondani) was determined using a Recombinant Inbred (RI) line population. Two sorghum-inbred lines were selected for this initial study, e.g., an inbred parent GBIK had been identified as highly resistant, while an inbred Redlan was highly susceptible. The 93 RI lines ($F_{5-6}$), along with the two parental lines were evaluated in the greenhouse of the Department of Agronomy at Kansas State University.

The mapping population was evaluated for greenbug resistance to Biotypes I (BioI-2) and K (BioK-2) at the 2–3 leaf stage. Greenbug screening assays were conducted in the greenhouse using a Randomized Complete Block Design with four replications. Individual plants were infested with about 50 greenbugs per plant using the technique described by Harvey et al. (1985). Greenbug resistance was quantified using a resistance rating that ranged from 1 (no damage) to 5 (plant death). The host-plant tolerance experiment was conducted in five replications and completely randomized. Differences in host-plant tolerance to greenbug Biotypes I (BioI-8) and K (BioK-8) were measured at the 8-leaf stage using a SPAD-502 Chlorophyll meter (Minolta Camera Co., Ltd, Japan) to quantify chlorophyll loss after greenbug feeding for 3 days (Deol et al. 1997). SPAD Index values were calculated for each entry as follow:

$$\text{SPAD Index} = (\text{SPADC} - \text{SPADT})/\text{SPADC},$$

where SPADC = uninfested control, and SPADT = infested area (where greenbugs feed).

From each of the 93 lines, 20–25 seeds were sown in the growth chamber and seedlings were bulked (Xiao et al. 1996) for DNA extraction. Twenty eight (Brown et al. 1996; Taramino et al. 1997) and 38 (Kong et al. 2000) SSR primers were evaluated. Amplification of SSRs was done using PCR reactions as described by Taramino and Tingey (1996) and Kong et al. (2000), except that 55 °C was used for primer annealing. Two hundred and twenty RAPD markers (Operon Kits A-K, OPERON Technologies, Alameda, Calif.) were screened for polymorphism using standard protocols (Tao et al. 1993). The SSR and RAPD reaction products were evaluated for polymorphisms on 3% Metaphor agarose gels (FMC Products, Rockland, Me., USA) and 1.6% agarose gels, respectively. Gels were stained in TBE buffer containing 1 μg $ml^{-1}$ of ethidium bromide for 30 to 60 min. Gel images and marker data were processed using Quantity One Software v 4.0.1 (Bio-Rad Laboratories, Hercules, Calif. USA). The SSR and RAPD bands were sized and then binary coded by 1 or 0 for their presence or absence in each genotype. The program MAPMAKER/EXP 3.0 (Lander et al. 1987) was used to establish the linkage map using the Kosambi function. Mapping of QTLs was performed using the single-factor analysis as described by Tuinstra et al. (1997) and Agrama et al. (1999). The PROC GLM procedure in SAS was used to detect significant associations between segregating markers and the resistance, as a quantitative trait. An estimate of the percentage of phenotypic variation explained by markers associated with resistance was determined by regression analysis using multiple regression (PROC GLM and PROC REG, SAS). The coefficient of determination ($R^2$) from the multiple regression, estimates the total proportion of phenotypic variation due to the additive effects.

## Results

The two parent lines differed significantly in greenbug resistance and tolerance (Table 1). In the host-plant resistance experiment, the parent line GBIK was more-resistant against both Biotypes I and K than Redlan at the 2-leaf stage (BioI-2, BioK-2). However, the Redlan line was completely dead when readings were taken. GBIK was also more-tolerant than Redlan to greenbug feeding at the 8-leaf stage (BioI-8, BioK-8). The tolerance was scored as the damage to sorghum leaves in terms of chlorophyll loss when greenbugs were allowed to feed only for 2 days. This damage was measured by the SPAD Index that takes into account normal changes in chlorophyll amount by comparing damaged to undamaged tissue. The GBIK parental line lost very little chlorophyll following BioI and BioK greenbug feeding as compared to the Redlan line. The recombinant inbred (RI) population means and the range of resistance and tolerance to GB Biotypes I and K at the 2 and 8 leaf stages are reported in Table 1. A significant difference was observed among the RIs. However, the RIs exhibited good variability that reflected the wide ranges of resistance at the 2-leaf and tolerance at the 8-leaf stages. The phenotypic correlation analysis was performed between resistance and tolerance to Biotypes I and K at the 2- and 8-leaf stages (Table 2). Significant associations were detected ($P < 0.01$) for resistance and tolerance to greenbug Biotypes I and K, and ranged from 0.36 to 0.70. The highest

**Table 1** Mean and range of greenbug damage at the 2-leaf (1–5; where 1 = no visible symptoms and 5 = completely damaged) and the 8-leaf (0.0–1.0; where the larger the SPAD Index is greater than the chlorophyll damage) stages observed for the two sorghum parents (GBIK and Redlan) and their $F_{5:6}$ recombination inbred line population

| Traits | GBIK | Redlan | RI lines | | |
|---|---|---|---|---|---|
| | Mean ± SE | Mean ± SE | Range | | Mean ± SE |
| BioI-2 | 3.95 ± 0.33 | 5.00 ± 0.00 | 2.25 | 5.00 | 4.57 ± 0.0617 |
| BioK-2 | 33.37 ± 0.32 | 5.00 ± 0.00 | 1.50 | 5.00 | 3.83 ± 0.1038 |
| BioI-8 | 0.106 ± 0.036 | 0.394 ± 0.055 | 0.0229 | 0.4173 | 0.1799 ± 0.0089 |
| BioK-8 | 0.172 ± 0.024 | 0.344 ± 0.084 | 0.0209 | 0.5066 | 0.2079 ± 0.0098 |

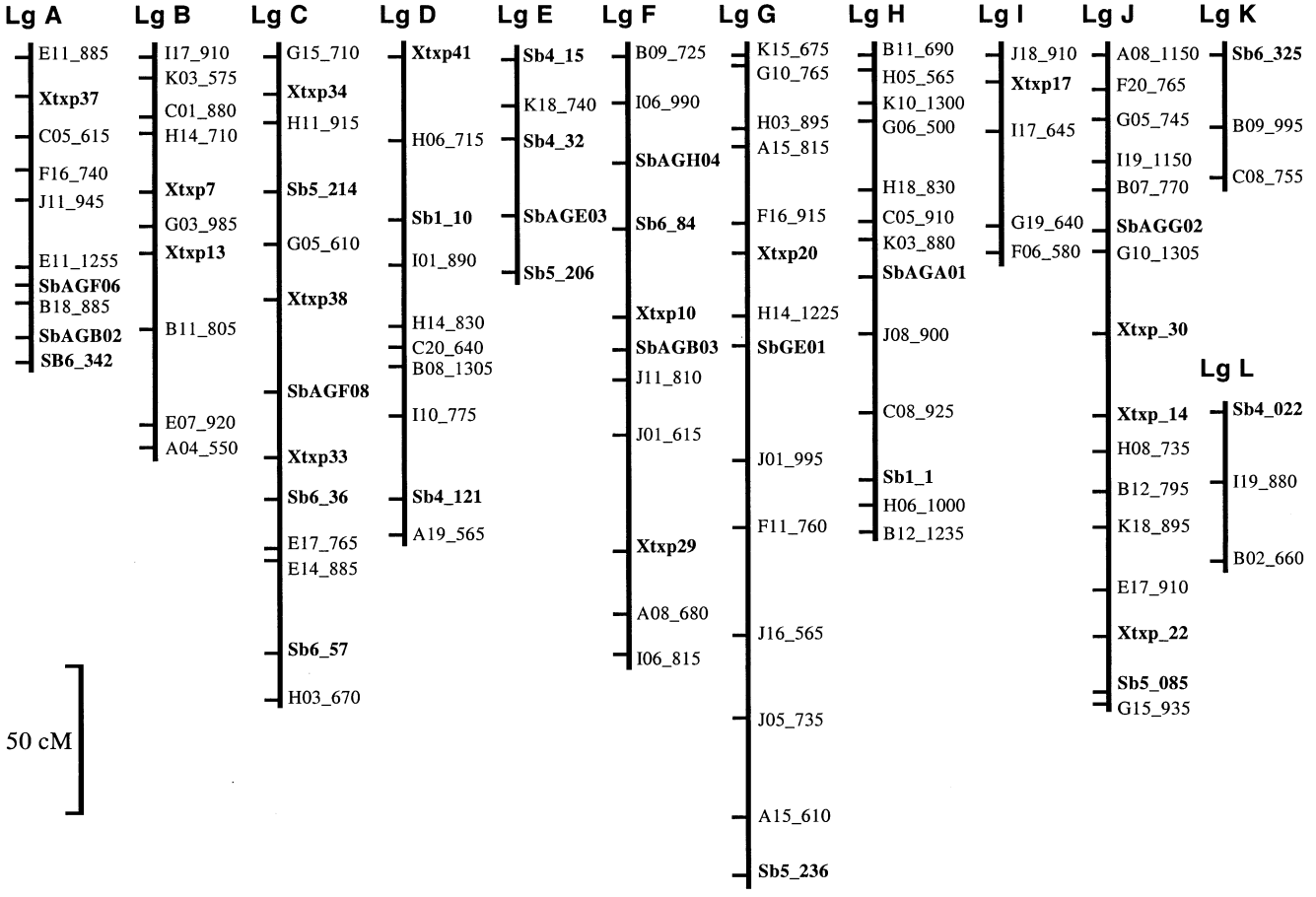


**Fig. 1** Molecular linkage map of the *S. bicolor* genome obtained from analysis of the RI population derived from the GBIK × Redlan cross. Symbols for the 38 SSRs are in *bold* and those for 75 RAPD loci are in *plain text* followed by the fragment size given in base-pairs, and interval distances (in centiMorgans, cM)

**Table 2** Phenotypic correlation coefficients (*r*) among greenbug resistant rating at the 2-leaf stage (BioI-2, BioK-2) and tolerance at the 8-leaf stage (BioI-8, BioK-8) for the two greenbug Biotypes I and K

| Item | BioK-2 | BioI-8 | BioK-8 |
|---|---|---|---|
| BioI-2 | 0.522** | 0.478** | 0.364** |
| BioK-2 | | 0.526** | 0.503** |
| BioI-8 | | | 0.696** |

correlation was between tolerance to BioI and BioK ($r$ = 0.696) and the lowest association was detected between resistance to BioI and tolerance to BioK ($r$ = 0.364).

One hundred and twenty nine markers were used to construct a genetic map of the 93 RI population. Only one hundred and thirteen loci (38 SSRs and 75 RAPDs) were linked. The map covered 1,530 cM with 113 loci distributed over 12 linkage groups (Fig. 1). These markers were evaluated for association with resistance or tolerance to the greenbug using PROC GLM.

Significant associations were identified for each trait. Nine putative QTLs located on linkage groups A, B, C, D, F (two QTLs), H, and J (two QTLs) were found to significantly affect resistance and tolerance to the green-

**Table 3** Genomic location and percentage of phenotypic variation ($R^2$) associated with QTLs significantly affecting resistance and tolerance to *S. graminum* Biotypes I and K

| Linkage group | Loci | BioI-2 | BioK-2 | BioI-8 | BioK-8 |
|---|---|---|---|---|---|
| A | B18-885 | – | 8.5 | – | – |
| B | OPC01-880 | 7.9 | – | – | – |
| C | Sb5-214 | 5.6 | 8.4 | 11.6 | 19.8 |
| D | Sb1-10 | 5.7 | 20.1 | 7.8 | 6.1 |
| F | SbAGB03 | 21.3 | 8.2 | 15.1 | 22.5 |
| F | Sb6-84 | – | – | 9.6 | – |
| H | SbAGA01 | 19.3 | 21.0 | 29.1 | 38.4 |
| J | OPA08-1150 | 10.4 | – | – | – |
| J | OPB12-795 | 6.8 | 10.3 | 11.0 | 9.3 |
| Total | | 58.9 | 53.3 | 67.5 | 78.6 |

bug (Table 3). Both resistance and tolerance to greenbug Biotypes I and K are controlled by QTLs linked to four SSRs (Sb5-214, Sb1-10, SbAGB03 and SbAGA01) and one RAPD (OPB12-795) marker. All these markers appear to be linked to biotype non-specific resistance and tolerance genes (Table 3). Four additional markers were associated with biotype-specific resistance or tolerance traits. The proportion of phenotypic variation explained by each of these genomic regions varied from 5.6 to 38.4%. The region linked to linkage group H accounted for the highest percentage of phenotypic variation. More than 50% of total phenotypic variation was explained by the QTLs for each trait. The total phenotypic variations were higher for tolerance at the 8-leaf stage than resistance to both biotypes.

## Discussion

Plant resistance to insects (PRI) can be an effective component of an integrated pest-management program. Utilization of sorghum cultivars with high levels of PRI would reduce the need for chemical insecticide applications, resulting in positive environmental and economic benefits. Antibiosis, antixenosis and tolerance are the three principal modes of PRI (Kogan and Ortman 1978; Bowling and Wilde 1996; Rector et al. 1999). The PRI showed antibiotic and antixenosis properties (All et al. 1989). The mechanisms of resistance to GB Biotype I were determined by antibiosis and tolerance (Wilde and Tuinstra 2000). Two approaches have been used to detect and locate factors controlling *S. graminum* (Rondani) Biotypes I and K in sorghum genotypes. In the first, we measured seedling-damage scores that represent the Antixenosis resistance (Bowling and Wilde 1996). The second, the SPAD Index, was used to screen for tolerance in terms of chlorophyll loss after 2 days of feeding by aphids (Girma et al. 1998). The two parents used to develop the recombinant inbred (RI) lines exhibited extreme phenotypes to the greenbug (GB) reaction. The inbred parent GBIK was highly resistant, and an inbred Redlan was highly susceptible. The RI populations have several advantages for use in mapping QTLs, which have been described by several authors (Knapp and Bridges 1990; Burr and Burr 1991; Austin and Lee 1996; Agrama et al. 1999).

In the present study, a sorghum genome map of 126 loci was constructed on the basis of the RI population using SSR and RAPD markers covering approximately 1,500 cM. This map consists of 12 linkage groups, although the basic chromosome number of sorghum is $x = 10$. Dufour et al. (1997) published two maps obtained from two RI populations which were built using 155 and 129 loci covering a total of 977 and 878 cM, respectively. These two maps were distributed in 13 and 12 linkage groups, and were used to construct a composite map of 188 loci spanning 1,095 cM in the 13 linkage groups. A saturated sorghum map was published by Boivin et al. (1999) which covers 1,325 cM for 343 loci distributed over 11 linkage groups plus two clusters of 2 and 3. However, two maps of 14 and 17 linkage groups were reported by Tuinstra et al. (1996) and Lijavetzky et al. (2000). All these maps were constructed using RFLPs, RAPDs and AFLPs. Recently, Kong et al. (2000) and Tao et al. (2000) published two maps of ten linkage groups constructed from RFLPs and SSRs.

Correlated traits often have QTLs mapping to the same chromosomal locations (Veldboom et al. 1994; Xiao et al. 1996). The same trend was observed in the current study. Trait correlations may result from either tight linkage of several genes controlling the traits or the pleiotropic effect of a single gene (Aastveit and Aastveit 1993; Agrama 1996). The age-related changes in the expression of QTLs were studied in radiata pine (Emebiri et al. 1998) and Douglas-fir (Carlson et al. 1994; Carlson and Agrama 1995). These studies revealed that QTL expression might not be stable across ages. However, in this study, tolerance to both Biotypes I and K at the 8-leaf stage was much more strongly correlated than resistance at the 2-leaf stage. Also, significant associations were detected for resistance and tolerance to greenbug Biotypes I and K. These results suggest that some host-plant resistance and tolerance genes are not biotype-specific and have functions across developmental stages. This association indicates that Marker-Assisted Selection (MAS) methods can improve the accuracy of early selection by direct identification of individuals carrying QTLs for resistance to Biotype I or K at the 2-leaf stage generally results in a correlated response for tolerance at later stages.

QTLs for correlated traits in this study seem in agreement with the idea of pleiotropic effects of the common genetic loci affecting the response of sorghum genotypes to the greenbug. Four SSRs and one RAPD marker were associated with the expression of all resistance and tolerance traits. These markers appear to be linked to biotype non-specific resistance and tolerance genes. The detection of more than one locus for each biotype supports the hypothesis that several regions, which represent different genes, control the expression of resistance and tolerance to the greenbug in sorghum.

There would be only nine genomic regions that should be transferred into a cultivated background. Introgression of this number of QTLs by MAS would not be difficult even though the precise locations of QTLs are not known (Dudley 1993; Sughroue and Rocheford 1994; Foold et al. 1997). This study identified several genomic regions on sorghum chromosomes with a significant association with greenbug resistance and tolerance. The results also revealed that resistance and tolerance were polygenically controlled, and can be used for the marker-assisted selection and breeding of greenbug-tolerant sorghum.

**Acknowledgements** This research was supported by a grant from the Plant Biotechnology Center at Kansas State University, Manhattan, Kansas.

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