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Genetic relationships between resistance to stalk-tunneling by the European corn borer and cell-wall components in maize population B73×B52

Abstract The objective of this study was to assess the relationships among quantitative trait loci (QTL) detected for European corn borer (ECB) tunneling and cell-wall components (CWC) neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) content in leaf-sheath and stalk tissues in a maize recombinant inbred line population derived from inbred lines B73 and B52. Most of the QTL for ECB resistance (10/13) were at QTL positions for one or more CWC. Of the 12 QTL for NDF and ADF in leaf-sheaths, five for each trait were at or near QTL for ECB tunneling. Four of these five QTL for NDF and ADF mapped to common locations. Four of the eight leaf-sheath ADL QTL were detected in the same genomic regions as ECB QTL. For stalk tissue, four regions contained common/overlapping QTL for ECB tunneling, NDF, and ADF. Six such regions were observed for stalk ADL and ECB tunneling. Seven of the ten QTL associated with both CWC and ECB tunneling contributed to the negative correlations observed between these traits, while relatively few QTL effects were positively correlated. This suggests that while CWC contribute to ECB resistance in this population, other mechanisms and other genes also are involved. Several QTL contributing to the negative correlations between ECB tunneling and CWC in the leaf-sheaths mapped to similar positions as QTL detected in tropical maize populations for resistance to leaf-feeding by *Diatraea grandiosella* Dyar and *Diatraea saccharalis* Fabricus. These regions may contain genes involved in the synthesis of cellulose, hemicellulose, and lignin in the leaf-blades and leaf-sheaths of maize.

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Introduction

Some cell-wall components (CWC), such as neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin, of maize leaf-sheaths and stalks have been associated with resistance to stalk-tunneling by the European corn borer (ECB) (*Ostrinia nubilalis* Hübner) (Coors 1987; Beeghly et al. 1997). These associations were confirmed in analyses that measured the correlated response to selection for resistance to ECB larvae feeding on the leaf-blade, leaf-sheath, collar, and stalk and the levels of these CWC in the tissues. Increases in the levels of NDF, ADF, cellulose, and lignin in leaf-sheaths were observed to correspond to increased resistance to ECB feeding on that tissue (Klenke et al. 1986; Coors 1988; Buendgen et al. 1990). Also, correlated responses in ECB feeding on stalks and leaf-sheaths were observed after one cycle of divergent selection for NDF and lignin content in those tissues (Ostrander and Coors 1997).

The relationship between the different CWC and resistance to the ECB varies among maize populations. For example, the populations WFISIHI and WIFISILO, which were created by divergent selection for leaf-sheath ADF, lignin, and silica contents, have a similar resistance to stalk-tunneling (Coors 1988; Buendgen et al. 1990). Nevertheless small negative genetic correlations were estimated between stalk-tunneling by the ECB and the CWC NDF, ADF, and lignin content of leaf-sheaths and stalks in S_1 families of these

and other maize populations (Beeghly et al. 1997). Additional divergent selection studies in these populations also produced contradictory results. After two cycles of selection for reduced NDF and lignin in the stalk and leaf-sheath in WFISILO, there was an increase in ECB leaf-sheath damage and tunneling (Ostrander and Coors 1997). However, changes in the resistance to ECB feeding on leaf-sheaths and stalks were not observed after two cycles of selection for increased NDF and lignin content of stalks and leaf-sheaths in WFISIHI (Ostrander and Coors 1997).

Rojanaridpiched et al. (1984) and Coors (1987, 1988) attempted to identify which CWC were most important for resistance to ECB tunneling. They did this by developing multiple regression equations to predict ECB damage based on levels of different CWC. This approach is effective when the independent variables are not highly correlated. Problems with regression methods occur, however, when at least one linear function of the independent variables is approximately equal to zero (Rawlings 1988). For example, a high correlation between two independent variables indicates a high dependency and that a linear function involving those variables can be found which will be close to zero. Whenever independent variables are highly collinear, their relative importance cannot be determined using either ordinary least-squares or biased regression methods since the data are inadequate for this purpose (Rawlings 1988). While Rojanaridpiched et al. (1984) and Coors (1987, 1988) did not address the possibility of correlations among CWC (their independent variables), several investigators have reported high genetic and phenotypic correlations among some CWC (Wolf et al. 1993; Jung and Buxton 1994; Marvin et al. 1995; Beeghly et al. 1997; Cardinal et al. 2003).

The primary objective of this study was to improve our understanding of the genetic relationship between stalk-tunneling by the ECB and CWC in a biallelic maize population. The population used to study these relationships was a recombinant inbred line (RIL) population from the cross of inbred lines B73 and B52. Since CWC were highly correlated in this population (Cardinal et al. 2003), regression methods will not be useful in understanding the association between specific CWC and ECB tunneling. In this situation, comparisons of quantitative trait loci (QTL) detected for CWC and ECB tunneling in the same maize population provide a more direct approach to understand the relationship between CWC and ECB tunneling. Consequently, additional objectives of this study were to (1) compare QTL locations and the effects of CWC and ECB tunneling previously reported by Cardinal et al. (2001, 2003) in order to elucidate the genetic relationships between them, and (2) compare these locations with QTL for resistance to other insect pests detected in other maize populations.

Materials and methods

Phenotypic data

The development of the population, description of the experiments, ECB (*Ostrinia nubilalis* Hübner) infestation methodology, ECB tunneling measurements, CWC determination and analysis are described in detail in Cardinal et al. (2001, 2003). Briefly, a recombinant inbred population was derived from the cross of maize inbred lines B73 and B52. B73 is susceptible to stalk-tunneling by the ECB and has lower NDF, ADF, and lignin content values than B52 (Cardinal et al. 2001, 2003). B52 is highly resistant to leaf-sheath feeding and stalk-tunneling by the ECB.

Two hundred RILs and parental lines were planted in single-row plots with two replications in two locations in 1997 and 1998. In 1998, 14 RILs were not grown in the experiments because their genotypic data indicated that they were contaminated. Plot sizes, seeding rates, experimental design, field management practices, and trait measurements are reported in Cardinal et al. (2001).

The ECB infestation and tunneling measuring protocols used in this study were reported by Cardinal et al. (2001). Six plants from each plot were infested with ECB larvae when 50% of the RILs were shedding pollen. Anthesis date and plant height were also recorded (Cardinal et al. 2001). ECB tunneling was measured 45–50 days following larvae application by splitting the stalks longitudinally and measuring all of the tunnels in the stalks from the soil surface to the second node below the tassel. Only the longest tunnel was recorded when parallel tunnels were observed. Holes in the stalk were counted as 1-cm-long tunnels. Two centimeters were added to the total length of a tunnel when the top of the plant was missing (Cardinal et al. 2001).

The trait 'ECB tunneling' was defined as the average total tunnel length per plant of the infested plants in a plot (Cardinal et al. 2001).

Stalk and leaf-sheath tissue sampling and CWC laboratory analysis techniques were reported by Cardinal et al. (2003). Four internodes (one below and three above the primary grain-bearing ear) and their leaf-sheaths were harvested from the last three non-ECB-infested plants of each plot for CWC analysis 8–12 days after the first larvae application. A detailed description of the sample processing, NIR analysis, and sequential detergent analysis to determine NDF, ADF, and ADL levels is provided in Cardinal et al. (2003). The samples were dried at 60°C, ground to particles less than 1 mm in size and scanned through a near-infrared reflectance spectrophotometer (NIRS) (model NIRS6500; FOSS NIR System, Eden Prairie, Minn,). Calibration sets were selected for each tissue type and year. These samples were analyzed in triplicate for NDF, ADF, and ADL following the ANKOM filter bag method of fiber analysis (Anonymous 1998a, b, c; Cardinal et al. 2003).

NIRS prediction equations were developed separately for NDF, ADF, and ADL for each tissue type and year using modified partial least-squares as described previously (Shenk and Westerhaus 1991; Cardinal et al. 2003). NDF, ADF, and ADL values were predicted for all samples and used in the analysis of the data (Cardinal et al. 2003). The traits "SHNDF", "SHADF", and "SHADL" were defined as the predicted NDF, ADF, and ADL content (in grams per kilogram), respectively, in the leaf-sheaths. The traits "STNDF", "STADF", and "STADL" were defined as the predicted NDF, ADF, and ADL contents (in grams per kilogram), respectively, in the stalks.

Least-squares means across environments for 183 RILs were estimated for each trait to use in QTL analysis reported by Cardinal et al. (2001, 2003). In this study, least-squares means for each RIL in each environment were used as the data for a multivariate analysis of variance analysis (PROC GLM) (SAS Institute 1990), which considered the RILs and environments to be random effects, to estimate entry-mean phenotypic and genotypic correlations among CWC and ECB tunneling (Cardinal et al. 2001, 2003). The parental lines and the contaminated RILs were eliminated from the data set for estimation of correlations (Cardinal et al. 2001, 2003). Approximate standard errors of the genetic correlations were estimated (Mode and Robinson 1959).

Genotypic data

One hundred eighty-three RILs were genotyped at 161 restriction fragment length polymorphism (RFLP) and simple sequence repeat (SSR) loci. A genetic linkage map was developed and was used in the QTL analysis published by Cardinal et al. (2001, 2003). Linkage analysis was performed with MAPMAKER/EXP ver. 3.0 (Lander et al. 1987). Loci were assigned to linkage groups (LGs) with a minimum LOD score of 3.0 and a maximum Haldane distance of 40 cM. A combination of three-point and multiple-point linkage analysis performed with ORDER, COMPARE, TRY, and RIPPLE commands were used to determine the "best" local locus orders for each LG.

QTL mapping

QTL analysis and methodology have been described (Cardinal et al. 2001, 2003). Composite interval mapping (CIM; Zeng 1994) was conducted with PLABQTL ver. 1.1 (Utz and Melchinger 1996) and QTL CARTOGRAPHER ver. 1.13 (Basten et al. 1999). The programs were used as searching tools for QTL that would be subsequently evaluated in a multiple regression model (Cardinal et al. 2001, 2003). QTL detected by either program were integrated in a single multiple regression model by PLABQTL. Model selection was performed by backward and forward stepwise regression using the AIC value to choose the best model (Jansen 1993; Cardinal et al. 2001, 2003).

QTL for ECB tunneling and CWC have been discussed in Cardinal et al. (2001, 2003). In this article, their genomic positions are compared, and phenotypic and genotypic correlations between ECB and CWC are evaluated in an attempt to further our understanding of the basis of native resistance to ECB in maize. To facilitate comparisons among linked QTL, we considered that two QTL overlapped when they were separated by less than 20 cM (Visscher 1996; Melchinger et al. 1998).

Results and discussion

All CWC (SHNDF, SHADF, SHADL, STNDF, STADF, STADL) were significantly negatively correlated, phenotypically and genetically, with ECB tunneling (Table 1). These negative correlations indicate that an increase in each CWC was associated with a decrease in ECB tunneling and, consequently, with an increase in ECB tunneling resistance. The highest genotypic correlations were between SHADF and ECB tunneling and between STADL and ECB tunneling (Table 1). The values of the correlations between ECB tunneling and the CWC estimated in this population are within the range observed in other maize populations (Beeghly et al. 1997).

Most (10/13) QTL detected for resistance to ECB tunneling are at, or linked to, regions associated with variation for one or more CWC (Fig. 1) (Cardinal et al. 2001, 2003). A comparison of genomic locations of QTL detected for ECB tunneling (across environments and for individual environments; Cardinal et al. 2001) and SHNDF (Cardinal et al. 2003) showed that five QTL are common to both traits (Fig. 1). Four of these five QTL contributed to the negative correlation among these traits, but the QTL effects for ECB tunneling and SHNDF on chromosome 7 (UMC59-UMC35) were positively correlated (i.e., the alleles that increased the value of ECB tunneling and SHNDF were inherited from the same parent) (Cardinal et al. 2001, 2003). Similarly, five QTL were detected in the same locations for both SHADF and ECB tunneling, four of which were at the same positions as for SHNDF. Four common QTL contributed to the negative correlation between SHADF and ECB tunneling. The QTL effects (UMC59-UMC35) for SHADF and ECB tunneling on chromosome 7, however, were positively correlated. Four QTL were detected in the same genomic positions for both SHADL and ECB tunneling (Fig. 1). The QTL effects (UMC81) for SHADL and ECB tunneling on chromosome 9 were positively correlated.

For stalk CWC, four QTL were detected for ECB tunneling, STNDF, and STADF in the same genomic locations. Two QTL were located on each of chromosomes 2 and 5 (Fig. 1). The effects of two QTL on

Table 1 Genotypic and phenotypic correlations on an entry-mean[a] basis for ECB tunneling and CWC in recombinant inbred lines of maize population B73×B52

SHNDF	SHADF	SHADL	STNDF	STADF	STADL
Genotypic correlations[b]					
ECB					
−0.326 (0.078)	−0.436 (0.072)	−0.267 (0.084)	−0.368 (0.075)	−0.364 (0.075)	−0.438 (0.072)
Phenotypic correlations[c]					
ECB					
0.283 (0.067)	−0.376 (0.063)	−0.209 (0.070)	−0.316 (0.066)	−0.312 (0.066)	−0.367 (0.063)

[a]SHNDF, Leaf-sheath neutral detergent fiber; SHADF, leaf-sheath acid detergent fiber; SHADL, leaf-sheath acid detergent lignin; STNDF, stalk neutral detergent fiber; STADF, stalk acid detergent fiber; STADL, stalk acid detergent lignin

[b]Genetic correlations were estimated from data gathered over 2 years, on two locations per year, and two replications per location. Standard errors are in brackets

[c]Phenotypic correlations were estimated from data gathered over 2 years, on two locations per year, and two replications per location. Standard errors are in brackets

chromosomes 2 (bnlg108) and 5 (UMC54-phi087) were positively correlated between each stalk fiber component (STNDF or STADF) and ECB tunneling (Cardinal et al. 2001, 2003). Four of six QTL detected for both STADL and ECB tunneling contributed to the negative correlation between these traits (Fig. 1). The effects of two QTL for STADL and ECB tunneling, one on chromosome 5 (UMC54-phi087) and one on chromosome 8 (UMC7-phi080), were positively correlated.

Two mechanisms by which an increase in CWC concentrations could cause reduced ECB tunneling have been proposed. First, an increase in fiber and lignin concentration may increase the bulk density in the diet of the ECB, which would reduce available nutrients and available energy and, consequently, reduce ECB larvae growth, and, ultimately, reduce tunneling (Bernays 1986; Beeghly et al. 1997; Coors 1988; Buendgen et al. 1990). Second, leaf toughness caused by a high concentration of CWC is associated with resistance to ECB feeding (Bergvinson et al. 1994). If these mechanisms are valid, QTL alleles that increase CWC should have a pleiotropic effect on ECB tunneling.

Although 10 out of the 13 QTL detected for ECB tunneling were associated with at least one CWC, the genetic effects at only seven QTL for ECB were consistent with a negative correlation between ECB tunneling and a CWC. Those QTL detected for both ECB tunneling and CWC at which the QTL effects were positively correlated are not expected to be involved in the proposed mechanisms of action. Only one-half of the genetic variance was explained by QTL for ECB tunneling and only half of these were negatively associated with QTL for CWC content. Therefore, other mechanisms for resistance to ECB tunneling must also be important in this population. Other possible candidate mechanisms contributing to ECB resistance are 2,4-dihydroxy-7-methoxy-1,4,-benzoxazin-3-one (DIMBOA) and silica contents of the leaf-sheaths, which have been associated with ECB tunneling in previous studies (Rojanaridpiched et al. 1984; Coors 1987). However, DIMBOA is expected to have a minor role in ECB tunneling resistance in this population because B52 has a low concentration of DIMBOA (Klun and Robinson 1969; Rojanaridpiched et al. 1984). Also, the *bx* genes involved in DIMBOA biosynthesis have been mapped to bin 4.01, and this region did not contain any QTL for ECB tunneling in this population (Frey et al. 1997).

Lignin may be the most important CWC associated with resistance to ECB tunneling since five of seven QTL contributing to negative correlations between ECB tunneling and a CWC involved lignin in the sheaths, stalks, or both as one of the CWC. Leaf-sheath NDF and ADF seem to be the second most important CWC associated with ECB resistance since five of the seven QTL having negative correlations between ECB tunneling and a CWC involved either SHNDF, SHADF, or both.

Several genomic regions contributing to a negative correlation between ECB tunneling and CWC content have also been shown to be associated with ECB tunneling in other maize populations (Jampantong et al. 2002; Krakowsky et al. 2002; Lee 1993). The genomic region on chromosome 3 (dupssr5) was associated with ECB tunneling in the B73×De811 maize population (Lee 1993; Krakowsky et al. 2002). This region is also associated with all three CWC in the leaf-sheaths and lignin content in the stalks in this study. The region on chromosome 9 (UMC81) was associated with ECB tunneling in MO17×B52 and B73×Mo47 maize populations (Lee 1993). This region is associated with leaf-sheath NDF and ADF content. Finally, the region on chromosome 5 (BNL10.12-UMC54) associated with SHNDF and ECB tunneling in this study was also associated with ECB tunneling and leaf-blade damage caused by the ECB in the B73×Mo47 population (Jampantong et al. 2002).

Three QTL for leaf damage by ECB, each detected in two different studies, were located in regions associated with QTL for ECB tunneling in the B73×B52 RI population (Cardinal et al. 1998, 2001; Jampantong et al. 2002). QTL for leaf-sheath CWC contents were detected in these same regions (Cardinal et al. 2003). The QTL on chromosome 5 (BNL10.12-UMC54) was detected both in the current study and in the B73×Mo47 populations (Jampantong et al. 2002). Two QTL on chromosomes 9
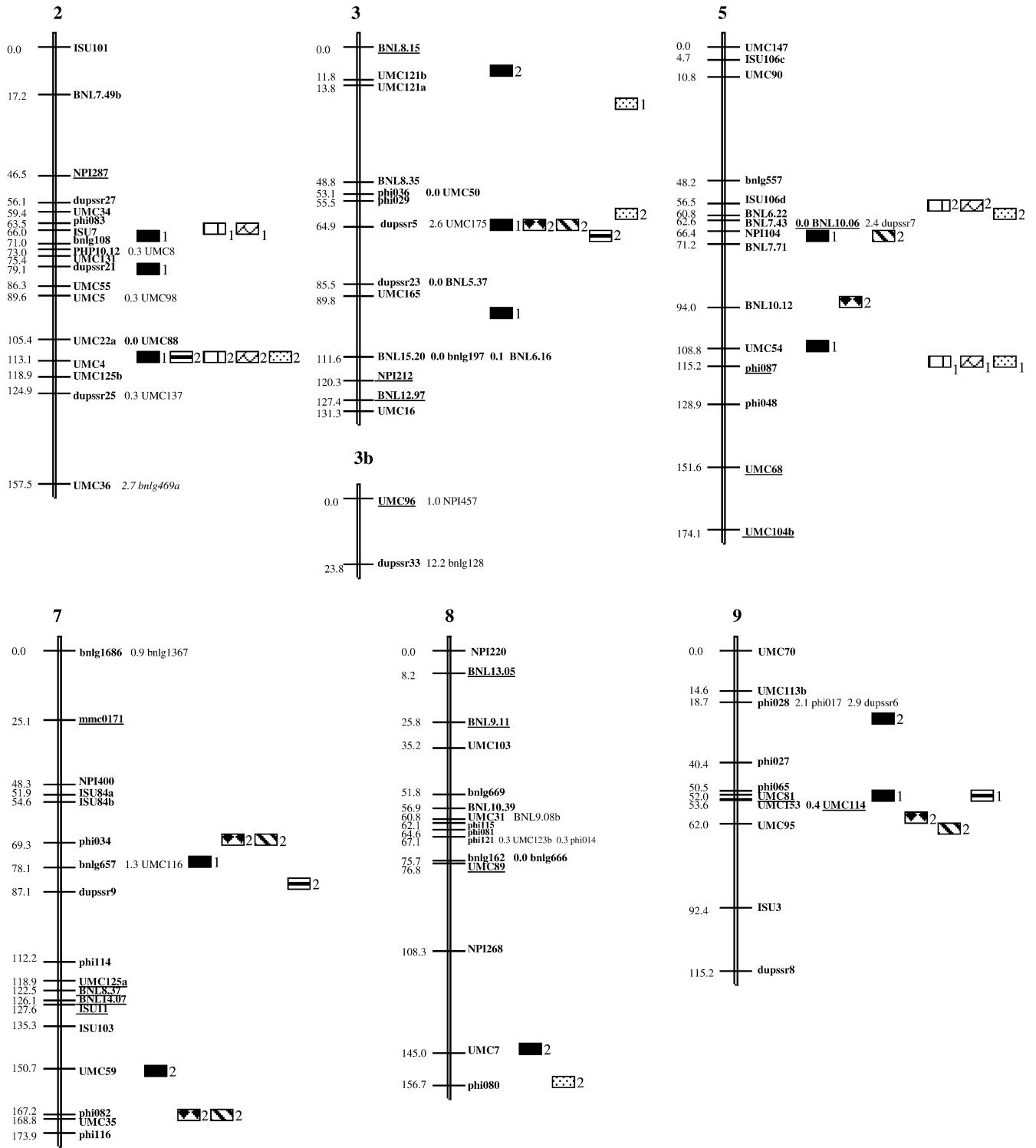
Fig. 1 Positions of ECB and CWC QTL and the linkage map of a B73×B52 RIL maize population (modified from Cardinal et al. (2001, 2003). Chromosome *number* is indicated at the *top* of each LG that contained a QTL, RFLP loci are in *uppercase letters*, SSR loci are in *lowercase letters*. *Underlined loci* indicate segregation distortion (*P* < 0.001). Loci placed at LOD < 2.0 are in *italics*. Values to the *left* of each LG indicates a locus position in centiMorgans. *Boxes* to the *right* of each LG indicate the position of a QTL. The *pattern of the box* indicates the trait: *solid black* ECB tunneling, *white diamond*, *black background* SHNDF, *black diagonal stripes* SHADF, *horizontal black and white stripes* SHADL, *vertical black lines on white background* STNDF, *broken hatching* STADF, *black dot on white background* STADL. The parental allele associated with an increase of the value of the trait at a given QTL is indicated by *1* = B73 and *2* = B52 to the *right* of each *box*

(UMC114) and 7 (bnlg657) were detected both in the current study and in the Mo17×H99 population (Cardinal et al. 1998).

In tropical maize, fiber and cell-wall phenolic contents of the leaf-blades may be involved in leaf-feeding resistance to sugarcane borer (SCB; *Diatraea saccharalis*) and southwestern corn borer (SWCB; *Diatraea grandiosella*) (Bonn et al. 1996; Cardinal et al. 2001). Several QTL for ECB tunneling resistance in the B73×B52 population coincide in their genomic position with QTL affecting resistance to leaf-feeding by SWCB and SCB in tropical maize populations (Bonn et al. 1996, 1997; Groh et al. 1998; Khairallah et al. 1998; Willcox et al. 2002; Cardinal et al. 2001). QTL on chromosomes 2 (UMC4), 5 (NPI104), and 7 (bnlg657) were detected for resistance to SCB in a tropical population (Bonn et al. 1996) and for resistance to ECB tunneling and for at least one leaf-sheath CWC in our study (Cardinal et al. 2001, 2003). QTL on chromosomes 2 (UMC4), 3 (dupssr5), 5 (UMC54), 7 (bnlg657), and 9 (UMC81) were detected for resistance to leaf feeding by SWCB or SCB in Bonn et al. (1997) and for ECB tunneling and at least one leaf-sheath CWC (Cardinal et al. 2001, 2003). A QTL on chromosome 9 (UMC81) was detected for resistance to SWCB, for ECB tunneling, and for SHNDF and SHADF (Willcox et al. 2002; Cardinal et al. 2001, 2003). Finally, QTL on chromosomes 5 (UMC54), 7 (bnlg657), and 9 (UMC81) were detected for resistance to SWCB or SCB in Groh et al. (1998) and for ECB tunneling and at least one sheath-leaf CWC herein.

The QTL on chromosome 5 (UMC54) was also reported to confer resistance to SWCB (Khairallah et al. 1998). All genomic regions except one associated with QTL for ECB tunneling in the B73×B52 population and for leaf-blade feeding of SCB and/or SWCB in tropical maize populations were associated with at least one CWC of the leaf-sheaths. This provides further evidence that CWC very likely are a mechanism of resistance to leaf-blade feeding in other corn borer species in tropical maize. Some of these regions may contain genes that are involved in hemicellulose, cellulose, and lignin synthesis early in the development of the leaf blades as well as later in the leaf-sheaths. For example, a putative cellulose synthase gene (ZmCesA-3) was mapped near UMC22a-UMC4 (Holland et al. 2000). Three putative cellulose synthase genes (ZmCes-A-4, ZMCesA-8, and ZmCesA-9) mapped to chromosome 7 (7.01 and 7.02) near QTL for SHNDF and SHADF in this study (Holland et al. 2000). Finally, the brown midrib mutation in maize (*bm1*) maps to bin 5.04 close to QTL near BNL7.43. The *bm1* mutants have reduced lignin content and reduced cinnamyl alcohol dehydrogenase activity (Bauchner et al. 1998).

QTL comparisons between different traits typically cannot distinguish pleiotropy from tight linkage if the positions of the QTL overlap. Either QTL for different traits in repulsion-phase linkage or QTL with pleiotropic effects on ECB tunneling and CWC content could cause the observed results. Fine-mapping of genomic regions containing such associations could provide evidence in favor of one or the other of the genetic explanations. This approach has been successful in resolving questions on QTL effects and heterosis for maize grain yield components (Graham et al. 1997).

The distribution of QTL for ECB tunneling and CWC in this population indicates that, despite the overall negative genetic correlation, it is possible to select for both decreased CWC and ECB tunneling, since several genomic regions were positively correlated for these traits. This is the goal of forage maize breeding programs—improving forage quality (i.e., decrease CWC content) and increasing or maintaining resistance to ECB tunneling at the same time. To achieve this goal, marker-assisted selection for particular combinations that would decrease CWC and ECB tunneling simultaneously would likely be more effective than phenotypic selection, and the selection for QTL with only small negative correlations could also contribute. For example, selection for lines that are homozygous for the B73 allele at the QTL on chromosome 2 near UMC4 is predicted to decrease the NDF content in stalks by 19.46 g kg^{-1} dry matter (2× additive effect) and increase ECB tunneling by only 2.6 cm (Cardinal et al. 2001, 2003). Thus, a knowledge of QTL effects and positions on unfavorably correlated traits is a useful tool for breeding and may improve our understanding of correlations among complex traits.

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