

# Natural Variation in Maize Defense against Insect Herbivores

L.N. MEIHLS,<sup>1</sup> H. KAUR,<sup>1</sup> AND G. JANDER

*The Boyce Thompson Institute for Plant Research, Ithaca, New York 14853-1801*

*Correspondence: jander@cornell.edu*

Genetic mapping projects with maize (*Zea mays*) have resulted in the identification of numerous quantitative trait loci (QTL) that influence resistance to insect herbivores. However, the underlying genetic basis of these QTL has been confirmed in only a small number of cases. Recent advances in genome sequencing, the development of large mapping populations, and advances in reverse genetic approaches will accelerate the discovery of novel herbivore resistance genes in maize. Areas that will merit particular research emphasis are natural variation in maize resistance to rootworms and phloem-feeding insects as well as the identification of previously unknown loci involved in the biosynthesis of maize defensive secondary metabolites.

Maize (*Zea mays*) is the world's most productive grain crop, with ~816 million metric tons harvested in 2011 (NCGA 2011). Both biotic and abiotic stress factors can severely limit maize yield (Machado et al. 2002). World-wide, 6% to 19% of global maize production is lost due to insects and other herbivores (Oerke 2006). Therefore, increased herbivore resistance has been the target of extensive research involving both classical breeding and transgenic approaches.

Most maize traits of agronomic importance are quantitative; they exhibit a range of phenotypes and are often under the control of several genes. The availability of molecular markers and the construction of linkage maps permit the identification of chromosomal regions containing quantitative trait loci (QTL) influencing traits of interest. Once identified, associated molecular markers may be used in marker-assisted breeding or for eventual gene identification. This form of forward genetics has been used since the early 1990's to map maize resistance to herbivores, pathogens, and abiotic stresses (McMullen and Simcox 1995). Current review articles describing QTL contributing to maize disease resistance (Wisser et al. 2006) and other agronomic traits (Tuberosa et al. 2003; Buckler et al. 2009; Brown et al. 2011) are available. However, there are few recent reviews of maize QTL related to insect resistance and associated traits (McMullen et al. 2009a). Therefore, this article seeks to summarize available information about maize insect resistance QTL and discuss these data in the context of the maize genome sequence.

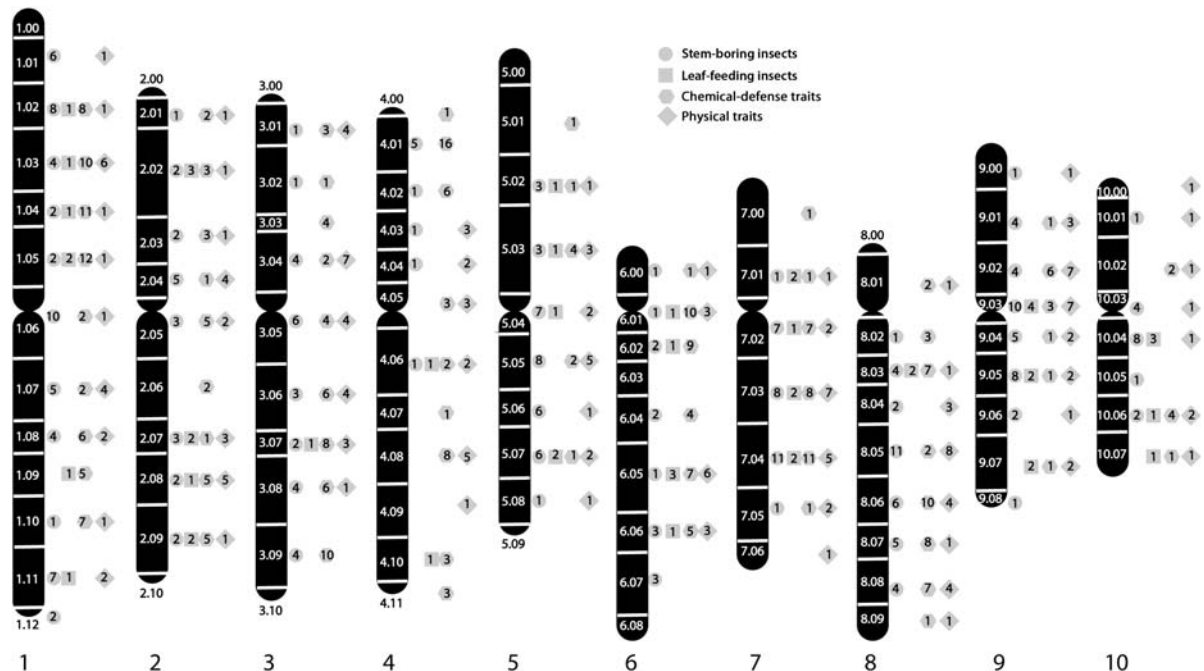
## MAPPING QUANTITATIVE TRAIT LOCI IN MAIZE

The natural diversity of maize germplasm is a valuable resource for investigating the genetic basis of phenotypic

variability. Traditional genetic approaches, as well as the introgression of chromosome segments from breeding lines that exhibit extreme variation in the trait of interest, have proved to be excellent tools for mapping novel insect resistance genes in maize cultivars. Such approaches have significantly advanced our basic scientific knowledge of insect resistance in maize and will allow us to develop more resistant maize lines. In particular, QTL mapping is a useful genetic tool for linking the trait of interest to genes that control phenotypic variation. In maize, each of the 10 chromosomes is divided into 8 to 12 "bins" (Fig. 1). A bin is a small section of approximately 20 cM (maize has 100 bins) and is designated by the respective chromosome number followed by a two-digit decimal (Gardiner et al. 1993). Each bin is defined by specific molecular markers on either side. Before the advent of large molecular marker sets and genome sequences, most genetic mapping was done at the bin level.

Extensively genotyped sets of inbred lines have been developed to assist in mapping maize quantitative traits. For instance, the IBM population of 304 lines, which was created by intermating B73 and Mo17 for four generations, followed by six generations of inbreeding (Lee et al. 2002), has been genotyped with thousands of molecular markers (Coe et al. 2002; Sharopova et al. 2002; Ganai et al. 2011). More recently, a diversity panel of 282 maize inbred lines and a large nested association mapping (NAM) population (Flint-Garcia et al. 2005; Yu et al. 2008; McMullen et al. 2009b) have been genotyped. The NAM population consists of ~5000 recombinant inbred lines that were made by crossing a genetically diverse population of 25 maize inbred lines to B73. From each of the crosses, 200 recombinant inbred lines (RILs) were developed by single-seed descent for at least six generations. All of the NAM lines have been genotyped with thousands of markers, resulting in a very dense genetic map. Numerous agronomically relevant maize

<sup>1</sup>These authors contributed equally to this work.



**Figure 1.** The 10 maize chromosomes showing locations of QTL that contribute to insect resistance. Mapped QTL from studies of stem-boring insects (circles), leaf-feeding insects (squares), chemical-defense traits (hexagons), and physical traits (diamonds) are indicated. Numbers within the shaded symbols indicate the number of QTL that has been identified in each bin. All QTL are positioned relative to molecular markers of the B73 genome.

traits have been mapped using this population, including kernel composition (Cook et al. 2012), inflorescence structure (Brown et al. 2011), flowering time (Buckler et al. 2009), aluminum tolerance (Krill et al. 2010), leaf architecture (Tian et al. 2011), abscisic acid levels (Setter et al. 2011), seed carotene content (Yan et al. 2010), and isocitrate dehydrogenase activity (Zhang et al. 2010).

### INSECT HERBIVORES THAT FEED ON MAIZE

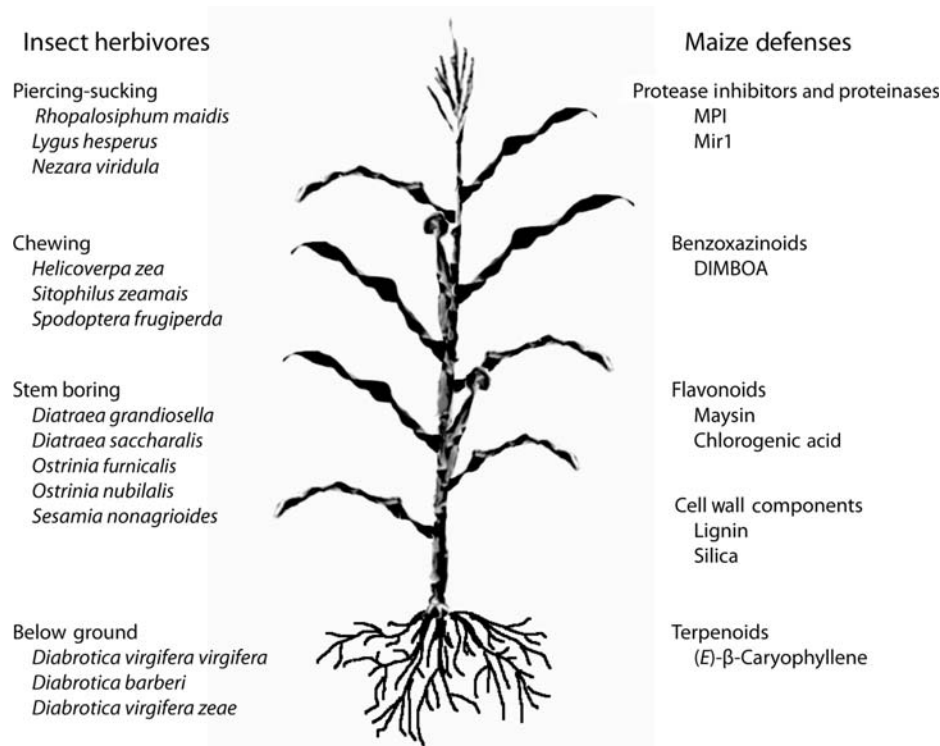
More than 90 insect species are known to feed on cultivated maize (Steffey et al. 1999). Virtually every part of the plant, from its roots to the tassel, is consumed by one or more insect pests (Fig. 2). Maize-feeding insects belong to different feeding guilds and can be broadly divided into four groups: leaf feeders, stem borers, phloem feeders, and root feeders.

Leaf feeders cause damage to the above-ground foliar and reproductive tissue of the plant. Fall armyworm (*Spodoptera frugiperda*), beet armyworm (*Spodoptera exigua*), corn earworm (*Helioverpa zea*), and grasshoppers (*Melanoplus* spp) feed on the whorls of young maize plants, producing small holes and irregular notching of the leaf margins. Heavy infestations of these pests can result in complete defoliation of the plant, leaving only the mid ribs. Excessive loss of photosynthetically active tissue inhibits the growth of the maize plants and causes severe reduction in grain yield. The female moths of fall armyworm and corn earworm are attracted to the silk of

maize plants for oviposition. Larvae remain within the husk of the ear, feeding on silk and developing kernels. Some herbivores, for instance the maize weevil (*Sitophilus zeamais*), feed almost exclusively on developing or mature kernels.

Stem borers, including the southwestern corn borer (*Diatraea grandiosella*), sugarcane borer (*Diatraea saccharalis*), Asian corn borer (*Ostrinia furnacalis*), European corn borer (*Ostrinia nubilalis*), and Mediterranean corn borer (*Sesamia nonagrioides*), damage maize by boring tunnels within the stems of the plant. Corn borers usually have two or more generations per year in the United States. Newly hatched corn borer larvae of the first generation feed on young whorl leaves of maize plants. As later instars, these larvae bore tunnels into the stalks to complete their development. In the second generation, newly hatched larvae feed on leaves, pollen, and ear tips. Later instars then tunnel into the stalks, leaf mid ribs, and ear shanks. Tunneling damages the vascular tissue, disrupts water and nutrient movement, provides sites for pathogen infection, and may cause stem lodging or breakage. This damage collectively causes serious yield losses in maize fields.

Phloem feeders are piercing-sucking insects that obtain nutrients from phloem sap of all above-ground plant tissues. Aphids typically found on maize include the corn leaf aphid (*Rhopalosiphum maidis*), greenbug (*Schizaphis graminum*), and bird cherry-oat aphid (*Rhopalosiphum padi*). Heavy infestations can cause wilting, curling, and discoloration of leaves. Aphid honeydew, a highly viscous, sugary liquid, coats surfaces of leaves,



**Figure 2.** Maize insect pests and plant defenses that can counteract them.

tassels, and silks. Mold growing abundantly on aphid honeydew can make it turn black, thereby lowering the photosynthetic efficiency of the affected leaves. Aphid-infested tassels fail to disseminate pollen, resulting in yield losses due to decreased pollination (Everly 1960; Carena and Glogoza 2004). In addition to the direct effects of reduced photosynthesis and removal of phloem liquid, aphids also transmit potentially damaging plant viruses (Carena and Glogoza 2004). Similar to aphids, western plant bug (*Lygus hesperus*) and southern green stink bug (*Nezara viridula*) also feed on phloem sap from all above-ground maize tissues.

Maize roots are attacked by a complex of *Diabrotica* species, including the western (*Diabrotica virgifera virgifera*), northern (*Diabrotica barberi*), and Mexican (*Diabrotica virgifera zea*) corn rootworms. Larvae of rootworms damage the roots of the maize plants, reducing the water and nutrient uptake and making plants more susceptible to lodging (Levine and Oloumi-Sadeghi 1991). In large numbers, adults can reduce pollination by feeding on maize silks (Culy et al. 1992).

## PLANT RESISTANCE MECHANISMS

Plant resistance to insect herbivory can be broadly categorized as antibiosis, antixenosis, or tolerance. Resistance is categorized as antibiosis if there is a negative effect on insect growth and/or reproduction. In contrast to antibiosis, plants exhibiting antixenosis do not negatively affect insect biology but instead are less attractive

hosts, leading to a delay in feeding or rejection of the host plant. Plants are described as tolerant when they are fed upon by insect pests but recover from the damage without measurable yield loss. In the majority of insect-resistant plants, antibiosis occurs together with either antixenosis or tolerance.

Antibiosis in maize can result from either chemical (e.g., secondary metabolites) or morphological (e.g., changes in plant tissue composition or structures) mechanisms (Widstrom and Snook 2001; Bushman et al. 2002; Szalma et al. 2002; Schnee et al. 2006; Frey et al. 2009; Ahmad et al. 2011; Schmelz et al. 2011). Plant volatiles, acting as an indirect defense through the attraction of natural enemies, are produced by maize in response to rootworms (Degenhardt et al. 2009), aphids (Du et al. 1998; Powell et al. 1998; Guerrieri et al. 1999), and lepidopteran herbivores (Turlings et al. 1998). Morphological traits such as lignin content and husk tightness are constitutive and typically do not change in response to insect feeding. Other morphological traits such as formation of callose, which plugs sieve elements and reduces phloem transport, can be induced locally upon aphid feeding.

Maize antixenosis has been demonstrated in the western corn rootworm (Bernklau et al. 2010), planthoppers (Costamagna et al. 2005), and European corn borer (Robinson et al. 1978). In some instances, trade offs in maize antixenosis have been identified, whereby the activation of a defense mechanism against one herbivore or pathogen makes the plant more attractive than another (Ballhorn 2011).

## SPECIFIC MAIZE DEFENSE SYSTEMS

### Benzoxazinoids

Benzoxazinoids, a class of defensive secondary metabolites found in grasses (Zúñiga et al. 1983), are among the best-studied maize chemical defenses. Abundance of benzoxazinoids tends to be highest in seedlings and decreases as the plants mature (Cambier et al. 2000). Both in vivo and in vitro assays demonstrate that benzoxazinoids provide defense against a wide variety of pathogens and herbivores (Niemeyer 1988). In most maize varieties, the predominant benzoxazinoid is DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one), which is stored in an inactive form as DIMBOA-glucoside (DIMBOA-Glc) (Fig. 3). The entire pathway for the biosynthesis of DIMBOA-Glc from indole in maize has been elucidated using a variety of biochemical and genetic approaches (Frey et al. 1995, 1997, 2003; Gierl and Frey 2001; von Rad et al. 2001; Jonczyk et al. 2008). Nine genes (*bx1*–*bx9*) catalyze successive steps in the pathway, with only the function of the last enzyme, a glucosyltransferase, being encoded by two partially redundant genes (*bx8* and *bx9*) (von Rad et al. 2001). With the exception of *bx9*, which is on chromosome 1, all of the *bx* genes are located in a small segment of maize chromosome 4, spanning a genetic distance of only 6 cM (bin 4.01 in Fig. 1) (Gierl and Frey 2001).

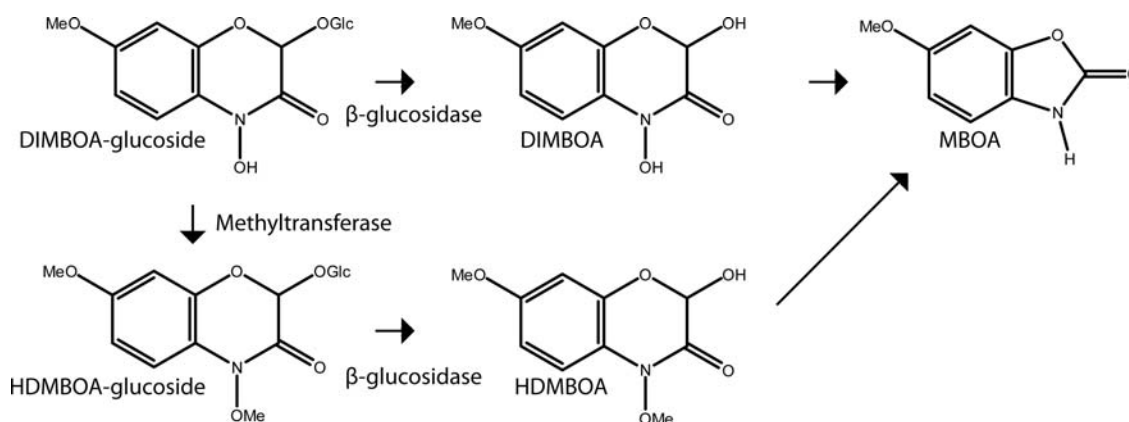
Tissue maceration during insect feeding brings vacuolar DIMBOA-Glc into contact with glucosidase, which is stored separately in the plastids and causes the release of DIMBOA (Fig. 3). Relatively slow, perhaps nonenzymatic, breakdown of DIMBOA results in the formation of an active, insect-deterrent compound called MBOA (Grambow et al. 1986). In response to caterpillar herbivory, DIMBOA-Glc is methylated to form HDMBOA (2-hydroxy-4,7-dimethoxy-1,4-benzoxazin-3-one)-Glc (Oikawa et al. 2004; Dafoe et al. 2011). HDMBOA-Glc is also activated by a glucosidase, but the conversion of HDMBOA to MBOA is more rapid than for DIMBOA.

Thus, production of DIMBOA-Glc to HDMBOA-Glc by an *O*-methyltransferase primes maize plants to respond more rapidly to subsequent caterpillar attack. Although the activity has been demonstrated enzymatically (Oikawa et al. 2002), the *O*-methyltransferases that catalyze the production of HDMBOA-Glc remain unidentified in maize and other grasses.

DIMBOA likely has multiple deleterious effects, having been found to inhibit trypsin and chymotrypsin proteases (Cuevas et al. 1990; Houseman et al. 1992), aphid cholinesterase (Cuevas and Niemeyer 1993; Escobar and Niemeyer 1993), and plasma membrane  $H^+$  ATPase (Friebe et al. 1997). Maize plants with higher levels of DIMBOA in whorl tissue are more resistant to European corn borer through increased larval mortality (Klun et al. 1967, 1970; Klun and Robinson 1969). Additionally, in a form of antixenosis, the larvae migrate away from high-DIMBOA maize varieties toward those with low DIMBOA content (Robinson et al. 1978). In the case of aphids, addition of DIMBOA to an artificial diet increases mortality, and a highly significant negative correlation was observed between in vivo maize DIMBOA content and aphid resistance (Long et al. 1977; Beck et al. 1983).

### Maysin

Maysin, a defensive C-glycosyl flavone, provides herbivore resistance in maize silk (Waiss et al. 1979; Elliger et al. 1980; Rector et al. 2003) and is synthesized via a pathway that is also the source of colored flavones in kernels and pollen. Chalcone synthase catalyzes the first committed step in the flavone biosynthesis pathway (Harborne 1988). Two maize loci, *Whp1* (*white pollen 1*) and *C2* (*colorless 2*), encode chalcone synthase and are required for maysin synthesis (Szalma et al. 2002). The *P* (*pericarp color*) locus, which encodes duplicate myb-like transcription regulators *P1* (*pericarp color 1*) and *P2* (*pericarp color 2*) (McMullen et al. 1998), is a principle regulatory locus in the flavone pathway. In silk



**Figure 3.** DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) is stored as an inactive glucoside, which is activated by coming into contact with a glucosidase through tissue damage. Likely spontaneous degradation to MBOA and other compounds leads to insect resistance. In a form of defense priming, DIMBOA-glucoside is methylated to HDMBOA-glucoside in response to insect feeding. After activation through cleavage by glucosidase, degradation of HDMBOA is more rapid than that of DIMBOA.



tissue, *C2* expression is regulated by P (Bruce et al. 2000; Bushman et al. 2002; Meyer et al. 2007), but regulation of *Whp1* remains unknown. Changes in other branches of the flavone pathway can result in increased maysin. With loss of function at *A1* (*anthocyaninless 1*), intermediates of the 3-deoxyanthocyanin pathway enter the flavone pathway, thereby increasing maysin content (McMullen et al. 2001).

### Chlorogenic Acid

Chlorogenic acid, a secondary metabolite that provides resistance against corn earworm (Cortés-Cruz et al. 2003), is a soluble phenylpropanoid-derived compound that accumulates in above-ground foliar tissue and silk in response to herbivory (Bushman et al. 2002). *PI* and *A1* mutations regulate flavonoid accumulation in maize, resulting in the production of a red cob with brown silk (Guo et al. 2010). These silk antibiotic compounds reduce corn earworm damage in the maize ear. Additionally, the *PI* locus increases the production of chlorogenic acid in the silks. Foliar chlorogenic acid accumulates in response to root abscisic acid treatment or herbivory, providing evidence of root-to-shoot communication in plant defense (Erb et al. 2009).

### Protease Inhibitors

Both protease inhibitors and proteases can be produced in response to insect damage of maize. *MPI*, a maize proteinase inhibitor gene, was shown to inhibit elastase and chymotrypsin-like protease activity in the mid gut of the Egyptian cotton leafworm (*Spodoptera littoralis*) (Tamayo et al. 2000). Feeding by the southern corn rootworm induces the activity of seven proteinase inhibitors in maize roots (Lawrence et al. 2012). In a related beetle, the western corn rootworm, proteinase inhibitors did not affect adults but, rather, acted as larval antifeedants (Kim and Mullin 2003; Bažok et al. 2005).

### Cysteine Protease

A cysteine proteinase, *Mir1*, was shown to be elevated in whorl tissue upon insect feeding (Pechan et al. 2000). *Mir1* accumulates at feeding sites, mainly in phloem of minor and intermediate veins (Lopez et al. 2007). Proteinase accumulation was correlated with reduced larval growth, possibly through damage to the peritrophic matrix of the larval mid gut (Pechan et al. 2002). It is hypothesized that *Mir1* binds chitin, localizing proteolytic activity to insect gut (Pechan et al. 2002). *Mir1* is induced within 1 h of insect feeding (Pechan et al. 2000), likely through regulation by the jasmonic acid pathway (Ankala et al. 2009).

### Ribosome-Inactivating Proteins

Ribosome-inactivating proteins (RIPs) inhibit protein synthesis by removing the purine ring from an adenine

residue of ribosomal RNA (Barbieri et al. 1993). RIPs have activity against a number of insect orders, depending on the plant origin of the RIP (Gatehouse et al. 1990; Dowd et al. 1998). In maize, two genes that encode RIP proteins (*Rip3:1* and *Rip3:2*) have been identified (Walsh et al. 1991; Bass et al. 1995), located in bins 8.05 and 7.04, respectively (Bass et al. 1995, 2004). Maize RIP1 must be proteolytically activated (Walsh et al. 1991; Bass et al. 1992; Mak et al. 2007), either during germination or through the activity of protease in insect guts (Dowd et al. 1998). RIP1 has demonstrated activity against the Indian meal moth (*Plodia interpunctella*) (Dowd et al. 1998), corn earworm (Dowd et al. 2003), cabbage looper (*Trichoplusia ni*) (Dowd et al. 1998), tobacco hornworm (*Manduca sexta*) (Dowd et al. 2003), and cigarette beetle (*Lasioderma serricorne*) (Dowd et al. 2003).

### Silica

As a component of the maize leaf blade, silica contributes to herbivore resistance by wearing down their chewing and grinding surfaces (Djain and Pathak 1967; Klein and Geis 1978; Bernays 1986). Maize plants grown in soil with high silica content experienced a 49% reduction of leaf blade damage by European corn borers (Coors 1987).

### Lignin

Lignin and other kinds of dietary fiber content promote insect resistance. Two possible causes for this observation are (1) increased bulk density of the diet, which reduces available nutrients and energy (Bernays 1986; Buendgen et al. 1990; Beeghly et al. 1997) and (2) increased leaf toughness caused by a high concentration of lignin and other cell wall components (cell-wall-bound phenolics such as *p*-coumaric acid, ferulic acid, and their derivatives) (Bergvinson et al. 1994).

## LOCALIZATION AND COLOCALIZATION OF MAIZE INSECT RESISTANCE QTL

A large number of maize inbred lines have been screened for resistance to leaf-feeding, stem-boring, piercing-sucking, and below-ground herbivores. However, to date, more QTL analyses involving RILs and other mapping populations have been completed only for leaf-feeding and stem-boring insects (Table 1). Additionally, the expression of several maize defense characteristics has been mapped as a quantitative trait (Table 2). We include older data that were generated before large molecular marker sets were available, so the location of specific QTL is shown only at the bin level in Tables 1 and 2 and in Figure 1. The majority of maize bins contain insect resistance QTL (Fig. 1), indicating that diverse insect resistance mechanisms are present in maize. Nevertheless, there seem to be concentrations of QTL in certain parts of the genome, for instance, at the top of chromosome 1, the bottom of chromosome 2, and on chromosome 7. Only 10 of 100 maize bins, mostly at

**Table 1.** Maize quantitative trait loci affecting insect resistance

Insect	Trait	Resistant parent	Susceptible parent	Mapping population	Bin(s)	Reference
<i>Diatraea grandiosella</i>	Insect resistance	CML139	Ki3	135 RILs	3.07–3.09; 5.05–5.07 (2); 6.04–6.05; 6.06; 8.02; 9.05	Khairallah et al. 1998
	Leaf damage	CML139	Ki3	135 RILs	1.03–1.04; 6.06; 8.06–8.08; 9.04; 9.05–9.06	Groh et al. 1998a
		CML67	CML131	171 F <sub>3</sub> families	1.06; 1.07; 1.11; 3.05; 5.06; 5.07; 7.02; 7.04; 9.05; 10.03–10.04	Bohn et al. 1997
		CML67	CML204	Backcross-277 families	7.04; 9.03; 10.03–10.06	Willcox et al. 2002
		CML67	CML131	170 RILs	1.01–1.02; 1.03; 1.06; 1.10; 5.05–5.06; 7.03; 8.05–8.06; 8.06–8.07; 9.02–9.04	Groh et al. 1998a
		CML67	CML131	166 test-cross progeny	1.06; 3.08–3.09; 7.03–7.04	Groh et al. 1998b
		Mp704	Mo17	230 F <sub>2:3</sub>	1.04; 1.11; 5.02; 6.02; 7.02–7.03; 9.03; 10.04	Brooks et al. 2005
		Mp704	Mo17	230 F <sub>2:3</sub> families	1.05; 1.11; 5.02; 7.02; 7.04; 8.03; 9.03; 10.04	Brooks et al. 2007
		Mp708	A619	214 F <sub>2:3</sub> families	1.02; 2.02; 5.04; 5.07; 6.05; 7.03; 9.03; 9.05	Brooks et al. 2007
		Mp708	A619	213 F <sub>2:3</sub> families	3.08; 5.04; 6.05; 9.05	Brooks et al. 2007
	Leaf toughness	CML139	Ki3	135 RILs	5.05–5.06; 8.06–8.08	Groh et al. 1998a
		CML67	CML131	170 RILs	1.06; 1.08; 4.04; 7.04–7.05; 8.06–8.07	Groh et al. 1998a
<i>Diatraea saccharalis</i>	Damage rating	CML67	CML131	171 F <sub>3</sub> families	1.11; 2.02–2.03; 5.04; 7.04; 9.02–9.03; 9.05–9.06; 10.04	Bohn et al. 1996
	Leaf damage	CML67	CML131	171 F <sub>3</sub> families	1.06; 1.07; 1.11; 3.05; 5.06; 5.07; 7.02; 7.04; 9.05; 10.03–10.04	Bohn et al. 1997
		CML67	CML131	170 RILs	1.03; 1.06; 1.11; 5.05–5.06; 7.03; 8.05–8.06; 8.06–8.07; 9.04	Groh et al. 1998a
<i>Helicoverpa zea</i>	Larval weight	GE37	FF8	250 F <sub>2:3</sub> families	1.04; 2.02; 2.09; 4.06; 6.01; 6.06; 10.04	Byrne et al. 1998
<i>Ostrinia furnacalis</i>	Feeding holes	Mc37	Zi330	162 F <sub>2:3</sub> families	2.05; 9.01	Xia et al. 2010
	Leaf damage	Mc37	Zi330	162 F <sub>2:3</sub> families	1.08; 2.04; 2.05; 4.01; 10.01	Xia et al. 2010
	Tunnel length/holes	Mc37	Zi330	162 F <sub>2:3</sub> families	1.01; 9.01–9.02	Xia et al. 2010
<i>Ostrinia nubilalis</i>	Cob damage	EP39	EP42	178 RILs	1.12	Ordas et al. 2010
		H99	Mo17	150 F <sub>2:3</sub>	4.01; 6.04; 7.02–7.03 (2); 9.03–9.05	Cardinal et al. 2006
		H99	Mo17	185 F <sub>6:8</sub>	1.06; 3.07–3.08; 4.01; 7.03; 8.03	Cardinal et al. 2006
	Leaf damage (first generation)	KW4773	WBB53	144 doubled haploid	5.04	Orsini et al. 2012
		Mo47	B73Ht	244 F <sub>2:3</sub> families	1.01; 1.06; 1.11; 2.09; 4.01; 4.06; 5.05; 6.02; 8.06	Jampatong et al. 2002
	Leaf damage (second generation)	Mo47	B73Ht	244 F <sub>2:3</sub> families	2.01; 5.05; 5.08; 6; 6.07; 8.03; 9.02	Jampatong et al. 2002
	Stalk tunnel length	EP39	EP42	178 RILs	8.05	Ordas et al. 2010
	Stalk breakage (second generation)	KW4773	WBB53	144 doubled haploid	2.07	Orsini et al. 2012
	Stalk damage rating	D06	D408	210 F <sub>2:3</sub>	1.02; 1.06; 6.07; 8.05	Papst et al. 2004
		D06 × D408 204 F <sub>2:3</sub>	D171	Test-cross progeny	1.01; 3.09; 6.06; 7.04; 8.04; 10.04	Papst et al. 2004
		Do6	D408	226 F <sub>3</sub> families	1.05; 5.05; 5.07; 6.07; 8.05	Bohn et al. 2000

(Continued)

Table 1. (Continued)

Insect	Trait	Resistant parent	Susceptible parent	Mapping population	Bin(s)	Reference
<i>Sesamia nonagrioides</i>	Stalk tunneling	B52	B73	183 RILs	2.04 (2); 2.07; 3.04; 3.06; 5.04 (2); 7.02; 7.04; 8.08; 9.01; 9.03	Cardinal et al. 2001
		B52	B73	200 RILs	2.04; 2.05; 2.08; 3.01; 3.04; 3.06; 5.04; 5.05; 7.02; 7.04; 8.08; 9.01; 9.03	Cardinal and Lee 2005
		De811	B73	147 F <sub>3</sub> lines	1.02–1.03 (2); 3.05; 4.03; 5.03; 5.07; 8.04–8.05	Krakowsky et al. 2002
		De811	B73	119 RILs	1.01; 1.02; 1.11; 2.07; 3.02; 3.04; 4.01–4.02 (2); 5.02; 5.07; 6.01; 6.05; 7.01–7.03 (3); 7.05; 8.03; 9.00; 9.08; 10.03; 10.06	Krakowsky et al. 2004
	Tunnel length	Do6	D408	226 F <sub>3</sub> families	1.07–1.08; 3.09; 5.03; 5.05; 9.03	Bohn et al. 2000
		EP39	EP42	178 RILs	1.02; 3.05; 8.05	Ordas et al. 2010
		D06	D408	210 F <sub>2:3</sub>	1.07; 2.04; 3.09; 5.03–5.04; 7.05; 8.05; 10.06	Papst et al. 2004
	Tunnel length (second generation)	B52	B73	300 F <sub>3</sub> families	1.01–1.02; 1.07–1.08; 2.03–2.04; 2.08–2.09; 3.04–3.06; 7.04; 10.04	Schön et al. 1993
	Cob damage	EP39	EP42	178 RILs	1.12	Ordas et al. 2010
	Kernel damage	B73	Mo17	243 RILs	8.05	Ordas et al. 2009
<i>Sitophilus zeamais</i>	Stalk tunnel length	EP39	EP42	178 RILs	8.05	Ordas et al. 2010
	Tunnel length	B73	Mo17	243 RILs	1.06; 9.04	Ordas et al. 2009
		EP39	EP42	178 RILs	1.02; 3.05; 8.05	Ordas et al. 2010
	Weevil susceptibility	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.05; 2.07; 3.07; 4.10; 7.01; 7.03; 9.05	García-Lara et al. 2009
	Grain damage	Muneng-8128	CML290	163 F <sub>2:3</sub> families	2.09; 5.03; 6.05; 7.01; 10.07	García-Lara et al. 2009
	Weevil adult progeny	Muneng-8128	CML290	163 F <sub>2:3</sub> families	2.07; 9.05; 10.06	García-Lara et al. 2009
	Leaf damage	Mp704	Mo17	230 F <sub>2:3</sub>	1.05; 1.11; 5.02; 7.02; 7.04; 8.03; 9.03; 10.04	Brooks et al. 2007
	Leaf damage	Mp704	Mo17	230 F <sub>2:3</sub>	1.09; 2.08; 6.02; 7.04; 8.03; 9.03; 10.04	Brooks et al. 2005
	Leaf damage	Mp708	A619	213 F <sub>2:3</sub> families	1.03; 2.02; 5.07; 6.05; 7.03; 9.03; 9.07	Brooks et al. 2007
	Leaf damage	Mp708	A619	213 F <sub>2:3</sub> families	1.02; 2.02; 5.04; 5.07; 6.05; 7.03; 9.03; 9.05	Brooks et al. 2007

the ends of chromosomes, are not known to be involved in some form of insect resistance.

QTL for stalk boring, leaf feeding, chemical defense, and plant physical traits colocalized in 24 bins. Chemical defense and plant traits colocalized in 53 bins. Stem-boring QTL, which have been studied in more detail than leaf-feeding QTL, colocalized with both chemical defense (51 bins) and plant traits (60 bins). Leaf feeding colocalized with chemical defense and plant traits in 29 bins each. Generally, QTL controlling resistance to stalk boring colocalize with those for leaf feeding (in 29 bins), suggesting that there are common defense mechanisms against these two classes of herbivores.

Not surprisingly, QTL for benzoxazinoid content are located in bin 4.01 (Table 2), which contains most of the known DIMBOA-glucoside biosynthetic loci. Several studies mapping stem-borer resistance also found QTL

in bin 4.01, suggesting a cause-and-effect relationship. Other benzoxazinoid QTL are found at the top of chromosome 1, in a location different from the known *bx9* locus on this chromosome. Colocalization of insect resistance QTL in this area (Fig. 1) might indicate the effects of novel benzoxazinoid regulatory or biosynthetic loci. Other likely benzoxazinoid QTL are found on chromosomes 3, 6, 7 and 8 (Table 2), where there are also no known biosynthetic or regulatory loci for this pathway.

Maysin QTL are localized on most chromosomes. *P1* and *P2*, located in bin 1.03, were found to colocalize with several maysin and stem-boring insect QTL. *Whp1* colocalized with several maysin and stem-boring insect QTL in bin 2.09. *A1*, which has been studied on the basis of loss-of-function mutations, colocalizes with both maysin content and stem-boring insect resistance QTL. *Rem1* (*recessive enhancer of maysin 1*), previously shown to

**Table 2.** Genetic mapping of maize traits that influence insect resistance

Trait	Insect species, if tested	Resistant parent	Susceptible parent	Mapping population	Bin(s)	Reference
5,5'-Diferulic acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	2.01; 2.06; 3.09; 6.01; 6.05; 8.03	García-Lara et al. 2010
8,5'-Diferulic acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.07; 1.10; 2.08; 4.10; 4.11; 8.01; 8.03; 8.07; 9.02	García-Lara et al. 2010
8,5'-Diferulic acid, benzofuran form	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.08; 2.02; 2.08; 3.03; 4.08; 6.01; 6.02; 6.05; 8.03; 9.02	García-Lara et al. 2010
8-O-4'-Diferulic acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.10; 3.09; 4.10; 5.01; 5.03; 6.04; 6.05; 8.03	García-Lara et al. 2010
cis-Ferulic acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.02; 1.10; 2.02; 3.06; 4.05; 6.05; 8.01; 8.03; 9.02; 10.02	García-Lara et al. 2010
trans-Ferulic acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	2.09; 3.01; 3.04; 3.06; 3.07; 3.09; 5.03; 6.04; 7.03; 10.06	García-Lara et al. 2010
Diferuloyl putrescine	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.10; 2.03; 4.11; 6; 7.03; 7.04; 9.05; 10.06; 10.07	García-Lara et al. 2010
Chlorogenic acid	<i>Helicoverpa zea</i>	W23 (c2 whp1 p1-wrb)	Mp708 (C2 Whp1 p1-wwb)	380 F <sub>2</sub>	1.03; 2.05; 2.09; 3.03; 3.05; 4.08	Szalma et al. 2002
	<i>Helicoverpa zea</i>	W23 (c2 whp1 p1-www)	Mp708 (C2 Whp1 p1-wwb)	437 F <sub>2</sub>	1.03; 2.05; 3.05; 3.07; 4.08; 9.03	Szalma et al. 2002
	<i>Helicoverpa zea</i>	W23 (c2 whp1 p1-www)	NC7A (C2 Whp1 p1-wwb)	450 F <sub>2</sub>	1.03; 2.05; 2.09; 3.05	Szalma et al. 2002
Crude fiber	<i>Ostrinia nubilalis</i>	D06 × D408	D171	Testcross progeny	3.01; 6.05; 9.02	Papst et al. 2004
DIMBOA	<i>Ostrinia furnacalis</i>	B73	CML322	RILs	1.04; 1.05; 4.01; 8.06; 8.07; 8.08	Butrón et al. 2010
	<i>Ostrinia furnacalis</i>	B73	IL14H	RILs	1.08; 1.09; 6.01; 6.02; 6.06	Butrón et al. 2010
	<i>Ostrinia nubilalis</i>	B73	CML322	RILs	1.04; 1.05; 4.01; 8.06; 8.07; 8.08	Butrón et al. 2010
	<i>Ostrinia nubilalis</i>	B73	IL14H	RILs	1.08; 1.09; 6.01; 6.02; 6.06	Butrón et al. 2010
	<i>Sesamia nonagrioides</i>	B73	CML322	RILs	1.04; 1.05; 4.01; 8.06; 8.07; 8.08	Butrón et al. 2010
	<i>Sesamia nonagrioides</i>	B73	IL14H	RILs	1.08; 1.09; 6.01; 6.02; 6.06	Butrón et al. 2010
DIMBOA and DIMBOA-glucoside	<i>Ostrinia furnacalis</i>	B73	CML322	RILs	1.04; 1.05; 3.07; 3.08; 3.09; 4.01; 7.02; 7.03; 8.06; 8.07; 8.08	Butrón et al. 2010
	<i>Ostrinia furnacalis</i>	B73	IL14H	RILs	1.02; 1.03; 4.01; 4.02; 6.01; 6.02	Butrón et al. 2010
	<i>Ostrinia nubilalis</i>	B73	CML322	RILs	1.04; 1.05; 3.07; 3.08; 3.09; 4.01; 7.02; 7.03; 8.06; 8.07; 8.08	Butrón et al. 2010
	<i>Ostrinia nubilalis</i>	B73	IL14H	RILs	1.02; 1.03; 4.01; 4.02; 6.01; 6.02	Butrón et al. 2010
	<i>Sesamia nonagrioides</i>	B73	CML322	RILs	1.04; 1.05; 3.07; 3.08; 3.09; 4.01; 7.02; 7.03; 8.06; 8.07; 8.08	Butrón et al. 2010
	<i>Sesamia nonagrioides</i>	B73	IL14H	RILs	1.02; 1.03; 4.01; 4.02; 6.01; 6.02	Butrón et al. 2010
DIMBOA-glucoside	<i>Ostrinia furnacalis</i>	B73	CML322	RILs	1.04; 1.05; 3.07; 3.08; 4.01; 8.06	Butrón et al. 2010
	<i>Ostrinia furnacalis</i>	B73	IL14H	RILs	4.01; 4.02	Butrón et al. 2010
	<i>Ostrinia nubilalis</i>	B73	CML322	RILs	1.04; 1.05; 3.07; 3.08; 4.01; 8.06	Butrón et al. 2010
	<i>Ostrinia nubilalis</i>	B73	IL14H	RILs	4.01; 4.02	Butrón et al. 2010
	<i>Sesamia nonagrioides</i>	B73	CML322	RILs	1.04; 1.05; 3.07; 3.08; 4.01; 8.06	Butrón et al. 2010

(Continued)



## MAIZE-INSECT INTERACTIONS

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Table 2. (Continued)

Trait	Insect species, if tested	Resistant parent	Susceptible parent	Mapping population	Bin(s)	Reference
	<i>Sesamia nonagrioides</i>	B73	IL14H	RILs	4.01; 4.02	Butrón et al. 2010
Husk coverage/tightness	<i>Helicoverpa zea</i>	GT119	GT-A1	250 F <sub>2:3</sub> families	1.04; 1.05; 1.07; 3.06; 3.07; 3.08; 4.08; 7.03; 7.04; 7.06	Widstrom et al. 2003
Hydroxyproline-rich glycoproteins, insoluble	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	2.02; 3.06; 5.05; 8.05; 9.03	García-Lara et al. 2010
Hydroxyproline-rich glycoproteins, soluble	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.08; 3.06; 5.05; 10.02	García-Lara et al. 2010
In vitro digestibility of organic matter	<i>Ostrinia nubilalis</i>	D06 × D408	D171	Testcross progeny	8.06; 9.07	Papst et al. 2004
Maysin	<i>Helicoverpa zea</i>	GE37	FF8	250 F <sub>2:3</sub> families	1.02; 2.07; 6.05–6.06; 8.05; 9.02	Byrne et al. 1998
	<i>Helicoverpa zea</i>	SC102 (P1-wrb)	B31857 (shrunk-2)	F <sub>2</sub>	1.03; 1.05; 1.06; 3.09; 4.07; 7.05; 8.09; 9.02	Guo et al. 2001
	<i>Helicoverpa zea</i>	W23 (c2 whp1 p1-wrb)	Mp708 (C2 Whp1 p1-wwb)	380 F <sub>2</sub>	2.09; 3.03; 4.08; 7.01	Szalma et al. 2002
	<i>Helicoverpa zea</i>	W23 (c2 whp1 p1-www)	Mp708 (C2 Whp1 p1-wwb)	437 F <sub>2</sub>	1.03; 4.08; 9.03	Szalma et al. 2002
	<i>Helicoverpa zea</i>	W23 (c2 whp1 p1-www)	NC7A(C2 Whp1 p1-wwb)	450 F <sub>2</sub>	1.03; 2.05; 2.09; 4.08; 8.03; 9.04	Szalma et al. 2002
	<i>Helicoverpa zea</i>	SIM	EPM	EPM × SIM (F <sub>2</sub> )	1.02; 2.08; 4.06; 5.03; 5.07; 6.01; 7.03	Meyer et al. 2007
	<i>Helicoverpa zea</i>	GT119	EPM	GT119 × EPM (F <sub>2</sub> )	1.02; 2.03; 2.08; 5.02; 7.03; 9.02	Meyer et al. 2007
	<i>Helicoverpa zea</i>	GT119	SIM	GT119 × SIM (F <sub>2</sub> )	1.02; 4.00; 4.08; 7.01	Meyer et al. 2007
	<i>Helicoverpa zea</i>	SIM8	EPM	EPM × SIM8 (F <sub>2</sub> )	4.05; 4.06; 8.02; 9.01	Meyer et al. 2007
Maysin and chlorogenic acid	<i>Helicoverpa zea</i>	GT-A1	GT119	250 F <sub>2:3</sub> families	1.03; 1.04; 1.05; 1.06; 1.07; 2.04; 2.05; 2.06; 3.02; 4.08; 4.10	Widstrom et al. 2003
p-Coumaric acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.09; 1.10; 3.06; 4.05; 6.02; 7; 8.02; 9.07	García-Lara et al. 2010
p-Coumaroyl-feruloyl putrescine	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.10; 3.01; 3.03; 3.04; 3.05; 3.06; 3.09; 5.03; 6.05; 8.02; 10.06	García-Lara et al. 2010
Sheath acid detergent fiber	<i>Ostrinia nubilalis</i>	B52	B73	200 RILs	3.04; 5.04; 7.05; 9.04	Cardinal and Lee 2005
	<i>Ostrinia nubilalis</i>	DE811	B73	200 RILs	1.01; 9.02; 9.03; 10.03; 10.07	Krakowsky et al. 2007
Sheath acid detergent lignin	<i>Ostrinia nubilalis</i>	B52	B73	200 RILs	2.08; 3.04; 7.03; 9.03	Cardinal and Lee 2005
Sheath neutral detergent and acid detergent fiber		De811	B73	147 F <sub>3</sub> families	1.03; 3.01; 3.04; 3.06; 4.05; 4.09; 7.03 (2); 8.04–8.05; 9; 10	Krakowsky et al. 2003
Sheath neutral detergent fiber	<i>Ostrinia nubilalis</i>	B52	B73	200 RILs	3.04; 5.05; 7.02; 7.05; 9.04	Cardinal and Lee 2005
Sheath neutral detergent fiber, adjusted	<i>Ostrinia nubilalis</i>	DE811	B73	200 RILs	2.04; 2.05; 2.08; 6.01; 9.02; 9.03; 10.06	Krakowsky et al. 2007
	<i>Ostrinia nubilalis</i>	DE811	B73	200 RILs	2.04; 2.05; 6.01; 6.05; 7.04; 9.02; 9.03	Krakowsky et al. 2007
Stalk acid detergent lignin	<i>Ostrinia nubilalis</i>	B52	B73	200 RILs	2.08; 3.01; 3.04; 5.03; 5.05; 8.08	Cardinal and Lee 2005
		De811	B73	147 F <sub>3</sub> families	1.07; 1.11; 2.07; 3.04; 3.06; 4.05; 6.05–6.06; 7.03; 7.05; 9.01	Krakowsky et al. 2003

(Continued)

Table 2. (Continued)

Trait	Insect species, if tested	Resistant parent	Susceptible parent	Mapping population	Bin(s)	Reference
Stalk fiber		De811	B73	147 F <sub>3</sub> families	1.03; 1.07; 2.04; 2.07; 3.04; 4.03; 6.06; 7.02; 7.03; 7.04; 8.04–8.05; 9.01	Krakowsky et al. 2003
Stalk neutral detergent fiber	<i>Ostrinia nubilalis</i>	B52	B73	200 RILs	2.04; 5.03; 5.05	Cardinal and Lee 2005
Total diferulic acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	1.10; 2.01; 2.08; 3.09; 6.04; 6.05; 8.03	García-Lara et al. 2010
Total phenolic acid	<i>Sitophilus zeamais</i>	Muneng-8128	CML290	163 F <sub>2:3</sub> families	2.03; 3.01; 3.09; 4.11; 6.04; 7.03; 10.06	García-Lara et al. 2010

enhance maysin production in the presence of a functional *Pl* allele (Lee et al. 1998) and estimated to be between *bz1* (bin 9.01–9.02) and *wx1* (bin 9.03) on chromosome 9, was found to colocalize with several QTL for maysin content. Interestingly, *C2*, which is thought to encode chalcone synthase required for maysin content, colocalized with QTL for maysin content but not stem-boring or leaf feeding insect resistance. Noteworthy is the lack of colocalization among genes encoding chalcone isomerase and maysin content QTL. Three *chi* genes encode chalcone isomerase, an enzyme upstream of the maysin biosynthetic pathway. Whereas *chi1* and *chi3* do not colocalize with relevant QTL, *chi2* colocalizes with both maysin content and stem-boring and leaf-feeding insect resistance QTL.

*Mir1* protease is encoded by a gene in bin 6.02, and *Mir1*-expressing plants have high resistance to lepidopteran herbivores (Pechan et al. 2000). However, only a small number of QTL for boring or chewing insect resistance was found in this bin (Fig. 1). This may be due to a lack of genetic variation at the *Mir1* locus in the mapping populations that have been investigated.

Genes encoding RIPs are located in bins 8.05 and 7.04 (Bass et al. 1995, 2004). Both of these bins have also been identified in 11 studies involving the identification of resistance QTL for stem-boring insects (Fig. 1). Further studies are needed to determine whether natural variation at *Rip3:1* and *Rip3:2* is the underlying cause of this natural variation in herbivore resistance.

## FUTURE PROSPECTS

Although numerous insect resistance QTL have been mapped in maize (Table 1 and Fig. 1), in most cases the underlying genetic differences that cause some maize inbred lines to be more susceptible to herbivores than others remain unknown. Given the importance of insect herbivory in maize cultivation, there is a clear need for more precise genetic mapping, identification of DNA sequence polymorphisms in the area of the QTL, and testing candidate genes through transgenic approaches. New tools that are available for maize research will permit the identification of insect resistance genes in a more systematic manner.

In the past few years, large sets of genotyped inbred lines and recombinant inbred populations (Coe et al. 2002; Sharopova et al. 2002; Flint-Garcia et al. 2005; Yu et al. 2008; McMullen et al. 2009b; Ganai et al. 2011) have become available for maize genetic mapping. QTL mapping experiments are greatly facilitated by high-resolution physical and genetic maps (Wei et al. 2009; Zhou et al. 2009; Ganai et al. 2011) that are based on the B73 genome sequence (Schnable et al. 2009). Although the reproducibility of insect bioassays and the feasibility of measuring insect performance on thousands of plants may limit such studies, it will almost certainly be possible to map maize insect resistance QTL to a relatively small number of genes.

The B73 genome sequence, combined with lower-level sequencing of a large number of maize lines (Chia et al. 2012), has identified many millions of sequence polymorphisms. Thus, once an insect resistance QTL has been mapped to within a few centimorgans in the maize genome using these molecular markers, it will be possible to identify likely candidate genes in the genomic area of interest. Furthermore, the large number of known maize DNA polymorphisms might allow direct identification of sequence differences in the candidate genes.

Once candidate genes have been identified, readily available reverse genetic approaches can be used to study their in vivo functions. Transposon insertion mutations can be used to investigate the effects of gene knockouts (Brutnell and Conrad 2003; Bai et al. 2007; Vollbrecht et al. 2010; Williams-Carrier et al. 2010). Should suitable transposon insertions be unavailable, individual genes identified from the maize genomic sequence also can be knocked out by TILLING for induced point mutations (Till et al. 2004). Finally, transgenic approaches can be used to overexpress targeted genes or silence their expression through RNA interference.

In some cases, additional information may be available for the identification of candidate genes in QTL regions. Many insect-defensive genes are induced in response to herbivory. Thus, gene expression profiling of maize, with and without herbivore attack, can increase the confidence level of identified candidate genes. Colocalization of QTL for insect resistance and chemical defense traits (Fig. 1) also provides additional opportunities for resistance gene

identification. Even if the biosynthetic enzymes for a specific metabolite are not known, it is possible to predict the type of enzymes that should be involved in the reaction. Given the currently available tools, it can be straightforward to move from the identification of a plant metabolite or enzymatic activity to the identification of candidates in a limited set of genes that are identified in a genetic mapping project.

It is noteworthy that, to date, all published QTL mapping of maize insect resistance has involved stem borers and chewing insects (Table 1). Both rootworms and phloem-feeding insects such as aphids have been absent from these QTL mapping projects. Given the significance of agricultural damage caused by rootworm herbivory (Gray et al. 2009) and the limited number of transgenic approaches that are available for controlling these pests, it will be important to take full advantage of natural variation in maize resistance in breeding programs. Thus, mapping rootworm resistance using a large maize diversity panel or recombinant inbred lines will provide essential information for future breeding programs.

Maize aphids grew significantly better on maize expressing *Bacillus thuringiensis* crystal toxin (Bt toxin) than on control plants (Faria et al. 2007). Thus, given the widespread planting of transgenic maize expressing Bt toxin, aphid herbivory may be an emerging problem in agriculture. Higher sensitivity of Bt transgenic lines, combined with predicted increases in global temperature, might allow aphid infestations to reach critical levels in areas where these pests are not currently relevant. The identification of *R* genes that provide high-level aphid resistance, combined with plant breeding to incorporate particularly strong alleles of these genes, has been effective for controlling aphids on crops such as wheat (Khan et al. 2009) and tomato (Rossi et al. 1998). Therefore, similar studies to identify natural variation in maize aphid resistance might also provide effective control methods.

Together, the diverse QTL studies that we have listed in Tables 1 and 2 provide evidence for significant natural variation in maize resistance to insect herbivory. Genome sequencing, large genetic mapping populations, and other research tools have opened up new opportunities for the discovery of insect resistance genes. In the coming years, the identification of genes underlying maize herbivore resistance QTL will be greatly accelerated, thereby providing new opportunities for crop plant improvement through breeding and transgenic approaches.

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L.N. Meihls, H. Kaur and G. Jander

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