Dissection of QTLs for Biotic Stress Resistance in Maize

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1   Introduction

Maize (*Zea mays* L.) is an important annual cereal crop of family Poaceae, having wider adaptability under varied environmental conditions, and popularly used for human food, animal feed and industrial usage (Shiferaw et al. 2011). It is originated in the highlands of Mexico (~8700 years ago) and known as 'queen of cereals', owing to its highest genetic yield potential (Piperno et al. 2009). Maize is grown on ~193.25 million hectare (mha) with a production of 1116.19 million tonnes (mt) with a productivity of 5.78 tha^{-1} (USDA 2020). The area under maize spans from the latitude 58° N to the latitude 40° S, and it is harvested every month of the year in one region or the other. Akin to any crop species, maize production is severely plagued by several abiotic and biotic stresses (Gong et al. 2014). Biotic stress includes stresses caused by virus, bacteria, fungi and nematodes, parasites and insect pests. Crops are regularly exposed to biotic stresses, which cause changes in metabolism and damages at various levels resulting in faltered productivity (Gimenez et al. 2018). The diseases are major culprits of biotic stress-induced

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damages in maize followed by insect pests and parasitic weeds mainly *Striga hermonthica* (Keno et al. 2018).

The outbreaks of diseases in maize are one of the well-documented crop epidemics in the world's history. For instance, the outbreak of southern corn leaf blight (SCLB), caused by *Bipolaris maydis* race T, was the first reported disease outbreak in maize during 1970–1971. This was mainly due to the indiscriminate use of T-type male sterile cytoplasm (cms – *T*exas) which occupied 85% of corn fields in the United States (Ullstrup 1972). With around 50–100% yield reduction, the economic loss due to this disease reached as high as one billion dollars. An outbreak due to northern corn leaf blight (NCLB) was observed in North China due to the extensive cultivation of a high-yielding, but susceptible, variety 'Xian Yu335' (Pu 2013). Similarly, a severe epidemic of maize lethal necrosis (MLN), a viral disease, was documented in Kenya in September 2011, which disseminated to other African countries. The yield loss due to this disease was estimated up to 126,000 metric tons which translated into $52 million in Kenya in 2012 (Mahuku et al. 2015; Terefe and Gudero 2019). Tar spot complex (TSC) caused by three fungal pathogens is another major disease in Latin American countries and has the reported potential of inciting up to 51% yield loss in maize. TSC first reported in 1904 in Mexico later spread to other countries (Mottaleb et al. 2019). Recently, FAW (fall armyworm) is causing devastation of maize crop across the countries (Prasanna et al. 2022). In India, it is first reported from Bangalore Rural and Chikkaballapur districts during May–June 2018 (Ganiger et al. 2018) and South Karnataka during the first fortnight of July 2018 (ICAR-NBAIR pest alert, 2018), the pest infected 40–70% of the crop, quickly spreading to the rest of the country (Tippannavar et al. 2019). Thus, disease and pests pose a serious threat to sustainable production of maize across the globe.

Breeding for stress-tolerant genotypes is an important and economically viable strategy to combat various biotic stresses. This can significantly reduce the dependence on chemical control for the management of diseases and pests and enhance the export value of the produce while ensuring the consumer safety. The information on the genetic control of the target trait is an important prerequisite of any breeding programme (Zunjare et al. 2015a; Muthusamy et al. 2016), which guides the breeders in choosing the most adequate breeding strategy. With the advent of molecular markers and statistical models, mapping of quantitative trait loci (QTLs) or genomic regions encoding a particular trait has picked up pace. The principle of 'linkage mapping' has been widely employed for mapping QTLs in crop plants through developing biparental segregating population for trait of interest (Collard et al. 2005). However, association mapping or linkage disequilibrium (LD) mapping is based on statistical associations of genetic markers with phenotypes in natural populations (Huang and Han 2013). With the rapid advancements in genomics, decreasing genotyping cost and available genome sequences, genome-wide LD mapping has become popular and powerful approach to dissect genetic architecture of complex traits (Huang and Han 2013). Both mapping techniques have their own pros and cons; for instance, the power of QTL detection is higher in case of biparental mapping study while resolution of QTL is higher for LD-based mapping. Several studies have been reported for identification of QTLs and the underpinning

candidate genes for various biotic stresses in maize. An attempt was made to review these reports in a systematic manner. The chapter was organized into different sections starting with a brief description of important pests and diseases of maize followed by defence mechanisms of biotic stress resistance, QTL mapping studies and attempts to improve maize genotypes using QTLs or genes.

2 Biotic Stresses: Types, Major Symptoms and Losses Caused

The most prevalent maize diseases are leaf blight, ear rot, maize rough dwarf disease, sugarcane mosaic disease, maize streak virus disease, maize dwarf mosaic disease, maize lethal necrosis virus disease and high plain disease, while the most prevalent insect pests are borers, fall armyworm, shoot fly and the storage weevils (Table 1). The detail of above biotic stresses are briefly described here under.

2.1 Major Diseases

Fungal Diseases

1. *Turcicum leaf blight*: Turcicum leaf blight (TLB) or northern corn leaf blight (NCLB) is the most important foliar disease in northern hills, northeastern hills and peninsular part of India. The fungus *Setosphaeria turcica* (anamorph *Exserohilum turcicum*) is the causal pathogen with characteristic symptom of 'cigar-shaped' tan or greyish lesions on leaf surface (Chen et al. 2016a). It is prevalent in majority of maize-cultivating countries of the world having cool climate (temperatures 20–25 °C), 90–100% relative humidity and low luminosity (Wu et al. 2014). Under favourable condition of infection with no treatment, it has potential to cause yield loss up to 70%.
2. *Gibberella ear rot (GER)*: It is caused by *Fusarium graminearum* fungus which also causes rot diseases in the stalks and roots of maize. The main symptoms include reddish grain formation at the ear tip initially. GER reduces the yield and quality of kernels and triggers the accumulation of mycotoxins (vomitoxin and zearalenone) which cause serious health problems in humans and animals (Brauner et al. 2017).
3. *Diplodia ear rot (DER)*: It is caused by pathogen *Stenocarpella maydis* and main symptoms are bleached husks, whitish fungal growth on grains and rotted ears. Early infections of DER lead to complete ear rotting, while late infections may result in partial rotting of ears. It results into loss of nutritive value of kernels and deposition of fungus causing mycotoxins (Baer et al. 2021).
4. *Aspergillus ear rot (AER)*: It is caused by fungus called *Aspergillus* that produces aflatoxin which is carcinogen and can potentially be dangerous to livestock

Table 1 List of the important biotic stresses prevalent in maize

S. no.	Name of pest	Scientific name	Major country prevalence (major area)	Typical symptoms	Damage caused	Reference(s)
Fungal diseases						
1.	*Turcicum* leaf blight	*Setosphaeria turcica*	Northern and northeastern hills and peninsular India	'Cigar-shaped' tan or greyish lesions on the leaf	Yield reduction up to 70%	Wu et al. (2014)
2.	*Gibberella* ear rot	*Fusarium graminearum*	Most of the maize-growing countries	Pinkish fungal growth on the tip of cob	Mycotoxin contamination	Woloshuk and Wise (2010) and Galiano-Carneiro et al. (2021b)
3.	*Diplodia* ear rot	*Stenocarpella maydis*	South America, Africa, United States and Canada	Tan spots on husks or bleached husks	Up to 80% reduction in yield	Baer et al. (2021)
4.	*Aspergillus* ear rot	*Aspergillus flavus*	Most of the maize-growing countries	Olive-green mould on ears	Aflatoxin contamination	Woloshuk and Wise (2011), Mitchell et al. (2016) and Womack et al. (2020)
5.	*Fusarium* ear rot	*Fusarium verticillioides*	China, United States and Southern Europe	Tan or brown kernels with white or pink fungal growth	Yield reduction up to 50% coupled with mycotoxin contamination	Ding et al. (2008) and Wen et al. (2021)
Viral diseases						
1.	Maize rough dwarf disease	Maize rough dwarf virus (MRDV), Mal de Rio Cuarto virus (MRCV), rice black-streaked dwarf virus (RBSDV) and southern rice black-streaked dwarf virus (SRBSDV)	Northern China, Europe and South America	Dwarfing, malformed tassel and dark green leaves	100% yield loss in severely affected areas	Zhang et al. (2021)

2.	Sugarcane mosaic disease	Sugarcane mosaic virus (SCMV)	Almost all maize-growing areas	Shades of green on a background of paler green to yellow chlorotic areas	Yield reduction can be up to 50%	Shepherd et al. (2010)
3.	Maize streak virus disease	Maize streak virus (MSV)	Primarily Africa, some parts of South Asia and the United States	Yellowish and light green streaks on leaves	100% yield loss in severely affected areas	
4.	Maize dwarf mosaic disease	Maize dwarf mosaic virus (MDMV)	Most of the maize-growing countries	Stippled (small, discoloured specks) mottle or mosaic of light and dark green	Up to 70% yield loss	Kannan et al. (2018)
5.	Maize lethal necrosis virus disease	Maize chlorotic mottle virus (MCMV)	Primarily Africa, some parts of Asia, North America and South America	Long yellow stripes on leaves	Up to 100% yield losses	Redinbaugh and Stewart (2018)
6.	High plains disease	Wheat mosaic virus (WMoV)	Prevalent in North America, some parts of Europe and South America	Stunted yellowish plants with one or more yellowish or reddish-purple bands	–	Jensen et al. (1996)
Insects						
1.	Spotted stem borer	*Chilo partellus*	Asia and in most countries of East and Southern sub-Saharan Africa	'Dead heart' symptom	Yield loss up to 26–80%	Ong'amo et al. (2016)

(continued)

Table 1 (continued)

S. no.	Name of pest	Scientific name	Major country prevalence (major area	Typical symptoms	Damage caused	Reference(s)
2.	Pink borer	*Sesamia inference*	Peninsular India	Younger plants show dead hearts while mature plants are prone to lodging	Yield loss up to 26–79%	Baladhiya et al. (2018)
3.	Mediterranean corn borer	*Sesamia nonagrioides* Lefebvre	Southern European countries and Africa	'Dead heart' and stem breakages	Yield loss of up to 80%	Zanakis et al. (2009)
4.	Fall army worm	*Spodoptera frugiperda*	Almost all maize-growing countries	Papery windows to oblong holes on leaves, complete defoliation. Damage to tassel and corn ears	Nearly complete yield loss	Ganiger et al. (2018), Tippannavar et al. (2019)
5.	Shoot fly	*Atherigona* spp.	Northwestern plain zone of India	'Dead heart' symptom	About 28–45% grain yield loss	Jindal (2013)
6.	Weevils	Maize weevil (*Sitophilus zeamais*), Rice weevil (*Sitophilus oryzae*), Granary weevil (*Sitophilus granaries*)	Almost all maize-producing countries	Moisture on seed leading to seed sprouting during storage, fungal growth	12–20% grain loss is quite common and may reach up to 80%	Zunjare (2012) and Nwosu (2018)

(Woloshuk and Wise 2011). Aflatoxin contamination of maize is a major problem in the southern parts of the United States (Mitchell et al. 2016). Symptoms of AER include green to yellowish fungal growth on and between grains near the ear tip mostly (Woloshuk and Wise 2011).

5. *Fusarium ear rot (FER)*: This maize disease is prevalent worldwide affecting grain yield and quality that is caused by fungus *Fusarium verticillioides* (Ding et al. 2008). Disease incidence is usually 10–20% in China, but in favourable conditions, it can reach up to 50% (Wen et al. 2021). The disease also poses a serious health hazard due to the accumulation of mycotoxin called fumonisin. Typical symptoms include scattered individual kernels with whitish pink to lavender *Fusarium* growth. Fungus-affected grains may have a 'starburst' pattern of white streaks.

Viral Diseases

1. *Maize rough dwarf virus disease (MRDV)*: It is a damaging viral disease with symptoms like internode shortening, malformed tassels and significant delays in vegetative growth (Wang et al. 2019). It is primarily caused by three viruses, namely, maize rough dwarf virus (MRDV), Mal de Rio Cuarto virus (MRCV) and rice black-streaked dwarf virus (RBSDV). MRDV and MRCV are prevalent in Europe and in South America, respectively, while RBSDV is prevalent in China. The small brown plant hopper *Laodelphax striatellus* is the carrier of RBSDV virus (Wang et al. 2003).

2. *Sugarcane mosaic virus disease (SCMV)*: It is one of the serious pathogens causing severe yield losses in both sugarcane and maize. SCMV was first detected in sugarcane in 1919 and in maize in 1963, both in the United States (Signoret 2008). High incidence of SCMV was also reported in maize in China and Argentina (Perera et al. 2009; Xu et al. 2008). The mosaic pattern with contrasting shades of green to yellow chlorotic areas typically appears on SCMV incidence. The complete plant may become stunted on early infection of SCMV. The disease is spread by several aphid species.

3. *Maize streak virus disease (MSV)*: It is endemic to sub-Saharan Africa, and yield losses due to this virus are reportedly as high as 100% with an annual economic loss of US$120 M and US$480 M (Martin and Shepherd 2009). Hence, it is considered as the biggest threat to the food security of sub-Saharan Africa (Shepherd et al. 2010). Among several strains of MSV, MSV-A causes economically tangible disease (Martin et al. 2001). The virus is mainly transmitted by leafhopper *Cicadulina* spp. frequently found in the late sown maize fields or with susceptible varieties (Muimba-Kankolongo 2018). The virus mainly damages the plants younger than six weeks old. The top and bottom surfaces of leaves have yellowish and light green streaks on younger plants while mature plants show whitish, yellow and light green streaks running parallel to the leaf veins. The infected plants can be severely stunted if the crop is attacked during the 4–5 leaf stages. Abnormal bunching of flowers and shoots and reddish pigmentation may also be observed in later stages.

4. *Maize dwarf mosaic virus disease (MDMV)*: This disease is caused by MDMV belonging to the genus *Potyvirus* and is the most common disease of monocotyledonous plants (Kannan et al. 2018). The yield loss due to MDMV disease can be up to 70% resulting from disturbed photosynthesis and increased respiration (Mikel et al. 1981). The stunted, bunchy infected plants with short internodes have a stippled mottle or mosaic of light and dark green on the youngest leaves. The more yellowing will appear as plants mature and temperatures rise. The virus is also transmitted by various aphid species (over 20).

5. *Maize lethal necrosis (MLN) disease*: This is due to maize chlorotic mottle virus (MCMV) which also belongs to Potyviridae. The disease is transmitted by maize thrips (*Frankliniella williamsi*). As mentioned earlier, this virus caused an outbreak in southern rift valley of Kenya during 2011 and later spread to other regions of Africa (Redinbaugh and Stewart 2018). MLN disease causes long yellow stripes on leaves which are wider than those caused by maize streak virus disease. As the disease progresses, the maize leaves turn yellow and dry out from the edges towards the midrib. MLN disease can also cause dwarfing and premature aging of the plants, and ultimately the plants die. Late infection prevents tassel formation and produces poorly filled cobs.

6. *High plains disease (HPD)*: This disease is caused by wheat mosaic virus (WMoV) and noted first time in the 1990s on maize in Idaho and later in Utah in 1994 (Jensen et al. 1996). This is one of the extremely difficult diseases to control since it is reported to be seed borne (Jensen et al. 1996). The symptoms include weakened root systems, stunted growth and yellowing of the leaves, sometimes with yellow streaks and flecks. Reddish-purple discolourations or wide yellow bands are often seen on mature leaves. The bands turn tan or pale brown as the tissue dies. HPD in sweet corn is transmitted by insect called wheat curl mite (*Aceria tosichella*).

2.2 Major Insect Pests

1. *Stem borer (SB):* SB (*Chilo partellus*) is a major insect pest and infests maize during the *kharif* season all over India causing a yield loss of about 26–80% in different agro-climatic regions. Typical symptoms involve a 'dead heart' due to the withering of central shoot. The larvae later mine and feed on internal tissues. When cut open, tunnel can be observed inside the stem wherever larvae have traversed. This is visible externally as bored holes on the stem near the nodes (Ong'amo et al. 2016). The younger larvae crawl and feed on tender folded leaves causing typical 'shot hole' symptom.

2. *Pink borer (PB):* PB (*Sesamia inferens*) affects maize crop with yield loss in the range of 25.7–78.9%. PB larvae feed inside the leaf sheath in groups on the epidermal layer, preferably on first three leaf sheaths. The larvae later enter the plant at the base by making a hole and damage the inner portion of the stem. The

younger plants show dead hearts while the old plants become weak and are prone to lodging due to heavy winds (Baladhiya et al. 2018).

3. *Mediterranean corn borer (MCB)*: MCB (*Sesamia nonagrioides* Lefebvre) or corn stalk borer is the most damaging pest of maize in Southern European countries. They can incite a yield loss of up to 80% (Zanakis et al. 2009). In the European Mediterranean area, MCB coexists with ECB, and this duo has the potential of causing a higher damage to the plants (Velasco et al. 2007). Larvae feed inside the stems led to 'dead heart' symptoms as terminal leaves die.

4. *Fall armyworm (FAW)*: FAW (*Spodoptera frugiperda*) is one of the most destructive pests of maize across the world. As referred before, this pest was under high alert during 2018 with outbreak starting from Karnataka state to other parts of India. Initially, the symptoms appear as elongated papery windows across the leaves caused by first and second instar FAW larvae which feed by scrapping on leaf surface. Once the larva enters third instar, its feeding causes ragged-edged round to oblong holes on leaves. The fifth instar starts feeding voraciously, consuming larger areas of leaves, while the sixth instar larva extensively defoliates the leaves. In reproductive stage of the maize crop, tassel and corn ears are the vulnerable parts. Tassel damage is most common, which does not lead to economic damage, but boring into corn ears directly affects the yield. Sweet corn ear is more prone to FAW damage, which render the ears unmarketable (Ganiger et al. 2018; Tippannavar et al. 2019).

5. *Shoot fly (SF):* SF (*Atherigona* spp.) is a serious pest in spring maize crop sown in February–March of the year in northwestern plain zone of India and reported to cause up to 60% plant loss. The SF affects the maize plants at the seedling stage where maggots feed on young growing plants resulting in drying of the seedlings or 'dead heart' (Jindal 2013).

6. *Weevils:* Post harvest grain loss due to weevil insects belonging to genus *Sitophilus* is a major biotic stress concern in maize. *Sitophilus zeamais* (maize weevil) is found in Latin America, Europe and Africa; and *Sitophilus granaries* (granary weevil) is prevalent in temperate climate, while *Sitophilus oryzae* (rice weevil) is supposedly originated in Indian sub-continent (Zunjare 2012). Larvae of weevils feed within the grain kernels and adults emerge making holes on the grain. Hence, eggs, larvae and pupae are not visible on the grain. Only adults can be found wandering over the surface of grain (Hossain et al. 2007; Zunjare et al. 2014, 2016). Nearly, 12–20% grain loss is quite common and may reach up to 80% under favourable conditions of infestation (Zunjare et al. 2015a, b, c).

In addition to above insect pests, there are other minor pests of maize such as cob borer (*Helicoverpa armigera* Hubner), tobacco caterpillar (*Spodoptera litura* Fabricius), flower chafer beetle (*Chiloloba acuta* Wiedemann), *Oxycetonia versicolor* (Fabricius), armyworm (*Mythimna separata* Walker), cut worm (*Agrotis ipsilon* Rott.), grasshopper (*Hieroglyphus nigrorepletus* Bol.), aphid (*Rhopalosiphum maidis* Fitch), leafhoppers (*Pyrilla perpusilla* Walker) and Angoumois grain moth (*Sitotroga cerealella* Olivier).

3   Defence Mechanisms in Maize Against Pathogens and Insects

Plants, being sessile in nature, have to either maintain harmony with these insect pests and diseases or fight against them for their survival since they cannot run away from the predators like animals. Maize plants recognize several kinds of elicitors released by insects. Oral secretion and ovipositional fluids of the herbivorous insects are the principal sources of these elicitors. For instance, oral secretions from *Mythimna separata* caterpillar contain >10 different kinds of fatty acid – amino acid conjugates, the most abundant being hydroxylated FAC volicitin (Qi et al. 2016). *M. separata* secretions trigger the enhanced production of jasmonic acid and its derivative JA-Ile (JA-isoleucine conjugate). In addition, maize plants can also detect other insect-derived elicitors, such as caeliferin and inceptin (Schmelz et al. 2011). Maize land races release some volatile compounds in response to oviposition by stem borer *Chilo partellus*, which attracts both egg and larval parasitosis (Tamiru et al. 2011).

3.1   Phytoalexins

After the recognition of elicitors, the plants put forth various defence mechanisms – physical and chemical to contain the damage being caused by the insect. Secondary metabolites constitute major class of chemical defence elicited in the plants, popularly referred to as 'phytoalexins' (Smith 1996). There are two types of secondary metabolites in plants – volatile and nonvolatile. The main objective of releasing volatile secondary metabolites is to attract natural enemies of invading pest, which is termed as indirect defence response. For instance, maize plants release indole, a volatile aromatic compound for protection against *S. littoralis* as direct defence (Veyrat et al. 2016). Another compound, methyl salicylate (MeSA), also acts as a strong deterrent against leafhoppers (*Cicadulina storeyi*) in maize (Oluwafemi et al. 2011). Both of these compounds can prime the plants against the attack of respective pests. The production of a terpene compound, (E)-β-caryophyllene, confers resistance to *Diabrotica virgifera* by attracting an entomopathogenic nematode *Heterorhabditis megidis* (Rasmann et al. 2005). This seems to be effective against stem borer as well (*C. partellus*) by attracting its natural enemy, an egg parasitoid *C. sesamiae* (Tamiru et al. 2011). The attack of *S. littoralis* was reported to incite the localized production of 1,3-benzoxazin-4-ones, phospholipids, N-hydroxycinnamoyl tyramines, azelaic acid and tryptophan in maize seedlings (Marti et al. 2013). Benzoxazinoids (BXs) are a group of well-characterized compounds which play a significant role in maize defence against herbivorous insects (Handrick et al. 2016). BXs are demonstrated to be toxic to European corn borer (*O. nubilalis*) and Asian corn borer (*O. furnacalis*). For instance, DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) is popularly reported to be effective against these corn borers;

however, the underlying mechanism still needs to be elucidated (Glauser et al. 2011). Lectins are glycoproteins which function in defending the plants against a range of pests. These are jasmonate inducible and were reported in maize apart from other monocots such as rice, barley, wheat and rye (Jiang et al. 2006). In addition, oxylipins such as 9-oxylipin and 10-oxo-11-phytoenoic acid are strongly induced in maize silks upon infection by corn earworm (*Helicoverpa zea*) (Christensen et al. 2014).

3.2 Phytoanticipins

These are constitutively produced defence-related compounds which are inactive in native state but are activated and recruited once there is an insect attack. Thus, these compounds are produced in anticipation of an insect attack, hence termed 'phytoanticipins'. For example, maize silks constitutively produce maysin which is a C-glycosyl flavone. However, the quinones which are derived from it are toxic to corn earworm (Waiss Jr et al. 1979). Sometimes, the dormant compound and its activator are localized in different organelles within the cell. Upon tissue disruption by the invading insect, they are brought together which leads to the production of active compound. Benzoxazinoids are stored in vacuoles as glucosides. Due to the tissue disruption, these glucosides are hydrolysed by plastid localized glucosidases leading to the production of toxic aglycones (Frey et al. 2009).

Several of the above mechanisms are also active against pathogens in maize. Phytoalexins such as kauralexins and zealexins are also induced against pathogens (Schmelz et al. 2011; Huffaker et al. 2011), and benzoxazinoids are produced mainly against fungal pathogens (Ahmad et al. 2011). In addition, maize utilizes certain physical barriers to ward off or curtail the spread of the pathogen. Increased accumulation of suberin offers barrier against *Fusarium graminearum* (Santiago et al. 2007) and *Aspergillus flavus* (Spangler 2008). Deposition of callose in the cell wall and local hypersensitivity reaction are the other physical barriers deployed by maize (Morris et al. 1998). Ribosome-inactivating proteins and PR (pathogenesis-related) proteins are also synthesized in response to pathogen attack (Moeller and Tiffin 2005). Thus, the mechanisms of maize tolerance to pathogens are poorly understood relative to insect pests and need further study.

4 QTL Analysis for Biotic Stresses

Host plant resistance in maize for the biotic stress is of two categories: (i) qualitative resistance based on single gene resistance (R genes) and (ii) quantitative resistance based on multi-gene resistance. Most of the genetic resistance exploited by maize breeders display quantitative inheritance. This may be because maize is relatively more genetically diverse than other cereals owing to its outcrossing (Buckler et al.

2001). Maize breeders, therefore, can access more diversity within adapted germplasm and identify major and minor QTLs to achieve effective levels of biotic stress resistance (Balint-Kurti and Johal 2009). Many of the QTLs governing biotic stress resistance in maize are minor with small additive effects which work in tandem. For instance, both NCLB and SCLB of maize show quantitative inheritance with the preponderance of both additive and non-additive gene actions (Ranganatha et al. 2017; Jakhar et al. 2021). Hence, reciprocal recurrent selection (RRS) is the suitable method for improving resistance to these diseases. We present here the details of QTLs/genomic regions identified so far for various diseases and insect pests based on analysis of both biparental mapping populations and association mapping panels (Table 2).

4.1 Turcicum *Leaf Blight/Northern Corn Leaf Blight*

Initially, Welz and Geiger (2000) re-analysed the data from previous authors (before 2000) and reported 23 QTLs, many being major QTLs with R^2 values as high as 25.6%. Nearly, 29 QTLs were identified using a large nested association mapping (NAM) population (5000 inbred lines) using 1.6 million SNPs, and most of the underlying candidate genes included protein kinases with plausible role in plant defence response (Poland et al. 2011). Van Inghelandt et al. (2012) reported four SNPs which showed significant association with NCLB resistance. The NCLB resistance corrected for flowering time each with phenotypic variability explained (PVE) of 0.36–14.29% in a set of 4149 maize inbred lines representing Europe and North America. Two stable QTLs were identified of which *qNCLB5*.04 explained about 19% and 20% of phenotypic variation in the experimental years 2012 and 2013, respectively, and it was associated with both NCLB score and lesion width and hence proposed as valuable candidate for marker-assisted selection (MAS) (Chen et al. 2016a). Tian et al. (2018) reported six QTLs in P178 × G41-based backcross inbred lines (BILs) with PVE range of 4–23%, including two stable QTLs on chromosomes 2 and 8. Another major QTL, *qNCLB7.02* with a PVE of 10.11–5.29% was reported by Wang et al. (2018). Three QTLs were identified for NCLB resistance, among which *qNCLB-8-2* contributed maximum PVE of 16.34% followed 10.24% by *qNCBL-5* (Ranganatha et al. 2021). Recently, GWAS (genome-wide association study) using three association panels revealed nearly 22 SNPs and 17 significant haplotypes which co-localized with previously reported genes and QTLs for NCLB resistance in maize (Rashid et al. 2020). In an intercontinental trial with a set of 742 F_1-derived doubled haploid (DH) lines along with test crosses, a total of 17 QTLs were identified accounting for a variance of 3.57–30.98%, of which two QTLs, *q4* and *q5*, were found stable across locations and seasons evaluated in Brazil and Europe (Galiano-Carneiro et al. 2021a).

Table 2 List of QTLs identified for different biotic stresses in maize

S. no.	Biotic stress	Parents	Mapping population	Number and types of markers used	Software and method	QTLs identified	Reference(s)
Disease resistance							
1	Turcicum leaf blight or northern corn leaf blight	Ki14 × B73	109 RILs	765 SNPs and 106 SSRs	MAPMAKER/EXP 3.0	7 QTLs	Zwonitzer et al. (2010)
		GWAS	1487 genotypes	8244 SNPs	Single marker analysis and multiple forward regression	4 SNPs	Van Inghelandt et al. (2012)
		NAM	5000 genotypes	1.6 million	SAS	29 QTLs	Poland et al. (2011)
		CM212 × CM 338	F$_{2:3}$ families	SSR	QTL cartographer 2.5 using composite interval mapping	2 QTLs	Singh and Srivastava (2015)
		K22 × By815	207 RILs	56,110 SNPs (MaizeSNP50 BeadChip)	CIM in Windows QTL Cartographer 2.5 and MCIM in QTL Network 2.0 software	5 QTLs	Chen et al. (2016a)
		PH234 × PHBP3 and PH234 × PH84K	569 F2:3 families	3315 SNPs	–	5 QTLs	Hegde et al. (2018)
		Qi319 × Ye478	314 F$_{11}$ lines	88,268 SNPs	CIM using IciMapping software 4.0	11 QTLs	Wang et al. (2018)
		CML153 × SKV50	344 F$_{2:3}$	768 SNPs	WinQTL Cartographer v 2.5	3 QTLs	Ranganatha et al. (2021)
		T1 × A1, T1 × A2, T1 × A10, T2 × A3, T2 × A4, T2 × A5 and T5 × A11	742 DH lines	15k SNP chip	RQTL	17 QTLs	Galiano-Carneiro et al. (2021a)

Table 2 (continued)

S. no.	Biotic stress	Parents	Mapping population	Number and types of markers used	Software and method	QTLs identified	Reference(s)
		BB (crossbred from B73 × B97) and BC (crossbred from B73 × CML322)	170 RILs of BB, 163 RILs of BC and 3 parental populations (B73, B97 and CML322) as controls	1100 SNPs	ICIM method in the QTL loci mapping software (version 3.2)	12 QTLs	Xia et al. (2020)
		GWAS	CAAM, DTMA and IMAS association panels	64,344 SNPs for CAAM, 69,254 for DTMA and 69,286 for IMAS panels	EMMAX model using SVS version 8.6.0	22 SNPs and 17 significant haplotypes	Rashid et al. (2020)
2	Gibberella ear rot	CG62 × CO387	144 RILs	162 SSR markers	Composite interval mapping (CIM) – QTL Cartographer version 2.0	11 QTLs (silk inoculation) 18 QTLs (kernel inoculation)	Ali et al. (2005)
		LP4637 × L4674	298 F$_5$ RILs	768 SNPs	MT-CIM, WinQTL Cartographer V2.5	4 QTLs	Giomi et al. (2016)
		B73 × Mo17-doubled haploid	298 inbred lines IBM Syn10 DH population	6618 recombination bin markers	CIM in QTL cartographer (version 2.5)	10 QTLs	Yuan et al. (2020)
		Cheng351 × ZW18, Dan598 × ZW18 and JiV203 × ZW18	F$_{2:3}$ families	GenoBaits Maize10K chip containing 10 K SNP markers	CIM in QTL cartographer (version 2.5)	17 QTLs	Wen et al. (2020)
		T3 × A6, T3 × A7, T3 × A8, T3 × A12, T4 × A4 and T4 × A5	DH lines	15 k SNP chip	CIM on mppR version 1.2.1	4 QTLs	Galiano-Carneiro et al. (2021b)

3	Diplodia ear rot	WL118-10 × CZL- 8	123, F$_{2:3}$ families	56 SSR primers	CIM in QTL cartographer (version 2.5_009)	3 QTLs	Tembo et al. (2014)
		03MZF-CK83 × 10MZF-L4LW 07MZF-VDF6 × 10MZF-L4LW 04MZF-KQF0 × 03MZF-CK83 07MZF-SCH9 × 10MZF-L4LW	DH lines (210, 232, 90 and 151, respectively)	15K SNP markers	CIM using mppR package in R	11 QTLs	Baer et al. (2021)
4	Fusarium ear rot	87-1 × Zong 3	187 RILs, F$_{7:8}$ population	246 SSR markers	CIM and MCIM methods, Wincartographer 2.0 software	6 QTLs	Ding et al. (2008)
		BT-1 × N6	250 RILs	207 SSRs	Mixed model using QTLNetwork-2.0	4 QTLs	Li et al. (2011)
		GWAS	279 inbreds	47,445 SNPs	TASSEL	3 MTAs	Zila et al. (2013)
		GWAS	16871 diverse inbred lines	200,978 SNPs	MLM in GAPIT	Inconclusive	Zila et al. (2014)
		Tropical maize inbred lines CML495 × LA POSTASEQ. C7 F64-2-6-2-2-B-B-B, CML492 × LPSMT, CML495 × LPSMT and CML449 × LPSMT	940 lines POP1, 201 lines; POP2, 277 families; POP3, 268 families; and POP4, 272 families	56,110 SNP markers (GWAS) 1250 SNPs (biparental QTL mapping)	MLM in TASSEL V3 IciMapping v3.2	45 SNPs, 15 haplotypes and 15 QTLs	Chen et al. (2016b)
		LP4637 × L4674	298 F$_5$ RILs	768 SNPs	MT-CIM, WinQTL Cartographer V2.5	4 QTLs	Giomi et al. (2016)
		BT-1 × N6	174 F$_{9:10}$ 217 inbred lines	207 SSRs (QTL mapping) GBS	IciMapping v4.0 MLM in TASSEL V5	8 QTLs 57 MTAs 43 genes	Ju et al. (2017)

(continued)

Table 2 (continued)

S. no.	Biotic stress	Parents	Mapping population	Number and types of markers used	Software and method	QTLs identified	Reference(s)
		CO441 × CO354	F$_{2:3}$ population of 188 progenies	369 SSR markers, 13,292 SNPs and 963 INDEL	MAPQTL 6.0 software	15 QTLs	Maschietto et al. (2017)
		GE440 × Sd7 and NC300 × Gm1002	F$_{2:3}$ population of 280progenies	7 SSRs and 1 STS marker	Map manager QTX version 0.22	7 QTLs	Abdel-Rahman et al. (2016)
		GWAS	183 genotypes	267,525	TASSEL version 5.2	14 MTAs	Coan et al. (2018)
		GWAS	242 maize inbred lines	23,153 DArT-seq markers	rrBLUP in R	12 MTAs	de Jong et al. (2018)
		GWAS	NAM B73 × CML333, B73 × CML52, B73 × CML69 and B73 × NC358	7386 SNPs	TASSEL version 5.2.37	110 QTLs	Morales et al. (2019)
		GWAS	256 inbred lines	990,000 SNP markers	MLM in Tassel V5.2.25	39 MTAs under 17 QTLs	Samayoa et al. (2019)
		GWAS	MAGIC (672 RILs) with eight founder parents (A509, EP17, EP43, EP53, EP125, F473, EP86 and PB130)	1, 0000, 000 SNPs	FarmCPU	13 QTLs	Butrón et al. (2019)
		GWAS	874 inbred lines	955,690 SNPs	GLM and MLM	GLM -3034 MTAs MLM – 19 MTAs	Liu et al. (2021)
		Cheng351 × ZW18, Dan598 × ZW18 and JiV203 × ZW18	F$_{2:3}$ families	GenoBaits Maize10K chip containing ten K SNP markers	CIM in QTL cartographer (version 2.5)	20 QTLs	Wen et al. (2020)

5	*Aspergillus* ear rot	B73 × Mp715	210 F$_{2:3}$ mapping population	562 SSR	CIM in Win-QTL Cartographer v 2.5	12 QTL	Dhakal et al. (2016)
		Mp715 × Va35	250 F$_{2:3}$ lines	1200 SNP and 29 SSR markers	CIM in QTL cartographer (version 2.5)	8 QTL	Smith et al. (2019)
		Mp705 × Mp719	241 F$_{2:3}$ families	1247 SNP and 29 SSR markers	CIM in QTL cartographer (version 2.5)	7 QTLs	Womack et al. (2020)
		CO441 × CO354	F$_{2:3}$ families	369 SSR markers and 13,292 SNPs and 963 INDELs	MAPQTL 6.0 software	32 QTLs	Mashietto et al. (2017)
6	Maize rough dwarf virus disease	Mo17 × BLS14	227 F$_{2:3}$ lines	180 SSRs	PLABQTL	2 QTLs	Di Renzo et al. (2004)
		90,110 × Ye478	102 RILs	512 SSRs	IciMapping v3.0	5 QTLs	Luan et al. (2012)
		X178 × B73	89 F8 RILs	514 SNPs, and 72 SSR markers	CIM in MapQTL version 5.0	2 QTLs	Shi et al. (2012)
		GWAS	50 F$_9$ lines	56,110 SNPs	TASSEL 2.0	1 QTL	Tao et al. (2013a)
		S221 × K36	Extreme genotypes (F$_2$ population)	709,670 SNPs	BSA-Seq	1 QTL	Li et al. (2018)
		Zheng58 × D863F and Zheng58 × ZS301	241 F$_8$ RIL and 242 F$_7$ RILs	181 SSR markers	ICIM method in IciMapping 4.0	10 QTLs	Wang et al. (2019)
		80,044 × 80,007	199 RILs	3k SNP makers	JoinMap (version 2.5)	1 QTL	Zhang et al. (2021)

Table 2 (continued)

S. no.	Biotic stress	Parents	Mapping population	Number and types of markers used	Software and method	QTLs identified	Reference(s)
7	Sugarcane mosaic virus disease	D32 × D145	219 F_3 or immortalized F_2 families	87 RFLP and 7 SSR	CIM in PLABQTL software	5 QTL	Xia et al. (1999)
		FAP1360A × F7	75 $BC_{4:5}$	RFLP (2), SSR (24) and AFLP (8) markers	MapMaker/Exp (version 3.0b)	2 genes	Xu et al. (1999)
		F6 × FAP0259A	121 F_3	2 SSRS from Xia et al. (1999)	CIM in e PLABQTL	2 QTLs	Duble et al. (2000)
		L520 × L19	150 F_2 individuals	19 SSRs	CIM in MapMaker/EXP 3.0	3 QTLs	De Souza et al. (2008)
8	Grey leaf spot	Mo17 × B73	302 RILs	–	CIM in MapQTL5	5 QTLs	Balint-Kurti et al. (2008a, b)
		Ki14 × B73	109 RILs	765 SNPs and 106 SSRs	MAPMAKER/EXP 3.0	7 QTLs	Zwonitzer et al. (2010)
		Y32 × Q11	161 $F_{2:3}$	183 polymorphic SSRs	CIM in QTL cartographer	4 QTLs	Zhang et al. (2012)
		YML32 × Ye478	204 $F_{2:3}$	167 polymorphic SSRs	IciMapping v3.1	7 QTLs	Liu et al. (2016a, b)
		NAM	25 NAM populations	–	–	16 QTLs	Benson et al. (2015)
		08-641 × 446	233 $F_{2:3}$ families	124 SSRs	WinQTL cartographer 2.5	5 QTLs	He et al. (2018)
		WGR × DZ01	30 extreme individuals (BC_1F_1)	–	BAS-Seq	1 major QTL	Sun et al. (2021)
		CML 550 × CML494 CML550 × CML504 CML550 × CML511 CZL0618 × LaPostaSeqC7-F71-1-2-1-1B CZL074 × LaPostaSeqC7-F103-1-2-1-1B	3 DH and 2 F_3 populations	1047–2699 SNPs	IciMapping version 4.1	22 QTLs	Kibe et al. (2020)
		GWAS	410 lines	337,110 SNPs	TASSEL ver5.2	10 MTAs	

9	Southern leaf blight	Mo17 × B73	158 RILs	234 markers (RFLP, isozyme and SSR)	PLABQTL	8 QTLs	Carson et al. (2004)
		NC300 × B104	133 RILs	113 SSRs	QTL cartographer v2.5	7 QTLs	Balint-Kurti et al. (2006)
		B73 × Mo17	158 RILs	–	QTL cartographer v2.5	4 stable QTLs	Balint-Kurti et al. (2007)
		H99 × B73 B73 × B52	142 and 186 lines, respectively	158 RFLP and 14 SSRs	QTL cartographer v2.5	3 QTLs	Balint-Kurti et al. (2008a, b)
		B73rhm1 × NC250A NC250A × B73	193 and 144, respectively	220 RFLPs, 32 SSRs and 78 SNPs	JoinMap® 3.0	9 QTLs	Zwonitzer et al. (2009)
		Ki14 × B73	109 RILs	765 SNPs and 106 SSRs	MAPMAKER/EXP 3.0	9 QTLs	Zwonitzer et al. (2010)
		NAM	5000 RILs	1106 SNPs	–	32 QTLs	Kump et al. (2011)
		NAM	25 NAM families	7386 SNPs		33 QTLs	Bian et al. (2014)
		NAM	5000 RILs	7386	Tassel 3.0	48 QTLs	Li et al. (2018)
		LM5 × CM140	207 RILs	80 polymorphic SSRs	QTL cartographer v2.5	4 QTLs	Kaur et al. (2019)

Table 2 (continued)

Insect resistance

S. no.	Biotic stress	Parents	Mapping population	Number and types of markers used	Software and method	QTLs identified	Reference(s)
1	Mediterranean corn borer (MCB)	A637 × A509	171 RILs	285 SNP markers	CIM in PlabMQTL,	5 QTLs	Jiménez-Galindo et al. (2017)
		B73 × CML103	121 inbred lines	1478 SNPs	CIM in PlabMQTL,	8 QTL	Samayoa et al. (2015a)
		GWAS	302 inbreds	50k SNPs	MLM using Tassel 4.1.26	25 SNPs	Samayoa et al. (2015b)
		EP42 × EP39	178 RILs	226 SSR markers	CIM in PLABQTL software	3 QTLs	Ordas et al. (2010)
		B73 × Mo17	243 RILs	587 markers	CIM in PLABQTL software	3 QTLs	Ordas et al. (2009)
		EP42 × A637	146 RILs	130 polymorphic SSRs	CIM in PlabMQTL software	6QTLs	Samayoa et al. (2014)
2	Maize weevil	CML290 × Muneng-8128 C0 HC1-18 -2-1-1	163 F$_2$ progeny	151 SSRs	CIM	23 QTLs	García-Lara et al. (2009)
		CML290 × Muneng-8128 C0 HC1-18 -2-1-1	163 F$_2$ progeny	151 SSRs	CIM	17 QTLs	García-Lara et al. (2010)
		P84 × Kilima	RILs	170 SSRs	CIM	15 QTLs	Castro-Álvarez et al. (2015)
3	European corn borer	B73 × B52	F$_2$ population	87 RFLP makers	IM using Mapmaker/QTL	8 QTLs	Schön et al. (1993)
		D06 × D408	226 F$_3$ families	93 RFLP +2 SSRs	CIM using PLABQTL	11 QTLs	Bohn et al. (2000)
		B73 × B52	183 RILs	65 SSRs	CIM using PLABQTL	9 QTLs	Cardinal et al. (2001)
		B73Ht × Mo47	244 F$_{2:3}$	582 RFLPs +1 SSR	CIM using QTL cartographer	16 QTLs	Jampatong et al. (2002)
		De811 × B73	147 F$_{2:3}$	103 RFLP	CIM using PLABQTL	7 QTLs	Krakowsky et al. (2002)
		D06 × D408	204 F$_{2:3}$	93 RFLP and 2 SSR	CIM	6 QTLs	Papst et al. (2004)

4	Southwestern corn borer	CML131 × CML67 Ki3 × CML139	215 $F_{2:3}$ 475 $F_{2:3}$	108 and 122 RFLPs	CIM	14 QTLs	Groh et al. (1998)
		Ki3 × CML139	472 F_2 individuals	282 RFLPs	CIM	7 QTLs	Khairallah et al. (1998)
		Mp704 × Mo17	230 $F_{2:3}$	73 SSRs	MIM using QTL Cartographer	10 QTLs	Brooks et al. (2005)
		A619 × Mp708	427 F_2	91 SSRs	MIM using QTL Cartographer	4 QTLs	Brooks et al. (2007)
		Mp704 × Mo17	230 $F_{2:3}$	224 SSRs and SNPs	CIM and MIM using QTL Cartographer 2.5	29 QTLs	Womack et al. (2018)
5	Fall army warm	Mp704 × Mo17	230 $F_{2:3}$	73 SSRs	MIM using QTL Cartographer	5 QTLs	Brooks et al. (2005)
		A619 × Mp708	427 F_2	91 SSRs	MIM using QTL Cartographer	7 QTLs	Brooks et al. (2007)
		Mp704 × Mo17	230 $F_{2:3}$	224 SSRs and SNPs	CIM and MIM using QTL Cartographer 2.5	24 QTLs	Womack et al. (2018)

4.2 Gibberella *Ear Rot (GER)*

One major QTL (28.9% PVE) was identified for GER on chromosome 3 (Ali et al. 2005). Around 17 QTLs were identified for GER in three mapping populations derived using three different donors (Cheng351, Dan598 and JiV203), of which *qRger7.1*, from the resistant parent, Cheng351, was a major QTL with 20.16–41.84% PVE (Wen et al. 2020). One stable QTL, *q1*, was also identified for GER with 10.17–21.84% PVE by Galiano-Carneiro et al. (2021b).

4.3 Diplodia *Ear Rot (DER)*

Tembo et al. (2014) identified the QTL '*Sm_4,1*' for resistance to *S. maydis*, causing DER on chromosome 4. Also, they have identified a QTL with pleiotropic effect on chromosome 1 which is 22 cM from *umc1269* marker. In another study, about eleven QTLs were identified for DER using multi-parent mapping populations and four different models of which one QTL on chromosome 5 showed maximum PVE of 7.18% (Baer et al. 2021).

4.4 Fusarium *Ear Rot (FER)*

FER is considered a complex trait controlled by many minor QTLs, with moderate heritability and high environmental influence posing significant hurdles for breeding-FER-resistant varieties. Genomic selection is the viable option for improving resistance against this disease. The first report on QTLs for resistance to FER was given by Perez-Brito et al. (2001) who found nine and seven QTLs in two F_2 populations with a PVE of 30–44%. In a subsequent study, two separate populations were utilized for mapping FER resistance and resistance to fumonisins. Seven QTLs were found with cumulative PVE of 47% for FER resistance and nine QTLs explained 67% of the variation for mean fumonisin concentration (Robertson-Hoyt et al. 2006). Two stable QTLs on chromosome 3 were reported by Ding et al. (2008) coupled with a major QTL with 13–22% PVE on the same chromosome. Four QTLs were identified on chromosomes 3, 4, 5 and 6, of which the one on chromosome 4 was a major QTL with PVE of 10.2% (Li et al. 2011). Another major QTL was reported on chromosome 4 (with PVE of 17.95%), which was later validated in near isogenic line (NIL) background (Chen et al. 2012). Seven QTLs and the associated markers were reported for FER resistance in terms of grain yield per main ear and test weight (Abdel-Rahman et al. 2016). Combined GWAS (using 818 tropical maize inbred lines) and QTL analysis (using four biparental mapping populations) revealed eight co-localized QTLs on chromosomes 2, 3, 4, 5, 9 and 10, with 38 putative candidate genes related to disease resistance (Chen et al. 2016b). In addition,

for 8 QTLs, 43 candidate genes (in vicinity of 57 SNPs) were mapped for *F. verticillioides* resistance. Among these genes, *GRMZM2G0081223*, *AC213654.3_FG004* and *GRMZM2G099255* were common across both mapping strategies and can be considered as valid candidate genes for FER resistance (Ju et al. 2017). This study has also validated the markers reported by previous authors. In another study, 15 and 17 QTLs were identified for FER resistance and fumonisin B1 (FB1) mycotoxin, respectively, and 24 candidate genes were validated by coupling with transcriptomic data (Maschietto et al. 2017). In contrast, a SNP-based GWAS study identified several minor QTLs governing FER resistance. Through mixed linear model (MLM), 19 marker trait associations (MTAs) were identified with an average PVE of 1.60% (Liu et al. 2021). Around 20 QTLs were identified for FER resistance among which *qRfer1*, *qRfer10*, and *qRfer17* were found to be major QTLs explaining phenotypic variation as high as 26.58 to 43.36%, 11.76 to 18.02%, and 12.02 to 32 21.81%, respectively (Wen et al., 2021). A combined QTL analysis for both FER and GER resistance unveiled four QTLs reflecting that LP4637 (donor) provides dual tolerance to both the ear rot genus (Giomi et al. 2016). Thirty-nine MTAs were identified for resistance to fumonisin accumulation in maize kernels separately which assembled into 17 QTLs (Samayoa et al. 2019). A multi-parent advanced generation intercross (MAGIC) population derived from eight founder parents was analysed for resistance to FER, and 13 putative QTLs were identified with minor affects. Nevertheless, there are distinct regions, 210–220 Mb on chromosome 3 and 166–173 Mb on chromosome 7 which harbour QTLs for FER and fumonisin content resistance in maize (Butron et al. 2019). NBS-LRR receptors and transcription factors involved in redox reaction and peroxidase activity seem to play a pivotal role in FER resistance (de Jong et al. 2018). This was discovered through DArT Seq-based GWAS study using 242 maize inbred lines. Two MTAs were found in the genes governing programmed cell death when 267 inbred lines were analysed using 47,445 SNPs (Zila et al. 2013). No disease resistance-related genes were identified in a GWAS study by Zila et al. (2014) despite a large panel of 1687 inbred lines iterating the complex nature of FER tolerance. A nested association mapping (NAM) population-based mapping (four populations with common parent) unveiled 110 QTLs for FER and fumonisin resistance (Morales et al. 2019). Four defence-related genes, a gibberellin 2-oxidase4, a glucosyltransferase, a Ras-related protein RHN1 and a phosphoribosylanthranilate transferase (PAT), are found to be putative candidate genes for FER in 183 field maize and popcorn inbred lines (Coan et al. 2018).

4.5   Stalk Rot

Two QTLs, *qRfg1* (major) and *qRfg2* (minor), were mapped from the resistant inbred 1145 (Yang et al. 2010; Zhang et al. 2012a). The *ZmCCT* gene was found to be the causal gene at *qRfg1* (Wang et al. 2017). The resistance in maize plants is governed by insertion or deletion activities of CACTA-like transposon in the

promoter of *ZmCCT* which causes histone modification and DNA methylation. The transposon insertion silences the gene and renders the plants susceptible to stalk rot. *ZmAuxRP1* is the candidate gene of *qRfg2*. Upon infection, the expression of this gene is downregulated resulting in the arrest of root growth, albeit increasing the resistance to stalk rot (Ye et al. 2019). *ZmAuxRP1* is reported to enhance the resistance of FER as well. Resistance of Anthracnose stalk rot (ASR) is governed by *Rcg1*, a major QTL which explained ~50% variation (Jung et al. 1994), and the underpinning candidate gene is an NB-LRR governing resistance gene (Frey et al. 2011). *Diplodia* stalk rot seems to be under the control of both additive and non-additive gene actions, and hence, RRS is the best breeding method for tolerance improvement (Carson and Hooker 1981; Badu-Apraku et al. 1987).

4.6   Maize Rough Dwarf Disease (MRDD)

Two QTLs were reported for disease susceptibility index (DSI) in Mo17 × BLS14-derived $F_{2:3}$ population. These two QTLs jointly governed 36.2% of PVE (Di Renzo et al. 2004). A major QTL, *qMrdd8*, was identified on chromosome 8 for MRDD resistance with a PVE of 24.6–37.3% across the environments (Shi et al. 2012). This was later fine-mapped to a region of 347 kb and coupled with RNA-Seq two candidate genes CG1 and CG2 that were identified (Liu et al. 2016a). A recessive major QTL, *qMrdd1*, was found on chromosome 8 using GWAS which was subsequently validated and fine-mapped to a 1.2 Mb region (Tao et al. 2013a). The underlying candidate gene was later found to be Rab GDP dissociation inhibitor alpha (*RabGDIα*) which is responsible for host susceptibility (Liu et al. 2020). Another major QTL *qMRD8* was identified on chromosome 8 with a PVE of 12.0–28.9% in addition to other QTLs, *qMRD2*, *qMRD6*, *qMRD7* and *qMRD10* (Luan et al. 2012). A single dominant locus was identified on chromosome 8 using SLAF-Seq-based bulked segregant analysis (BSA), and two SSR markers *6F29R29* and *6F34R34* were reported to be linked to this QTL. This region harbours around 32 candidate genes with defence-related functions (Li et al. 2018). Recently, a partially dominant resistance QTL, *qMrdd2*, for MRDD (with 20.4% PVE) was identified on chromosome 2 in recombinant inbred line (RIL) population derived from 80,007 (resistant) × 80,044 (sensitive) (Zhang et al. 2021).

4.7   Sugarcane Mosaic Virus (SCMV) Disease

Initial report on QTLs for resistance to SCMV came from Xia et al. (1999) who identified five QTLs located on chromosomes 1, 3, 5, 6 and 10, with two stable and prominent QTLs on chromosomes 3 and 6. Later, these QTLs were validated in a different mapping population (F_3 from F_6 × FAP0259A) and named as *Scm1* (chromosome 6) and *Scm2* (chromosome 3), the resistant alleles of *Scm1* matched with those reported by Xia et al. (1999), whereas the alleles of *Scm2* were different.

However, later by saturating these two regions with a greater number of microsatellite markers, Yuan et al. (2003) demonstrated that *Scm1* locus houses two QTLs. Similarly, two QTLs, *Scm1* and *Scm2*, were reported for SMV resistance on chromosomes 6 and 3, respectively (Xu et al. 1999). Three QTLs were identified for SMV disease, two QTLs (*Scm2a*, PVE of 13.34%, and *Scm2b*, PVE of *41.85%*) clustered together on chromosome 3, whereas third QTL was found on chromosome 6, *Scm1* with a PVE of 7.66% (De Souza et al. 2008). Thus, regions on chromosomes 3 and 6 seem to harbour genes for SCMV disease resistance in maize which was further confirmed by a meta-QTL analysis (Lü et al. 2008).

4.8 Grey Leaf Spot (GLS)

Resistance to GLS is under the control of multitude of genes with cumulative additive effects and a significant G × E interaction (Lyimo et al. 2011). An advanced generation intercross RIL population derived from the cross Mo17 × B73 was utilized to identify five QTLs, and drawing parallels with previously reported QTLs, two hotspots were identified (Balint-Kurti et al. 2008a). Two stable and major QTLs, *qRgls1* and *qRgls2* on chromosomes 8 and 5, were consistently detected across locations. Furthermore, *qRgls1* was fine-mapped to an interval of 1.4 Mb (Zhang et al. 2012). QTLs identified for flowering time and GLS resistance were found to overlap reflecting the relation between these two traits in YML32 × Ye478-based $F_{2:3}$ population. A major QTL, *qRgls.yaas-8-llqFt.yaas-8* with PVE of ~18% and 16.2%, was identified for GLS disease score and flowering time, respectively (Liu et al. 2016b). Three major QTLs, *qGLS1.04*, *qGLS2.09* and *qGLS4.05* with PVE of >10%, were reported using a NAM population. Later, *qGLS1.04* was fine-mapped to two intervals of 6.5 Mb and 5.2 Mb, and the underpinning candidate gene was also identified, that is, putative flavin monooxygenase gene (Benson et al. 2015). Four stable QTLs *qRgls.CH-4*, *qRgls.CH-1*, *qRgls.CH-2* and *qRgls.CH-6* were in $F_{2:3}$ population (08-641 and 446 as parents), of which *qRgls.CH-6* was novel (He et al. 2018). Through linkage mapping, 22 QTLs were identified with *qGLS7–105* on chromosome 7 being the major QTL (PVE of 28.2%), and 14 QTLs were found through GWAS with PVE of 6–8% individually (Kibe et al. 2020). A major QTL, *qRgls1.06*, explaining 55% of the total variance was identified through BSA-Seq for resistance to GLS which was later fine-mapped to 2.38 Mb region (Sun et al. 2021).

4.9 Southern Corn Leaf Blight (SCLB)

Three major QTLs on chromosomes 1, 2 and 3 were identified for SLLB resistance in a RIL population derived from Mo17 × B73 (Carson et al. 2004). Similarly, two major QTLs accounting for 80% of phenotypic variance were identified on chromosomes 3 and 9 using a RIL population of the cross NC300 × B104 (Balint-Kurti

et al. 2006). Later, same group identified four stable QTLs in a different mapping population, B73 × Mo17, two on chromosome 3 (within same interval) and one each on chromosomes 1 and 8 (Balint-Kurti et al. 2007). The QTL found on chromosome 3 almost matched in its location with the one identified previously by Carson et al. (2004). This QTL was further fine-mapped to a 0.5 cM interval using two sets of populations, NIL $F_{2:3}$ one derived from the initial cross Mo17 × B73 and a RIL $F_{2:3}$ from two RILs of B73 × Mo17, and the candidate genes were elucidated (Kump et al. 2010). Three QTLs were identified using two more mapping populations developed from H99 × B73 and B73 × B52. Furthermore, a cursory comparison with previously reported QTLs revealed two QTL hotspots on chromosomes 3 and 6 (Balint-Kurti et al. 2008b). Nine QTLs each were identified in two sets of mapping populations – B73 rhm1 × NC250A and NC250A × B73 – one developed specifically for SCLB and Ki14 × B73 developed for exploring multiple disease resistance (Zwonitzer et al. 2009, 2010). Similarly, in NAM populations, ~35 QTLs with small additive effects were identified for SCLB resistance along with several underlying defence-related genes such as LRR receptor kinase, AP2 transcription factors, etc. (Kump et al. 2011; Bian et al. 2014). In another study, a large NAM population (5000 recombinant inbred lines from 25 parents with B73 as a common parent) was used to map 48 QTLs for SCLB resistance. Further, among the candidate genes identified, three genes encoding AN1-like zinc finger domain containing protein, LRR protein and BCL-2-associated athanogene 3 protein were separately validated (Li et al. 2018). Four putative QTLs on chromosomes 3, 8 and 9 were found to confer resistance to SLB with a cumulative PVE of 54% (Kaur et al. 2019).

In a QTL analysis for multiple disease resistance, a single RIL population derived from Ki14 × B73, nine, eight and six QTLs were identified for SCLB, GLS and NCLB resistance, respectively, with many QTLs overlapping across diseases (Zwonitzer et al. 2010). Combined QTL mapping for three SCLB, NCLB and GLS using four donors (NC304, NC344, Ki3, NC262) and two recurrent parents (Oh7B, H100) revealed QTLs overlapping for two or more diseases – two QTLs for SCLB and NCLB, seven QTLs for SCLB and GLS and two QTLs for NCLB and GLS and six for all the three diseases (Lopez-Zuniga et al. 2019). Around 44 QTLs identified for resistance against NCLB, SCLB and GLS in previous studies were validated using 12 $F_{2:3}$ populations, of which 16 QTLs were confirmed and can serve as valuable candidates for MAS (Martins et al. 2019).

5   QTLs for Insect Resistance

5.1   *Mediterranean Corn Borer (MCB)*

The resistance to MCB is assessed through length of stem tunnels made by MCB larvae. Grain yield under infestations also seems to be equally important trait for screening for MCB tolerance. In an initial report, three QTLs were reported, one for kernel damage and two for stalk tunnelling. Two of these QTLs co-localized with

previously reported QTLs for European corn borer (Ordas et al. 2009). In a similar study, three more QTLs were identified for MCB resistance, and underlying five candidate genes involved in cell wall biosynthesis were proposed. Thus, cell wall characteristics primarily decide feeding behaviour of borers (Ordas et al. 2010). Six QTLs were found for various MCB-resistant traits such as tunnel length (1), stalk lodging (1) and ear resistance (4), with PVE of 19.8%, 11.5% and 25–63%, respectively. QTLs governing yield under infestation seem to control MCB tolerance (Samayoa et al. 2014). However, in another study by the same group, no genetic correlation was obtained between tunnel length and grain yield reflecting that this association is background specific. Samayoa et al. (2015a) identified eight QTLs for MCB resistance, most of them being major QTLs including one QTL that can reduce tunnel length up to 8 cm (Samayoa et al. 2015a). A GWAS study using a panel of 302 inbreds revealed 25 MTAs for MCB resistance with PVE of 6–9%. The genes with or close to these SNPs are mostly defence related (Samayoa et al. 2015b). Five QTLs were reported for MCB resistance in terms of tunnel length (3), kernel resistance (1) and stalk damage (1), of which one QTL (in the bin 10.02–10.03) displayed major effect (PVE – 13% for stalk damage and 10% for tunnel length) (Jimenez-Galindo et al. 2017). Interestingly allelic variants of markers linked to these QTLs provided yield advantage as in previous study.

5.2 *European Corn Borer (ECB)*

Like MCB, resistance to ECB is a quantitative trait with tunnel length being the suitable proxy for mapping studies. Genomic regions responsible for resistance from donor inbred line B52 were found on chromosomes 1, 2, 3 and 4 in a first study (Onukogu et al. 1978). Later, eight QTLs were reported for tunnel length which showed cumulative PVE of 38%, among which two were major QTLs with PVE >13% (Schon et al. 1993). Likewise, six QTLs for tunnel length and five for silk damage rating were reported with a total genotype variance of 50%, and only one QTL was common between these two traits (Bohn et al. 2000). Using RILs derived from the same cross (B73 × B52) as that of Schon et al. (1993), nine QTLs were identified for ECB resistance with a cumulative PV of 59%. However, only one QTL coincided with the previous study (Cardinal et al. 2001). Jampatong et al. (2002) reported nine QTLs (on chromosomes 1, 2, 4, 5, 6 and 8) for first-generation ECB and seven (on chromosomes 2, 5, 6, 8 and 9) for second-generation ECB. However, majority of QTLs were inconsistent across environments. Using De811 as a donor, seven QTLs were detected for ECB resistance. In comparison with the population derived from B73 × B52, only one QTL could match reflecting different genes contributing resistance to ECB (Krakowsky et al. 2002). Two sets of populations were utilized in another study – $F_{2:3}$ and a test cross population. Four and eight QTLs were found for stalk damage rating (SDR) and tunnel length using $F_{2:3}$ of the original cross, while six QTLs were identified using test cross progenies. However, of these, only three QTLs for SDR matched between two populations (Papst et al. 2004).

5.3   Southwestern Corn Borer (SWCB)

Resistance to SWCB is a polygenic trait with primarily additive gene action and is assessed phenotypically by observing leaf damage area. Using two mapping populations, CML131 × CML67 and Ki3 × CML139, nine QTLs (chromosomes 1, 5, 7, 8 and 9) were identified in former and five QTLs (chromosomes 1, 6, 8 and 9) in latter population, and no common QTLs were observed between two populations (Groh et al. 1998). In the same year, seven QTLs were reported using a F_2 population derived from the cross, Ki3 × CML139, which accounted for a cumulative PV of 30% (Khairallah et al. 1998). Brooks et al. (2005) reported around eight QTLs and two interactions for SWCB resistance using a population generated from the cross of Mp704 and Mo17. Furthermore, *mir* family of genes and *glossy15* locus located on chromosomes 6 and 9, respectively, were proposed as candidate genes for SWCB resistance. In continuation of this work, addition of 151 more SSR markers resulted into 29 QTLs (through CIM) explaining up to 29% of PVE (Womack et al. 2018). Four more QTLs were unveiled for SWCB resistance using Mp708 as a donor parent. The QTLs found on chromosomes 1, 5, 7 and 9 corroborated with those identified using Mp704 in previous study (Brooks et al. 2007).

5.4   Fall Armyworm (FAW)

The resistance to FAW seems to show close association with resistance to SWCB facilitating simultaneous improvement of both these traits. As a testament to this, QTL studies have coupled analysis of both insect pests, and many of the QTLs coincided for these two pests. Brooks et al. (2005) found seven QTLs governing resistance to FAW, of which two QTLs coincided with those identified for SWCB. Similarly, in 2007, the same group reported seven QTLs using a different donor parent. Of these, the QTLs found on chromosomes 1, 5, 7 and 9 overlapped with the QTLs identified for SWCB resistance (Brooks et al. 2007). By enriching the linkage map of Brooks et al. (2005) with additional SSR and SNP markers, Womack et al. (2018) reported 24 and 36 QTLs for FAW resistance through CIM and MIM, respectively.

Thus, many of the genomic regions governing different herbivorous insect pests coincide, indicating few genetic entities confer broad-spectrum resistance against a variety of herbivorous pests in maize and in turn suggesting the apparent possibility of simultaneous improvement of resistance to these pests. This was further attested by a GWAS study using 341 maize genotypes where single candidate gene was responsible for multiple QTNs for pest resistance (Badji et al. 2020). Additionally, a meta-QTL analysis of these QTLs revealed that majority of the regions governing resistance to herbivorous insects in maize harbour QTLs for cell wall constituents such as members of hydroxycinnamate group as well as fibre components indicating their vital role in resistance (Badji et al. 2018).

5.5 Maize Weevil (MW)

There are limited reports on identifying the genomic regions governing MW resistance. In a first report by Garcia-Lara et al. (2009), five QTLs were found for grain damage, six QTLs for grain weight loss, seven for MW susceptibility index and three for number of adult progenies explaining 28%, 22%, 27% and 10% of PVE, respectively. Almost half of these QTLs showed significant G × E interaction. Later, using the same population, Garcia-Lara et al. (2010) reported 17 QTLs for 11 biochemical parameters with PVE ranging from 25% to 47%. Similarly, 15 QTLs were identified for MW resistance in a RIL population derived from P84 × Kilima with a PVE of 14–51%. Individually, six QTLs were found for grain weight loss, four QTLs for flour production and five for adult progeny (Castro-Álvarez et al. 2015). Badji et al. (2020) recently conducted GWAS using 341 tropical maize lines to study the genetic control of resistance to multiple insect pests like MW, SB and FAW. They identified revealed 62 quantitative trait nucleotides (QTNs) associated with FAW and MW resistance traits across the maize genome. Sixteen QTNs were closely associated with multiple traits and six were associated with resistance to both FAW and MW, discovering the pleiotropic genetic control.

6 Qualitative Resistance: R Genes

Qualitative resistance is generally correlated with hypersensitive response at infection site and is also exploited in maize (Steffenson 1992). Examples of *Ht* genes for resistance to NCLB (Welz and Geiger 2000) and the *Rp* genes for resistance to common rust (Ramakrishna et al. 2002) have been used in maize breeding. *Hm1* was the first reported disease resistance gene conferring resistance to maize leaf blight and ear mould caused by *Cochliobolus carbonum* (race 1). This gene encodes an NADPH-dependent HC-toxin reductase which neutralizes HC-toxin responsible for the disease (Johal and Briggs 1992). The locus *rp1* on chromosome 10 harbours around 14 race-specific resistance genes for common rust in maize caused by *P. sorghi* (Hulbert 1997). Among these genes, *Rp1-D* was characterized and is a NB-LRR resistance gene (Collins et al. 1999). However, races virulent to this gene emerged later. At least 18 race-specific genes have been identified for resistance to southern rust in maize, which is more notorious than common rust (Zhu et al. 2021). *ZmWAK* is the underpinning gene for the major QTL, *qHSR1*, governing resistance to head smut caused by *Sphacelotheca reiliana* on chromosome 2 (Zuo et al. 2015). *ZmWAK* codes for a wall-associated receptor-like protein kinase which primarily functions to restrict the spread of the soil-borne pathogen from root to aboveground parts. A closely related gene, *ZmWAK-RLK1*, was found to be a candidate gene in *Htn1* locus mapped for NCLB resistance (Hurni et al. 2015). *ZmREM6*.3 is a candidate gene of another NCLB resistance QTL *qNLB1.02$_{B73}$* (Jamann et al. 2016), whereas *ZmREM1*.3 overexpression in maize plants gave resistance to southern rust

(Wang et al. 2019). Another NB-LRR gene, *Rcg1*, which governs resistance to ASR was characterized using transposon tagging (Frey et al. 2011). *ZmCCoAOMT2* was proposed as candidate gene for GLS resistance which encodes caffeoyl-CoA O-methyltransferase involved in lignin production (Yang et al. 2017). This gene was also found to be responsible for resistance to SCLB. In addition, *rhm1*, another locus conferring SCLB resistance, contains only one causal gene encoding lysine histidine transporter 1 (Zhao et al. 2012).

ZmFBL41 was identified as gene responsible for quantitative resistance against banded leaf and sheath blight in maize. A mutant with two amino acid substitutions in *ZmFBL41* prevented its interaction with *ZmCAD* thwarting the degradation of the latter and resulting in lignin accumulation and resistance (Li et al. 2019). As mentioned before, *ZmCCT* and *ZmAuxRP1* are the causal genes of *qRfg1*, a major QTL, and *qRfg2*, a minor QTL governing resistance to stalk rot, respectively. The expression of *ZmCCT* is regulated by CACTA-like transposon. The insertion of transposon silences the gene with minimum or no response to pathogen attack (Wang et al. 2017). *ZmAuxRP1* enhances the synthesis of auxin indole-3-acetic acid (IAA) while repressing benzoxazinoid defence compounds (BXs). It also provides resistance to FER (Ye et al. 2019). Mutants (knockdown) of *LOX3* (lipoxygenase) gene displayed reduced ear rot symptoms with decreased conidia formation of *Fusarium verticillioides* and the subsequent production of mycotoxin fumonisin B1 (Gao et al. 2007, 2009). Another gene, *ZmLOX12*, however, supressed the disease production (Christensen et al. 2015).

Similarly, h-type thioredoxin encoding gene *ZmTrxh* is the causal gene of *Scmv1*, a major locus for SCMV resistance mapped on chromosome 6 (Tao et al. 2013b). *ZmABP1* is the causal gene for *Scmv2*, another SCMV resistance locus which encodes an auxin-binding protein acting during the later stages of viral infection (Leng et al. 2017). *ZmGDIα* gene is associated with a major QTL, *qMrdd1*, for MRDD resistance, which encodes a Rab GDP dissociation inhibitor alpha (RabGDIα) (Liu et al. 2020). The recessive allele of the gene *ZmGDIα-hel* generated by the insertion of helitron transposon into intron 10 renders an alternative splice variant which reduces disease severity by ~30%. *Pythium* stalk rot in maize is caused by *Pythium aphanidermatum* and *Pythium inflatum*. Two dominant genes, *RpiQI319-1* and *RpiQI319-2*, reportedly confer resistance to *Pythium* stalk rot (Song et al. 2015). Thus, several candidate genes underpinning resistance to biotic stresses, particularly diseases, in maize have been elucidated and characterized, and many more need to be discovered and characterized in the future.

7 Utilization of QTLs Identified in MAS Programmes

MAS provides valuable alternative for conventional breeding for accelerated development of improved crop varieties with host plant resistance. MAS significantly reduces the time through efficient selection, irrespective of stage. Marker-assisted

backcross breeding (MABB) can be utilized to correct a specific defect of otherwise popular variety using linked or gene-based marker (Zunjare et al. 2018; Xu et al. 2020). This is particularly relevant in maize biotic stress breeding because of extensive QTL and GWAS reports available in literature. Further many of these QTLs were fine-mapped and validated making them suitable inputs for MAS. However, only few introgression studies exist for biotic stress resistance genes in maize compared to rice and wheat. Zhao et al. (2012) introgressed head smut resistance QTL, qHSR1 (ZmWAK gene), through MABC into ten diverse inbred lines that exhibited improved head smut resistance and yield (Zuo et al. 2015). The introgression of ZmWAK into a Chinese maize line Tongsipingtou led to the development of head smut-resistant variety, Jidan558. Marker-assisted gene pyramiding of two genes, *Scmv1* and *Scmv2*, into the background of maize line, F_7, resulted into a completely tolerant line (nearly isogenic line) against sugarcane mosaic virus (Xing et al. 2006). Yang et al. (2017) also developed a multiple disease-resistant line (against SCLB and GLS) by introgression of *qMdr9.02*. Three putative QTLs for southwestern corn borer were simultaneously mapped and transferred from CML67 into recurrent parent CML204 (Willcox et al. 2002). A major QTL for MRDD, *qMrdd8*, was introgressed from the donor X178 into the background of seven recipient parents, Huangzao4, Chang7-2, Ye478, Zheng58, Zhonghuang68, B73 and Ji846 using four foreground markers (Xu et al. 2020). MLND resistance QTLs were transferred from KS23-6 into nine locally adapted inbreds using KSAP assays (Awata et al. 2021). Except these, to the best of our knowledge, there were no attempts to introgress genes/QTLs for biotic stress resistance in maize despite the availability of many well-characterized and cloned genes.

8 Conclusion

Diseases and pests are the important stresses encountered by maize crop which often result in complete yield loss. Available literature suggests report of numerous QTLs for various biotic stresses. Many of them have been fine-mapped, and the causal candidate genes have been identified and characterized. Methodical deployment of these genes and QTLs into the susceptible inbreds is highly essential to evolve biotic stress-resilient maize hybrids. Relative to diseases, mapping studies for insect pests received lesser attention, though they are more devastating than diseases. Lack of easy-to-adopt screening protocols might be the reason for this. However, the silver lining here is that resistance to herbivorous insects seems to be controlled by few genomic hot spots, thus facilitating multiple insect resistance by the transfer of a few QTLs. With the advent of high-throughput genotyping techniques, MAS should be exploited to a maximum extent to fast track the development of biotic stress-tolerant maize varieties.

References

Abdel-Rahman MM, Bayoumi SR, Barakat MN (2016) Identification of molecular markers linked to Fusarium ear rot genes in maize plants *Zea mays* L. Biotechnol Biotechnol Equip 30(4):692–699

Ahmad S, Veyrat N, Gordon-Weeks R, Zhang Y, Martin J, Smart L, Glauser G, Erb M, Flors V, Frey M, Ton J (2011) Benzoxazinoid metabolites regulate innate immunity against aphids and fungi in maize. Plant Physiol 157:317–327

Ali ML, Taylor JH, Jie L, Sun G, William M, Kasha KJ, Reid LM, Pauls KP (2005) Molecular mapping of QTLs for resistance to Gibberella ear rot, in corn, caused by Fusarium graminearum. Genome 48(3):521–533

Awata LAO, Ifie BE, Danquah E, Jumbo MB, Suresh LM, Gowda M, Marchelo-Dragga PW, Olsen MS, Shorinola O, Yao NK, Boddupalli PM, Tongoona PB (2021) Introgression of maize lethal necrosis resistance quantitative trait loci into susceptible maize populations and validation of the resistance under field conditions in Naivasha, Kenya. Front Plant Sci 12:699

Badji A, Otim M, Machida L, Odong T, Kwemoi DB, Okii D, Agbahoungba S, Mwila N, Kumi F, Ibanda A, Mugo S, Kyamanywa S, Rubaihayo P (2018) Maize combined insect resistance genomic regions and their co-localization with cell wall constituents revealed by tissue-specific QTL meta-analyses. Front Plant Sci 9:895

Badji A, Kwemoi DB, Machida L, Okii D, Mwila N, Agbahoungba S, Kumi F, Ibanda A, Bararyenya A, Solemanegy M, Odong T (2020) Genetic basis of maize resistance to multiple insect pests: integrated genome-wide comparative mapping and candidate gene prioritization. Genes 11(6):689

Badu-Apraku B, Gracen VE, Bergstrom GC (1987) A major gene for resistance to anthracnose stalk rot in maize. Phytopathology 77:957–959

Baer O, Laude T, Reano C, Gregorio G, Diaz M, Pabro L, Tamba L, Baltazar N, Fabreag M, Pocsedio A, Kumar A (2021) Diplodia ear rot resistance QTL identified in maize (*Zea mays* L.) using multi-parent double-haploid population mapping. SABRAO J Breed Genet 53(1)

Baladhiya HC, Sisodiya DB, Pathan NP (2018) A review on pink stem borer, *Sesamia inferens* Walker: a threat to cereals. J Entomol Zool Stud 6(3):1235–1239

Balint-Kurti PJ, Johal GS (2009) Maize disease resistance. In: Handbook of maize: its biology. Springer, New York, pp 229–250

Balint-Kurti PJ, Krakowsky MD, Jines MP, Robertson LA, Molnár TL, Goodman MM, Holland JB (2006) Identification of quantitative trait loci for resistance to southern leaf blight and days to anthesis in a maize recombinant inbred line population. Phytopathology 96(10):1067–1071

Balint-Kurti PJ, Zwonitzer JC, Wisser RJ, Carson ML, Oropeza-Rosas MA, Holland JB, Szalma SJ (2007) Precise mapping of quantitative trait loci for resistance to southern leaf blight, caused by *Cochliobolus heterostrophus* race O, and flowering time using advanced intercross maize lines. Genetics 176(1):645–657

Balint-Kurti PJ, Wisser R, Zwonitzer JC (2008a) Use of an advanced intercross line population for precise mapping of quantitative trait loci for gray leaf spot resistance in maize. Crop Sci 48(5):1696–1704

Balint-Kurti PJ, Zwonitzer JC, Pe ME, Pea G, Lee M, Cardinal AJ (2008b) Identification of quantitative trait loci for resistance to southern leaf blight and days to anthesis in two maize recombinant inbred line populations. Phytopathology 98:315–320

Benson JM, Poland JA, Benson BM, Stromberg EL, Nelson RJ (2015) Resistance to gray leaf spot of maize: genetic architecture and mechanisms elucidated through nested association mapping and near-isogenic line analysis. PLoS Genet 11(3):e1005045

Bian Y, Yang Q, Balint-Kurti PJ, Wisser RJ, Holland JB (2014) Limits on the reproducibility of marker associations with southern leaf blight resistance in the maize nested association mapping population. BMC Genomics 15(1):1–15

Bohn M, Schulz B, Kreps R, Klein D, Melchinger AE (2000) QTL mapping for resistance against the European corn borer (*Ostrinia nubilalis* H.) in early maturing European dent germplasm. Theor Appl Genet 101(5):907–917

Brauner PC, Melchinger AE, Schrag TA, Utz HF, Schipprack W, Kessel B, Ouzunova M, Miedaner T (2017) Low validation rate of quantitative trait loci for Gibberella ear rot resistance in European maize. Theor Appl Genet 130:175–186

Brooks TD, Willcox MC, Williams WP, Buckley PM (2005) Quantitative trait loci conferring resistance to fall armyworm and southwestern corn borer leaf feeding damage. Crop Sci 45(6):2430–2434

Brooks TD, Bushman BS, Williams WP, McMullen MD, Buckley PM (2007) Genetic basis of resistance to fall armyworm (Lepidoptera: Noctuidae) and southwestern corn borer (Lepidoptera: Crambidae) leaf-feeding damage in maize. J Econ Entomol 100(4):1470–1475

Buckler ES, Thornsberry JM, Kresovich S (2001) Molecular diversity, structure and domestication of grasses. Genet Res 77:213–218

Butron A, Santiago R, Cao A, Samayoa LF, Malvar RA (2019) QTLs for resistance to fusarium ear rot in a multiparent advanced generation intercross (MAGIC) maize population. Plant Dis 103(5):897–904

Cardinal AJ, Lee M, Sharopova N, Woodman-Clikeman WL, Long MJ (2001) Genetic mapping and analysis of quantitative trait loci for resistance to stalk tunneling by the European corn borer in maize. Crop Sci 41(3):835–845

Carson ML, Hooker AL (1981) Inheritance of resistance to stalk rot of corn caused by *Colletotrichum graminicola*. In: Carson ML (ed). The American Phytopathological Society, Phytopathology, vol 71, p 1190

Carson ML, Stuber CW, Senior ML (2004) Identification and mapping of quantitative trait loci conditioning resistance to southern leaf blight of maize caused by *Cochliobolus heterostrophus* race O. Phytopathology 94(8):862–867

Castro-Álvarez FF, William M, Bergvinson DJ, García-Lara S (2015) Genetic mapping of QTL for maize weevil resistance in a RIL population of tropical maize. Theor Appl Genet 128(3):411–419

Chen J, Ding J, Li H, Li Z, Sun X, Li J, Wang R, Dai X, Dong H, Song W, Chen W (2012) Detection and verification of quantitative trait loci for resistance to Fusarium ear rot in maize. Mol Breed 30:1649–1656

Chen G, Wang X, Long S, Jaqueth J, Li B, Yan J, Ding J (2016a) Mapping of QTL conferring resistance to northern corn leaf blight using high-density SNPs in maize. Mol Breed 36:4. https://doi.org/10.1007/s11032-015-0421-3

Chen J, Shrestha R, Ding J, Zheng H, Mu C, Wu J, Mahuku G (2016b) Genome-wide association study and QTL mapping reveal genomic loci associated with Fusarium ear rot resistance in tropical maize germplasm. G3: Genes, Genomes, Genetics 6(12):3803–3815

Christensen SA, Nemchenko A, Park YS, Borrego E, Huang PC, Schmelz EA, Kunze S, Feussner I, Yalpani N, Meeley R, Kolomiets MV (2014) The novel monocot-specific 9-lipoxygenase ZmLOX12 is required to mount an effective jasmonate-mediated defense against Fusarium verticillioides in maize. Mol Plant-Microbe Interact 27(11):1263–1276

Christensen SA, Huffaker A, Kaplan F, Sims J, Ziemann S, Doehlemann G, Ji L, Schmitz RJ, Kolomiets MV, Alborn HT, Mori N, Jander G, Ni X, Sartor RC, Byers S, Abdo Z, Schmelz EA (2015) Maize death acids, 9-lipoxygenase-derived cyclopente(a)nones, display activity as cytotoxic phytoalexins and transcriptional mediators. Proc Natl Acad Sci U S A 112(36):11407–11412

Coan MMD, Senhorinho HJC, Pinto RJB, Scapim CA, Tessmann DJ, Williams WP, Warburton ML (2018) Genome-wide association study of resistance to ear rot by *Fusarium verticillioides* in a tropical field maize and popcorn core collection. Crop Sci 58:564–578

Collard B, Jahufer Z, Brouwer JB, Pang E (2005) An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: the basic concepts. Euphytica 142:169–196

Collins N, Drake J, Ayliffe M, Sun Q, Ellis J, Hulbert S, Pryor T (1999) Molecular characterization of the maize RP1-D rust resistance haplotype and its mutants. Plant Cell 11:1365–1376

de Jong G, Pamplona AKA, Von Pinho RG, Balestre M (2018) Genome-wide association analysis of ear rot resistance caused by *Fusarium verticillioides* in maize. Genomics 110(5):291–303

De Souza IRP, Schuelter AR, Guimarães CT, Schuster I, De Oliveira E, Redinbaugh M (2008) Mapping QTL contributing to SCMV resistance in tropical maize. Hereditas 145(4):167–173

Dhakal R, Windham GL, Williams WP, Subudhi PK (2016) Quantitative trait loci (QTL) for reducing aflatoxin accumulation in corn. Mol Breed 36(12):1–11

Di Renzo MA, Bonamico NC, Díaz DG, Ibañez MA, Faricelli ME, Balzarini MG, Salerno JC (2004) Microsatellite markers linked to QTL for resistance to Mal de Río Cuarto disease in *Zea mays* L. J Agric Sci 142(3):289–295

Ding JQ, Wang XM, Chander S, Yan JB, Li JS (2008) QTL mapping of resistance to Fusarium ear rot using a RIL population in maize. Mol Breed 22(3):395–403

Duble CM, Melchinger AE, Kuntze L, Stork A, Lubberstedt T (2000) Molecular mapping and gene action of Scm1 and Scm2, two major QTL contributing to SCMV resistance in maize. Plant Breed 119(4):299–303

Frey M, Schullehner K, Dick R, Fiesselmann A, Gierl A (2009) Benzoxazinoid biosynthesis, a model for evolution of secondary metabolic pathways in plants. Phytochemistry 70:1645–1651

Frey TJ, Weldekidan T, Colbert T, Wolters PJCC, Hawk JA (2011) Fitness evaluation of Rcg1, a locus that confers resistance to *Colletotrichum graminicola* (Ces.) GW Wils. Using near-isogenic maize hybrids. Crop Sci 51:1551–1563

Galiano-Carneiro AL, Kessel B, Presterl T, Miedaner T (2021a) Intercontinental trials reveal stable QTL for Northern corn leaf blight resistance in Europe and in Brazil. Theor Appl Genet 134(1):63–79

Galiano-Carneiro AL, Kessel B, Presterl T, Gaikpa DS, Kistner MB, Miedaner T (2021b) Multi-parent QTL mapping reveals stable QTL conferring resistance to Gibberella ear rot in maize. Euphytica 217(1):1–13

Ganiger PC, Yeshwanth HM, Muralimohan K, Vinay N, Kumar ARV, Chandrashekara K (2018) The occurrence of the new invasive pest, fall armyworm, Spodoptera frugiperda (JE Smith) (Lepidoptera: Noctuidae), in the maize fields of Karnataka, India. Curr Sci 115(4):25

Gao X, Shim WB, Gobel C, Kunze S, Feussner I, Meeley R, Balint-Kurti P, Kolomiets M (2007) Disruption of a maize 9-lipoxygenase results in increased resistance to fungal pathogens and reduced levels of contamination with mycotoxin fumonisin. Mol Plant-Microbe Interact 20(8):922–933

Gao X, Brodhagen M, Isakeit T, Brown SH, Göbel C, Betran J, Feussner I, Keller NP, Kolomiets MV (2009) Inactivation of the lipoxygenase ZmLOX3 increases susceptibility of maize to Aspergillus spp. Mol Plant-Microbe Interact 22(2):222–231

Garcia-Lara S, Khairallah MM, Vargas M, Bergvinson DJ (2009) Mapping of QTL associated with maize weevil resistance in tropical maize. Crop Sci 49(1):139–149

Garcia-Lara S, Burt AJ, Arnason JT, Bergvinson DJ (2010) QTL mapping of tropical maize grain components associated with maize weevil resistance. Crop Sci 50(3):815. https://doi.org/10.2135/cropsci2009.07.0415

Gimenez E, Salinas M, Manzano-Agugliaro F (2018) Worldwide research on plant defense against biotic stresses as improvement for sustainable agriculture. Sustainability 10(2):391

Giomi GM, Kreff ED, Iglesias J, Fauguel CM, Fernández M, Oviedo MS, Presello DA (2016) Quantitative trait loci for Fusarium and Gibberella ear rot resistance in Argentinian maize germplasm. Euphytica 211(3):287–294

Glauser G, Marti G, Villard N, Doyen GA, Wolfender JL, Turlings TC, Erb M (2011) Induction and detoxification of maize 1, 4-benzoxazin-3-ones by insect herbivores. Plant J 68(5):901–911

Gong F, Yang L, Tai F, Hu X, Wang W (2014) "Omics" of maize stress response for sustainable food production: opportunities and challenges. Omics: J Integr Biol 18(12):714–732

Groh S, González-de-León D, Khairallah MM, Hoisington DA (1998) QTL mapping in tropical maize: III. Genomic regions for resistance to Diatraea spp. and associated traits in two RIL populations. Crop Sci 38(4):1062–1072

Handrick V, Robert CA, Ahern KR, Zhou S, Machado RA, Maag D, Glauser G, Fernandez-Penny FE, Chandran JN, Rodgers-Melnik E, Schneider B, Buckler ES, Boland W, Gershenzon J, Jander G, Erb M, Köllner TG (2016) Biosynthesis of 8-O-methylated benzoxazinoid defense compounds in maize. Plant Cell 28(7):1682–1700

He W, Yang L, Leng Y, Zhang B, Yang J, Li L, Chen Y, Kang J, Tang H, Deng L, Wu Y (2018) QTL mapping for resistance of maize to grey leaf spot. J Phytopathol 166(3):167–176

Hegde S, Kumar M, Mahantesh G, Meenakshi GN (2018) Mapping QTLs for resistance to Northern Leaf Blight in Tropical Maize (*Zea mays* L.). Int J Curr Microbiol App Sci 7(6):1940–1946

Hossain F, Boddupalli PM, Sharma RK, Kumar P, Bahadur Singh B (2007) Evaluation of quality protein maize genotypes for resistance to stored grain weevil Sitophilus oryzae (Coleoptera: Curculionidae). Int J Trop Insect Sci 27:114–121

Huang X, Han B (2013) Natural variations and genome-wide association studies in crop plants. Annu Rev Plant Biol. https://doi.org/10.1146/annurev-arplant-050213-035715

Huffaker A, Kaplan F, Vaughan MM, Dafoe NJ, Ni X, Rocca JR, Alborn HT, Teal PEA, Schmelz EA (2011) Novel acidic sesquiterpenoids constitute a dominant class of pathogen-induced phytoalexins in maize. Plant Physiol 156(4):2082–2097

Hulbert SH (1997) Structure and evolution of the rp1 complex conferring rust resistance in maize. Annu Rev Phytopathol 35:293–310

Hurni S, Scheuermann D, Krattinger SG, Kessel B, Wicker T, Herren G, Fitze MN, Breen J, Presterl T, Ouzunova M, Keller B (2015) The maize disease resistance gene Htn1 against northern corn leaf blight encodes a wall-associated receptor-like kinase. Proc Natl Acad Sci USA 112(28):8780–8785

Jakhar DS, Singh R, Singh SK (2021) Assessment of genetics for turcicum leaf blight resistance in maize (Zea mays L.). Bangladesh J Bot 50(1):195–198

Jamann TM, Luo X, Morales L, Kolkman JM, Chung CL, Nelson RJ (2016) A remorin gene is implicated in quantitative disease resistance in maize. Theor Appl Genet 129(3):591–602

Jampatong C, McMullen MD, Barry BD, Darrah LL, Byrne PF, Kross H (2002) Quantitative trait loci for first-and second-generation European corn borer resistance derived from the maize inbred Mo47. Crop Sci 42(2):584–593

Jensen SG, Lane LC, Seifers DL (1996) A new disease of maize and wheat in the High Plains. Plant Dis 80:1387–1390

Jiang JF, Han Y, Xing LJ, Xu YY, Xu ZH, Chong K (2006) Cloning and expression of a novel cDNA encoding a mannose-specific jacalin-related lectin from *Oryza sativa*. Toxicon 47(1):133–139

Jimenez-Galindo JC, Ordas B, Butrón A, Samayoa LF, Malvar RA (2017) QTL mapping for yield and resistance against mediterranean corn borer in maize. Front Plant Sci 8:698

Jindal J (2013) Incidence of insect pests and management of shoot fly, Atherigona spp. in spring sown maize. Doctoral dissertation, PAU Ludhiana

Johal GS, Briggs SP (1992) Reductase-activity encoded by the Hm1 disease resistance gene in maize. Science 258:985–987

Ju M, Zhou Z, Mu C, Zhang X, Gao J, Liang Y, Chen J, Wu Y, Li X, Wang S, Wen J (2017) Dissecting the genetic architecture of *fusarium verticillioides* seed rot resistance in maize by combining QTL mapping and genome-wide association analysis. Sci Rep 7(1):1–11

Jung M, Weldekidan T, Schaff D, Paterson A, Tingey S, Hawk J (1994) Generation-means analysis and quantitative trait locus mapping of anthracnose stalk rot genes in maize. Theor Appl Genet 89(4):413–418

Kannan M, Ismail I, Bunawan H (2018) Maize dwarf mosaic virus: from genome to disease management. Viruses 10(9):492

Kaur M, Vikal Y, Kaur H, Pal L, Kaur K, Chawla JS (2019) Mapping quantitative trait loci associated with southern leaf blight resistance in maize (*Zea mays L.*). J Phytopathol 167(10):591–600

Keno T, Azmach G, Gissa DW, Regasa MW, Tadesse B, Wolde L, Deressa T, Abebe B, Chibsa T, Mahabaleswara S (2018) Major biotic maize production stresses in Ethiopia and their management through host resistance. Afr J Agric Res 13(21):1042–1052

Khairallah MM, Bohn M, Jiang C, Deutsch JA, Jewell DC, Mihm JA, Melchinger AE, González-De-León D, Hoisington DA (1998) Molecular mapping of QTL for southwestern corn borer resistance, plant height and flowering in tropical maize. Plant Breed 117(4):309–318

Kibe M, Nair SK, Das B, Bright JM, Makumbi D, Kinyua J, Suresh LM, Beyene Y, Olsen MS, Prasanna BM, Gowda M (2020) Genetic dissection of resistance to gray leaf spot by combining

genome-wide association, linkage mapping, and genomic prediction in tropical maize germplasm. Front Plant Sci 11:1602

Krakowsky MD, Brinkman MJ, Woodman-Clikeman WL, Lee M (2002) Genetic components of resistance to stalk tunneling by the European corn borer in maize. Crop Sci 42(4):1309–1315

Kump KL, Holland JB, Jung MT, Wolters P, Balint-Kurti PJ (2010) Joint analysis of near-isogenic and recombinant inbred line populations yields precise positional estimates for quantitative trait loci. Plant Genome 3(3)

Kump KL, Bradbury PJ, Wisser RJ, Buckler ES, Belcher AR, Oropeza-Rosas MA, Holland JB (2011) Genome-wide association study of quantitative resistance to southern leaf blight in the maize nested association mapping population. Nat Genet 43:163–168

Leng P, Ji Q, Asp T, Frei UK, Ingvardsen CR, Xing Y, Studer B, Redinbaugh M, Jones M, Gajjar P, Liu S, Li F, Pan G, Xu M, Lubberstedt T (2017) Auxin binding protein 1 reinforces resistance to sugarcane mosaic virus in maize. Mol Plant 10(10):1357–1360

Li ZM, Ding JQ, Wang RX, Chen JF, Sun XD, Chen W, Song WB, Dong HF, Dai XD, Xia ZL, Wu JY (2011) A new QTL for resistance to fusarium ear rot in maize. J Appl Genet 52(4):403–406

Li YX, Chen L, Li C, Bradbury PJ, Shi YS, Song Y, Zhang D, Zhang Z, Buckler ES, Li Y, Wang T (2018) Increased experimental conditions and marker densities identified more genetic loci associated with southern and northern leaf blight resistance in maize. Sci Rep 8(1):1–12

Li N, Lin B, Wang H, Li X, Yang F, Ding X, Yan J, Chu Z (2019) Natural variation in Zm FBL41 confers banded leaf and sheath blight resistance in maize. Nat Genet 51(10):1540–1548

Liu C, Hua J, Liu C, Zhang D, Hao Z, Yong H, Xie C, Li M, Zhang S, Weng J, Li X (2016a) Fine mapping of a quantitative trait locus conferring resistance to maize rough dwarf disease. Theor Appl Genet 129(12):2333–2342

Liu L, Zhang YD, Li HY, Bi YQ, Yu LJ, Fan XM, Tan J, Jeffers DP, Kang MS (2016b) QTL mapping for gray leaf spot resistance in a tropical maize population. Plant Dis 100(2):304–312

Liu Q, Deng S, Liu B, Tao Y, Ai H, Liu J, Zhang Y, Zhao Y, Xu M (2020) A helitron-induced RabGDIα variant causes quantitative recessive resistance to maize rough dwarf disease. Nat Commun 11(1):1–14

Liu Y, Hu G, Zhang A, Loladze A, Hu Y, Wang H, Qu J, Zhang X, Olsen M, San Vicente F, Crossa J (2021) Genome-wide association study and genomic prediction of Fusarium ear rot resistance in tropical maize germplasm. Crop J 9(2):325–341

Lopez-Zuniga LO, Wolters P, Davis S, Weldekidan T, Kolkman JM, Nelson R, Hooda KS, Rucker E, Thomason W, Wisser R, Balint-Kurti P (2019) Using maize chromosome segment substitution line populations for the identification of loci associated with multiple disease resistance. G3: Genes, Genomes, Genetics 9(1):189–201

Lü X, Li X, Xie C, Hao Z, Ji H, Shi L, Zhang S (2008) Comparative QTL mapping of resistance to sugarcane mosaic virus in maize based on bioinformatics. Front Agric China 2(4):365–371

Luan J, Wang F, Li Y, Zhang B, Zhang J (2012) Mapping quantitative trait loci conferring resistance to rice black-streaked virus in maize (*Zea mays* L.). Theor Appl Genet 125(4):781–791

Lyimo HJ, Pratt RC, Mnyuku RS (2011) Heritability and gene effect estimates for components of partial resistance to grey leaf spot of maize by generation mean analysis. Plant Breed 130(6):633–639

Mahuku G, Lockhart BE, Wanjala B, Jones MW, Kimunye JN, Stewart LR, Cassone BJ, Sevgan S, Nyasani JO, Kusia E, Kumar PL (2015) Maize lethal necrosis (MLN), an emerging threat to maize-based food security in sub-Saharan Africa. Phytopathology 105(7):956–965

Marti G, Erb M, Boccard J, Glauser G, Doyen GR, Villard N, Robert CAM, Turlings TC, Rudaz S, Wolfender JL (2013) Metabolomics reveals herbivore-induced metabolites of resistance and susceptibility in maize leaves and roots. Plant Cell Environ 36(3):621–639

Martin DP, Shepherd DN (2009) The epidemiology, economic impact and control of maize streak disease. Food Secur 1(3):305–315

Martin DP, Willment JA, Billharz R, Velders R, Odhiambo B, Njuguna J, James D, Rybicki EP (2001) Sequence diversity and virulence in Zea mays of Maize streak virus isolates. Virology 288(2):247–255

Martins LB, Rucker E, Thomason W, Wisser RJ, Holland JB, Balint-Kurti P (2019) Validation and characterization of maize multiple disease resistance QTL. G3: Genes, Genomes, Genetics 9(9):2905–2912

Maschietto V, Colombi C, Pirona R, Pea G, Strozzi F, Marocco A, Rossini L, Lanubile A (2017) QTL mapping and candidate genes for resistance to Fusarium ear rot and fumonisin contamination in maize. BMC Plant Biol 17(1):1–21

Mikel MA, D'arcy CJ, Rhodes AM, Ford RE (1981) Yield loss in sweet corn correlated with time of inoculation with maize dwarf mosaic virus. Plant Dis 65(11):902–904

Mitchell NJ, Bowers E, Hurburgh C, Wu F (2016) Potential economic losses to the US corn industry from aflatoxin contamination. Food Addit Contam Part A 33(3):540–550

Moeller DA, Tiffin P (2005) Genetic diversity and the evolutionary history of plant immunity genes in two species of Zea. Mol Biol Evol 22(12):2480–2490

Morales L, Zila CT, Moreta Mejía DE, Montoya Arbelaez M, Balint-Kurti PJ, Holland JB, Nelson RJ (2019) Diverse components of resistance to Fusarium verticillioides infection and fumonisin contamination in four maize recombinant inbred families. Toxins 11(2):86

Morris SW, Vernooij B, Titatarn S, Starrett M, Thomas S, Wiltse CC, Frederiksen RA, Bhandhufalck A, Hulbert S, Uknes S (1998) Induced resistance responses in maize. Mol Plant-Microbe Interact 11(7):643–658

Mottaleb KA, Loladze A, Sonder K, Kruseman G, San Vicente F (2019) Threats of tar spot complex disease of maize in the United States of America and its global consequences. Mitig Adapt Strateg Glob Chang 24(2):281–300

Muimba-Kankolongo A (2018) Food crop production by smallholder farmers in Southern Africa: challenges and opportunities for improvement. Academic

Muthusamy V, Hossain F, Thirunavukkarasu N, Saha S, Agrawal PK, Gupta HS (2016) Genetic analyses of kernel carotenoids in novel maize genotypes possessing rare allele of β-carotene hydroxylase gene. Cereal Res Commun 44:669–680

Nwosu LC (2018) Maize and the maize weevil: advances and innovations in postharvest control of the pest. Food Qual Saf 2(3):145–152

Oluwafemi S, Bruce TJ, Pickett JA, Ton J, Birkett MA (2011) Behavioral responses of the leafhopper, Cicadulina storeyi China, a major vector of maize streak virus, to volatile cues from intact and leafhopper-damaged maize. J Chem Ecol 37(1):40–48

Ong'amo G, Khadioli N, Le Ru B, Mujica N, Carhuapoma P (2016) Spotted stemborer, *Chilo partellus* (Swinhoe 1885). In: Kroschel J, Mujica N, Carhuapoma P, Sporleder M (eds) Pest distribution and risk atlas for Africa. Potential global and regional distribution and abundance of agricultural and horticultural pests and associated biocontrol agents under current and future climates. International Potato Center (CIP), Lima. ISBN 978-92-9060-476-1

Onukogu FA, Guthrie WD, Russell WA, Reed GL, Robbins JC (1978) Location of genes that condition resistance in maize to sheath-collar feeding by second-generation European corn borers. J Econ Entomol 71(1):1–4

Ordas B, Malvar RA, Santiago R, Sandoya G, Romay MC, Butron A (2009) Mapping of QTL for resistance to the Mediterranean corn borer attack using the intermated B73 × Mo17 (IBM) population of maize. Theor Appl Genet 119(8):1451–1459

Ordas B, Malvar RA, Santiago R, Butron A (2010) QTL mapping for Mediterranean corn borer resistance in European flint germplasm using recombinant inbred lines. BMC Genomics 11(1):1–10

Papst C, Bohn M, Utz HF, Melchinger AE, Klein D, Eder J (2004) QTL mapping for European corn borer resistance (*Ostrinia nubilalis* Hb.), agronomic and forage quality traits of testcross progenies in early-maturing European maize (*Zea mays* L.) germplasm. Theor Appl Genet 108(8):1545–1554

Perera MF, Filippone MP, Ramallo CJ, Cuenya MI, Garcia ML, Ploper LD, Castagnaro AP (2009) Genetic diversity among viruses associated with sugarcane mosaic disease in Tucumán, Argentina. Phytopathology 99(1):38–49

Perez-Brito D, Jeffers D, Gonzales-de-Leon D, Khairallah MM, Cortes-Cruz M, Velazquez-Cardelas G, Azpíroz S, Srinivasan G (2001) QTL mapping of *Fusarium moniliforme* ear rot resistance in highland maize, Mexico. Agrociencia 35:181–196

Piperno DR, Ranere AJ, Holst I, Iriarte J, Dickau R (2009) Starch grain and phytolith evidence for early ninth millennium BP maize from the Central Balsas River Valley, Mexico. Proc Natl Acad Sci USA 106(13):5019–5024

Poland JA, Bradbury PJ, Buckler ES, Nelson RJ (2011) Genome-wide nested association mapping of quantitative resistance to northern leaf blight in maize. Proc Natl Acad Sci 108(17):6893–6898

Prasanna BM, Bruce A, Beyene Y, Makumbi D, Gowda M, Asim M, Martinelli S, Head GP, Parimi S (2022) Host plant resistance for fall armyworm management in maize: relevance, status and prospects in Africa and Asia. Theor Appl Genet 135:3897–3916

Pu Z (2013) Dynamic analysis on the disease progression of maize leaf blight between Xianyu335 and improved Xianyu335 in Western region of Heilongjiang Province. J Maize Sci 21(4):119–123

Qi J, Sun G, Wang L, Zhao C, Hettenhausen C, Schuman MC, Baldwin IT, Li J, Song J, Liu Z, Xu G (2016) Oral secretions from *Mythimna separata* insects specifically induce defence responses in maize as revealed by high-dimensional biological data. Plant Cell Environ 39(8):1749–1766

Ramakrishna W, Emberton J, Ogden M, SanMiguel P, Bennetzen JL (2002) Structural analysis of the maize Rp1 complex reveals numerous sites and unexpected mechanisms of local rearrangement. Plant Cell 14:3213–3223

Ranganatha HM, Lohithaswa HC, Anand SP (2017) Understanding the genetic architecture of resistance to northern corn leaf blight and southern corn rust in maize (*Zea mays* L.). Indian J Genet Plant Breed 77(3):357–363

Ranganatha HM, Lohithaswa HC, Pandravada A (2021) Mapping and validation of major quantitative trait loci for resistance to northern corn leaf blight along with the determination of the relationship between resistances to multiple foliar pathogens of maize (*Zea mays* L.). Front Genet 11:1764

Rashid Z, Sofi M, Harlapur SI, Kachapur RM, Dar ZA, Singh PK, Zaidi PH, Vivek BS, Nair SK (2020) Genome-wide association studies in tropical maize germplasm reveal novel and known genomic regions for resistance to Northern corn leaf blight. Sci Rep 10(1):1–16

Rasmann S, Kollner TG, Degenhardt J, Hiltpold I, Toepfer S, Kuhlmann U, Gershenzon J, Turlings TC (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. Nature 434(7034):732–737

Redinbaugh MG, Stewart LR (2018) Maize lethal necrosis: an emerging, synergistic viral disease. Annu Rev Virol 5(1):301–322

Robertson-Hoyt LA, Jines MP, Balint-Kurti PJ, Kleinschmidt CE, White DG, Payne GA, Maragos CM, Molnár TL, Holland JB (2006) QTL mapping for Fusarium ear rot and fumonisin contamination resistance in two maize populations. Crop Sci 46(4):1734–1743

Samayoa LF, Butron A, Malvar RA (2014) QTL mapping for maize resistance and yield under infestation with *Sesamia nonagrioides*. Mol Breed 34(3):1331–1344

Samayoa LF, Malvar RA, McMullen MD, Butron Gomez AM (2015a) Identification of QTL for resistance to Mediterranean corn borer in a maize tropical line to improve temperate germplasm. BMC Plant Biol 15:265

Samayoa LF, Malvar RA, Olukolu BA, Holland JB, Butron A (2015b) Genome-wide association study reveals a set of genes associated with resistance to the Mediterranean corn borer (Sesamia nonagrioides L.) in a maize diversity panel. BMC Plant Biol 15(1):1–15

Samayoa LF, Cao A, Santiago R, Malvar RA, Butrón A (2019) Genome-wide association analysis for fumonisin content in maize kernels. BMC Plant Biol 19(1):1–11

Santiago R, Reid LM, Arnason JT, Zhu X, Martinez N, Malvar RA (2007) Phenolics in maize genotypes differing in susceptibility to Gibberella stalk rot (*Fusarium graminearum* Schwabe). J Agric Food Chem 55:5186–5193

Schmelz EA, Kaplan F, Huffaker A et al (2011) Identity, regulation, and activity of inducible diterpenoid phytoalexins in maize. Proc Natl Acad Sci USA 108:5455–5460

Schon CC, Lee M, Melchinger AE, Guthrie WD, Woodman WL (1993) Mapping and characterization of quantitative trait loci affecting resistance against second-generation European corn borer in maize with the aid of RFLPs. Heredity 70(6):648–659

Shepherd DN, Martin DP, Van der Walt E, Dent K, Varsani A, Rybicki EP (2010) Maize streak virus: an old and complex 'emerging' pathogen. Mol Plant Pathol 11(1):1–12

Shi LY, Hao ZF, Weng JF, Xie CX, Liu CL, Zhang DG, Li MS, Bai L, Li XH, Zhang SH (2012) Identification of a major quantitative trait locus for resistance to maize rough dwarf virus in a Chinese maize inbred line X178 using a linkage map based on 514 gene-derived single nucleotide polymorphisms. Mol Breed 30(2):615–625

Shiferaw B, Prasanna B, Hellin J, Banziger M (2011) Crops that feed the world 6. Past successes and future challenges to the role played by maize in global food security. Food Secur 3:307–327

Signoret PA (2008) Cereal viruses: maize/corn. In: Encyclopedia of virology, pp 475–482. https://doi.org/10.1016/b978-012374410-4.00700-7

Singh R, Srivastava RP (2015) New quantitative trait loci (QTLs) for turcicum leaf blight in maize. J Biotech Crop Sci 5:35–43

Smith CJ (1996) Accumulation of phytoalexins: defence mechanism and stimulus response system. New Phytol 132:1–45

Smith JS, Williams WP, Windham GL, Xu W, Warburton ML, Bhattramakki D (2019) Identification of quantitative trait loci contributing resistance to aflatoxin accumulation in maize inbred Mp715. Mol Breed 39(6):1–14

Song FJ, Xiao MG, Duan CX, Li HJ, Zhu ZD, Liu BT, Sun SL, Wu XF, Wang XM (2015) Two genes conferring resistance to pythium stalk rot in maize inbred line Qi319. Mol Gen Genomics 290(4):1543–1549

Spangler LM (2008) Impact of lignin and caffeoyl coenzyme a O-methyltransferase 1 on Aspergillus flavus growth in maize cobs. MSc thesis, The Pennsylvania State University, State College, PA, USA

Steffenson BJ (1992) Analysis of durable resistance to stem rust in barley. Euphytica 63:153–167

Sun H, Zhai L, Teng F, Li Z, Zhang Z (2021) qRgls1.06, a major QTL conferring resistance to gray leaf spot disease in maize. Crop J 9(2):342–350

Tamiru A, Bruce TJ, Woodcock CM, Caulfield JC, Midega CA, Ogol CK, Mayon P, Birkett MA, Pickett JA, Khan ZR (2011) Maize landraces recruit egg and larval parasitoids in response to egg deposition by a herbivore. Ecol Lett 14(11):1075–1083

Tao Y, Liu Q, Wang H, Zhang Y, Huang X, Wang B, Lai J, Ye J, Liu B, Xu M (2013a) Identification and fine-mapping of a QTL, qMrdd1, that confers recessive resistance to maize rough dwarf disease. BMC Plant Biol 13(1):1–13

Tao Y, Jiang L, Liu Q, Zhang Y, Zhang R, Ingvardsen CR, Lübberstedt T, Xu M (2013b) Combined linkage and association mapping reveals candidates for Scmv1, a major locus involved in resistance to sugarcane mosaic virus (SCMV) in maize. BMC Plant Biol 13(1):1–13

Tembo L, Asea G, Gibson PT, Okori P (2014) Quantitative trait loci for resistance to Stenocarpella maydis and Fusarium graminearum cob rots in tropical maize. J Crop Improv 28(2):214–228

Terefe H, Gudero G (2019) Distribution and association of factors influencing emerging maize lethal necrosis disease epidemics in Southern Ethiopia. Cogent Food Agric 5(1):1683950

Tian Z, Ai T, Deng C, You S, Shi Q, Ma Y, Li Z, Ding J (2018) QTL mapping of resistance to northern corn leaf blight in maize inbred line P178 and effect analysis. J Henan Agric Sci 47(2):73–97

Tippannavar PS, Talekar SC, Mallapur CP, Kachapur RM, Salakinkop SR, Harlapur SI (2019) An outbreak of fall armyworm in Indian subcontinent: a new invasive pest on maize. Maydica 64(1):10

Ullstrup AJ (1972) The impacts of the southern corn leaf blight epidemics of 1970-1971. Annu Rev Phytopathol 10:37–50

United States Department of Agriculture (2020) Retrieved from USDA: https://apps.fas.usda.gov/psdonline/circulars/production.pdf

Van Inghelandt D, Melchinger AE, Martinant JP, Stich B (2012) Genome-wide association mapping of flowering time and northern corn leaf blight (*Setosphaeria turcica*) resistance in a vast commercial maize germplasm set. BMC Plant Biol 12(1):1–15

Velasco P, Revilla P, Monetti L, Butron A, Ordas A, Malvar RA (2007) Corn borers (Lepidoptera; Noctuidae; Crambidae) in northwestern Spain: population dynamics and distribution. Maydica 52:195–203

Veyrat N, Robert CAM, Turlings TCJ, Erb M (2016) Herbivore intoxication as a potential primary function of an inducible volatile plant signal. J Ecol 104(2):591–600

Waiss AC Jr, Chan BG, Elliger CA, Wiseman BR, McMillian WW, Widstrom NW, Zuber MS, Keaster AJ (1979) Maysin, a flavone glycoside from corn silks with antibiotic activity toward corn earworm. J Econ Entomol 72(2):256–258

Wang ZH, Fang SG, Xu JL, Sun LY, Li DW, Yu JL (2003) Sequence analysis of the complete genome of rice black-streaked dwarf virus isolated from maize with rough dwarf disease. Virus Genes 27(2):163–168

Wang C, Yang Q, Wang W, Li Y, Guo Y, Zhang D, Ma X, Song W, Zhao J, Xu M (2017) A transposon-directed epigenetic change in ZmCCT underlies quantitative resistance to Gibberella stalk rot in maize. New Phytol 215(4):1503–1515

Wang J, Xu Z, Yang J, Lu X, Zhou Z, Zhang C, Zheng L, Tian R, Hao Z, Yong H, Li M, Zhang D, Li X, Weng J (2018) qNCLB7. 02, a novel QTL for resistance to Northern corn leaf blight in maize. Mol Breed 38(5):1–12

Wang X, Yang Q, Dai Z, Wang Y, Zhang Y, Li B, Zhao W, Hao J (2019) Identification of QTLs for resistance to maize rough dwarf disease using two connected RIL populations in maize. PLoS One 14(12):e0226700

Welz HG, Geiger HH (2000) Genes for resistance to northern corn leaf blight in diverse maize populations. Plant Breed 119:1–14

Wen J, Shen Y, Xing Y, Wang Z, Han S, Li S, Yang C, Hao D, Zhang Y (2020) QTL mapping of resistance to Gibberella ear rot in maize. Mol Breed 40(10):1–11

Wen J, Shen Y, Xing Y, Wang Z, Han S, Li S, Yang C, Hao D, Zhang Y (2021) QTL mapping of Fusarium ear rot resistance in maize. Plant Dis 105(3):558–565

Willcox MC, Khairallah MM, Bergvinson D, Crossa J, Deutsch JA, Edmeades GO, Gonzalez-de-Leon D, Jiang C, Jewell DC, Mihm JA, Williams WP, Hoisington D (2002) Selection for resistance to southwestern corn borer using marker-assisted and conventional backcrossing. Crop Sci 42(5):1516

Woloshuk C, Wise K (2010) Gibberella ear rot. Purdue University Extension. Retrieved from: https://www.extension.purdue.edu/extmedia/BP/BP-77-W.pdf

Woloshuk C, Wise K (2011) Aspergillus ear rot. Purdue University Extension. Retrieved from: https://www.extension.purdue.edu/extmedia/bp/bp-83-w.pdf

Womack ED, Warburton ML, Williams WP (2018) Mapping of quantitative trait loci for resistance to fall armyworm and southwestern corn borer leaf-feeding damage in maize. Crop Sci 58(2):529–539

Womack ED, Williams WP, Windham GL, Xu W (2020) Mapping quantitative trait loci associated with resistance to aflatoxin accumulation in maize inbred MP719. Front Microbiol 11:45

Wu F, Shu J, Jin W (2014) Identification and validation of miRNAs associated with the resistance of maize (Zea mays L.) to *Exserohilum turcicum*. PLoS One 9:e87251

Xia X, Melchinger AE, Kuntze L, Lubberstedt T (1999) Quantitative trait loci mapping of resistance to sugarcane mosaic virus in maize. Phytopathology 89(8):660–667

Xia H, Gao W, Qu J, Dai L, Gao Y, Lu S, Zhang M, Wang P, Wang T (2020) Genetic mapping of northern corn leaf blight-resistant quantitative trait loci in maize. Medicine 99(31):e21326

Xing Y, Ingvardsen C, Salomon R, Lubberstedt T (2006) Analysis of sugarcane mosaic virus resistance in maize in an isogenic dihybrid crossing scheme and implications for breeding potyvirus-resistant maize hybrids. Genome 49(10):1274–1282

Xu ML, Melchinger AE, Xia XC, Lubberstedt T (1999) High-resolution mapping of loci conferring resistance to sugarcane mosaic virus in maize using RFLP, SSR, and AFLP markers. Mol Gen Genet MGG 261(3):574–581

Xu DL, Park JW, Mirkov TE, Zhou GH (2008) Viruses causing mosaic disease in sugarcane and their genetic diversity in southern China. Arch Virol 153(6):1031–1039

Xu Z, Hua J, Wang F, Cheng Z, Meng Q, Chen Y, Han X, Tie S, Liu C, Li X, Wang Z, Weng J (2020) Marker-assisted selection of qMrdd8 to improve maize resistance to rough dwarf disease. Breed Sci 70(2):183–192

Yang Q, Yin G, Guo Y, Zhang D, Chen S, Xu M (2010) A major QTL for resistance to Gibberella stalk rot in maize. Theor Appl Genet 121:673–687

Yang Q, He Y, Kabahuma M, Chaya T, Kelly A, Borrego E, Bian Y, El Kasmi F, Yang L, Teixeira P, Kolkman J, Nelson R, Kolomiets M, Dang JL, Wisser R, Caplan J, Li X, Lauter N, Balint-Kurti P, Balint-Kurti P (2017) A gene encoding maize caffeoyl-CoA O-methyltransferase confers quantitative resistance to multiple pathogens. Nat Genet 49(9):1364–1372

Ye J, Zhong T, Zhang D, Ma C, Wang L, Yao L, Zhang Q, Zhu M, Xu M (2019) The auxin-regulated protein ZmAuxRP1 coordinates the balance between root growth and stalk rot disease resistance in maize. Mol Plant 12(3):360–373

Yuan L, Dussle CM, Melchinger AE, Utz HF, Lubberstedt T (2003) Clustering of QTL conferring SCMV resistance in maize. Maydica 48(1):55–62

Yuan G, Chen B, Peng H, Zheng Q, Li Y, Xiang K, Liu L, Zou C, Lin H, Ding H, Pan G, Zhang Z (2020) QTL mapping for resistance to ear rot caused by Fusarium graminearum using an IBM Syn10 DH population in maize. Mol Breed 40(9):1–12

Zanakis GN, Mariolis NA, Rodiatos AJ, Kesoglou AP, Paraskevakos EP, Dimou KN, Theodosiadis CA, Zampogianis CT (2009) Chemical control of maize pests Ostrinia nubilalis (Lepidoptera: Crambidae) and Sesamia nonagrioides (Lepidoptera: Noctuidae) in Greece. In: Proceedings of 13th Panhellenic entomological congress. Copycity, Thessaloniki, pp 302–303

Zhang Y, Xu L, Fan X, Tan J, Chen W, Xu M (2012) QTL mapping of resistance to gray leaf spot in maize. Theor Appl Genet 125(8):1797–1808

Zhang D, Liu Y, Guo Y, Yang Q, Ye J, Chen S, Xu M (2012a) Fine-mapping of qRfg2, a QTL for resistance to Gibberella stalk rot in maize. Theor Appl Genet 124(3):585–596

Zhang W, Deng S, Zhao Y, Xu W, Liu Q, Zhang Y, Ren C, Cheng Z, Xu M, Liu B (2021) qMrdd2, a novel quantitative resistance locus for maize rough dwarf disease. BMC Plant Biol 21(1):1–11

Zhao Y, Lu X, Liu C, Guan H, Zhang M, Li Z, Cai H, Lai J (2012) Identification and fine mapping of rhm1 locus for resistance to southern corn leaf blight in maize. J Integr Plant Biol 54(5):321–329

Zhu M, Tong L, Xu M, Zhong T (2021) Genetic dissection of maize disease resistance and its applications in molecular breeding. Mol Breed 41(5):1–22

Zila CT, Fernando Samayoa L, Santiago R, Butron A, Holland JB (2013) A genome-wide association study reveals genes associated with fusarium ear rot resistance in a maize core diversity panel. G3: Genes Genomes Genetics 3(11):2095–2104

Zila CT, Ogut F, Romay MC, Gardner CA, Buckler ES, Holland JB (2014) Genome-wide association study of Fusarium ear rot disease in the USA maize inbred line collection. BMC Plant Biol 14(1):1–15

Zunjare RU (2012) Genetic analyses of resistance to stored grain weevil (Sitophilus oryzae) in maize. MSc Thesis submitted to Post graduate School, Indian Agricultural Research Institute, New Delhi India, p 123

Zunjare R, Hossain F, Thirunavukkarasu N, Muthusamy V, Jha SK, Kumar P, Gupta HS (2014) Evaluation of specialty corn inbreds for responses to stored grain weevil (Sitophilus oryzae L.) infestation. Indian J Genet Plant Breed 74:564–567

Zunjare R, Hossain F, Muthusamy V, Jha SK, Kumar P, Sekhar JC, Guleria SK, Singh NK, Thirunavukkarasu N, Gupta HS (2015a) Genetics of resistance to stored grain weevil (Sitophilus oryzae L.) in maize. Cogent Food Agric 1:1075934. https://doi.org/10.1080/23311932.2015.1075934

Zunjare RU, Hossain F, Muthusamy V, Vishwakarma A, Pandey N, Kumar P, Sekhar JC, Jha SK, Thirunavukkarasu N, Gupta HS (2015b) Analyses of genetic diversity among exotic-and indigenous-maize inbreds differing for responses to stored grain weevil (Sitophilus oryzae L) infestation. Maydica 60:1–7

Zunjare R, Hossain F, Muthusamy V, Choudhary M, Kumar P, Sekhar JC, Guleria SK, Singh NK, Thirunavukkarasu N, Gupta HS (2015c) Popping quality attributes of popcorn hybrids in relation to weevil (*Sitophilus oryzae*) infestation. Indian J Genet Plant Breed 75:510–513

Zunjare R, Hossain F, Muthusamy V, Jha SK, Kumar P, Sekhar JC, Thirunavukkarasu N, Gupta HS (2016) Genetic variability among exotic and indigenous maize inbreds for resistance to stored grain weevil (*Sitophilus oryzae* L.) infestation. Cogent Food Agric 2:1137156. https://doi.org/1 0.1080/23311932.2015.1137156

Zunjare RU, Hossain F, Muthusamy V, Baveja A, Chauhan HS, Bhat JS, Thirunavukkarasu N, Saha S, Gupta HS (2018) Development of biofortified maize hybrids through marker-assisted stacking of *β-carotene hydroxylase, lycopene-ε-cyclase* and *opaque2* genes. Front Plant Sci 9:178

Zwonitzer J, Bubeck D, Bhattramakki D, Goodman M, Arellano C, Balint-Kurti PJ (2009) Use of selection with recurrent back-crossing and QTL mapping to identify loci contributing to southern leaf blight resistance in a highly resistant maize line. Theor Appl Genet 118:911–925

Zwonitzer JC, Coles ND, Krakowsky MD, Arellano C, Holland JB, McMullen MD, Pratt RC, Balint-Kurti PJ (2010) Mapping resistance quantitative trait loci for three foliar diseases in maize recombinant inbred line population-evidence for multiple disease resistance. Phytopathology 100(1):72–79