



Susceptibility of maize genotypes to *Rhizopertha dominica* (F.)

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Abstract

This work examined the survival of *Rhizopertha dominica* on maize kernels differing either for specific traits or for their genetic background. Maize traits comprised endosperm starch composition, and accumulation of pigments, i.e., carotenoids and anthocyanins, in the aleurone, while maize genotypes included the B73 reference line, the high oil content RAlexo line and the commercial variety *Zea mays everta* (popcorn). Kernels of the different genotypes were classified according to the endosperm texture. The number of adults of *R. dominica* developing from neonate larvae on both whole and sectioned kernels was measured. Differences were only observed in experiments with whole kernels. The lowest value was observed for the B73 line, and the highest for the popcorn variety. These two genotypes have the lowest and highest proportions of vitreous endosperm, respectively. In our experimental conditions, variations in the insect attack were observed in different lines, thus indicating that the insect–kernel interaction is influenced by quantitative more than single-gene traits.

Keywords Lesser grain borer · Larvae · *Zea mays* · Endosperm mutants · Maize seed traits

Introduction

Rhizopertha dominica (F.) (Coleoptera, Bostrichidae) is one of the economically most important beetles infesting cereal grains on a worldwide scale (www.plantwise.org), and its feeding can reduce kernels to the pericarp (Winterbottom 1922; Campbell and Sinha 1976).

Females lay eggs on the surface and newly born larvae drill into the kernels, preferring breaks or the germ area where the covering testa is loose (Birch 1945a). On

damaged kernels, first instar larvae mortality decreases (Birch 1945a, b; Howe 1950; Breese 1960), and progeny production increases (Throne et al. 2000), while hardness of kernels has no effect on *R. dominica* reproduction (Bhatia and Gupta 1969; Amos et al. 1986; Sinha et al. 1988; Towes et al. 2000). This insect can also develop on twigs of different plants, legume seeds and various other substances (Edde 2012). It can also develop on milled media, such as semolina, but in this case, it needs at least a 6-mm layer (Limonta et al. 2011).

Stored product beetles are resistant to many grain protectants: the first records date back to 1965 (Parkin 1965). In particular, resistance of *R. dominica* was recorded to organophosphates and pyrethroids (Navarro et al. 1986; Zettler and Cuperus 1990; Lorini and Galley 1996, 1999; Guedes et al. 1996, 1997; Collins 2006), phosphine (Bell et al. 1977; Herron 1990; Zettler and Cuperus 1990; Lorini and Collins 2006; Opit et al. 2012; Collins et al. 2017), juvenile hormone analogues (Collins et al. 1993; Collins 1998; Lorini and Galley 1999; Daglish et al. 2013). The selection of host-plant genotypes that restrain insect pest development could be an alternative to treatment with insecticides for any cereal crops that suffer from grain damage by postharvest pests. New sources of resistance to the insects would be useful in breeding programs; however, this approach has not yet been considered as a method of control.

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In rice, kernel soundness and integrity are generally considered the most important characters for conferring resistance to *R. dominica* infestation. A correlation between cracked and split hulls and susceptibility was observed (Chanbang et al. 2008a, b; Kavallieratos et al. 2012), and varieties with thicker hulls have been shown to be more tolerant (Chanbang et al. 2008a). Moreover, a work conducted on African varieties has established that hardness and husk protection can confer tolerance to *R. dominica* (Chougourou et al. 2013), while the work of Astuti et al. (2013) conducted in Indonesia has shown that high phenolic content and hardness can increase resistance to *R. dominica* infestation. In wheat, susceptibility is negatively correlated with kernel hardness and is instead positively correlated with the percentage of total protein (Watts and Dunkel 2003).

Studies on *R. dominica* effects on maize varieties mostly go back to the 1990s. These studies examined local varieties and hybrids cultivated in India (Pandey and Singh 1974; Singh and Pandey 1977; Kurdikeri et al. 1994, 1995) and in Egypt (El Halfawy and Hassan 1978) and found that some of them were less susceptible to *R. dominica*. Although they did not provide an explanation for the different susceptibility, they provide a first indication of the existence of variability for this trait in the maize germplasm. The analysis of additional genotypes will show whether other sources of resistance are present in different maize germplasm collections and will also be of help in unraveling the biochemical characteristics that confer tolerance to the host plant.

The maize seed comprises two major compartments: the embryo and the endosperm (Consonni et al. 2005). The embryo represents the next sporophytic generation, while the endosperm, which is the largest seed compartment, provides nutrients and signals for embryo development and seedling germination. The maize endosperm comprises different domains, among which are the central region that accumulates starch and reserve proteins, and the aleurone, which is the outer layer of the endosperm (Li and Berger 2012). Starch is composed of two types of glucose homopolymers, linear amylose and branched amylopectin, while proteins include mainly zeins, a unique storage protein found only in cereals. Several genes have been described that are involved in starch biosynthesis. Among them is the *Sugary1* (*Su1*) gene (James et al. 1995) that encodes an isoamylase that hydrolyzes α -1,6 bonds in amylopectin. Mutants in this gene change starch composition, causing a decrease in amylopectin and an increase in the more highly branched and soluble polymer, phytoglycogen. As a consequence, mutants show changes in endosperm texture and seed appearance.

The aleurone layer is characterized by the accumulation of secondary metabolites that include important antioxidant compounds. In particular, genotypes, anthocyanins and carotenoids accumulate, thus conferring on the kernels

the dark red and orange colored appearance, respectively (Dooner et al. 1991; Tan et al. 1997).

The susceptibility of maize lines, differing for specific seed traits and for their genetic constitution, to *R. dominica* was examined in this work. The general aim was to identify genotypes showing resistance to the attack. This information will be a prerequisite for developing resistant varieties useful in storage of products of organic agriculture, whose regulation precludes the use of pesticides in both field and storage. Moreover, resistant varieties allow the farmer to save the cost of using controlled atmospheres, which are unaffordable in developing countries.

Materials and methods

Plant material

The endosperm-related mutants and inbred lines used in this study were provided by the Maize Genetics Cooperation Stock Center (<http://maizecoop.cropsci.uiuc.edu/>). Plants were grown and propagated in an open field at the University of Milan. The harvested seeds were dried to about 12–13% moisture content and stored at room temperature.

Mutant lines were propagated through selfing heterozygous plants; tests were performed with homozygous mutants and related wild-type kernels selected from F_2 segregating ears. Inbred lines were propagated via siblings mating. The seeds of the popcorn variety (*Zea mays everta*) were purchased at a local supermarket.

Maize genotypes description

The B73 line, developed at Iowa State University (Russell 1972), exhibits high yield, and it is the most used laboratory accession and the main source of commercially important germplasm. Its genome sequence was released in 2009 (Schnable et al. 2009). The RALexo genetic stock, also known as Alexander High Oil Synthetic, is the result of a selection carried out at the University of Illinois for grain with high oil content (<http://www.maizegdb.org>, Gerdes et al. 1993; Goldman et al. 1994).

Popcorn (*Zea mays everta*) is one of the favorite maize varieties around the world. Its commercialization started in the 1880s (Erwin 1949), and the modern varieties are the result of modern breeding methods which have improved the desired characters, such as flavor and pericarp strength.

The *sugary1* (*su1*) gene, located on the short arm of chromosome 4, encodes isoamylase-type starch debranching1 enzyme, belonging to the family of α -amylase starch hydrolytic enzymes (Pan and Nelson 1984). Loss of *su1* gene function results in the accumulation of sugars and the highly branched water-soluble polysaccharide phytoglycogen in the

endosperm. The endosperm of mutant seeds is wrinkled and translucent when dry, sweet at the milk stage.

Su1 and su1 kernels show accumulation of anthocyanin pigments in the region surrounding the embryonic axis, due to the presence of an allele of the *anthocyaninless1* (*a1*) gene, referred to as *a1-eap* (*embryonic axis profile*) (Gavazzi et al. 2004).

The *yellow endosperm1* (*y1*) gene, located on the long arm of chromosome 6, controls the production of the enzyme phytoene synthase (PSY), involved in the first step of the biosynthesis of carotenoids in the endosperm (Buckner et al. 1996). Homozygous *y1/y1* mutant seeds, characterized by low carotenoids content in the endosperm, can be easily distinguished on segregating ears for their pale yellow color.

Colored seeds were from the W23 line carrying the dominant alleles required for anthocyanin pigmentation in the aleurone, i.e., *A1*, *C1* and *R1* alleles; colorless seeds were from the same line.

Insect rearing

Rhyzopertha dominica was reared on maize kernels at 29 ± 1 °C, $70 \pm 5\%$ R.H. and a photoperiod of 16:8 (light/dark). Mixed maize kernels, 450 g, and 100 adults were put in a glass jar (13 cm Ø; 20 cm height) with a lid provided with a hole (3 cm Ø) closed by a stainless steel wire mesh to allow gaseous exchange. Adults were allowed to oviposit for three days and were then removed, in order to obtain coeval adults progeny.

To collect eggs, 20 g of kernels and 20 coeval adults were put in a Petri dish, with the bottom covered with black cardboard. After three days, kernels and adults were removed from the petri dish and the eggs were daily checked to collect first instar larvae characterized by a terminal median spine.

Tests

The tests were carried out by placing 40 maize kernels in glass containers (35 mm Ø; height 20 mm) with 20 first instar larvae, 0–24 h old. Such containers, closed with a net (120 mesh) to provide ventilation, were placed in an incubator at 29 ± 1 °C, $70 \pm 5\%$ R.H. and 16 h of light alternating with 8 h of darkness. For each of the five maize genotypes, tests were carried out with 40 entire kernels and with 40 longitudinally sectioned kernels. Four replicates were carried out for each test.

To analyze the effect of starch composition on *R. dominica* attack, insect development in presence of seeds with an altered starch composition (*su1/su1*; Fig. 1) was compared with insect development in the presence of wild-type seeds obtained from selfing either homozygous (*Su1/Su1*) or heterozygous (*Su1/-*) F_1 plants. The effect of pigment presence was analyzed by comparing seeds accumulating carotenoids (*Y1/-*) or anthocyanin (W23 *ACR*—Colored) with sibling seeds devoid of pigment, i.e., *y1/y1* and colorless seeds (W23 *ACR*—colorless), respectively. Tests were carried out on both whole and sectioned kernels, and the number of adults which emerged was recorded.

Fig. 1 Phenotypic diversity of kernels used in this work. Kernels of *su1* and *y1* mutant and relative wild-type genotypes and of colorless and colored W23 seeds (a) and inbred lines (b)

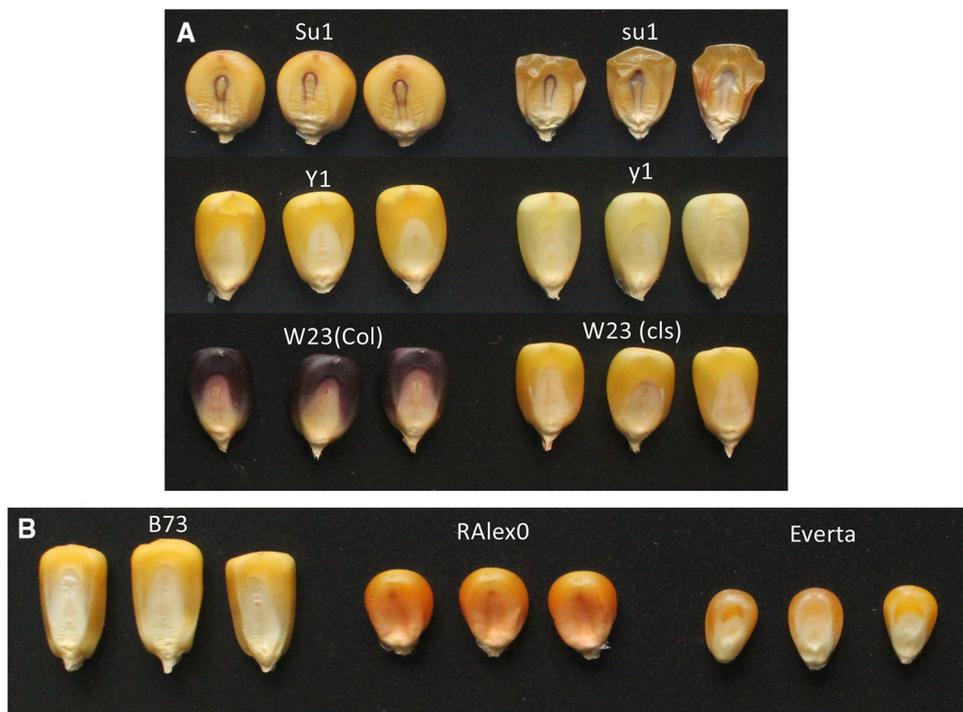


Table 1 Adults of *Rhyzopertha dominica* (\pm SE) emerged from the whole and sectioned Su1 wild-type (*Su1/Su1* and *Su1/-*) versus homozygous *su1/su1* mutant kernels

Genotype	Kernel phenotype	Whole	Sectioned
<i>Su1/Su1</i>	Wild type	3.2 \pm 1.25	13.5 \pm 0.96
<i>Su1/-</i>	Wild type	4.2 \pm 0.48	10.5 \pm 0.87
<i>su1/su1</i>	Sugary—wrinkled	5.7 \pm 1.03	11.5 \pm 1.19

Anova: whole grain $F_{2, 9} = 1.664$ $P = 0.243$ n.s.; sectioned grain $F_{2, 9} = 2.27$ $P = 0.159$ n.s.

Table 2 Adults of *Rhyzopertha dominica* (\pm SE) emerged from the whole and sectioned Y1 wild-type (*Y1/-*) versus homozygous *y1/y1* mutant kernels

Genotype	Kernel phenotype	Whole	Sectioned
<i>Y1/-</i>	Wild type—yellow	1.2 \pm 0.63	12.0 \pm 1.47
<i>y1/y1</i>	Mutant—white	2.2 \pm 0.25	12.5 \pm 1.55

Student's *t* test: whole $t = 1.477$ n.s.; sectioned $t = 0.234$ n.s.

Table 3 Adults of *Rhyzopertha dominica* (\pm SE) emerged from the whole and sectioned W23 ACR colored versus colorless kernels

Genotype	Kernel phenotype	Whole	Sectioned
W23	Colored	2.7 \pm 0.48	8.2 \pm 0.48
W23	colorless	4.5 \pm 1.04	9.2 \pm 2.21

Student's *t* test: whole $t = 1.528$ n.s.; sectioned $t = 0.442$ n.s.

Data analysis

The number of emerged adults and the days from the beginning of the test were recorded. Data, when normally distributed, were submitted to one-way ANOVA, LSD test and Student's *t* test ($\alpha = 0.05$); otherwise, Kruskal–Wallis test and multiple comparisons of groups were performed (IBM Statistics SPSS 25.0 per Windows).

Results

Kernels of genotypes adopted in this study differ for their appearance, starch composition and pigment accumulation (Fig. 1).

The comparison between emerged adults in *su1* and *y1* mutant and relative wild-type seeds (Tables 1, 2), as well as between colored and colorless seeds (Table 3), did not show any significant differences.

An additional analysis was performed by comparing the data obtained from the three different genetic lines among themselves, without considering the homozygous mutant seeds. In this comparison, we include three additional

**Fig. 2** Sectioned wild-type kernels. In the sectioned kernels, the vitreous region appears lucid and darker, while the floury region is white and opaque (white bar: 3 mm in length)**Table 4** Adults of *Rhyzopertha dominica* (\pm SE) emerged from the whole and sectioned kernels of different maize genotypes

Genotype/line	Proportion of vitreous endosperm	Adults	
		Whole	Sectioned
B73	Low	0.7 \pm 0.48c	10.0 \pm 0.41
<i>Y1/-</i>	Intermediate	1.2 \pm 0.63bc	12.0 \pm 1.47
W23 ACR Col	Intermediate	4.5 \pm 1.04ab	9.2 \pm 2.21
RAlExo	Large	2.2 \pm 1.31bc	8.2 \pm 2.95
<i>Su1/Su1</i>	Large	3.2 \pm 1.25bc	13.5 \pm 1.71
Popcorn	Large	7.0 \pm 0.71a	13.0 \pm 1.91

Anova: whole grain $F_{5, 18} = 5.855$ $P < 0.01$; sectioned grain $F_{5, 18} = 1.336$ $P = 0.294$ n.s. Values followed by different letters are significantly different (LSD test)

genotypes, i.e., the reference line B73, the RAlExo line, and the popcorn variety.

All these genotypes are characterized by endosperm with a different texture (Fig. 2; Table 4). The B73 seeds show a high proportion of starchy endosperm and low presence of vitreous endosperm. In the rest of the genotypes, there is a higher presence of vitreous endosperm. RAlExo seeds have

a large proportion of vitreous endosperm and are characterized by the presence of a large embryo. The vitreous region is particularly abundant in the endosperm of the popcorn variety, which can thus be classified as hard endosperm (Larkins et al. 2017).

Despite the difference in the endosperm texture, we did not observe any statistically significant differences in the number of adults developed from sectioned seeds. Statistically significant differences were instead observed in the whole seeds test. The lowest value was observed for the B73 line and the highest for the popcorn variety. These two genotypes have the lowest and highest proportions of vitreous endosperm, respectively.

Data on development days are reported in Table 1S. Even if data on the days required to complete the development from neonate larva to adult on whole kernels are normally distributed, the presence of heterogeneous numbers weakened the statistical analysis. Data on development on sectioned kernels do not present a normal distribution, and this prevented the possibility of comparing them with those on whole kernels.

Discussion

Our results indicate that differences in the susceptibility to *Rhyzopertha dominica* attack may not be attributable to variations in single genes affecting specific traits, such as starch composition and pigment accumulation in the host plant. Differences were observed when different genetic backgrounds were compared. This suggests that the susceptibility to this insect attack might be attributable to quantitative traits, such as kernel texture and nutrient composition, which are controlled by multiple genetic factors.

At present, different maize genotypes have been developed to meet different nutritional and usage demands. Selection and genetic improvement have led to different quality and quantity of seed storage molecules and therefore to different seed hardness. Hard, flint maize varieties, with a large proportion of vitreous endosperm, are often considered to be often more resistant than soft, floury varieties, in which the proportion of vitreous endosperm is very low. It has been proposed that the vitreous endosperm strengthens the kernel making it less fragile. The hardness of seeds has been demonstrated to affect the successful and rapid multiplication of insect pests in *opaque2* (*o2*) mutants, which do not form vitreous endosperm and thus show a high degree of susceptibility to attack by *S. zeamais* and *S. cerealella* (Rhine and Staples 1968). Differently, Towes et al. (2000) demonstrated that in rice grain hardness did not influence the reproduction of *R. dominica*.

Accordingly, in our study, in the whole kernels experiment the highest number of adults was observed in the

popcorn, which is a hard variety, and the lowest number in the B73 line, which is dent line with high soft starch grain content (Table 4). Our interpretation is that seed hardness does not prevent *R. dominica* attack. In addition, the presence of vitreous endosperm, which is rich in proteins, at the periphery of the popcorn kernels, positively influences insect number. When fed with the protein-rich popcorn, however, *R. dominica* has a longer mean developmental period than on B73 line that is rich in starch (Table 1S).

In sectioned kernels, different ratios of vitreous and floury endosperm did not affect insect number (Table 4). This observation can be explained by the fact that sectioned kernels facilitate the finding of appropriate nutrients.

Susceptibility to insect attack might be investigated more extensively through the comparison of a large number of maize accessions, including landraces and local varieties, as well as modern commercial genotypes. Variations in these traits are envisaged and will be informative for unraveling their complex genetic basis. On this basis, programs aimed at improving the resistance to insect damage can be designed.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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