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The impacts of maize seed phenology and nutritive traits imparting tolerance to the rice weevil (*Sitophilus oryzae* L.)

Značaj osobina i nutritivne vrednosti semena kukuruza u tolerantnosti semena kukuruza prema pirinčanom žišku (*Sitophilus oryzae* L.)

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ABSTRACT

Maize is an important food, industrial, and energy crop. In recent years, the maize production has been increasing globally, but also seed losses during storage caused by the stored product pests, particularly the rice weevil (*Sitophilus oryzae*). This emphasizes the need to minimize postharvest losses, possibly including the development of resistant genotypes. It requires resistance level monitoring across genotypes and understanding phenotypic, biochemical (starch, protein, oil, phenolics, antioxidative capacity) and biophysical (kernel hardness, moisture, and weight) traits that influence insect development. This study assessed the susceptibility of 39 maize genotypes to *S. oryzae* and determined how different seed traits affect the pest development (progeny production - PP) and feeding intensity. Genotypes of the hardest seeds were found among flint (328.93-481.00 N) and popcorn types (324.17-449.20 N). NIR spectroscopy revealed the highest protein content in popcorn (12.07%), starch in dent (65.0%), and oil in white (13.63%) and sweet maize (10.97%) types. Phenolic compounds content varied significantly among genotypes, while antioxidant capacity showed no statistical difference. PP positively correlated with seed moisture (%), content of phenolic compounds, and antioxidative capacity, but strongly negatively correlated with percentage of oil content. After four generations, the biotest revealed the lowest number of emerged adults on flint, semi-flint, and sweet maize genotypes. The most tolerant/resistant genotypes - 605413 NS (semi-dent), MB 982 (flint), Crveni Kosjerić (semi-flint), and Beli osmak II (flint) - showed reduced seed consumption and progeny production in *S. oryzae*. Cultivating these genotypes can be recommended to reduce storage losses and support maize production stability.

Keywords: storage pests, genotypes, tolerance, susceptibility, postharvest losses, progeny production

SAŽETAK

Kukuruz predstavlja značajnu prehrambenu i industrijsku biljku, ali i izvor energije. Poslednjih godina, beleži se trend porasta setvenih površina i prinosa kukuruza u svetu, ali i gubitaka uzrokovanih štetočinama uskladištenog semena, poput pirinčanog žiška (*Sitophilus oryzae*). Ovo ukazuje na neophodnost smanjenja gubitaka semena tokom skladištenja u cilju postizanja održivosti proizvodnje. Kako bi se izbegla kontinuirana primena pesticida, strategija “tolerantnih/otpornih genotipova” je sve aktuelnija u zaštiti bilja. U cilju razvoja tolerantnih genotipova, potrebno je utvrditi osnove specifične tolerantnosti detaljnom fenotipizacijom (tvrdoća, vlaga, masa zrna i drugo) i analizom biohemijskih osobina semena (sadržaj skroba, proteina, ulja, fenolnih komponenti), ispitivanjem što većeg broja genotipova. Cilj istraživanja je bio ispitivanje tolerantnosti 39 genotipova kukuruza na *S. oryzae* i pogodnost za razviće (produkcija potomstva kroz četiri generacije – PP i % konzumirane hrane), zavisno od fenotipskih i biohemijskih osobina. Genotipovi sa najtvrđim zrnom su bili u tipu tvrdunca (328.93-481.00 N) i kokičara (324.17-449.20 N). NIR je detektovala najveći % proteina u tipu kokičara, skroba u tipu zuban, a ulja kod belog kukuruza (13.63%) i šećerca (10.97%). Sadržaj fenolnih komponenti se statistički visoko razlikovao među genotipovima, ali antioksidativni kapacitet nije. PP je u značajnoj pozitivnoj korelaciji sa % vlage zrna i sadržajem fenolnih komponenti, ali negativno sa % ulja u zrnu. Nakon razvića četvrte generacije, prosečno najmanja PP je na svim genotipovima u tipu tvrdunca, polu-tvrdunca i šećerca. Najtolerantniji genotipovi su 605413 NS (polu-zuban), MB 982 (tvrdunac), Crveni Kosjerić (polu-tvrdunac), Beli osmak II (tvrdunac). Na osnovu % konzumirane hrane i niskoj produkciji potomstva trebalo bi davati prednost u izboru za setvu, jer mogu obezbediti očuvanje kvaliteta semena tokom skladištenja.

Ključne reči: štetočine uskladištenog semena, genotip, tolerantnost/otpornost, osetljivost, posležetveni gubici, produkcija potomstava

INTRODUCTION

Maize (*Zea mays* L.) is one of the most common and widely cultivated crops, primarily due to a wide range of uses – for food and feed and various industrial applications (biofuel, bioplastics). It is a primary source of energy in developing countries and contributes up to 60% and 30% of the diet's energy and protein, respectively (Mlyneková and Čerešňáková, 2013). In 2023, maize was the second crop in the world in terms of cultivated area (ha) and production (t), after wheat. According to FAOSTAT (2025), the total maize production is increasing globally, although in Serbia, yield per ha is stable, but cultivated area and production are declining (SORS, 2025).

Whether we are facing an increase or a decrease in area or yields, it is of paramount importance to provide safe storage of maize seeds as an important input for annual production. Maize storage plays a key role in the entire production cycle, and many studies indicate that the highest losses occur during the post-harvest period (Majumder et al., 2016). It is assumed that storage pests alone may cause 30-40% of losses (Kumar and Kalita, 2017), depending on the storage technology, environmental conditions, and pest management measures applied. Losses can be quantitative (seed weight loss) and qualitative, related to reduced nutritional values, development of molds (including the production of mycotoxins), and presence of insect particles and excrements (Nietupski et al., 2021). Reduced germination and seed viability can also be the result of seed damage, which subsequently affects emergence in the field. One of the insect species that is becoming an increasing threat to stored maize, cereal seeds and products due to global warming is the rice weevil, *Sitophilus oryzae* (Linnaeus, 1763) (Coleoptera: Curculionidae).

The main strategy for controlling *S. oryzae* is the use of chemical insecticides and toxic fumigants (Peña-Flores et al., 2025). Their inadequate and frequent use resulted in several consequences, such as insect resistance to insecticides, residues in food and feed, negative impacts on human health, and seed quality after storage (Arthur, 1996; Żeber-Dzikowska et al., 2025). Therefore, there has been an ongoing effort to find other pest control options. For instance, *S. oryzae* is considered one of the most resistant stored product insect species to pyrethroids and usually cannot be controlled by application rates that are effective against most other species in storage (Samson and Parker, 1989; Arthur, 1994, 1999).

Due to high costs and a variety of risks of insecticide use, host plant resistance is a promising tool for effective control of storage (seed) weevil species (Acheampong et al., 2019). It is a sustainable and eco-friendly strategy and provides economical means to minimize post-harvest losses caused by store product pests (Mwololo et al., 2013). In developing countries, where most farmers rely on subsistence crop production, growing resistant genotypes may significantly reduce storage losses caused by grain weevils and other storage pests (Acheampong et al., 2019). However, breeding for resistance towards stored product insects, as a strategy, is not yet being exploited by the breeders to its full potential. Consequently, modern high-yielding genotypes are more susceptible to insect pests than their predecessors (Kossou et al., 1993). It is a well-known fact that a single trait is not sufficient to develop stable resistant/tolerant genotypes; thus, exploring multiple traits that underlie the resistance against stored product insects is needed. It was previously reported that stored grain insect pests, including *S. oryzae*, could be controlled by cultivating resistant or tolerant varieties (Sousa et al., 2010; Bottega et al., 2012). However, a comprehensive investigation into the tolerance/resistance of maize to *S. oryzae* attack and development is still lacking. The knowledge of tolerance mechanisms and the underlying genetic bases of resistance to a specific insect pest provides valuable inputs in creating new breeding strategies to develop resistant genotypes (Dhilwayo et al., 2005; Dari et al., 2010). In that sense, producing more information about the resistance potential of maize genotypes to *S. oryzae* would guide researchers in the selection of germplasm for genetic improvement and breeding of cultivars resistant to this pest.

This work aimed to screen 39 maize genotypes for susceptibility to the *S. oryzae* attack and suitability for the weevil development, in correlation with physiochemical and nutritive traits of seeds.

MATERIAL AND METHODS

Maize varieties

The experiment involved 39 genotypes (Table 1) of different maize types, representing high-quality hybrids and inbred lines. The selection of genotypes was based on preliminary field performance and market opportunities. The maize genotypes were classified by types of endosperms, and a comparison was made between the groups dent, semi-dent, semi-flint, flint, popcorn, and sweet maize (sweet corn).

Table 1. Maize genotypes used in the experiment

Type	Genotype	Type	Genotype
Dent	NSU2	Semi-dent	♂ 605413 NS
	♀ 611904 NS		Crveni Dragačevo (red)
	22-742 F1		
	NS exp 53w		
	White maize I	Semi-flint	White maize II
	MB 1492		Šareni osmak
	♀ 604314 NS		Crveni Kosjerić (red)
	22-1187 F1		IP 7456
	♂ 606747 NS		Bosanac
	NS 5004 F1		MB 1581
	♂ 66791 NS	Flint	MB 982
	22-1305 F1		Beli osmak II (white)
	♀ 602402 NS		Požegrmac osmak
	♀611903 NS		Staklarac
	NS exp 6		MB 1833
	♀ 602906 NS		Beli osmak I (white)
	♂ 603814 NS	Pop corn	ZP 6170k
	22-921 F1		MB 1172
	MB 2259		MB 2267
	MB 1584 (red)	Sweet corn	Krupni šećerac (SC021su)
	NS exp 76 (red)		

Phenotyping and biochemical properties of seeds

A detailed seed phenotyping of 39 maize genotypes was performed.

Morphological characterization of maze seeds was performed according to the UPOV descriptor, determining seed type and 100 kernel/seed weight.

Seed hardness was evaluated based on the external force (N) applied to seeds that managed to crush them. These tests were performed at the Laboratory for Biosystem Engineering, Faculty of Agriculture, University of Novi Sad, on an FTC TMS-pro device. A cell with a load capacity of 500 N was used in the experiment. The speed of the pre-test was 60 mm/min, and the test was 30 mm/min. The probe displacement is set to 2 mm.

Biochemical analysis encompassed the determination of nutrient composition (NIR analysis), phenolic compounds (total phenols, tannins and flavonoids), as well as antioxidative capacity on maize seeds.

Nutrient composition of maize seeds (NIR analysis)

The nutrient composition of maize seeds was analyzed using the DA 7250™ Diode Array Near Infrared Analysis System (PerkinElmer, Inc., Waltham, Massachusetts, USA). The analysis of 39 maize genotypes was carried out by means of a rapid and accurate indirect method. Samples were analyzed in real time, with results available online 24/7 through the NetPlus Reports software. The maximum analyzed surface area reached up to 108 cm^2. The instrument operated in measurement mode using down-view reflection or transflectance. The detector wavelength range was 900–1700 nm, with an operational range of 950–1650 nm, and a resolution of <0.05 nm. The detector type was a thermoelectrically cooled, 256-pixel, high-detectability indium gallium arsenide (InGaAs).

Depending on the size, seeds of each genotype were placed into small trays, and the surface was levelled using a ruler with gentle shaking. On average, 100-150 g of seeds per genotype was used for analysis. Each measurement was performed in five replicates. Two tray types were applied in the measurements: rotating and static. The following traits were measured without additional processing of maize seeds: moisture, protein, oil and starch. For all measured parameters, predefined minimum and maximum ranges were set in the device. The operational ranges were as follows: moisture 4-44%, protein 3.5–15.8%, oil 1.5–13.6%, starch 40–73%, and density 1.13–1.35 g/cm^3.

Phenolic compounds content

Preparation of seed material for biochemical analyses

Methanol extracts of seeds were used to determine the content of total phenols, tannins, and flavonoids, as well as the determination of antioxidant activity measured by DPPH (2,2-diphenyl-2-picrylhydrazyl), ABTS [2,2'-azino-bis-(3-ethylbenzothiazolin-6-sulfonic acid)], and FRAP (Ferric Reducing Antioxidant Power). For the preparation of methanol extracts, 2 g of seeds from each maize genotype is weighed, homogenized in a porcelain bowl with 10 ml of 70% methanol, and the obtained extracts are kept in a cool and dark place with occasional stirring. After 24 hours, the samples are centrifuged for 15 minutes at 5000 rpm (U-320, Boeco, Hamburg, Germany), poured into clean plastic tubes with caps, and stored at -18 °C.

Total phenols

Total phenols were determined spectrophotometrically, using the Folin-Ciocalteu (FC) reagent, according to the procedure described by Nagavani and Raghava Rao (2010), with slight modifications.

Total tannin content

Total tannin content was determined by the same method as the content of total phenols, after removing the tannin components from the extracts on an insoluble polyvinylpolypyrrolidone matrix.

Total flavonoid content

Total flavonoid content was determined according to the protocol described by Saha et al. (2013), with slight modifications. This spectrophotometric method is based on the ability of flavonoids to form a stable colored metallo-complex with aluminium(III)-chloride ($AlCl_3$).

Antioxidative capacity tests

Determination of ABTS•+ radical neutralization ability

Generation of ABTS•+ radicals is performed by mixing 7.4 $mmol/dm^3$ aqueous solution of ABTS reagent with 2.6 $mmol/dm^3$ aqueous solution of K2S2O8, in a 1:1 ratio, during 12 hours at room temperature in the dark (Kalinowska et al., 2022).

Determination of DPPH• radical neutralization ability

The determination of the antioxidant capacity of the tested kernel/seed extracts by the DPPH method is based on the reduction of the purple DPPH• radical by the antioxidants present, whereby DPPH• is transformed into its neutral, yellow-colored form (DPPH-H), as it builds the corresponding hydrazine. The DPPH method is performed according to the procedure of Lai and Lim (2011).

Determination of the reduction capacity by the FRAP method

The protocol described by Spiegel et al. (2020) was used.

Insect biotests

Parental insect population

The initial population of *S. oryzae* was reared at the Institute of Field and Vegetable Crops, National Institute of the Republic of Serbia, Novi Sad, on maize seeds (hybrid NS444) for at least ten generations, in transparent glass jars (5 L), at 27±2 °C, R.H. 70±10% and 16:8 (L : D) photoperiod. To maintain the parenteral population, healthy maize seeds were sieved to remove the fractions of grain particles or insects, and then sterilized by freezing (–18 °C) for 48 h to eliminate visible and hidden insect and mite infestations. The live weevils are transferred to a 5 kg jar containing 4 kg of healthy, insecticide-free and uninfested maize seeds for further mass rearing. For proper aeration and fast rearing, the jar was covered with a cloth attached with rubber bands. In order to obtain test insects of known age, weevils were allowed to oviposit on the maize seeds (hybrid NS444) for a week, after which they were removed. Newly emerged weevils were collected daily, transferred to separate containers and used for further experiments 7-15 days' post-emergence. The same procedure for maintaining parenteral population and collecting new specimens for experiments was performed throughout the entire experimental period and held under the laboratory conditions (27±2 °C, 70% R.H., 16:8 L:D).

Seed susceptibility and/or resistance assessment

The susceptibility and/or resistance of maize seeds to *S. oryzae* was assessed based on progeny production (PP) and the feeding intensity measured as % of consumed seeds (%CS), by weighing, in "No-choice" tests. The tests were performed in Petri dishes, and the 20 young (up to 15 days old) weevils (sex ratio approximately 1:1) were introduced into each dish on 50 g of seeds of each genotype (39 treatments). For the progeny production assessment, the number of newly emerged weevils was counted after 1 month (F1), and continued after 2, 3 and 4 months, where the total number of weevils that had emerged in four months was marked PP 4 Gen. Both dead and alive insects were counted after each reading and recorded separately for each Petri dish. The percentage of consumed seeds (%CS) was calculated based on the amount of seeds consumed after 4 months of feeding on each genotype. The experiment was set in five replicates.

Based on % CS, the tested genotypes were classified into different susceptibility groups, created by the authors as follows: 0-10%, tolerant/resistant; 10-25%, moderately tolerant/ resistant; 25-50%, susceptible; 50-75%, highly susceptible; >75%, extremely susceptible. Different levels of tolerance were marked in different colors in the Tables in the Results section.

The "No-choice" tests were carried out under the same conditions as rearing of parenteral population, under the laboratory conditions, at 27±2 °C, 70% R.H., 16:8 L: D. The seeds used in the bioassay were previously stored in a freezer at –18°C for seven days in order to eliminate any external insect infestation and promote seed moisture balance. After removal from the freezer, seeds are transferred to glass containers and kept in the laboratory at room temperature for ten days to reach hygroscopic balance/ to obtain equilibration moisture content with this R.H.

Data analysis

All data collected in phenotyping and biochemical analysis, as well as in biotests (number of emerged weevils after 1, 2, 3 and 4 months, and % of consumed seeds), were subjected to the Kruskal-Wallis test because none of the tested variables followed normal distribution. Multiple comparison was performed using the Bonferroni test, which grouped variables in homogeneous subsets based on genotype. Significance level was 0.05. Correlation between all variables was determined and visually presented in Corrplot (Heat map). A scatter plot was used to group genotypes based on progeny production after 4 months (PP 4 Gen) and % of consumed seeds. The coefficient of variation is also presented, indicating the variations among different maize seed traits. The results were processed using JASP 0.95.3 (2025) software.

RESULTS

Phenotyping and biochemical properties of seeds

Seed hardness

Results on seed hardness obtained on an FTC TMS-pro device indicate highly significant differences among genotypes ($t_{(39)}$=135.82, *P*<0.01). The differences can be related to the types of genotypes. The genotypes with the lowest force (N) needed to crush the seed belonged to the dent type and ranged from (155.20-341.63 N), and the sweet maize type (184.33 N). The hardest seed was of flint (328.93-481.00 N) and popcorn genotypes (324.17-449.20 N). Differences among genotypes were statistically highly significant. Among all tested genotypes, MB 1833, Staklarac, MB 1172, Bosanac, and Beli osmak II (white) had the hardest seeds (481.00, 464.70, 449.20, 437.97, 435.17 N, respectively). The results are presented in Figure 1.

100 seed weight. This trait differed highly significantly among genotypes, based on results from the Kruskal-Wallis test ($t_{(39)}$=117.65, *P*<0.001).

Nutrient composition of maize seeds (NIR analysis)

The results on moisture, protein, starch, and oil content (%) are also presented on Figure 1. The moisture content (%) differed significantly among genotypes ($t_{(39)}$=136.88, *P*<0.01). NIR analysis revealed significant differences among genotypes in protein content ($t_{(39)}$= 146.91, *P*<0.01), which can be related to the type of maize. Statistically the highest protein content was in all three popcorn types [MB 2267 (12.07%), ZP 6170k (10.48%) and MB 1172 (10.45%)], in two flint types [Crveni Kosjerić (red - 11.01%) and MB 1581 (10.47%)],

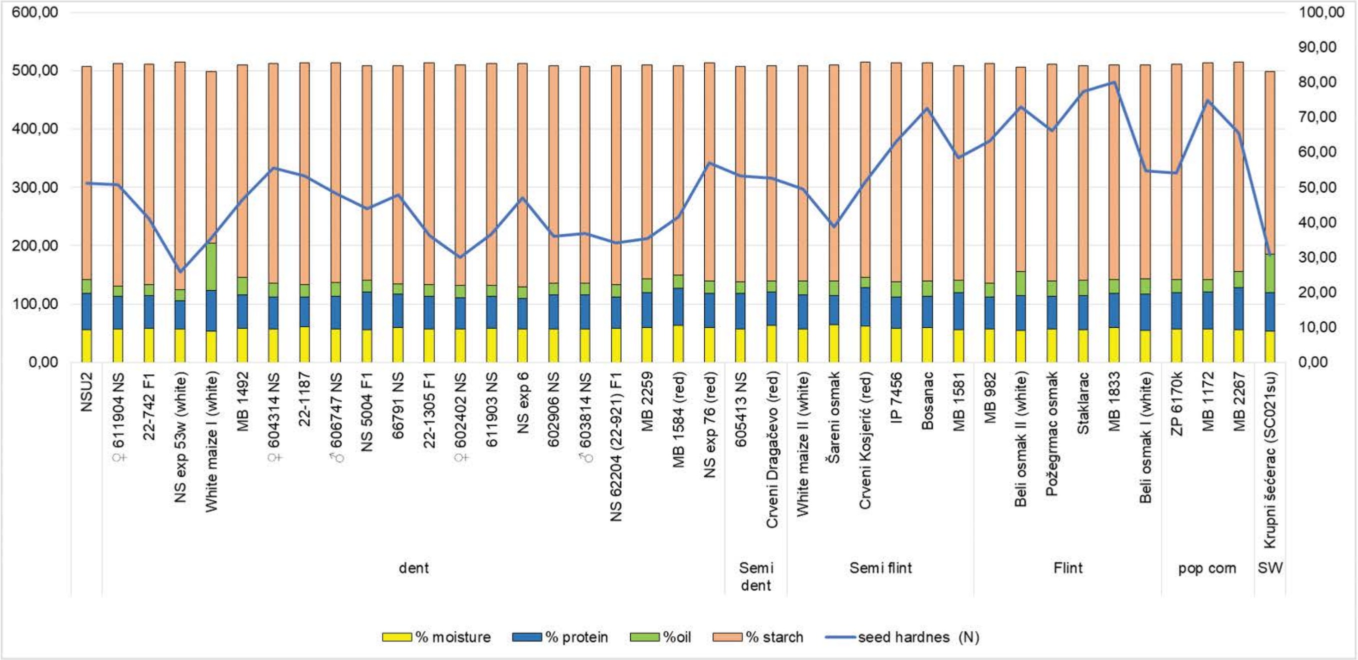


Figure 1. NIR analysis of 39 maize genotypes encompassed the content of moisture (%), proteins (%), oil (%), and starch (%) (right axis). The Figure is also pointing out seed hardness (N) tested on the FTC TMS pro device, presented as a blue line (left axis)

and four dent types [White maize I (white-11.62%), NS 5004 F1 (10.78%), MB 1584 (red - 10.53%), and NSU2 (10.32%)].

The starch content (%) also differed significantly among genotypes ($t_{(39)}=143.95$, $P<0.01$). The highest content was detected in dent-type genotypes NS exp 53w (white-65.00%), NS exp 6 (63.80%), ♀ 611904 NS (63.50%), 22-1187 F1 (63.23%), 22-742 F1 (63.00%), 611903 NS and 22-1305 F1 (63.43%), and ♀ 604314 NS (62.83%).

The oil content was the highest in White maize I (white - 13.63%) and in sweet maize type Krupni šećerac (SC021su - 10.97%), while in other genotypes it ranged from 2.98 - 7.02%. Differences were statistically significant ($t_{(39)}=144.46$, $P<0.01$).

Phenolic compounds content and antioxidative capacity tests

The content of phenolic compounds, phenols, tannins, and flavonoids differed significantly among genotypes ($t_{(39)}=95.11$, 91.88, 101.83, $P<0.01$, respectively). Maize genotypes 22-742 F1, 22-1187 F1, MB 2259, and Krupni šećerac (SC021su) had significantly higher content of the mentioned compounds in comparison to other genotypes. Antioxidative capacity of maize seeds, analyzed in tests of total AO activity, FRAP, and ABTS, did not differ significantly between genotypes ($t_{(39)}=37.77$, 37.33, 29.99, $P>0.05$, respectively) (Table 2).

Insect biotests

Progeny production

Figure 2 presents *S. oryzae* progeny production expressed in the number of emerged weevils after 1, 2, 3 and 4 months on each maize genotype, grouped in maize types (dent, semi dent, semi flint, flint, popcorn, and sweet maize). Kruskal-Wallis test detected significant and highly significant differences in this variable ($t_{(39)}=61.66$, $P>0.001$, 78.28, 76.33, 76.34, $P<0.01$, respectively).

Recordings of the progeny production after each observation period (each month), show statistically significantly lower number of weevils in several genotypes, continuously. The most tolerant/resistant regarding progeny production after 4 months was ♂ 605413 NS (semi-dent), followed by MB 982 (flint), Crveni Kosjerić (red) (semi flint), and Beli osmak II (white) (flint). When observed in general, on average, a significantly lower number of weevils developed on genotypes belonging to all flint, semi-flint, semi-dent, and sweet maize genotypes, regardless of the observation period. After 4 months, the most tolerant/resistant genotypes, based on the progeny production (PP 4 Gen), from the dent group were NSU2, ♀ 611903 NS, ♀ 611904 NS, 22-1305 F1, MB 1492, White maize I, 22-1187 F1 and ♀ 602906 NS, where the number of emerged weevils ranged from 51.67 to 74.33. In the semi-dent group, the most tolerant/resistant was ♂ 605413 NS, where only 16.33 weevils developed after 4 months. For the semi-flint group, the most tolerant/resistant, when observed in progeny production, were Crveni Kosjerić (red), with only 31.33 weevils and MB 1581, with 39.34 weevils, which emerged. In the flint group, the most tolerant/resistant were MB 982 and Beli osmak II (white), with 22.21 and 38.33 weevils, respectively, that emerged after the fourth month. Based on the PP 4 Gen data, Sweet maize genotype SC0221su was at the same level of tolerance as most tolerant/resistant dent-type maize genotypes.

Progeny production and % of consumed seeds after 4 months

In Table 3, PP 4 Gen (total number of emerged weevils in four months) and % of consumed seeds are presented for each genotype. Additionally, genotypes are grouped based on the % of consumed seeds for each maize type (dent, semi-dent, semi-flint, flint, popcorn, and sweet maize). Kruskal-Wallis test detected highly significant differences (Table 5) in the number of emerged adults and % of consumed seeds ($t_{(39)}= 76.34$, 68.27, $P<0.001$, respectively). The Bonferroni test enabled us to divide genotypes into homogenous groups based on the analysis of PP 4 Gen and % or consumed seeds (Table 3).

Table 2. Biochemical analysis of 39 maize genotypes determined the content of total phenols (mg quercetin/g d.m.), tannins (mg quercetin/g d.m.), flavonoids (mg quercetin/g d.m.), and tested antioxidative capacity in the following tests: total AO activity, DPPH, ABTS, and FRAP (mg trolox/g d.m.)

	Maize genotype	Phenols	Tannins	Flavonoids	Total AO	DPPH	ABTS	FRAP
1	NSU2	7.067	2.022	2.501	5.191	1.705	2.099	0.845
2	♀ 611904 NS	7.134	2.079	3.456	5.203	1.703	2.070	0,880
3	22-742 F1	8.269	3.020	3.436	5.170	1.747	2.123	0.891
4	NS exp 53w	7.188	2.031	2.603	5.116	1.670	1.974	0.887
5	White maize I	7.141	2.129	2.691	5.155	1.758	2.104	0.853
6	MB 1492	7.158	2.165	2.918	5.162	1.742	2.137	0.824
7	♀ 604314 NS	7.195	2.063	2.708	5.295	1.673	2.143	0.859
8	22-1187 F1	8.510	3.111	3.596	5.204	1.654	2.105	0.876
9	♂ 606747 NS	7.206	2.125	2.675	5.190	1.682	2.071	0.937
10	NS 5004 F1	7.120	2.094	2.816	5.285	1.645	2.072	0.787
11	♂ 66791 NS	7.152	2.106	2.770	5.121	1.717	2.102	0.851
12	22-1305 F1	7.073	2.130	2.779	5.068	1.683	2.077	0.845
13	♀ 602402 NS	7.171	2.045	2.660	5.179	1.656	2.068	0.824
14	♀ 611903 NS	7.105	2.168	2.789	4.976	1.671	1.988	0.825
15	NS exp 6	7.224	2.221	2.923	5.170	1.688	2.124	0.798
16	♀602906 NS	7.186	2.138	2.713	5.165	1.654	2.082	0.877
17	♂ 603814 NS	7.219	2.097	2.628	5.302	1.658	2.139	0.866
18	22-921 F1	7.196	2.158	2.669	5.109	1.704	2.138	0.845
19	MB 2259	8.064	3.088	3.732	4.933	1.742	2.045	0.812
20	MB 1584 (red)	6.980	2.073	3.651	5.114	1.602	2.086	0.838
21	NS exp 76 (red)	7.063	2.148	2.653	5.238	1.697	2.131	0.864
22	♂ 605413 NS	7.171	2.113	2.647	5.087	1.673	2.128	0.919
23	Crveni Dragačevo (red)	5.232	1.354	1.509	6.102	2.501	3.057	0.521
24	White maize II	7.232	2.096	2.540	5.294	1.648	2.159	0.908
25	Šareni osmak	7.093	2.173	2.654	5.174	1.659	2.165	0.835
26	Crveni Kosjerić (red)	7.200	1.980	2.674	5.089	1.692	2.123	0.849
27	IP 7456	7.151	2.058	2.563	5.225	1.660	2.132	0.885
28	Bosanac	7.145	2.048	2.513	5.246	1.719	2.103	0.833
29	MB 1581	7.092	2.105	2.714	5.153	1.712	2.075	0.893
30	MB 982	7.076	2.147	2.965	5.260	1.687	2.126	0.837
31	Beli osmak II (white)	7.086	2.115	2.753	5.084	1.695	2.111	0.831
32	Požegrmac osmak	7.279	2.152	2.814	5.210	1.831	2.119	0.877
33	Staklarac	7.252	2.106	2.618	5.133	1.681	2.057	0.825
34	MB 1833	7.202	2.035	2.635	5.067	1.707	2.134	0.832
35	Beli osmak I (white)	7.116	2.103	2.738	5.292	1.660	2.133	0.826
36	ZP 6170k	7.117	2.068	2.838	5.308	1.716	2.015	0.778
37	MB 1172	7.109	2.047	2.635	5.178	1.792	2.081	0.835
38	MB 2267	7.175	2.075	2.626	5.142	1.721	2.067	0.833
39	Krupni šećerac (SC021su)	8.520	2.947	3.555	5.265	1.710	2.124	0.881

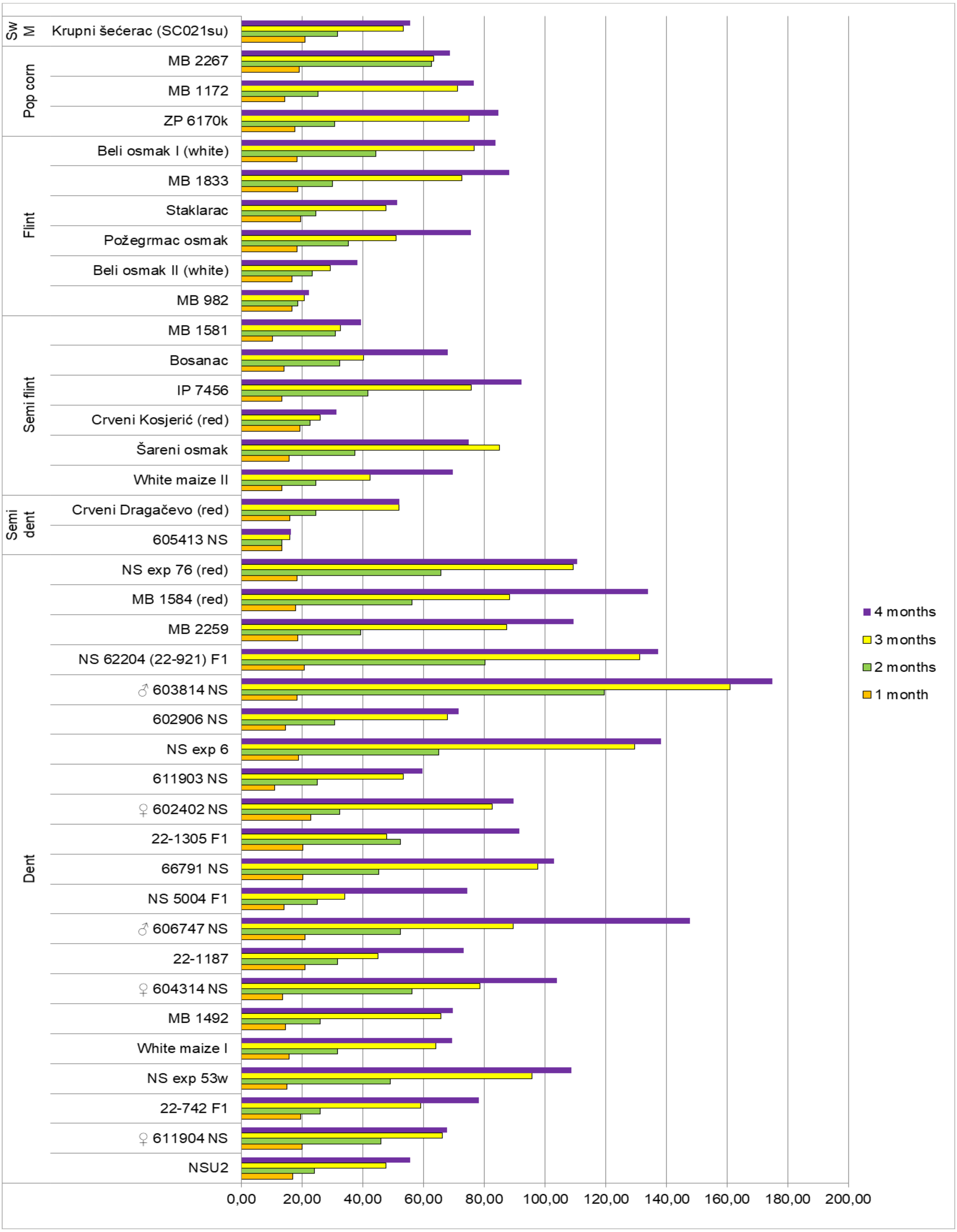


Figure 2. Progeny production expressed as the number of emerged weevils after 1, 2, 3 and 4 months

Table 3. Progeny production (PP 4 Gen), % of consumed seeds after 4 months, classification of genotypes based on susceptibility level to *S. oryzae*

Type	Genotype	PP 4 Gen	% consumed seed	Level of susceptibility	Type	Genotype	PP 4 Gen	% consumed seed	Level of susceptibility
Dent	NSU2	55.7^{d}	0.27^{a}	🟩	Semi-dent	♂ 605413 NS	16.3^{f}	5.27^{b}	🟩
	♀ 611904 NS	67.8^{cd}	2.93^{a}	🟩		Crveni Dragačevo (red)	52.0^{d}	6.71^{b}	🟩
	22-742 F1	78.3^{c}	7.48^{b}	🟩					
	NS exp 53w	108.7^{b}	7.03^{b}	🟩					
	White maize I	69.3^{cd}	7.25^{b}	🟩	Semi-flint	White maize II	69.7^{cd}	3.27^{a}	🟩
	MB 1492	69.7^{cd}	9.84^{bc}	🟩		Šareni osmak	75.0^{c}	4.99^{a}	🟩
	♀ 604314 NS	104.0^{b}	10.15^{c}	⬜		Crveni Kosjerić (red)	31.3^{e}	9.61^{bc}	🟩
	22-1187 F1	73.3^{c}	11.53^{c}	⬜		IP 7456	92.0^{bc}	10.22^{c}	⬜
	♂ 606747 NS	147.7^{ab}	11.88^{c}	⬜		Bosanac	68.0^{cd}	11.55^{c}	⬜
	NS 5004 F1	14.3^{f}	12.88^{c}	⬜		MB 1581	39.33	17.44^{d}	⬜
	♂ 66791 NS	103.00	12.95^{c}	⬜	Flint	MB 982	22.2^{ef}	0.00^{a}	🟩
	22-1305 F1	51.6^{d}	13.98^{cd}	⬜		Beli osmak II (white)	38.3^{e}	0.86^{a}	🟩
	♀ 602402 NS	89.7^{c}	15.91^{d}	⬜		Požegrmac osmak	55.9^{d}	2.14^{a}	🟩
	♀ 611903 NS	59.8^{d}	16.10^{d}	⬜		Staklarac	51.3^{d}	3.51^{a}	🟩
	NS exp 6	138.3^{ab}	18.69^{d}	⬜		MB 1833	88.3^{c}	5.26^{ab}	🟩
	♀ 602906 NS	71.7^{c}	20.97^{e}	⬜		Beli osmak I (white)	83.7^{c}	7.61^{b}	🟩
	♂ 603814 NS	175.00^{a}	20.99^{e}	⬜	Pop corn	ZP 6170k	84.7^{c}	3.07^{a}	🟩
	22-921 F1	137.3^{ab}	21.31^{e}	⬜		MB 1172	76.9^{c}	3.38^{a}	🟩
	MB 2259	109.33^{b}	21.98^{e}	⬜		MB 2267	68.7^{cd}	5.13^{ab}	🟩
	MB 1584 (red)	134.0^{ab}	28.78^{e}	🟧	Sweet corn	Krupni šećerac (SC021su)	55.7^{d}	8.22^{b}	🟩
	NS exp 76 (red)	110.7^{b}	44.33^{f}	🟧					

Value; t value – Bonferroni test; Values with the same letter are on the same level of significance for the confidence interval 95%; ** $P < 0.01$; * $P < 0.05$; NS – $P > 0.05$;Values in the table are presented as means values; significance levels based of Bonferroni test; Classification of genotypes based on tolerance to *S. oryzae*: 🟩 0-10% - resistant; ⬜ 10-25% moderately resistant; 🟧 25-50%, susceptible, 🟫 50-75% highly susceptible; 🟥 >75% extremely susceptible.

Scatter plot grouped genotypes based on progeny production after 4 months (PP 4 Gen) and % of consumed seeds (Figure 3).

The coefficient of variation is also presented, indicating the variations among different traits (Table 4). The strongest deviations from the average values were recorded for % of consumed seeds (52.0%), PP 4 Gen (31.4%), and % oil (64.80%).

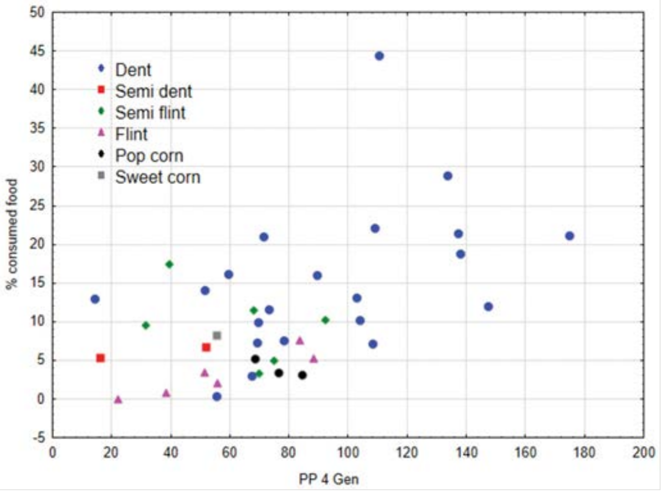


Figure 3. Grouped maize genotypes based on PP 4 Gen and % of consumed seeds

Table 4. Coefficients of variation for each analyzed seed and *S. oryzae* bionomy trait

Trait	Coefficient of variation (%)	Trait	Coefficient of variation (%)
100 seed weight	5.80	Total AO activity	2.87
Seed hardness (N)	17.60	DPPH	5.70
% of moisture	13.80	ABTS	1.77
% of protein	13.50	FRAP	2.88
% of oil	64.80	% of consumed seed	52.0
% of starch	3.72	PP after 1 month	0.4
Phenols	12.90	PP after 2 months	7.88
Tannins	2.26	PP after 3 months	15.70
Flavonoids	3.22	PP after 4 months	31.4

PP - progeny production

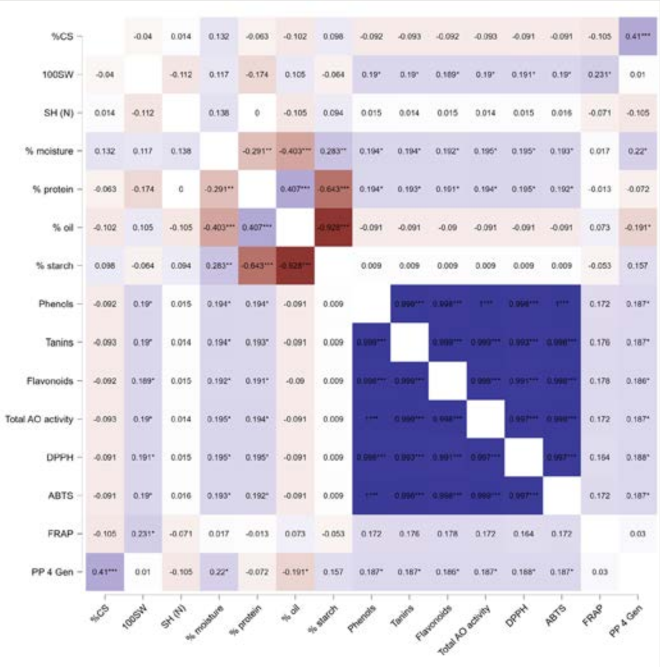
Correlation analysis

Correlation between seed traits

A strong positive correlation was detected between the content of total phenols, tannins, flavonoids, total AO activity, DPPH, and ABTS, as well as between other parameters (Figure 5). The starch content was strongly negatively correlated with % of oil (-0.982***) and protein content (-0.643***). Oil content (%) was in strong positive correlation with protein content (0.407***) but in strong negative correlation with moisture (%) content (-0.403***, -0.291**, respectively).

Correlation between seed traits and S. oryzae progeny production and feeding intensity

Progeny production, expressed in the number of emerged weevils and % of consumed seeds, was correlated with all phenotyping and biochemical traits for each genotype (Figure 4). Significant positive correlations were detected between PP 4 Gen (number of emerged weevils after 4 months) and % of seed moisture, content of phenols, tannins and flavonoids, as well as antioxidative activity detected by total AO tests, DPPH, ABTS and FRAP tests (0.187*, 0.186*, 0.187*, 0.188*, 0.187*). Significant negative correlation for this trait was with % of oil (-0.191*). The % of consumed seed was in strong positive correlation with PP 4 Gen (0.41***).



	%CS	100SW	SH (N)	% moisture	% protein	% oil	% starch	Phenols	Tanins	Flavonoids	Total AO activity	DPPH	ABTS	FRAP	PP 4 Gen
%CS		-0.04	0.014	0.132	-0.063	-0.102	0.098	-0.092	-0.093	-0.092	-0.093	-0.091	-0.091	-0.105	0.41***
100SW	-0.04		-0.112	0.117	-0.174	0.105	-0.064	0.19*	0.19*	0.189*	0.19*	0.191*	0.19*	0.231*	0.01
SH (N)	0.014	-0.112		0.138	0	-0.105	0.094	0.015	0.014	0.015	0.014	0.015	0.016	-0.071	-0.105
% moisture	0.132	0.117	0.138		-0.291**	-0.403***	0.283**	0.194*	0.194*	0.192*	0.195*	0.195*	0.193*	0.017	0.22*
% protein	-0.063	-0.174	0	-0.291**		0.407***	-0.643***	0.194*	0.193*	0.191*	0.194*	0.195*	0.192*	-0.013	-0.072
% oil	-0.102	0.105	-0.105	-0.403***	0.407***		-0.928***	-0.091	-0.091	-0.09	-0.091	-0.091	-0.091	0.073	-0.191*
% starch	0.098	-0.064	0.094	0.283**	-0.643***	-0.928***		0.009	0.009	0.009	0.009	0.009	0.009	-0.053	0.157
Phenols	-0.092	0.19*	0.015	0.194*	0.194*	-0.091	0.009		0.999***	0.998***	1***	0.998***	1***	0.172	0.187*
Tanins	-0.093	0.19*	0.014	0.194*	0.193*	-0.091	0.009	0.999***		0.999***	0.999***	0.993***	0.996***	0.176	0.187*
Flavonoids	-0.092	0.189*	0.015	0.192*	0.191*	-0.09	0.009	0.998***	0.999***		0.998***	0.991***	0.998***	0.178	0.186*
Total AO activity	-0.093	0.19*	0.014	0.195*	0.194*	-0.091	0.009	1***	0.999***	0.998***		0.997***	0.999***	0.172	0.187*
DPPH	-0.091	0.191*	0.015	0.195*	0.195*	-0.091	0.009	0.998***	0.993***	0.991***	0.997***		0.997***	0.164	0.188*
ABTS	-0.091	0.19*	0.016	0.193*	0.192*	-0.091	0.009	1***	0.996***	0.998***	0.999***	0.997***		0.172	0.187*
FRAP	-0.105	0.231*	-0.071	0.017	-0.013	0.073	-0.053	0.172	0.176	0.178	0.172	0.164	0.172		0.03
PP 4 Gen	0.41***	0.01	-0.105	0.22*	-0.072	-0.191*	0.157	0.187*	0.187*	0.186*	0.187*	0.188*	0.187*	0.03	

Figure 4. Pairwise relationships between phenotyping traits, biochemical characteristics, progeny production (expressed in the number of emerged weevils) and % of consumed seed. %CS - % of consumed seeds; 100SW - 100 seed weight; SH (N) - seed hardness; PP 4 Gen – progeny production after 4 months.

DISSCUSSION

The results of the present study revealed that the *S. oryzae* population developed differently on maize genotypes in terms of progeny production (expressed as the number of emerged weevils) after one, two, three, and four months, and feeding intensity observed as % of consumed seeds after four months, indicating different seed susceptibility and/or resistance levels.

Significant difference was detected among 39 maize genotypes in terms of seed hardness (N), 100-seed weight, and moisture content (%). Also, genotypes differed in protein, oil, and starch content (%) that can be related to the type of maize involved in the tests. The content of phenolic compounds, phenols, tannins, and flavonoids differed significantly among genotypes, with the highest content detected in several dent and sweet maize genotypes. A number of studies indicate the influence of each of the mentioned parameters on the progeny production and % of consumed food. For instance, secondary metabolites such as tannins have a strong feeding deterrent activity, while flavonoid derivatives such as flavans with a double bond have proven to have a defensive role affecting behaviour, development, and the number of insects in sorghum grain (Lattanzio et al., 2006).

In our study, the progeny production after 1, 2, 3 and 4 months significantly differed among genotypes. However, on several genotypes, significantly lower numbers of weevils emerged in all four generations. In that respect, the most resistant were as follows: 605413 NS (semi-dent), MB 982 (flint), Crveni Kosjerić (red) (semi-flint), and Beli osmak II (white) (flint). Based on the progeny production and % of consumed seeds, we divided genotypes into homogenous groups. The results are in accordance with the results previously reported by Gvozdenac et al. (2018), who reported that maize genotypes exhibited different degrees of susceptibility to rice weevil attack and suitability for its development and feeding. The least susceptible was the popcorn type of maize, while white and red-aleurone genotypes were the most suitable for the rice weevil development and feeding, which is correlated to the seed hardness and nutrient content. Moreover, our work has proven a strong positive correlation between progeny production after four months and % of consumed seeds. The progeny production increased after each month for susceptible genotypes, while it remained constant for the tolerant/resistant ones (MB 982, Beli osmak (white), NSU2, and Požegrmac osmak). Higher progeny production of S. oryaze on dent genotypes and significantly lower on flint once, indicating higher tolerance, is in accordance with results presented by Jiménez-Galindo et al. (2023), who reported that the flint varieties showed significantly higher mortality of adults before entering the seed, a lower quantity of emerged adults of the first generation in the obligate-antibiosis bioassay, and lower net consumption and percentage. Tiwari et al. (2020) presented observations on susceptibility index, % of maize seed damage, and % of weight loss, revealing that none of the tested genotypes was tolerant/resistant to *S. oryzae*, but genotype HKi161 had the lowest susceptibility, indicating an opportunity to exploit this genotype in breeding programs and cultivar improvement. Abebe et al. (2009) observed the tolerance of maize against *S. zeamais* and found that the resistant variety produced low numbers of F1 progeny, and a low percentage of seed damage and seed weight loss. Similar results were presented by Muzemu et al. (2013), namely, *S. zeamais* resistant varieties had low F1 emergence, lower grain weight loss, and lower grain damage.

The % of consumed seeds strongly positively correlated with progeny production after four months. The finding is in accordance with the findings of Jiménez-Galindo et al. (2023), who detected a positive correlation between the 1st adult generation and the net consumption and percentage.

S. oryzae progeny production was positively correlated with % of seed moisture but not with the 100-seed weight, which indirectly indicates seed size, thus would be expected to affect infestation level as well, as suggested by Stejskal and Kučerová (1996) and Campbell (2002). There were significant differences in the 100-

seed weight among genotypes, although there was no strong correlation with the progeny production nor % of maize seeds consumed. The studies on sorghum, on the other hand, suggest otherwise. Seed traits such as size and moisture content determine the resources available for larval development (Mwenda et al., 2019). Stejskal and Kučerová (1996) reported a higher number of laid eggs compared to a smaller seed size. Also, female weevils accepted large seeds more quickly than small ones, which affected oviposition (Campbell, 2002), all resulting in a lower number of emerged weevils, in the case of sorghum seeds.

Seed hardness is very important for the determination of grain quality. The hardness has been useful in food processing and plays a great role in resistance against pests, including seed weevils, as it creates a physical barrier to infestation. This was proven in our work, as this seed trait was negatively correlated with progeny production after four generations, but not so strongly with % of consumed seeds, indicating it only takes a female to penetrate the seed coat and pass the first barrier. Seed hardness, among other physical properties such as length, width, thickness, and weight, is a basis for resistance to the attack of *S. zeamais* and some other insect pests of stored maize (Dobie, 1974; Osipitan and Odebiyi, 2007). Several researchers documented that a harder sorghum seed is more resistant to insect attack compared to a softer seed (Dasbak et al, 2009). Prasad et al. (2015) reported a significantly negative relationship between sorghum seed hardness and weight loss, which is not our case. However, this study also found a significantly positive link between median development period, seed hardness, and 100-seed weight. Varieties with harder seeds were not so affected by this pest (Mwenda et al., 2019), which can be related to our results, as progeny production after 4 months (PP 4 Gen) was also negatively correlated with this trait, although not strongly. Tolerance, i.e. resistance to seed pests, can be a key for future breeding programs aiming to develop varieties with desirable traits for long storage and processing, and it can be used in integrated pest management programs (Chandrashekar and Satyanarayana, 2006). The difference in seed hardness in maize is due to differences in the ratio of vitreous (hard) and floury (soft) endosperm, zein protein content and composition, and starch characteristics. Genotypes like flint maize are characterized by hard seeds rich in vitreous endosperm, while in floury maize, kernels are rich in floury endosperm (Oas and Adams, 2021), and dent maize, where there is a mix of vitreous and floury endosperm, making it an intermediate hardness (Khan et al., 2019). This variability influences the seed's overall hardness, its processing suitability, and its composition, with genetics playing the dominant role.

The protein content (%) was in strong negative correlation with oil and moisture content (%) in our work, but did not affect observed traits of S. oryaze progeny production. On the other hand, Nwosu (2016) reported that significant protein, starch, and minerals rendered maize susceptible to *S. zeamais*. Starch and protein are the main components of maize endosperm, and both are related to seed hardness (Gayral et al., 2016). Higher seed protein of zeins, specific maize endosperm prolamin-like proteins, is correlated with seed hardness (Gerde et al., 2016; Kljak et al., 2018; Pratt et al., 1995; Robutti et al., 1997). A debate based on maize resistance to *S. zeamais* infestation and damage is still on (Dobie, 1974; Nwosu et al., 2015).

The correlation analysis in our work detected positive correlation between progeny production and % of moisture and content of phenols, tannins, and flavonoids, as well as antioxidative non-enzymatic compounds detected by total AO tests, DPPH, ABTS, and FRAP tests. Gowda et al. (2019) presented results confirming ours. Namely, the authors indicate that the morphological and biochemical composition of the seeds was the most important factor in determining which rice varieties were resistant to or preferred by *S. oryzae*. Biochemical grain characteristics were found to have a positive correlation with insect emergence, weight loss, and preference index. Astuti et al. (2019) proved that maize seeds resistant to *S. zeamais* contained phenolic acids, trypsin inhibitors, and high fiber content, while susceptible varieties had high protein and starch content; however, this is the opposite of what we found in our study, where there was a positive correlation between PP 4 Gen and phenolic content. García-Lara et al (2004) presented results on how the lower phenol content (0.32%) in maize genotype Pioneer 21 caused the *S. zeamais* adult insects to choose this variety as their host. Nwosu et al. (2015) indicate the lack of information on the relationship of chemical constituents of maize seeds with resistance to *S. zeamais* infestation and that there is a need for extensive studies on the chemical bases for maize response to *S. zeamais* infestation, as can be concluded for *S. oryzae* as well.

The overall findings of this study are consistent with the conclusion proposed by Singh and Sharma (2021), that a single parameter is insufficient for the precise prediction of grain resistance to *S. oryzae*.

CONCLUSION

The presented study analyzed phenotypic traits of maize seeds associated with their susceptibility and resistance to *S. oryzae* infestation.

- The study clearly shows that some genotypes were more resistant when compared to other genotypes, based on the progeny production and % of consumed seeds.
- The most resistant were as follows: 605413 NS (semi-dent), MB 982 (flint), Crveni Kosjerić (red) (semi-flint), and Beli osmak II (white) (flint).
- On resistant genotypes, significantly lower numbers of weevils emerged after each observation during four months.
- A single seed trait is insufficient for defining maize tolerance to *S. oryzae*.
- When developing breeding strategies for the rice weevil-tolerant/resistant maize genotypes, it is crucial to consider biochemical parameters such as starch and protein content, as well as biophysical traits like seed hardness, seed moisture, and seed weight.
- Additional seed analysis should be performed, such as amylose content and the presence of protein inhibitors.
- Breeding for quality requires a clear understanding of the heritability of each of the traits responsible for tolerance to *S. oryzae*.
- Highly tolerant/resistant maize genotypes such as 605413 NS (semi-dent), MB 982 (flint), Crveni Kosjerić (red) (semi-flint), and Beli osmak II (white) (flint) should be promoted for cultivation.

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