original scientific paper
Ratar. Povrt. 2026, 63(2): 116-128
doi: 10.5937/ratpov63-69762
Manuscript submitted: 31 July 2026
Manuscript accepted: 24 August 2026
Published online: 27 August 2026

Does the host shift affect the body size of the rice weevil (*Sitophilus oryzae* L.) as a response to developmental stress: Wheat-Maize-Sorghum case?

Jelena Ačanski[1]* · Marko Radenković[1] · Dejan Prvulović[2] · Marija Stajić[1] · Aleksandra Ilić[3] · Anja Dolapčev Rakić[3] · Sonja Gvozdenac[3]

[1]University of Novi Sad, BioSense Institute, Novi Sad, Serbia
[2]University of Novi Sad, Faculty of Agriculture, Novi Sad, Serbia
[3]Institute of Field and Vegetable Crops, Novi Sad, Serbia

* Corresponding author email: acanski@biosense.rs

Summary: The rice weevil, *Sitophilus oryzae* (L.) is recognised as one of the most polyphagous and extremely destructive pests of stored cereal grains worldwide. It develops under a wide range of environmental conditions, however, there have been some indications about alterations in specimen morphology when observed across populations originating from different commodities. While responses to different stressors have mainly been evaluated using survival, progeny production, and developmental time, body size as an indicator of developmental stress has received limited attention. This study investigated whether centroid size (CS), assessed through geometric morphometrics, reflects the influence of hosts changes, i.e whether these responses are associated with seed traits. A parental population reared on wheat was transferred to maize and sorghum, and progeny production and body size were analysed. Adults from maize were statistically significantly smaller than those from wheat, despite similar progeny production. Sorghum significantly reduced progeny production but did not significantly affect body size. Phenotypic variability in CS was the highest in the maize population. According to two-block Partial Least Squares analysis, larger body size was associated with higher protein content, while seed hardness and increased total phenolic contents, including flavonoids and tannins, were linked to reduced CS. These results indicate that body size must be measured as an indicator of developmental responses. Also, our study suggests the importance of integrating complementary biological parameters to provide a more comprehensive understanding of developmental responses to host shifts and other stressors, and helps to identify host characteristics associated with insect performance.
Key words: body size, centroid size, developmental plasticity, developmental stress, host shift, partial least squares, grain traits, *Sitophilus oryzae*, stored-product pests

Introduction

Cereal grains, like wheat and maize, are among the most widely cultivated crops globally (Kumar and Kalita, 2017), serving as a key source of food for humans and livestock, as well as for different industrial products (Ranum et al., 2014). More than 2.5 billion people rely on wheat as a primary food source, with global production exceeding 800 million tons annually (FAOSTAT, 2025). The European Union is the world's second-largest producer (approximately 135 million tons)

(USDA FAS, 2025), and Serbia ranks among the 20 major wheat producers (estimated production of around 3 million tons) in 2024 (SORS, 2024). Maize 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 & Čerešňáková, 2013). In 2023, according to cultivated area (ha) and total production (t), it ranked as the world's second most important cereal crop (FAOSTAT, 2025) with an increasing production trend globally. FAOSTAT (2025) also identifies sorghum as the fifth most important cereal crop worldwide. Although sorghum is cultivated on a much smaller scale than wheat and maize, it has a longstanding production tradition in Serbia (Berenji et al., 2011). In Serbia, sorghum is grown on approximately 2,600 hectares, with an average grain yield exceeding 3,100 kg ha^{-1}. Its notable tolerance to drought and high temperatures enhances its potential significance under changing climatic conditions (Dolapčev Rakić et al., 2025). *Sitophilus oryzae* is a well-documented and economically significant pest of stored sorghum, causing substantial grain damage across various sorghum varieties (Hendrival et al., 2019; Liba et al., 2026).

Given the existential significance of these three crops, considerable progress has been made in postharvest technologies and grain storage systems. However, wheat, maize, and sorghum continue to experience substantial postharvest losses during storage caused by stored product insects (Gvozdenac et al., 2022; Kebede et al., 2024), with the rice weevil, *Sitophilus oryzae* (Linnaeus, 1763) (Coleoptera: Curculionidae), being a major threat. Globally, it is one of the most economically significant primary pests of stored cereal grains. Aside from quantitative and qualitative (decreased nutritional content, change in content of carbohydrates, starch and proteins) losses, this pest causes significant economic losses by contamination (body fragments, toxic substance occurrence like metabolic byproducts, uric acid, etc.), and reduction of nutritional and commercial value of the grain, diminishing consumer confidence (García-Lara et al., 2019). Its widespread distribution, larval development within grains, high reproductive capacity, and broad host range facilitate persistent infestations that result in considerable quantitative and qualitative losses during storage (Rees, 2004; Hagstrum et al., 2013).

Developmental environments (including the quality of feeding substrate) in stored-product insects significantly influence key life-history traits, including developmental rate, survival, fecundity, and population growth (Longstaff, 1981; Rees, 2004), even though they are polyphagous. All those contribute significantly to overall population developmental stability (DS). DS refers to an organism's capacity to maintain normal development in the face of genetic and environmental perturbations (Debat & David, 2001). Environmental stress may disrupt developmental processes, resulting in alterations to developmental and fitness-related traits such as body size, morphology, fluctuating asymmetry, survival, and reproduction. The extent of these changes depends on the specific nature and intensity of the stressor. In Sitophilus species, larvae complete their entire development within a single grain, thus, environmental physical and chemical characteristics of the grain itself are the major factors influencing immature stage development, but also the entire developmental cycle is primarily determined by the characteristics of the grain itself (Gvozdenac et al, 2022). On the other hand, adult size is particularly informative because larval development is entirely completed within a single grain, resulting in adult morphology that is closely determined by the developmental environment. Previous research has demonstrated that the developmental substrate can affect adult body size in *Sitophilus* spp., although the extent of this effect varies depending on the host grain and population examined (Ungsunantwiwat & Mills, 1985). Additionally, body size has been linked to reproductive success in *S. oryzae* (Holloway & Smith, 1987). Therefore, body size serves as a biologically relevant trait for investigating developmental responses in stored-product insects. Insect body size exhibits high plasticity and may respond to factors such as nutrition, host quality, temperature, and population density experienced during development (Nijhout et al., 2014; Koyama & Mirth, 2018). Since body size is closely associated with multiple fitness components, including fecundity, dispersal capacity, and competitive ability (Nylin & Gotthard, 1998; Honěk, 1993; Blanckenhorn, 2000; Eck et al., 2015), elucidating how host

shifts influence structural growth is essential for understanding developmental plasticity and life-history evolution.

Although body size has occasionally been quantified in taxonomic, developmental, and reproductive studies of Sitophilus species, experimental research evaluating insecticides, fumigants, essential oils, and botanical extracts has assessed morphological responses almost exclusively using body mass. Linear or geometric estimates of body size have rarely been considered in these contexts. In contrast, body size and morphometric measurements, such as body length, body width, pronotal and rostral dimensions, or landmark-based morphometric analyses, have been used primarily in taxonomic, developmental, biological, and species-identification studies, rather than for evaluating responses to chemical or botanical stressors (Shakthi et al., 2025).

Centroid size (CS) is the standard measure of scale in geometric morphometrics. CS is calculated from the entire landmark configuration as the square root of the summed squared distances of all landmarks from their centroid. This measure reflects the overall size of the analysed configuration rather than a single interlandmark distance (Bookstein, 1991; Zelditch et al., 2012; Webster & Sheets, 2010). CS also serves as the scaling factor in Generalized Procrustes Analysis (GPA), where landmark configurations are translated, rotated, and scaled to unit centroid size. This process allows for the examination of shape variation independently from variation in position, orientation, and scale (Rohlf & Slice, 1990; Dryden & Mardia, 1998; Mitteroecker & Gunz, 2009). CS is commonly used in geometric morphometric analyses because it is based on all landmarks rather than a single anatomical axis (Klingenberg, 2016).

For stored-product insects, understanding how nutritive traits of grains influence body size has implications that extend beyond basic developmental biology. They may affect different components of the insect phenotype, but not all developmental responses are necessarily reflected in shape variation or developmental instability. Consequently, factors that do not produce detectable changes in shape or fluctuating asymmetry may still influence growth. This influence can affect biologically important traits associated with insect bionomy, such as survival, dispersal capacity, reproductive potential, or competitive ability. In the longer term, identifying developmental factors that promote or constrain growth may improve understanding of pest biology and provide a foundation for refining existing management strategies or developing novel approaches for the control of stored-product insects.

This study aimed to investigate whether body size in *S. oryzae*, quantified using landmark-based geometric morphometrics, corresponds to grain physical and nutritive traits. By evaluating size as an independent morphological characteristic, the study assessed its potential to provide biologically meaningful information on developmental responses and to establish a foundation for future research exploring its relevance in stored-product insect biology and pest management.

Material and methods

Insect rearing and experimental design

The initial *S. oryzae* population was obtained from a population reared for 10 generations on wheat grains (var. Pobeda), in controlled conditions, at 27 ± 1 °C, 70 ± 5% RH and in continuous darkness (Trematerra, 2013), at the Institute of Field and Vegetable Crops, National Institute of the Republic of Serbia, Novi Sad. The population was maintained throughout the experimental period under laboratory conditions, at 27±2 °C, 70% RH, 16:8 L:D. In Petri dishes (Ø 9 cm) containing 50 g of wheat grains (variety Pobeda), maize (hybrid NS 644) and sorghum (variety Titan), 20 adult weevils, non-destructively screened based on rostrum morphology to obtain an approximately 1:1 sex ratio, were placed. The population maintained on wheat represented the control population, whereas the populations transferred to maize and sorghum represented the experimental populations exposed to a change in grain type. Petri dishes were incubated in the dark, under the same conditions as rearing the parental population. Each grain type represented one treatment, replicated three times (9 Petri dishes in total). Insects were allowed to develop and

reproduce continuously on the three grain types, and newly emerged adults (progeny production, PP) were counted at 30-day intervals, i.e. after 30, 60, 90, and 120 days. Adults from the preceding generation were removed after each assessment to allow successive generations to be monitored. Young, live adults emerging in the fourth generation were collected and used for geometric morphometric analyses.

Grain traits

To analyse the content of moisture, starch, protein, and dry gluten in wheat, maize, and sorghum grains, a Near Infrared Spectrometry analyser, model DA 7250, was used. For further analysis, grains were ground to a fine powder prior to analysis and extracted in ethanol (1 g of ground grains was homogenised with 5 mL of 70% ethanol). The extracts were kept in the dark at room temperature for 24 h with occasional stirring. Each biochemical assay was performed in six replicates. Total phenolic content was determined spectrophotometrically using the Folin–Ciocalteu (FC) colourimetric method, which measures the reducing capacity of phenolic compounds toward the FC reagent (Hudz et al., 2019). Absorbance was recorded at 730 nm, and phenolic concentration was calculated from a quercetin standard curve. Total tannin content was determined using a polyvinylpolypyrrolidone (PVPP) binding assay, followed by Folin–Ciocalteu measurement of non-tannin phenolics, and expressed as quercetin equivalents per 100 g dry weight (mg QE/100 g dw). Total flavonoid content was measured using an aluminium chloride ($AlCl_3$) colourimetric assay, with maximum absorbance at 430 nm (Martono & Muninggar, 2020) and expressed as quercetin equivalents per 100 g dry weight (mg QE/100 g dw). Ferric reducing antioxidant power (FRAP) was measured using the Fe^{3+}–TPTZ reduction assay, with absorbance read at 593 nm (Lim & Lim, 2013). Results were calculated from a Trolox standard curve. Seed hardness was measured using an FTC TMS-pro texture analyser (FTC, USA) at the Laboratory for Biosystem Engineering, Faculty of Agriculture, University of Novi Sad. Hardness was quantified as the maximum force (N) required to crush individual seeds. Measurements utilised a 500 N load cell, a pre-test speed of 60 mm min^{-1}, a test speed of 30 mm min^{-1}, and a probe displacement of 2 mm. For each seed type, five replicate measurements were conducted, and the mean value was used for subsequent statistical analyses. Wheat, maize, and sorghum grain physical, nutritive and biochemical traits were used as predictor variables in the two-block partial least squares (PLS) analysis.

Geometric morphometric analysis - centroid size

Eighty *S. oryzae* specimens were included in the geometric morphometric analysis (wheat 31, maize 24, and sorghum 25). Following collection, specimens were stored at -18°C until further processing. To enhance visibility of the ventral body surface, legs were removed prior to imaging. Specimens were rinsed with distilled water, followed by 75% ethanol, and positioned horizontally on microscope slides using a clay mould. Each specimen received a unique identification code. High-resolution images of the ventral body side were obtained using a Leica MZ16 stereomicroscope with a Leica DFC320 digital camera. Twelve homologous two-dimensional landmarks were digitised per specimen (Fig. 1) using TPSDig 2.05 software (Rohlf, 2006). Measurement error was estimated by digitising each specimen twice by the same person. ANOVA showed that centroid size did not differ significantly between males and females ($P > 0.05$). Therefore, data from both sexes were pooled for subsequent analyses.

Landmark configurations were superimposed using Generalized Procrustes Analysis implemented in MorphoJ version 2.0 (Klingenberg, 2011). During GPA, CS was automatically calculated for each specimen as the square root of the summed squared distances of all landmarks from their centroid (Bookstein, 1991). In the present study, centroid size was used as a proxy for overall body size in the analysed ventral configuration. For ease of biological interpretation, CS values were converted from digital units to millimetres using the calibration scale obtained during image acquisition.

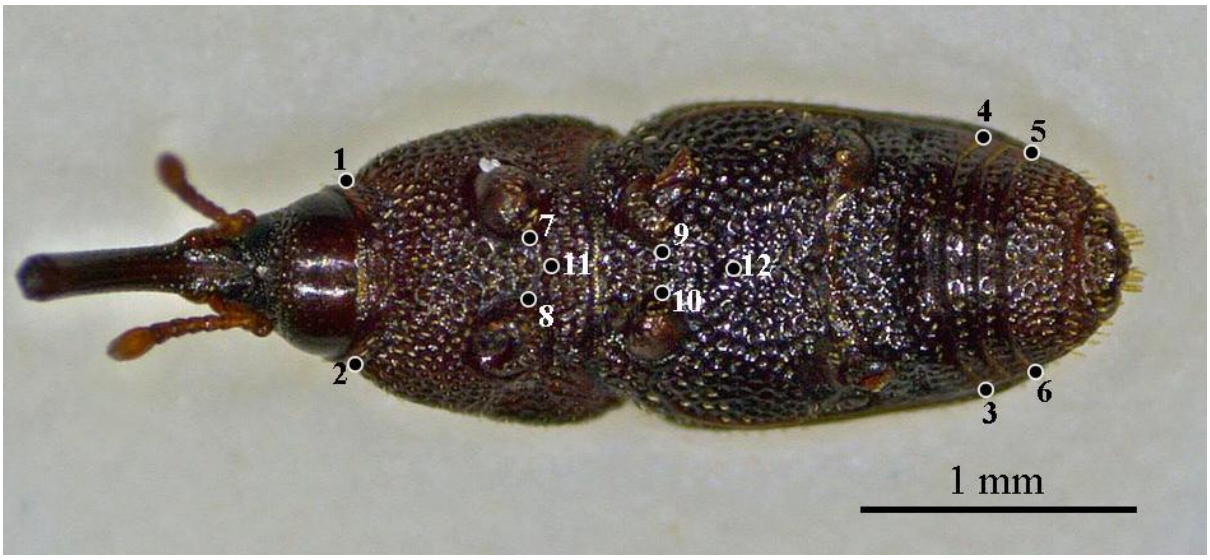

Figure 1. Locations of the twelve landmarks used in the geometric morphometric analysis of ventral body shape in *Sitophilus oryzae*

Differences in centroid size among experimental groups were evaluated using one-way analysis of variance (ANOVA) and Dunnett's post hoc test to test the difference in CS between parental and experimental populations. Variation in body size was quantified using the coefficient of variation (CV; standard deviation divided by the mean) for each laboratory population, including the control group. Differences in the coefficients of variation among populations were evaluated using the Modified Signed Likelihood Ratio Test (MSLRT) implemented in the R package cvequality (Krishnamoorthy & Lee, 2014; Marwick & Krishnamoorthy, 2019).

Correlation between CS and graintraits

Associations between seed traits and CS were assessed using two-block PLS analysis implemented in the geomorph package in RStudio. Block 1 (X) included seven seed traits (moisture content, protein content, starch content, total phenolic content, flavonoid content, tannin content, and seed hardness), while Block 2 (Y) consisted of the CS values for each specimen. Prior to the analysis, seed trait variables were standardised using the scale function in RStudio (z-score transformation) to remove differences in measurement scales and ensure equal contribution of all variables to the analysis.

Results

Progeny production of S. oryaze

Cumulative progeny production increased over time in all grain types and differed substantially among treatments. Wheat and maize supported similarly high offspring production, reaching 658 and 635 specimens, respectively, after four months, whereas sorghum yielded only 159 specimens (Figure 2A).

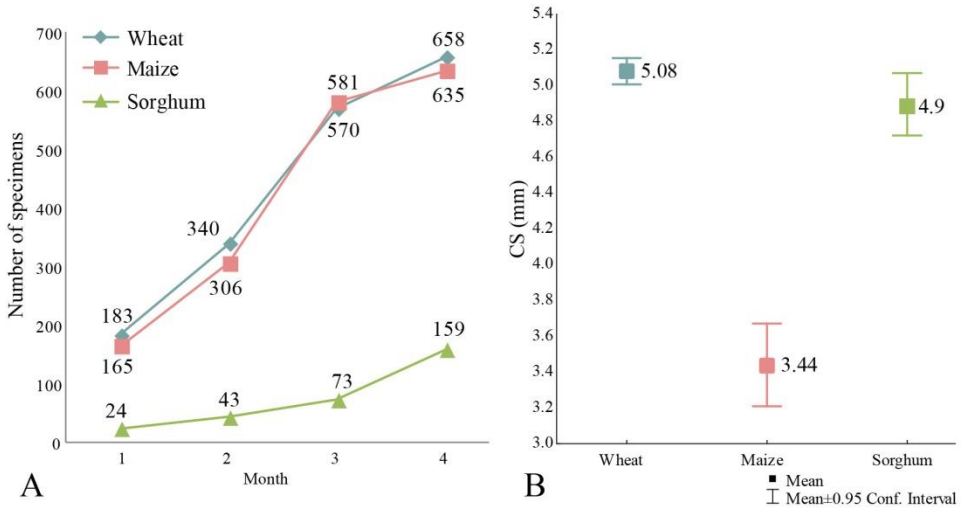

Figure 2. Cumulative progeny production and centroid size of *S. oryzae* reared on wheat (parental population), maize and sorghum. A. Cumulative progeny production. B. Mean centroid size (mm) of *Sitophilus oryzae* adults

Size analyses

ANOVA with Dunnett's post hoc test identified significant differences in CS among populations ($F_{2, 76} = 130.169$, $P < 0.001$). Specimens reared on maize had a significantly smaller centroid size than the control population (Dunnett's test, MSerror = 0.158; df = 76; all $P < 0.001$), while no significant difference was observed between specimens reared on sorghum and the control ($P = 0.158$).

Differences in centroid size, measured in millimetres, are illustrated in a mean plot with 95% confidence intervals (Figure 2B). The mean centroid size was largest in the parental population originating from wheat (5.08 mm), followed by the sorghum population (4.9 mm). In contrast, specimens reared on maize exhibited a substantially lower mean body size (3.44 mm). The coefficient of variation for centroid size varied substantially among populations (Figure 3). The maize population exhibited the highest value (15.9%), followed by the sorghum population (8.4%), while the parental wheat population showed the lowest variability (3.9%). The MSLRT confirmed significant differences in centroid size variability among the three populations (MSLRT = 44.59, $P < 0.001$).

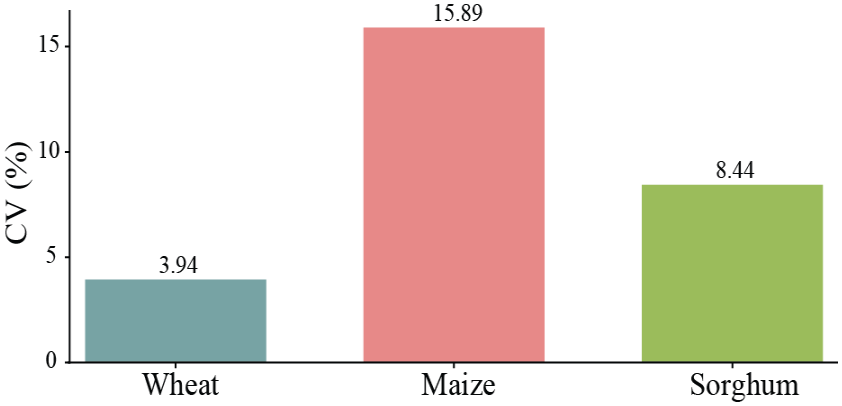

Figure 3. Coefficient of variation (CV) of centroid size in *S. oryzae* populations reared on different seed types. The wheat population exhibited the lowest phenotypic variability (CV = 3.94%), whereas specimens reared on maize showed the highest variability (CV = 15.89%), followed by those reared on sorghum (CV = 8.44%)

Grain physical, nutritive and biochemical traits

The highest moisture was detected in samples of wheat grains (10.13%), protein content in sorghum grains (17.03%) and starch, also in wheat (72.63%), as presented in Table 1. Biochemical parameters all differed significantly across grain types, with all being the highest in maize grains (Table 1). Seed hardness (N) was also the highest in maize (323.1 N).

Table 1. Wheat, maize, and sorghum grain physical, nutritive and biochemical traits.

Seed type	Moisture (%)	Proteins (%)	Starch (%)	Total phenols (mg QE 100 g^{-1} DW)	Flavonoids (mg QE 100 g^{-1} DW)	Tannins (mg QE 100 g^{-1} DW)	Seed hardness (N)
Maize	8.24 b	6.98 c	64.34	7.37	2.26	2.28	323.1
Wheat	10.13 a	13.40 b	72.63	2.24	0.24	0.59	79.6
Sorghum	7.48 b	17.03 a	50.98	1.45	0.43	0.17	120.82
F value	7.11*	26.66*					

Correlation between CS and grain traits

Two-block partial least squares (PLS) analysis demonstrated a strong and significant covariation between grain traits and centroid size (r-PLS = 0.875, $P = 1 \times 10^{-4}$). Protein content exhibited the strongest positive association with centroid size (PLS loading = 0.924), while flavonoids, total phenolic content, seed hardness, and tannins showed strong negative associations (PLS loadings, respectively: -0.997; -0.991; -0.988; -0.979). Moisture and starch contributed minimally to the first PLS axis (PLS loadings, respectively: 0.299; -0.054). The first PLS axis accounted for all variation in the grain traits block and distinguished the maize population from the wheat and sorghum populations. Specimens reared on wheat and sorghum, which had larger centroid sizes, were associated with higher protein content, whereas maize, with the smallest centroid size, was positioned at the opposite end of the PLS axis (Figure 4).

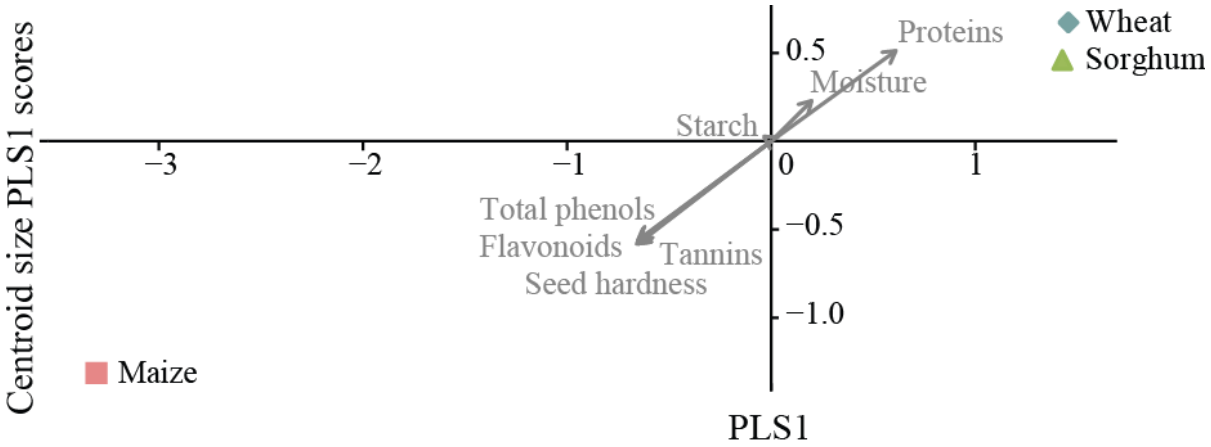

Figure 4. Two-block Partial Least Squares analysis illustrating the relationship between seed traits and centroid size in *S. oryzae*. Arrows represent the loadings of grain traits, indicating their direction and strength of association with centroid size

Discussion

The present study demonstrates that a host shift acts as a developmental stressor and influences progeny and body size of *S. oryzae*. While progeny production on maize did not differ significantly compared to PP on wheat, adults emerging from maize were significantly smaller. In contrast, sorghum markedly reduced progeny production but produced adults of similar size to those reared on wheat. Host shifts alter the nutritional, physical, and defensive environment in which larvae complete development. The coefficient of variation for centroid size was also substantially higher in host-shift populations than in the parental wheat population, with the highest value observed in maize, indicating greater heterogeneity in developmental responses among specimens. Importantly, these contrasting responses demonstrate that different components of insect performance do not necessarily respond uniformly to changes in host quality. Rather, host shifts appear to influence different fitness-related traits through partly independent developmental pathways, emphasising that host suitability is a multidimensional rather than a single-trait phenomenon.

In insects, adult size is determined by environmental conditions during developmental stages, the size threshold for developmental transitions, and the duration of the terminal growth period (Nijhout et al, 2006; Callier & Nijhout, 2013). For example, when stress decreases food assimilation, and larvae cannot compensate before metamorphosis, adults often become smaller. But the direction of the body-size response to stressed environmental conditions should not be assumed a priori. Insects can also preserve or even increase final size by extending development, adding an instar, or engaging in catch-up growth (Esperk & Tammaru, 2010; Saastamoinen et al., 2013). Also, hormesis can influence size, when low-dose toxic stress can increase rather than depress fitness, like higher adult body mass after sublethal pyrethroid exposure in the Colorado potato beetle (Margus et al., 2019). The present results fit well within this framework of developmental plasticity, illustrating that host shifts may reduce body size, maintain it despite reduced performance, or potentially increase it depending on the interaction between host characteristics and insect developmental responses.

The contrasting responses observed in maize and sorghum further demonstrate why evaluating only one component of insect performance may overlook biologically relevant developmental effects. Changes in adult body size may instead reveal biologically meaningful developmental responses that remain undetected by other measures. Furthermore, the strong covariation between centroid size and seed traits in this paper, as revealed by the two-block PLS analysis, indicates that these differences are linked to variation in the nutritional and defensive characteristics of the host grains. Collectively, these findings suggest that body size provides complementary information regarding the developmental consequences of host shifts and assists in identifying the seed characteristics most strongly associated with these responses.

Research on phosphine-resistant *S. oryzae* has demonstrated that adults display significantly reduced body weight, and that insecticide resistance correlates with body-mass variation and fluctuating asymmetry (Guedes et al., 2006; Cordeiro et al., 2017; Park et al., 2025). In addition, investigations of different host grains have primarily focused on progeny production, developmental time, fecundity, emergence, longevity, and life-table parameters (Baker, 1988; Abedi et al., 2024), while measurements of body length or other linear dimensions have been less frequently reported (Thakkar & Parikh, 2018; Prasad et al., 2025; Guarino et al., 2026). Botanical insecticide studies have likewise emphasised mortality, repellency, progeny emergence, and asymmetry (Stefanazzi et al., 2011; Ačanski et al., 2023; Hariani et al., 2024). Although these parameters provide valuable information on pesticidal or host-shift efficacy, they do not offer a complete understanding of how they influence insect size. In a rice-derived laboratory population of *S. oryzae,* maize produced the shortest development and the largest adults, whereas pearl millet prolonged development and reduced performance, showing that host-associated delays and size outcomes (Thakkar & Parikh, 2018; Prasad et al., 2025). An earlier study by Baker (1988) showed that development of *S. oryzae*

differed across barley, maize, rice, and wheat, with the lowest progeny production in maize, contrary to our and the above-mentioned study.

Insect adult size is associated with fecundity, longevity, stress resistance, and mating success (Koyama & Mirth, 2018), and behavioural interactions (Kalinkat et al., 2015). In many insect species, larger adult size is correlated with increased fitness (Andersson, 1994). In *S. oryzae,* the fitness relevance of size is direct, as females prefer large males, indicating that size affects competitive mating success (Holloway & Smith, 1987). Body size can capture sublethal developmental consequences likely to matter for subsequent reproduction and population dynamics, which points out why adult body size deserves attention as a fitness-linked trait.

Our study illustrates that assessment of adult body size can provide complementary information on developmental responses to stressors. Within that context, our PLS result is particularly important because it links size to a multivariate host-trait axis rather than to a single grain characteristic. The positive association of centroid size with protein, and the negative association with total phenolics, flavonoids, tannins, and seed hardness, suggests that centroid size covaried with a multivariate gradient of host quality and host defence. It is known that phenolic-based defences in seed are associated with resistance to Sitophilus infestation, including negative relationships between phenolic acids or diferulate-linked wall chemistry of maize and susceptibility to the maize weevil (Classen et al., 1990; Arnason et al., 1992; Arnason et al., 1993). Gvozdenac et al. (2026) reported that the rice weevil progeny production positively correlated with maize grain moisture (%), content of total phenols, tannins and flavonoids, but negatively with grain hardness. Sorghum studies have also shown that soluble phenolics, especially proanthocyanidin-rich fractions, and grain hardness are repeatedly associated with resistance to *S. oryzae* (Ramputh et al., 1999; Russell, 1966; Prasad et al., 2015). Regarding grain hardness, a recent study showed that it is strongly and negatively correlated with *S. oryzae* progeny output (Abedi et al., 2024). The results demonstrate the importance of measuring body size as a trait, particularly in maize specimens. Considering only progeny production to assess the impact of host change would suggest that maize has no significant effect on development and fitness. However, progeny production varied substantially among the three seed types throughout the experiment. Maize supported progeny production levels comparable to wheat but resulted in significantly smaller adults. In contrast, sorghum markedly reduced progeny production, while adult body size remained similar to that of the parental wheat population. These contrasting outcomes indicate that different seed properties affect distinct components of fitness. The significant PLS association between seed composition and centroid size further supports the hypothesis that nutritional and defensive seed traits contribute to developmental responses. Higher protein content was associated with larger body size, whereas increased levels of phenolic compounds, flavonoids, tannins, and seed hardness were linked to reduced centroid size.

The low progeny production observed on sorghum aligns with previous studies that identify this cereal as a relatively unsuitable or resistant host for *S. oryzae* (Reddy et al., 2002; Prasad et al., 2015). The reduced progeny production in the present study may result from several pre-emergence processes, such as decreased oviposition, slower developmental rates, or increased immature mortality. One explanation for the absence of reduced adult size among specimens reared on sorghum is that the extended developmental period commonly associated with this host enables surviving larvae to acquire and allocate additional resources prior to metamorphosis. Alternatively, selective survival may occur, whereby resistant sorghum eliminates larvae with lower physiological capacity, resulting in a smaller subset of specimens capable of completing development and achieving normal adult size. High progeny production in maize indicates that the maize variety used in this analysis did not limit successful development at the population level; however, adults were significantly smaller than those emerging from wheat. The position on the PLS axis suggests that maize may support high offspring production while imposing nutritional or biochemical constraints on specimen growth**.** Phenolic compounds and tannins may contribute to resistance by reducing

oviposition, progeny emergence, or food utilisation, although their effects depend strongly on concentration, grain genotype, and interactions with other seed traits. In the present study, higher levels of phenolic compounds, tannins, and seed hardness were associated with reduced centroid size but not with lower progeny production. This pattern suggests that body size and progeny production may reflect different developmental responses to host characteristics.

This study demonstrates the importance of integrating multiple complementary parameters to obtain a comprehensive understanding of developmental responses of *S. oryzae* to host shifts or other stressors. Such an integrative framework not only improves our understanding of stress but also helps identify traits associated with insect performance. Expanding the integrative approach to a broader range of host species, cultivars, and successive generations will further clarify the mechanisms underlying host use and can support the development of more sustainable management strategies for *S. oryzae* and other economically important stored-product pests.

Author contributions: Conceptualization, J.A., S.G. and M.R.; methodology, J.A., S.G. and M.R.; software, J.A., S.G. and M.R.; validation, J.A., S.G. and D.P.; formal analysis, J.A., S.G., M.R. and M.S.; investigation, J.A., M.R., D.P., M.S., A.I., A.D.R. and S.G.; resources, D.P., M.S., A.I., A.D.R. and S.G.; data curation, S.G. and M.R.; writing—original draft preparation, J.A., M.R., D.P., M.S., A.I., A.D.R. and S.G.; writing-review and editing, J.A., S.G. and M.R.; visualization, J.A., S.G. and M.R.; supervision, J.A. and S.G.; project administration, J.A. and S.G.; funding acquisition, J.A. and S.G. All authors have read and agreed to the published version of the manuscript.

Competing interests statement: No competing interests were disclosed.

Funding statement: This research was supported by the Provincial Secretariat for Higher Education and Scientific Research of the Autonomous Province of Vojvodina (Project title: Stress biomarkers as a basis for the development of environmentally friendly control measures against the rice weevil (*Sitophilus oryzae*); Contract Number: 003875718 2025 09418 003 000 000 001 04 004; Jelena Ačanski) and the Science Fund of the Republic of Serbia (Project title: New biorational methods for stored seed pest control and protection: To serve and prevent - SafeSeed; Contract Number: #6691; Sonja Gvozdenac) and the Ministry of Science, Technological Development and Innovation of the Republic of Serbia (Contract Number: 451-03-33/2026-03/200358 and 4451-03-33/2026-03/ 200032). This work was performed as part of the activities of the Centre of Excellence for Innovations in Breeding of Climate-Resilient Crops - Climate Crops, Institute of Field and Vegetable Crops, Novi Sad, Serbia.

Data availability statement: The data presented in this study are available from the corresponding author upon reasonable request.

Ethical issues statement: Grammarly Pro was used for language editing and formatting; no AI tools were used for data analysis or research activities.

References

Abedi, Z., Razmjou, J., Rafiee Dastjerdi, H., & Ebadollahi, A. (2024). Physical and biochemical characteristics of cereal grains affect population growth parameters of *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae). *Journal of Stored Products Research, 109*, 102459. https://doi.org/10.1016/j.jspr.2024.102459

Ačanski, J., Gvozdenac, S., Radenković, M., Prvulović, D., Tanasković, S., & Horvatović, M. (2023). Effect of four plant extracts on the mortality, population growth, and fluctuating asymmetry of *Sitophilus oryzae*. *Entomologia Experimentalis et Applicata, 171*(8), 611–620. https://doi.org/10.1111/eea.13325

Andersson, M. (1994). *Sexual selection*. Princeton University Press.

Arnason, J. T., Gale, J., Conilh de Beyssac, B., Sen, A., Miller, S. S., Philogene, B. J. R., Lambert, J. D. H., Fulcher, R. G., Serratos, A., & Mihm, J. (1992). Role of phenolics in resistance of maize grain to the stored grain insects, *Prostephanus truncatus* (Horn) and *Sitophilus zeamais* (Motsch.). *Journal of Stored Products Research, 28*(2), 119–126. https://doi.org/10.1016/0022-474X(92)90019-M

Arnason, J. T., Lambert, J. D. H., Gale, J., Mihm, J., Bjarnason, M., Jewell, D., Serratos, J. A., Fregeau-Reid, J., & Pietrzak, L. (1993). Is "quality protein" maize more susceptible than normal cultivars to attack by the maize weevil *Sitophilus zeamais*? *Postharvest Biology and Technology, 2*(4), 349–358. https://doi.org/10.1016/0925-5214(93)90039-6

Baker, J. E. (1988). Development of four strains of *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) on barley, corn (maize), rice, and wheat. *Journal of Stored Products Research, 24*(4), 193–198. https://doi.org/10.1016/0022-474X(88)90018-5

Hendrival, H., Putra, R. L., & Aryani, D. S. (2019). Susceptibility of sorghum cultivars to *Sitophilus oryzae* L.(Coleoptera: Curculionidae) during storage. *Planta Tropika*, *7*(2), 110-116.

Berenji, J., Dahlberg, J., Sikora, V., & Latkovi, D. (2011). Origin, history, morphology, production, improvement, and utilization of broomcorn [*Sorghum bicolor* (L.) moench] in Serbia1. *Economic botany*, *65*(2), 190–208.

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The Quarterly Review of Biology, 75*(4), 385–407. https://doi.org/10.1086/393620

Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge University Press.

Callier, V., & Nijhout, H. F. (2013). Body size determination in insects: A review and synthesis of size- and brain-dependent and independent mechanisms. *Biological Reviews, 88*(4), 944–954. https://doi.org/10.1111/brv.12033

Classen, D., Arnason, J. T., Serratos, J. A., Lambert, J. D. H., Nozzolillo, C., & Philogène, B. J. R. (1990). Correlation of phenolic acid content of maize to resistance to *Sitophilus zeamais*, the maize weevil, in CIMMYT's collections. *Journal of Chemical Ecology, 16*(2), 301–315. https://doi.org/10.1007/BF01021766

Cordeiro, E. M. G., Corrêa, A. S., Rosi-Denadai, C. A., Tomé, H. V. V., & Guedes, R. N. C. (2017). Insecticide resistance and size assortative mating in females of the maize weevil (*Sitophilus zeamais*). *Pest Management Science, 73*(5), 823–829. https://doi.org/10.1002/ps.4437

Debat, V., & David, P. (2001). Mapping phenotypes: Canalization, plasticity and developmental stability. *Trends in Ecology & Evolution, 16*(10), 555–561. https://doi.org/10.1016/S0169-5347(01)02266-2

Dolapčev Rakić, A., Prodanović, S., Sikora, V., Vasiljević, S., Župunski, V., Jevtić, R., & Uhlarik, A. (2025). Potential for enhancing forage sorghum yield and yield components in a changing Pannonian climate. *Agriculture*, 15(13), 1439. https://doi.org/10.3390/agriculture15131439

Dryden, I. L., & Mardia, K. V. (1998). *Statistical analysis of shape*. John Wiley & Sons.

Eck, D. J., Shaw, R. G., Geyer, C. J., & Kingsolver, J. G. (2015). An integrated analysis of phenotypic selection on insect body size and development time. *Evolution, 69*(9), 2525–2532. https://doi.org/10.1111/evo.12744

Esperk, T., & Tammaru, T. (2010). Size compensation in moth larvae: Attention to larval instars. *Physiological Entomology, 35*(3), 222–230. https://doi.org/10.1111/j.1365-3032.2010.00739.x

Food and Agriculture Organization of the United Nations. (2025). *FAOSTAT: Food and agriculture data* [Data set]. Retrieved February 12, 2026, from https://www.fao.org/faostat/en/

Food and Agriculture Organization of the United Nations. (2025). *FAOSTAT: Production—Crops and livestock products: Wheat production* [Data set]. Retrieved February 12, 2026, from https://www.fao.org/faostat/en/

García-Lara, S., García-Jaimes, E., & Bergvinson, D. J. (2019). Mapping of maize storage losses due to insect pests in central Mexico. *Journal of Stored Products Research, 84*, 101529. https://doi.org/10.1016/j.jspr.2019.101529

Guarino, S., Gasparro, S., Cerasa, G., Moliterno, A. A. C., Ingraffia, R., Porto, A. L., Gargano, G., Ruisi, P., Giambalvo, D., & Peri, E. (2026). Resistance grade of different *Triticum* species toward *Sitophilus oryzae* L. (Coleoptera: Curculionidae). *Journal of Stored Products Research, 116*, 102892. https://doi.org/10.1016/j.jspr.2026.102892

Guedes, R. N. C., Oliveira, E. E., Guedes, N. M. P., Ribeiro, B., & Serrão, J. E. (2006). Cost and mitigation of insecticide resistance in the maize weevil, *Sitophilus zeamais*. *Physiological Entomology, 31*(1), 30–38. https://doi.org/10.1111/j.1365-3032.2005.00479.x

Gvozdenac, S., Dedić, B., Mikić, S., Ovuka, J., & Miladinović, D. (2022). Impact of climate change on integrated pest management strategies. In *Climate change and agriculture: Perspectives, sustainability and resilience* (pp. 311–372). Wiley. https://doi.org/10.1002/9781119789789.ch14

Gvozdenac, S., Škorić, M., Prvulović, D., Kolarov, R., Ovuka, J., Tanasković, S., Lozanov-Crvenković, Z., Stanisavljević, D., Nastasić, A., Babić, V., Radojčin, M., Pavkov, I., & Marković, D. (2026). The impacts of maize seed phenology and nutritive traits imparting tolerance to the rice weevil (*Sitophilus oryzae* L.). *Journal of Central European Agriculture, 27*(1), 204–219. https://doi.org/10.5513/JCEA01/27.1.5081

Hagstrum, D. W., Phillips, T. W., & Cuperus, G. (Eds.). (2013). *Stored-product protection*. Kansas State University.

Hariani, N., Lestari, R., & Zulfitri, A. (2024). Evaluating the efficacy of citronella essential oil (*Cymbopogon nardus*) as a control agent for warehouse rice weevil (*Sitophilus oryzae*). *Jurnal Pendidikan Matematika dan IPA, 15*(3), 346–354. https://doi.org/10.26418/jpmipa.v15i3.80589

Holloway, G. J., & Smith, R. H. (1987). Sexual selection of body weight in *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae). *Journal of Stored Products Research, 23*(4), 197–202. https://doi.org/10.1016/0022-474X(87)90003-8

Honěk, A. (1993). Intraspecific variation in body size and fecundity in insects: A general relationship. *Oikos, 66*(3), 483–492. https://doi.org/10.2307/3544943

Hudz, N., Yezerska, O., Shanaida, M., Horčinová Sedláčková, V., & Wieczorek, P. P. (2019). Application of the Folin-Ciocalteu method to the evaluation of *Salvia sclarea* extracts. *Pharmacia, 66*(4), 209–215. https://doi.org/10.3897/pharmacia.66.e38976

Kalinkat, G., Jochum, M., Brose, U., & Dell, A. I. (2015). Body size and the behavioral ecology of insects: Linking individuals to ecological communities. *Current Opinion in Insect Science, 9*, 24–30. https://doi.org/10.1016/j.cois.2015.04.017

Kebede, L. M., Garbaba, C. A., Kuyu, C. G., Atnafu, B., & Mendesil, E. (2024). Evaluation of the performance of

maize storage facilities for control of storage insect pests in Ethiopia. *Journal of Stored Products Research, 107*, 102336. https://doi.org/10.1016/j.jspr.2024.102336

Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources, 11*(2), 353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x

Klingenberg, C. P. (2016). Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution, 226*(3), 113–137. https://doi.org/10.1007/s00427-016-0539-2

Koyama, T., & Mirth, C. K. (2018). Unravelling the diversity of mechanisms through which nutrition regulates body size in insects. *Current Opinion in Insect Science, 25*, 1–8. https://doi.org/10.1016/j.cois.2017.11.002

Krishnamoorthy, K., & Lee, M. (2014). Improved tests for the equality of normal coefficients of variation. *Computational Statistics, 29*(1), 215–232. https://doi.org/10.1007/s00180-013-0445-2

Kumar, D., & Kalita, P. (2017). Reducing postharvest losses during storage of grain crops to strengthen food security in developing countries. *Foods, 6*(1), Article 8. https://doi.org/10.3390/foods6010008

Liba, T., Zhu, K. Y., & Scheff, D. S. (2026). Evaluating the Long-Term Efficacy of Four Active Ingredients Against *Rhyzopertha dominica* (F.)(Coleoptera: Bostrichidae) and *Sitophilus oryza*e (L.)(Coleoptera: Curculionidae) on Stored Sorghum in the United States. *Insects*, *17*(3), 273. https://doi.org/10.3390/insects17030273

Lim, C. S. H., & Lim, S. L. (2013). Ferric reducing capacity versus ferric reducing antioxidant power for measuring total antioxidant capacity. *Laboratory Medicine, 44*(1), 51–55. https://doi.org/10.1309/LM93W7KTFNPZIXRR

Longstaff, B. C. (1981). Biology of the grain pest species of the genus *Sitophilus* (Coleoptera: Curculionidae): A critical review. *Protection Ecology, 3*, 83–130.

Margus, A., Piiroinen, S., Lehmann, P., Tikka, S., Karvanen, J., & Lindström, L. (2019). Sublethal pyrethroid insecticide exposure carries positive fitness effects over generations in a pest insect. *Scientific Reports, 9*, Article 11320. https://doi.org/10.1038/s41598-019-47473-1

Martono, Y., & Muninggar, J. (2020). Optimization infusion condition on flavonoid and antioxidant activity of herb beverages using response surface methodology. *IOP Conference Series: Materials Science and Engineering, 959*(1), 012029. https://doi.org/10.1088/1757-899X/959/1/012029

Marwick, B., & Krishnamoorthy, K. (2019). *cvequality: Tests for the equality of coefficients of variation from multiple groups* (Version 0.3.1) [Computer software]. https://CRAN.R-project.org/package=cvequality

Mitteroecker, P., & Gunz, P. (2009). Advances in geometric morphometrics. *Evolutionary Biology, 36*(2), 235–247. https://doi.org/10.1007/s11692-009-9055-x

Mlyneková, Z., & Čerešňáková, Z. (2013). Degradation of starch and crude protein in dent and dent × flint maize hybrids in different stages of maturity. *Slovak Journal of Animal Science, 46*(2), 61–67.

Nijhout, H. F., Davidowitz, G., & Roff, D. A. (2006). A quantitative analysis of the mechanism that controls body size in *Manduca sexta*. *Journal of Biology, 5*(5), Article 16. https://doi.org/10.1186/jbiol43

Nijhout, H. F., Riddiford, L. M., Mirth, C., Shingleton, A. W., Suzuki, Y., & Callier, V. (2014). The developmental control of size in insects. *Wiley Interdisciplinary Reviews: Developmental Biology, 3*(1), 113–134. https://doi.org/10.1002/wdev.124

Nylin, S., & Gotthard, K. (1998). Plasticity in life-history traits. *Annual Review of Entomology, 43*, 63–83. https://doi.org/10.1146/annurev.ento.43.1.63

Park, J., Kim, D., Yang, J., Yu, J.-W., Song, M.-H., Lee, J.-H., Choi, E.-S., Lee, J.-H., Kim, B.-S., & Lee, S.-E. (2025). Metabolomic and partial proteomic analyses of phosphine resistance in *Sitophilus oryzae* adults: Significant reduction in body weight after acquiring resistance. *Pesticide Biochemistry and Physiology, 213*, 106549. https://doi.org/10.1016/j.pestbp.2025.106549

Prasad, G., Babu, K. S., Sreedhar, M., Padmaja, P. G., Subbarayudu, B., Kalaisekar, A., & Patil, J. V. (2015). Resistance in sorghum to *Sitophilus oryzae* (L.) and its association with grain parameters. *Phytoparasitica, 43*(3), 391–399. https://doi.org/10.1007/s12600-015-0458-1

Prasad, G., Biswal, L., Parija, S., Sasmal, A., Gupta, A. K., & Khulbe, D. (2025). Biology and morphological analysis of rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) on different stored cereals. *Entomon, 50*(4), 423–430. https://doi.org/10.33307/entomon.v50i4.1579

Ramputh, A., Teshome, A., Bergvinson, D. J., Nozzolillo, C., & Arnason, J. T. (1999). Soluble phenolic content as an indicator of sorghum grain resistance to *Sitophilus oryzae* (Coleoptera: Curculionidae). *Journal of Stored Products Research, 35*(1), 57–64. https://doi.org/10.1016/S0022-474X(98)00030-7

Ranum, P., Peña-Rosas, J. P., & García-Casal, M. N. (2014). Global maize production, utilization, and consumption. *Annals of the New York Academy of Sciences, 1312*(1), 105–112. https://doi.org/10.1111/nyas.12396

Reddy, K. P., Singh, B. U., & Reddy, K. D. (2002). Sorghum resistance to the rice weevil, *Sitophilus oryzae* (L.): Antixenosis. *International Journal of Tropical Insect Science, 22*(1), 9–19. https://doi.org/10.1017/S1742758400015010

Rees, D. (2004). *Insects of stored products*. CSIRO Publishing. https://doi.org/10.1071/9780643101128

Rohlf, F. J. (2006). *tpsDig* (Version 2.05) [Computer software]. Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf, F. J., & Slice, D. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology, 39*(1), 40–59. https://doi.org/10.2307/2992207

Russell, M. P. (1966). Effects of four sorghum varieties on the longevity of the lesser rice weevil, *Sitophilus oryzae* (L.). *Journal of Stored Products Research, 2*(1), 75–79. https://doi.org/10.1016/0022-474X(66)90042-7

Saastamoinen, M., Ikonen, S., Wong, S. C., Lehtonen, R., & Hanski, I. (2013). Plastic larval development in a butterfly has complex environmental and genetic causes and

consequences for population dynamics. *Journal of Animal Ecology, 82*(3), 529–539. https://doi.org/10.1111/1365-2656.12034

Shakthi, V. V., Santhanambika, M. S., & Maheswari, G. (2025). Quantitative morphometric analysis of *Sitophilus* species for accurate species identification in stored grain ecosystems. *Journal of Stored Products Research, 114*, 102787. https://doi.org/10.1016/j.jspr.2025.102787

Stefanazzi, N., Stadler, T., & Ferrero, A. (2011). Composition and toxic, repellent and feeding deterrent activity of essential oils against the stored-grain pests *Tribolium castaneum* (Coleoptera: Tenebrionidae) and *Sitophilus oryzae* (Coleoptera: Curculionidae). *Pest Management Science, 67*(6), 639–646. https://doi.org/10.1002/ps.2102

Thakkar, B., & Parikh, P. (2018). Effects of host grains on the rice weevil, *Sitophilus oryzae* (L.). *Indian Journal of Entomology, 80*(4), 1427–1430. https://doi.org/10.5958/0974-8172.2018.00300.0

Trematerra, P. (2013). Aspects related to decision support tools and integrated pest management in food chains. *Food Control, 34*(2), 733–742. https://doi.org/10.1016/j.foodcont.2013.06.020

U.S. Department of Agriculture, Foreign Agricultural Service. (2025). *Production—Wheat: Commodity: Wheat* [Data set]. Retrieved February 12, 2026, from https://www.fas.usda.gov/

Ungsunantwiwat, A., & Mills, R. B. (1985). Influence of rearing medium on size and weight of adults of four *Sitophilus* populations and on weight loss of host kernels (Coleoptera: Curculionidae). *Journal of Stored Products Research, 21*(2), 89–93. https://doi.org/10.1016/0022-474X(85)90027-X

Webster, M., & Sheets, H. D. (2010). A practical introduction to landmark-based geometric morphometrics. *The Paleontological Society Papers, 16*, 163–188. https://doi.org/10.1017/S1089332600001868

Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2012). *Geometric morphometrics for biologists: A primer* (2nd ed.). Academic Press.

Uticaj promene domaćina na veličinu tela pirinčanog žiška (*Sitophilus oryzae* L.): studija na pšenici, kukuruzu i sirku

Jelena Ačanski · Marko Radenković · Dejan Prvulović · Marija Stajić · Aleksandra Ilić · Anja Dolapčev Rakić · Sonja Gvozdenac

Sažetak: Pirinčani žižak (*Sitophilus oryzae* L.) je jedna od ekonomski najznačajnijih štetočina uskladištenih žitarica u svetu. Izuzetno je polifagna vrsta, ali ishrana na semenima nekih biljnih vrsta dovodi do promenama u morfološkim karakteristikama jedinki. Dosadašnja istraživanja bila su uglavnom usmerena na preživljavanje, brojnost potomstva i dužinu razvića. Veličina tela kao pokazatelj razvojnog stresa znatno je manje proučavana prema dostupnoj literaturi. Cilj ovog istraživanja bio je da utvrdi da li veličina centroida (CS), određena primenom geometrijske morfometrije, odražava uticaj pomene biljke domaćina (semena). Praktično da li se uočene promene u veličini imaga mogu povezati sa nutritivnim i morfoloskim osobinama semena. Populacija izvorno gajena na pšenici podeljena je u tri eksperimentalne grupe: gajenje je nastavljeno na pšenici kao kontrolnoj grupi, dok su preostale dve grupe preusmerene na kukuruz i sirak. Nakon toga analizirani su brojnost i veličina tela potomstva. Jedinke razvijene na kukuruzu bile su statistički značajno manje u odnosu na jedinke sa pšenice, iako brojnost potomstva nije pokazala značajne razlike. Na semenu sirka je registrovan značajno manji broj potomaka, ali nije utvrđen značajan uticaj na veličinu tela. Fenotipska varijabilnost centroidne veličine bila je najveća u populaciji sa kukuruza. Rezultati Partial Least Squares analize dva bloka pokazali su da je veličina tela pozitivno korelisana sa većim sadržajem proteina u semenu. Tvrdoća semena i viši sadržaj ukupnih fenolnih jedinjenja, uključujući flavonoide i tanine, su negativno korelisani sa centroidnom veličinom. Dobijeni rezultati ukazuju da veličina tela predstavlja značajan pokazatelj razvojnih odgovora na stres pirinčanog žiška. Takođe, naglašava značaj integracije ovog parametra u istraživanja u cilju sticanja potpunijih razvojnih odgovora pirinčanog žiška na promenu biljke domaćina i druge stresore, kao i prepoznavanje osobina domaćina koje negativno utiču na uspešnost razvoja štetočine.

Ključne reči: centroidna veličina, osobine semena, parcijalna analiza najmanjih kvadrata, promena domaćina, razvojna plastičnost, razvojni stres, skladišne štetočine, veličina tela