Suitability of three different legumes for Acanthoscelides obtectus development and population growth

Pogodnost tri različite vrste leguminoza za razviće i rast populacije Acanthoscelides obtectus

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ABSTRACT

Legumes are a rich source of valuable nutrients thus represent important component in human and animal nutrition. The most important and often a limiting factor in legume production is the presence of seed pests, such as the bean weevil *Acanthoscelides obtectus* (Say, 1831). This work tested the suitability of three different legume species (common bean, faba bean and grass pea), the species with a growing interest in the human diet, for the development of the bean weevil, aiming to provide a reliable forecast of its population growth. After four months, been weevils consumed the highest percentage of the common bean kernels (70.79%), followed by the grass pea (53.13%), and faba bean (0.42%). The progeny production and population growth were significantly affected by the tested legume species. After each month, the total number of adults was the highest on the common bean, indicating its best suitability for the weevil's development. Based on the number of the emerged specimens after each month of the observation, the bean weevil development was unhampered and continuous also on the grass pea. The lowest number of emerged adults, in all observation periods, was in faba bean, indicating its low preference and suitability for the weevil's development. The population growth of the bean weevil was the highest on the common bean, followed by grass pea, and it fitted best to the quadratic equation model that enabled the prediction of the population growth of the bean weevil for each legume species in the next generations.

Keywords: bean weevil, common bean, faba bean, grass pea, population growth, modelling

SAŽETAK

Leguminoze su višestruko značajne, jer predstavljaju dragocen izvor različitih nutrijenata u ljudskoj i životinjskoj ishrani. Njihovim uzgojem doprinosi se raznolikosti agroekosistema i pozicioniraju se kao klimatski prilagodljiv usev. Najvažniji ograničavajući faktor u proizvodnji leguminoza predstavljaju štetotočine zrna (semena), poput pasuljevog žiška *Acanthoscelides obtectus* (Say, 1831). U ovom radu ispitana je pogodnost tri različite leguminoze (pasulj, sastrica i bob) sa rastućom popularnošću u ljudskoj ishrani, za razviće i rast populacije pasuljevog žiška. S ciljem utvrđivanja pouzdanog modela za prognozu populacijskog rasta štetočine, rezultati su korišćeni u matematičkom modelovanju. Istraživanja pokazuju da je, posle četiri meseca, zrno pasulja konzumirano u najvišem procentu (70,79%), manje sastrice (53,13%) i najmanje zrna boba (0,42%). Na produkciju potomstva i rast populacije statistički značajno je uticala vrsta leguminoze u ishrani. Ukupan broj eklodiralih imaga, na kraju svakog meseca u eksperimentalnom periodu, bio je najveći

na pasulju, što pokazuje pogodnost ove biljke hraniteljke za razviće insekta. Eklozija imaga ukazuje da je razviće moguće i na sastrici. Najmanji broj imaga je eklodirao na zrnima boba, što ukazuje na nisku preferentnost i nepogodnost za razviće ovog insekta. Rast populacije žiška najintenzivniji je na pasulju, pa na sastrici, što je u potpunosti podržano kvadratnim regresionim modelom, koji omogućava prognozu rasta populacije pasuljevog žiška u svakoj narednoj generaciji.

Ključne riječi: pasuljev žižak, pasulj, bob, sastrica, rast populacije, modelovanje

INTRODUCTION

The legume family is globally distributed and highly diverse, with about 19,000 species (Azani, 2017). Their significant role in total agricultural turnover has been corroborated by growing production and area under cultivation. Common bean (Phaseolus vulgaris L.) is among the most important crops for human consumption. It is rich in healthy proteins, starch, fibers and minerals (especially iron and zinc), which are becoming more and more deficient in the modern human diet. For people in less industrialized countries various legume species are often the only source of these nutrients (Broughton et al., 2003). In Serbia, common bean was grown as a sole crop on 8.512 ha in 2020 (Vasić et al., 2021), and its production manly relies on modern cultivars. However, people in marginal and rural areas still grow and maintain landraces for personal consumption (Savić et al., 2020). Besides common bean, the legumes faba bean (Vicia faba L.) and grass pea (Lathyrus sativus L.) were also traditionally grown in local communities, with no available official data. However, these two species are designated as less cultivated and neglected, although an effort is being made towards their reintroduction incrop production. Faba bean in particular, is regaining its place in human and animal nutrition worldwide as a result of rich protein, carbohydrates, dietary fibers and micronutrient contents (Mulualem et al., 2012). Compared to common bean, faba bean and grass pea intended for human nutrition are mainly grown in family home gardens. Moreover, these two species are being recognized by the producers and consumers for their preserved medicinal value, as well as better tolerance to adverse environments (Ramya et al., 2022; Multari et al., 2015). Therefore, they are important components in sustainable and diversified cropping systems, but, also, they can be considered climate smart crops (Kopke and Nemecek, 2010; Pathania et al., 2014).

Unfortunately, legume production is often hampered and limited by insect pests, and major losses are caused by the bean weevil, Acanthoscelides obtectus (Say, 1813) (Coleoptera: Chrysomelidae: Bruchinae). A. obtectus infests different hosts in the field and storages (Thakur and Renuka, 2014; Vera-Graziano and Cruz-Izquierdo, 2016; Njoroge et al., 2017; Vuts et al., 2018). However, its populations are commonly detected in legume storages because their life cycle is well adapted for reproduction in a closed environment (Nascimento et al., 2020). A. obtectus larvae feed inside kernels and cause losses often higher than 30% (Pemonge et al., 1997). Therefore, they inflict quantitative damage by reducing seed weight and/or volume, as well as qualitative losses by reducing physiological quality and germination capacity, increasing temperature and moisture content in a seed bulk, and spoiling the seed's purines with insect residues and excrements (Faroni et al., 2006). This species can complete its entire life cycle on dry beans in storages without returning to the field (Labeyrie, 1962). The authors report severe damage on both Phaseolus vulgaris L. and P. lunatus L. in Africa (Nchimbi-Msolla and Misangu, 2002; Paul et al., 2009), Australia (Bailey, 2007), Europe (Schmale et al., 2002, Alvarez et al., 2005), America (Kingsolver, 2004; Romero-Napoles, 2010), the Mediterranean area (Regnault-Roger et al., 2004; Ayvaz et al., 2010) and some other regions of the world (Southgate, 1979). A. obtectus may adapt to different legume species: a) its host plant, i.e. common bean; b) non-host plants, i.e. Vigna unguiculata Walp., Cicer arietinum L. and Vicia faba L. (Hamraouiand and Regnault-Roger, 1995). Also, it causes the destruction of stored runner beans, Phaseolus coccineus L., lima beans, Ph. lunatus, cow peas, V. unguiculata, chickpeas, C. arietinum, and other stored pulses worldwide (Larson and Fisher, 1938; Schoonhoven et al., 1983).

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Investigations of A. obtectus began back in 1919, although its significance was first recorded in 1938 by Larson and Fisher (1938). Larson and Fisher (1938) emphasided that wherever common bean (Ph. vulgaris), lima bean (Ph. lunatus macrocarpus Benth.), and cowpea (Vigna sinensis (Torner) Savi.) varieties were grown, seed losses occurred, and damage caused by this weevil was usually visible as seed injuries. The first researches were focused on systematics, biology, ecology and control (Săvescu, 1961; Beratlief, 1978; Săpunaru and Pricop, 1997), forecast and signalisation methods for this pest (Săvescu, 1978; lacob, 1980), and its biological control (Săpunaru et al., 2006). Even though there are many studies on A. obtectus bionomy and ecology, research on weevil preference, concurrent (simultaneous) development and population growth on different legumes is lacking. In recent research, Savković et al. (2019) evaluated potential of A. obtectus to invade and sustain population growth on two suboptimal host plants, chickpeas and mung beans. However, several questions are still pending. How wide is actually the host range of the A. obtectus? Which factors associated with seed quality facilitate its survival and development? And, do unsuitable hosts still enable the development and population growth of this weevil?

This work tested the suitability of three different legumes (common bean, faba bean, and grass pea), of growing interest in the human diet, for the development and population growth of *A. obtectus*, with the main goal of providing a reliable forecast of its population growth.

MATERIAL AND METHODS

The development of the A. *obtectus* and its population growth on three different legume species (common bean, faba bean, and grass pea) were studied in a "no-choice" test under laboratory conditions. The accessions chosen for the study were typical representatives of each legume species (typical seed weights, shapes, and colors within the respective species). Seeds were not treated with pesticides prior to the experiment but were exposed to -80 °C for 30 min to eliminate potential contamination with fungi and infestation with insects and mites.

The laboratory population of A. obtectus used in this research was reared under laboratory conditions in glass jars (5 L), on the common bean variety 'Belko' (a commercial variety created by the Institute of Field and Vegetable Crops, Novi Sad, Serbia), at a constant temperature of 26 ± 2 °C and a relative humidity of 50%, under a light regime of 16:8 (day/night), as described by Szentesi (1972). Newly emerged adults (60 specimens per jar) were placed in separate jars on common bean, faba bean and grass pea seeds and were allowed to develop for four months (120 days) on the pre-measured amount (200 g) of each legume species. Seed weight was measured on an electronic scale (Kern & SOHN GmbH, Germany), with a precision of 0.01 g. The jars with weevils were incubated in a climatic chamber during the entire experiment, under the same conditions as for the rearing of the parental population. After each month, the number of newly emerged weevils was counted, and they were allowed to develop further. After four months (120 days), seed damage was estimated based on the amount of consumed kernels/seeds (g and %), and also the final population density was estimated.

The results were expressed as the percentage of consumed kernels. It was determined for each legume species after the final weighing at the end of the emergence period (four months) using the following formula:

$$LM = Mi - \frac{Mf}{Mi} \times 100$$

LM = weight loss (%), Mi = initial weight (g), Mf = final weight (g).

We performed an experiment in a completely randomized design with 4 replicates.

Data on the total number of emerged insects per legume species and after each month, consumed grain weight (g), and percentage of consumed grain (%) as well as the number of emerged beetles (progeny production) were subjected to a one-way ANOVA, and the corresponding means were compared by Duncan's multiple range test (with a 0.05 significance level) using the SPSS software (SPSS, 2017). Data on the number of emerged weevils after each month were analyzed using several regression models (linear, quadratic, and exponential) in order to determine the best fit that would predict the population growth of *A. obtectus*.

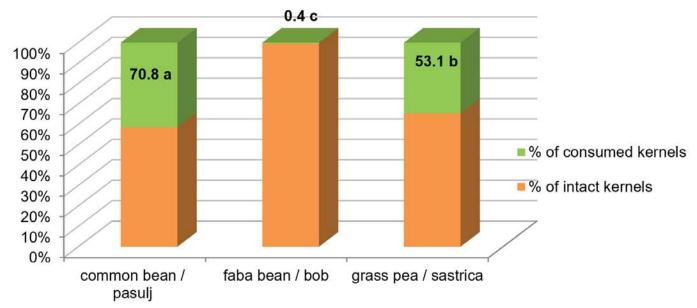
RESULTS

The highest percentage of consumed kernels was on common bean, on average 70.79% after four months, followed by significantly lower seed consumption on grass pea (53.13%). The lowest percentage of consumed kernels was recorded on faba bean, only 0.42% in four months. The difference between the percentage of consumed kernels among tested legume seeds, common bean, faba bean and grass pea, was statistically highly significant ($F_{2.12}$ =849.6^{**}, P<0.001) (Figure 1).

The progeny production (the number of emerged beetles) and population growth of *A. obtectus* were significantly affected by the legume species on which the feeding and development occurred (Table 1). The number of emerged adults differed significantly among the legume species after each observation month (1-4) (*P*<0.000; Table 1). On common bean and grass pea, significantly

higher numbers of weevils emerged, regardless of the observation period. On common bean, the average number of specimens increased from one observation to the next, and was 83.0 after the 1st month, 251.5 after the 2nd, 762.3 after the 3rd and 1193.3 after the 4th month. On the grass pea, the average number of weevil specimens was 80.0, 191.7, 633.5 and 1007.4, respectively. Nevertheless, the total number of emerged adults did not significantly differ between the common bean and grass pea, after the 1st month, but it was significantly different after two, three and four months of observation (Table 1). The lowest total number of emerged *A. obtectus*, regardless of the observation period, was on faba bean: 12.0 after the 1st month, 68.0 after the 2nd, 103.0 after the 3rd and 175.3 after the 4th month.

The data on the number of emerged beetles after each month were fitted in the regression analysis, using different models. The quadratic equation was proven to be the best fit for the population growth of *A. obtectus*, on all three legume species. The results of the regression analysis fit, including the regression equations of *A. obtectus* population growth on the seeds of all three legume species, are presented in Figures 2-4.



Mean values differ significantly thus are marked with different letters; Different letters represent different levels of significance

Figure 1. Percentage of consumed and intact legume kernels after four months

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Legume species	1 month	2 months	3 months	4 months
Beans	83.0 ± 2.4^{a}	251.5 ± 12.1ª	762.3 ± 39.8ª	1193.3 ± 55.8ª
Faba bean	$12.0 \pm 8,1^{b}$	68.0 ± 11.3°	103.0 ± 15.1°	175.3 ± 25.1°
Grass pea	$80.0 \pm 6,5^{\circ}$	$191.7 \pm 17.5^{\text{b}}$	633.5 ± 20.9 ^b	$1007.4 \pm 43.4^{\text{b}}$
<i>F</i> value	261.5**	507.1**	851.2**	3067.9**
<i>P</i> value	0.001	0.000	0.000	0.000

Table 1. Number of emerged A. obtectus beetles on different legumes after one, two, three and four months

Values represent mean number of newly emerged beetles \pm SD; Values with the same letters are at the same level of significance between the rows (legume species); ** - P<0.01

Based on the results presented in Figures 2–4, the population growth of *A. obtectus* on all three legume species, as mentioned above, best fitted the quadratic equation $(65.625x^2 + 56.025x + 59.75)$. The regression equations enabled the calculation of the population growth of *A. obtectus* when reared on the legume species tested. The models for prediction of population growth obtained for all three legumes are highly reliable, since the determination coefficient (R²) was very high and ranged from 0.985 to 0.988. These coefficients indicate that the statistical models presented can predict the outcome (population growth in this case) with certainty ranging from 98.5 to 98.9%.

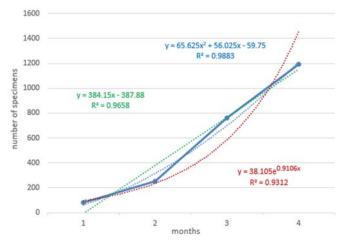


Figure 2. Population growth of *A. obtectus* on common bean (dash curves on the graph represent fitted linear (green), quadric (blue) and exponential (red) regression curves, with corresponding equations; blue line represents regression line with data points)

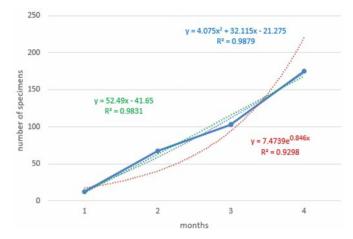


Figure 3. Population growth of *A. obtectus* on faba bean (dash curves on the graph represent fitted linear (green), quadric (blue) and exponential (red) regression curves, with corresponding equations; blue line represents regression line with data points)

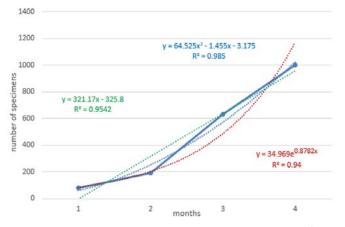


Figure 4. Population growth of *A. obtectus* on grass pea (dash curves on the graph represent fitted linear (green), quadric (blue) and exponential (red) regression curves, with corresponding equations; blue line represents regression line with data points)

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DISCUSSION

This work aimed to assess the suitability of three different legume species (legumes for human nutrition) for the development of the *A. obtectus*, as well as to estimate its population growth, and enable the prediction of its population growth using mathematical models. Early reports on *A. obtectus* host range imply that this species is a seed pest that attacks only *Phaseolus* species and cultivated cowpea, *Vigna* spp. (Larson and Fisher, 1938; Johnson 1981). However, up to now, studies have proved that the range of potential wild and cultivated host species of *A. obtectus* are wider, although it is not entirely explored. Szentesi (2021) divided potential host plants into:

- Hosts (H) plant species that fully support development through generations and regularly harbour natural infestations. For example, in Hungary, there are only two species that fulfil these conditions – the common bean (*Ph. vulgaris*) and the scarlet runner bean (*Ph. coccineus*);
- II) Acceptable non-hosts (ANH) non-recognised species that can be used as suitable substrates for larval development in nature. Their development is asynchronous, both temporally and spatially, with weevil phenology, and thus females can only occasionally use them for progeny production, mainly on seeds in storages. On such hosts, adults may emerge, but developmental time is typically prolonged and larval mortality is high (e.g. chickpea and faba bean) and
- III) Non-hosts (NH) plants that are nutritionally unsuitable or even toxic and that never enable weevil development, although occasional oviposition may occur on seeds in storages.

A. obtectus is an oligophagous species feeding on plant species belonging to the tribe Phaseoleae (Fabaceae), which comprises the genera *Phaseolus*, *Glycine*, *Lablab* and *Vigna* (Szentesi, 2020). Occasional reports exist on the weevil occurrence on other legume species, such as lupine (tribe Genisteae), chickpea (Cicereae), within species of *Vicia* genus, lentils and *Lathyrus* species (Fabeae) (Jermy and Szentesi, 1978; Jarry and Bonet, 1982; Hamraoui and Regnault-Roger, 1995). On the seeds of preferred hosts, under favourable conditions, practically every larva becomes an adult, but on NH or even ANH seeds, such as faba beans, only a very small percentage of larvae reach maturity (Larson and Fisher, 1938). Our results are in accordance with these findings taking into consideration that the lowest number of adults emerged from faba bean seeds, regardless of the observation period (1–4 months), and the population growth was the lowest throughout the experiment.

The studies on the preference-performance of a wide range of bean weevil host and non-host species are missing due to the usually narrow host specialisation of all bruchids including A. obtectus (Janzen, 1977; Johnson, 1989). Nevertheless, A. obtectus, along with several other bruchid species, can develop and reproduce under stored conditions on leguminous seeds, as was proven in practice. This provides a scope of possibilities to study the host specificity, as was done in this work. In this work, the number of emerged A. obtectus adults and the population growth after each observation month were statistically significantly lower on faba beans than on common beans and grass peas. This is in accordance with the reports of Szentesi (2021). The author found that bruchid females deposited a decreasing number of eggs on the seeds of different legumes, in the following order: H, ANH and NH. Not surprisingly, A. obtectus oviposition was the highest on the members of the tribe Phaseoleae, as was the case in our work, although nonhost species like faba bean are known as occasional hosts. Significantly more adults emerged from H species than from ANH species or NH species, which was also proven in this work, where the highest number of adult weevils emerged from common bean, in comparison to grass pea and, particularly, faba bean. Besides the Phaseolus species, occasional infestations are possible and present in storages on garden pea or faba bean (Szentesi, pers. comm.); therefore, our work supports these results, since the weevil continued its development on faba bean seeds, although in lower numbers.

In a study performed by Szentesi (2020), common bean was a host that provided a better preference/ performance ratio, as was also previously confirmed by Leroi and Jarry (1981). Several authors (Johnson, 1989; Zhang and Liu 2006; Cronin and Abrahamson, 2001) noted that some species belonging to the ANH group, such as Vicia (faba bean included) and Lathyrus spp. (grass pea included), allowed larval development at some extent. However, the seeds of the genus Lathyrus were more preferent and suitable for A. obtectus development, while the development was much lower on the seeds of Vicia species, as was also proven in our work. Savković et al. (2019) estimated the invading potential and assessed the population dynamics of A. obtectus during an experimentally induced host-shift. The authors aimed to determine if beetles, reared on their optimal host, change their oviposition behaviour when placed on an alternative host in no-choice experiments, which represents the first phase of potential host shifts in storages. The results presented by Savković et al. (2019) showed a slight decrease in population growth on new hosts, nonetheless beetles managed to secure survival of their populations on chickpeas and mung beans as alternative seeds.

We can speculate that lower A. obtectus development and progeny production on faba bean was due to biochemical characteristics as well as seed coat thickness. Based on Bleiler et al. (1988), Mitri et al. (2009) results and Szentesi pers. comm., the levels of canavanine can represent a significant factor or a primary plant weapon influencing the survival of A. obtectus in NH Vicia seeds, even though the larvae expressed a significant tolerance to this compound. However, some other toxic compounds occur in many legume species and in combination with other chemical groups they form the chemical resistance profile of a seed (Thiery, 1984). In the present study, we considered only the legume species as a factor that may affect preference-performance relationship. Other important factors (biochemistry of a seed, physical properties, environmental conditions, life-history traits, species mobility, host genotype, etc.) which may also influence the host selection (Larsson and Ekbom, 1995; Cronin and Abrahamson, 2001; de la Masselière et al., 2017) were not investigated and will be the subject of further investigations.

CONCLUSION

The results of this work show that A. obtectus, after four months, consumed the highest percentage of common bean kernels, followed by grass pea, while the percentage of consumed faba bean kernels was statistically the lowest. The progeny production and population growth of A. obtectus was significantly affected by the legume species. According to the data obtained (the highest adult emergence), common bean was the most suitable feeding and reproductive host. The data obtained indicated that the development was concurrent also on grass pea. On the other hand, faba bean kernels exhibited a low feeding preference and proved to be an unsuitable substrate/host for A. obtectus development. The population growth of the A. obtectus was the highest on common bean, followed by grass pea, and it fitted best to the quadratic equation model, which enabled the prediction of the population growth of A. obtectus for each legume species in the next generation and/or month.

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REFERENCES

Alvarez, N., Hossaert-McKey, M., Rasplus, J.Y., McKey, D., Mercier, L., Soldati, L., Aebi, A., Shani, T., Benrey, B. (2005) Sibling species of bean bruchids: A morphological and phylogenetic study of *Acanthoscelides obtectus* Say and *Acanthoscelides obvelatus* Bridwell. Journal of Zoological Systematics and Evolutionary Research, 43, 29–37.

DOI: https://doi.org/10.1111/j.1439-0469.2004.00286.x

Ayvaz, A., Sagdic, O., Karaborklu, S., Ozturk, I. (2010) Insecticidal activity of the essential oils from different plants against three storedproduct insects. Journal of Insect Science, 10, 21. DOI: <u>https://doi.org/10.1673/031.010.2101</u>

Azani, N., Babineau, M., Bailey, C.D., Banks, H., Barbosa, A.R., Pinto, R.B., Bruneau, A. (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny The Legume Phylogeny Working Group (LPWG). Taxon, 66, 44–77.

- Bailey, P.T. (2007) Pests of Field Crops and Pastures: Identification and Control. CSIRO Publishing, Collingwood, VIC 3066, Australia, pp, 456
- Beratlief, C. (1978) New methods for controlling the pests from storehouses. Agricultural Library of Bucharest.
- Bleiler, A.J., Rosenthal, G.A., Janzen, D.H. (1988) Biochemical Ecology of Canavanine-Eating Seed Predators. Ecology, 69 (2), 427–433.
- Broughton, W.J., Hernandez, G., Blair, M., Beebe, S., Gepts, P., Vanderleyden, J. (2003). Beans (*Phaseolus* spp.) – Model food legumes. Plant and Soil, 252, 55–128.

DOI: https://doi.org/10.1023/A:1024146710611

Chittenden, F.H. (1899) Insects Injurious to Beans and Peas. U. S. Department of Agriculture, Yearbook 1898, 233–260, illus.

Cronin, J.T., Abrahamson, W.G. (2001) Goldenrod stem galler preference and performance: effects of multiple herbivores and plant genotypes. Oecologia, 127 (1), 87–96. DOI: https://doi.org/10.1007/s004420000561

- De la Masselière, C., Facon, B.M., Hafsi, A., Duyck, P.F. (2017) Diet breadth modulates preference - performance relationships in a phytophagous insect community. Scientific Reports, 7, 16934.
- Faroni, L.R.A., Sousa, A.H. (2006) Aspectos Biologicos e Taxonomicos dos Principais Insetos-Praga de Produtos Armazenados. In: Almeida, F.A.C., Duarte, M.E.M, Mata, M.E.R.M.C., eds. Tecnologia de Armazenagem em Sementes, UFCG, Campina Grande, Brazil, pp, 371–402.
- Hamraoui, A., Regnault-Roger, C. (1995) Oviposition and larval growth of *Acanthoscelides obtectus* Say (Col., Bruchidae) in regard to host and non-host plants from Leguminosae family. Journal of Applied Entomology, 119, 195–99.

DOI: https://doi.org/10.1111/j.1439-0418.1995.tb01269.x

- lacob N. (1980) Economic damaging limits in integrated control of main pests from crops. Vegetal Production. Cereale și plante tehnice, 4, Bucharest.
- Janzen, D.H. (1977) How southern cowpea weevil larvae (Bruchidae: *Callosobruchus maculatus*) die on nonhost seeds. Ecology, 58, 921–927.
- Jarry, M., Bonet, A. (1982) La bruche du haricot, Acanthoscelides obtectus Say (Coleoptera, Bruchidae), est-elle un danger pour le cowpea, Vigna unguiculata (L.) Walp.? Agronomie, 2, (10), 963–968. DOI: https://doi.org/10.1051/agro:19821009

Jermy, T., Szentesi, Á. (1978) The role of inhibitory stimuli in the choice of oviposition site by phytophagous insects. Entomologia Experimentalis et Applicata, 24, 458–71.

DOI: https://doi.org/10.1111/j.1570-7458.1978.tb02806.x

- Johnson, C.D. (1981) Seed beetle host specificity and systematics of the Leguminosae. In: Polhill, R.M., Raven, P.H., eds. Advances in legume systematics. Royal Botanical Gardens Kew, pp. 995–1027.
- Johnson, C.D. (1989) Adaptive radiation of Acanthoscelides in seeds: examples of legume-bruchid interactions. In: Stirton, C.H., Zarucchi, J.L., eds. Advances in legume biology. Missouri Botanical Garden, 29. pp. 755- 780.

Kingsolver, J.M., (2004) Handbook of the bruchidae of the United States and Canada (Insecta, Coleoptera). Vols. 1 & 2, Technical Bulletin 1912, U.S. Department of Agriculture, USA, 1–524. Kopke U., Nemecek, T. (2010) Ecological services of faba bean. Field Crops Research, 115, 217–233.

DOI: https://doi.org/10.1016/j.fcr.2009.10.012 Labeyrie, V., (1962) Les Acanthoscelides. In: Balachowsky, A.S., ed.

- Entomologie Appliquee a l'Agriculture, Volume 1: Traite, Masson, Paris, France, 469-490.
- Larson, A. O., Fisher, C. K. (1938) The bean weevil and the southern cowpea weevil in California. U.S. Department of Agriculture Technical Bulletin, 593, 1–170.
- Larsson, S., Ekbom, B. (1995) Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plants. Oikos, 72, 155–60.
- Leroi, B., Jarry, M. (1981) Relations d'*Acanthoscelides obtectus* ave différentes espèces de *Phaseolus*: influence sur la fécondité et possibilités de développement larvaire. Entomologia experimentalis et applicate, 30, 73–82.

DOI: https://doi.org/10.1111/j.1570-7458.1981.tb03587.x

- Mitri, C., Soustelle, L., Framery, B., Bockaert, J., Parmentier, M. L., Grau,
 Y. (2009) Plant insecticide L-canavanine repels Drosophila via the insect orphan GPCR DmX. PLoS biology, 7(6), e1000147.
 DOI: https://doi.org/10.1371/journal.pbio.1000147
- Multari, A., Stewart, D., Russell, W.R. (2015) Potential of fava bean as future protein supply to partially replace meat intake in the human diet. Comprehensive Reviews in Food Science and Food Safety, 14 (5), 511–522.
- Mulualem, T., Dessalegn, T., Dessalegn, Y. (2012) Participatory varietal selection of faba bean (*Vicia faba* L.) for yield and yield components in Dabat district. Ethiopia. Wudpecker Journal of Agricultural Research, 1 (7), 270–274.
- Nascimento, J.M., Lopez, M.L., Rocha, J.F., dos Santos V.B., de Sousa, A.H. (2020) Population Development of Bean Weevils (Coleoptera: Chrysomelidae: Bruchinae) in Landrace Varieties of Cowpeas and Common Beans. The Florida Entomologist, 103 (2), 215–220.
- Nchimbi-Msolla, S., Misangu, R.N. (2002) Seasonal distribution of common bean (*Phaseolus vulgaris* L.) bruchid species in selected areas in Tanzania. Proceedings of the Bean Seed Workshop, January 12-14, 2002, Arusha, Tanzania, 1-5.
- Njoroge, A.W., Affognon, H., Mutungi, C., Richter, U., Hensel, O., Rohde, B., Mankin, R.W. (2017) Bioacoustics of *Acanthoscelides obtectus* (Coleoptera: Chrysomelidae: Bruchinae) on *Phaseolus vulgaris* (Fabaceae). Florida Entomologist, 100, 109–115.
- Pathania A., Sharma S.K., Sharma P.N. (2014) Common bean. In: Singh M., Bisht I., Dutta M., eds. Broadening the Genetic Base of Grain Legumes. Springer, New Delhi.
- Paul, U.V., Lossini, J.S., Edwards, P.J., Hilbeck, A. (2009) Effectiveness of products from four locally grown plants for the management of *Acanthoscelides obtectus* (Say) and *Zabrotes subfasciatus* (Boheman) (both Coleoptera: Bruchidae) in stored beans under laboratory and farm conditions in Northern Tanzania. Journal of Stored Products Research, 45 (2), 97–107.
- Pemonge, J., Pascual-Villalobos, M.J., Regnault-Roger, C. (1997) Effects of material and extracts of *Trigonella foenum-graecum* L. against the stored product pests *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) and *Acanthoscelides obtectus* (Say) (Coleoptera: Bruchidae). Journal of Stored Products Research, 33 (3), 209–217. DOI: https://doi.org/10.1016/S0022-474X(97)00007-6
- Ramya, K.R., Tripathi, K., Pandey, A., Barpete S., Gore, P.G., Raina, A.P., Khawa,r K.M., Swain, N., Sarker, A. (2022) Rediscovering the potential of multifaceted orphan legume grass pea – a sustainable resource with high nutritional values. Frontiers in Nutrition, 8. DOI: https://doi.org/10.3389/fnut.2021.826208

- Regnault-Roger, C., Ribodeau, M., Hamraoui, A., Bareau, I., Blanchard, P., Gil-Munoz, M.I., Barberan, F.T. (2004) Polyphenolic compounds of Mediterranean Lamiaceae and investigation of orientational effects on Acanthoscelides obtectus (Say). Journal of Stored Products Research, 40, 395–408.
- Romero-Napoles, J. (2010) A new species of *Acanthoscelides Schilsky*, 1905 (Coleoptera: Bruchidae) from Nuevo Leon, Mexico, with a key to the obtectus species-group. Coleopterists Bulletin, 64 (2), 125–128.
- Săpunaru, T., Pricop, M. (1997) Studies on the bean weevil (*Acanthoscelides obtectus* Say) biology, ecology and control. Cercetari Agronomice in Moldova 30 (1), 281–288.
- Săpunaru, T., Filipescu, C., Georgescu T., Bild, Y.C. (2006) Bioecology and Control of Bean Weevil (*Acanthoscelides obtectus* Say.) Cercetări Agronomice în Moldova, 39 (2), 5–12.
- Săvescu, A. (1961) Contribution on the study of biology, ecology and control of bean weevil *Acanthoscelides obtectus* Say. Scientific works. Horticulture-Viticulture. Agrosilvica Publishing House, Bucharest.
- Săvescu A., Rafailă C. (1978) Prognoses in plant protection. Ceres, Bucharest.
- Savić, A., Zorić M., Brdar-Jokanović, M., Zdravković, M., Dimitrijević, M., Petrović, S., Živanov, D., Vasić, M. (2020) Origin and diversity study of local common bean (*Phaseolus vulgaris* L.) germplasm from Serbia: phaseolin and phenotyping approach. Genetic Resources and Crop Evolution, 67 (8), 2195–2212.
- Savković, U., Đorđević, M., Stojković, B. (2019) Potential for Acanthoscelides obtectus to adapt to new hosts seen in laboratory selection experiments. Insects. 29, 10(6), 153. DOI: https://doi.org/10.3390%2Finsects10060153
- Schmale, I., Wackers, F.L., Cardona, C., Dorn, S. (2002) Field infestation of *Phaseolus vulgaris* by *Acanthoscelides obtectus* (Coleoptera: Bruchidae), parasitoid abundance and consequences for storage pest control. Environmental Entomology, 31 (5), 859–863. DOI: https://doi.org/10.1603/0046-225X-31.5.859
- Schoonhoven, A. V., Cardona, C., Valor, J. (1983) Resistance to the bean weevil (Acanthoscelides obtectus) and the Mexican bean weevil (Zabrotes subfasciatus) in noncultivated common bean (Phaseolus vulgaris) accession. Journal of Economic Entomology, 76 (6), 1255– 1259.

- Southgate, P.J., (1979) Biology of the Bruchidae. Annual Review of Entomology, 24, 449–473.
- Szentesi, Á. (1972) Studies on the mass-rearing of *Acanthoscelides obtectus* Say (Col., Bruchidae). Acta Phytopathologica 7, 453–63.
- Szentensi, Á. (2020) How bean weevil (*Acanthoscelides obtectus*, Coleoptera, Bruchinae) larvae die on legume seeds. 18 November 2020, PREPRINT (Version 2) available at Research Square. DOI: https://doi.org/10.21203/rs.3.rs-44834/v2
- Szentesi, Á. (2021) How the seed coat affects the mother's oviposition preference and larval performance in the bean beetle (*Acanthoscelides obtectus*, Coleoptera: Chrysomelidae, Bruchinae) in leguminous species. BMC ecology and evolution, 21 (1), 171. DOI: https://doi.org/10.1186/s12862-021-01892-9
- Thakur, D.R., Renuka, D. (2014) Biology and biointensive management of Acanthoscelides obtectus (Say) (Coleoptera: Chrysomelidae) – a pest of kidney beans worldwide. In: Arthur, F.H., Kengkanpanich, R., Chayaprasert, W., Suthisut, D., eds. Proceedings of the 11th International Working Conference on Stored Product Protection. Department of Agriculture, Ministry of Agriculture and Cooperatives Entomology and Zoology Association of Thailand Thai Phytopathological Society, 115–126.
- Thiery, D. (1984) Hardness of some fabaceous seed coats in relation to larval penetration by *Acanthoscelides obtectus* (Say) (Coleoptera: Bruchidae). Journal of Stored Products Research, 20 (4), 177–81.
- Vasić, M., Šeremešić, S., Marinković, J., Tepić-Horecki, A., Zdravković, M., Ilić, A., Ječmenica, M. (2021) Production and assortment of dry beans in Serbia. Biljni lekar, 49 (6), 729–744.
- Vera-Graziano, J., Cruz-Izquierdo, S. (2016) Insect population parameters of *Acanthoscelides obtectus* (Say.) in grains of five cultivars of common bean (*Phaseolus vulgaris* L.). Agrociencia, 50, 347–353.
- Vuts, J., Woodcock, C.M., Konig, L., Powers, S.J., Pickett, J.A., Szentesi, A., Birkett, M.A. (2018) Host shift induces changes in mate choice of the seed predator *Acanthoscelides obtectus* via altered chemical signalling. PLoS ONE 13(11), e0206144. DOI: https://doi.org/10.1371/journal.pone.0206144
- Zhang, P.J., Liu, S.S. (2006) Experience induces a phytophagous insect to lay eggs on a nonhost plant. Journal of Chemical Ecology, 32 (4), 745–53. DOI: https://doi.org/10.1007/s10886-006-9032-0