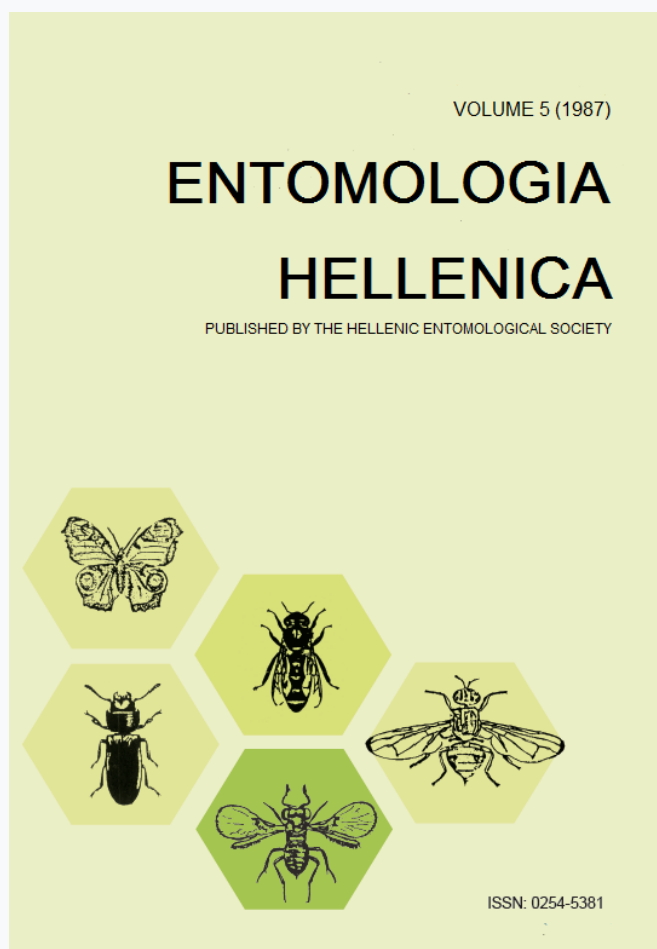


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Influence of the Leguminosae Secondary Substances on the Ecology and Biology of Bruchidae¹

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ABSTRACT

Secondary substances of leguminous seeds, suggest themselves to be the main defense mechanisms against Bruchidae which also develop their own mechanisms to avoid and/or detoxify these compounds. These interactions between plants and insects through the secondary substances, lead to the appearance of divergent or convergent defence mechanisms at the plant level and to the specialist or generalist at the insect one. Among the most widespread secondary compounds in the Leguminosae, are the tannins, lignins, lectins, alkaloids, enzyme inhibitors, polysaccharides, non protein amino acids, toxic glycosides and miscellaneous toxins.

Introduction

Secondary plant substances (SPS) or secondary plant metabolites are compounds that have no known metabolic function even though some of them are implicated as storage compounds and regulators of plant metabolism and growth (Rhoades 1979). The ecological role of SPS is of high importance because these compounds are also implicated as defensive agents for plant-herbivore, plant-pathogen and plant-plant (allelopathic) interactions. We must also have in mind that SPS could act in many cases as phagostimulants or as nutritive substances for the herbivores. The presence of the SPS in the plants and the fluctuations of their concentrations during the year act as a mechanism of natural selection against herbivores which must in turn evolve their own defensive mechanisms and strategies or find the appropriate pathways to avoid or detoxify these compounds.

The SPS in relation to some anatomical characteristics of the plant (hardness of plant tissue, hairs or other devices of the seeds that render the entrance of the young larvae more difficult) and how apparent or not are the resources, lead to the appearance of specialist or generalist herbivores. This continuous interaction between plants and

herbivores through the SPS is the main cause of their coevolution. This coevolving system, is always under evolution which results in the appearance of divergent or convergent defences at the plant level and the appearance of specialists or generalists at the herbivore level (Rhoades 1979).

The purpose of this paper is to provide a brief account of various types of SPS which are known to exist in the leguminous seeds and suggest how these substances may play a role in Leguminosae - Bruchidae interrelationships.

Bruchidae and Leguminosae

The relationship of the Bruchidae to their leguminous host plants, towards a more or less strict oligophagy which is exhibited, is considered a rare case among insects because these beetles seem to be extremely specialised to attack leguminous seeds; in fact, this adaptation of the bruchids to the species of this family is a typical example of plant-herbivore coevolution where the presence of different kinds of SPS on one hand and a great number of strategies and/or detoxification pathways on the other, shows that the whole system plant-herbivore is in dynamic balance in time and space. The preference of the Bruchidae for legumes is noted at two levels. The first is that of host selection and the second - developmental compatibility - denotes the ability to complete larval development on the preferred host. The utili-

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sation of a preferred plant as food, implies, the ability to digest its individual compounds (Applebaum 1964).

As Janzen (1977a) pointed out, each species of Bruchidae can develop in a limited number of leguminous species. In fact, of the 78 species of bruchids studied, 57 have only those 1 species of plant as host, 12 have 2, 5 have 3, 3 have 4 and 1 has 6. To explain these findings Janzen suggested that at the level of legume seeds there are many kinds of toxic compounds whose toxic action excludes a great number of bruchid species and allows the development of only species which are capable of detoxifying or avoiding these substances. Johnson and Slobodchikoff (1979), considered that the specialists can develop on seeds rich in SPS because they possess an appropriate enzymatic equipment adapted for the assimilation of the nutrient substrate while the generalists develop in seeds less rich in SPS and possess an enzymatic mechanism less specific.

Secondary Plant Substances of Leguminosae and their Biological Role on Bruchids

Leguminous seeds contain various types of SPS which belong to different chemical groups and have deterrent or toxic properties against bruchids. Among the most significant ones are tannins, lectins or phytohaemagglutinins, alkaloids, cyanogenic glycosides, saponins, enzyme inhibitors, non-protein amino acids, heteropolysaccharides and lignins. The kind of SPS and their concentration in the seeds depends on many factors such as: the plant species, the phenological stage of plant, the post-harvest period elapsed and the storage conditions. Their distribution within a seed is not even and they are absent from some parts of it.

Tannins

Tannins, as well as lignins are phenolic compounds that are found in high concentrations in all classes of vascular plants. Swain (1979) classifies tannins in four groups according to their chemical structure, molecular weight, water solubility and tannin action: (i) proanthocyanidins (condensed tannins), (ii) hydrolyzable tannins, (iii) oxytannins, and (iv) a miscellaneous group referred as b-tannins. The presence of tannins in the diet of herbivores is generally considered to be a disadvantage. The protein-precipitating properties of the tannins in ingested food result in poor digestion and, consequently, effectively reduce the nutritive value of the food. The tannins, can also act as enzyme inhibitors or, after hydrolysis by appropriate esterases, can release gallic acid that results in damage to the peritrophic membrane of the herbivores (Tanguy-Martin et al. 1977, Bernays 1978).

In the case of the leguminous seeds, tannins are present in high concentrations at the tegument of the colored varieties and constitute from this point of view a non desirable antinutritional factor in the diet of farm animals but at the same time an effective agent against phytophagous insects. Boughdad et al. (1986) have produced evidence that condensed tannins of the tegument of the seeds of *Vicia faba*, have a toxic effect against *Callosobruchus maculatus* F. and their presence in these seeds can reduce considerably the damage caused by this bruchid. Preliminary experiments conducted in our laboratory, showed that *Acanthoscelides obtectus* Say prefers to lay its eggs in tannins-free varieties of *Phaseolus vulgaris* and that the mortality of the first instar larvae during penetration into seeds containing tannins in their teguments was about two to four times higher than in tannins-free seeds (Table 1).

TABLE 1. Host selection and L_1 mortality of *A. obtectus* in the presence of 3 tannins-free varieties of *P. vulgaris* and of one (Aise), containing tannins in its seed-coat*.

Variety	Total eggs laid	Number of hatched eggs	% L_1 mortality during penetration (with respect to number of hatched eggs)
Soissons	506 (24.0%) a	399 (78.8%)	5.5 a
Aridaia	460 (21.8%) a	354 (76.9%)	13.0 b
Gigantes	996 (47.2%) b	760 (76.3%)	8.0 a
Aise	145 (7.0%) c	113 (77.9%)	22.1 c

* Multiple choice test with 8 replications and 8 females per replication. Means not followed by the same letter are significantly different at $P = 0.01$ (z criterion).

Lectins

Lectins or phytohaemagglutinins are a somewhat heterogeneous collection of molecules which have been grouped together because of their ability to cause the clumping of human and animal red blood cells in vitro (Bell 1978). The presence of lectins in legume seeds is related to: (i) protection of the plants against fungal attack, (ii) ability of the mature plant to fix atmospheric nitrogen within root nodules after infection of root tissues by strains of *Rhizobium*, (iii) hyphal cell wall synthesis, and (iv) sugar transport (Janzen et al. 1976, Fountain et al. 1977). Most lectins are toxic to higher animals and this toxicity is not necessarily related to the ability to agglutinate red blood cells.

In nature, one of the most toxic substances is the lectin of the seeds of *Ricinus communis* (Leguminosae). The lectin isolated from *P. vulgaris* exerts its toxic effect on the rats by interfering with their digestion and/or absorption, by the formation of intestinal and other lesions or by an impairment of body defences and the consequent tissue invasion by normally innocuous gut bacteria (Pusztai et al. 1979). Two lectins isolated from the cotyledons of *P. vulgaris* (red var.) (Mialonier et al. 1973) and from the tegument of the «Soissons» variety (Stamopoulos 1980) were tested against the larvae of *A. obtectus* at concentrations similar to those existing at the seed level. Neither of the two tested lectins showed a deleterious effect against the larvae of this bruchid (Table 2). On the other hand, Janzen et al. (1976) had recorded a very toxic effect of the *P. vulgaris* lectin against *C. maculatus* which in nature do not attack this plant. If we destroy the lectins of *P. vulgaris* by autoclaving the seeds at 125° C for 20 min., *C. maculatus*

larvae are able to develop without any problem in this non-host plant. As these authors pointed out, the above example shows: (i) the *P. vulgaris* lectin would be toxic to *C. maculatus* because cowpeas which are its host seeds, do not show phytohaemagglutinin activity and therefore, this bruchid is not likely to have evolved the respective detoxification mechanisms, (ii) the major part of the adaptive significance of lectins to *P. vulgaris* and other legume seeds is to protect them from attack by seed insects.

Alkaloids

The alkaloids are synthesized from the plants, from amino acids or from derived products of the carbohydrate catabolism, especially acids. The role these compounds play in plants is not very clear. Some authors suggest that they may be storage products and others that they may serve to protect the plants from predators.

Although many leguminosae contain alkaloids (*Lupinus*, *Ervum*, *Genista*, *Sophora*) knowledge of their biological action against the bruchids is limited to the work of Janzen et al. (1977) who tested ten alkaloids by incorporating them into the artificial diet of *C. maculatus*; of the alkaloids they tested only one (sparteine from *Genista tinctoria*) occurs in leguminosae. From their results Janzen et al. suggested that colchicine, gramine, strychnine, reserpine, nicotine, atropine, ephedrine and spartein were lethal at a concentration of 0.1% and the remaining two (caffeine and theobromine) which reduced adult beetle emergence at 0.1%, were lethal at 1.0%. In a complementary experiment Janzen (1977b) studied the fate of larvae of *C. maculatus* on seeds of legumes other than

TABLE 2. Effect of the seed-coat lectin of *P. vulgaris* (v. Soissons) and of PHA-C* on the development of *A. obtectus* (D. Stamopoulos 1980).

Content of the artificial diet	Number of eggs laid	Number of hatched eggs	Emergent adults (with respect to hatched eggs)
Cotyledon powder + 1% of seed-coat lectin	40**	38	37 (0.97)
Cotyledon powder + 1.4% PHA-C	100***	70	56 (0.80)
Cotyledon powder only (control)	44****	40	32 (0.80)

* PHA-C = Lectin isolated from the cotyledons of a red variety of *P. vulgaris* (Mialonier et al. 1973).

** 20 rep. × 2 eggs, ***50 rep × 2 eggs, ****22 rep. × 2 eggs.

Vigna unguiculata. The larvae died without penetrating the cotyledons of alkaloid-containing species *Ormosia venezolana*, *Sophora macrocarpa* and *Erythrina flabelliformis*; in the latter, only the bruchid *Specularius erythrinae* could develop.

Miscellaneous glycosides

Glycosides are derivatives of sugars in which the aglycon portion could be sterols, triterpenes, derivatives of HCN or other. The enzymatic hydrolysis of these compounds can release toxic molecules into the alimentary tract of a herbivore which can lead to death.

Applebaum et al. (1969), studied the influence of saponins isolated from the seeds of *Cicer arietinum*, *Pisum sativum*, *Vicia faba*, *Lens esculenta*, *Ph. vulgaris* and *Arachis hypogea* on the biology of the multivoltine bruchid *Callosobruchus chinensis* L. He found there is a correlation between the toxicity of these substances to the larvae of the insect and the relative resistance of these plant species to attack by this seed beetle.

Various legumes are potentially toxic because they contain glycosides from which HCN may be released through their hydrolysis. The case of the lima bean *Phaseolus lunatus* is the best known example because its consumption in some tropical countries has been implicated in fatal cases of poisoning. In fact, the glycoside phaseolunatin may be hydrolysed by β -glucosidase in glucose and 2-cyano-2-propanol which gives acetone and HCN after hydrolysis by oxynitrilase. Some varieties of

lima bean can yield as much as 300 mg of HCN/100 gr of bean and it is considered that these seeds can be extremely toxic to vertebrates and also to insects which are vulnerable to HCN (Liener 1980). Janzen (1977b) suggested that the failure of larvae of many Bruchidae to develop in the seeds of this plant, might be the result of the toxic action of this glycoside. Yet, two Bruchidae (*Zabrotes subfasciatus* and *Acanthoscelides argillaceus*), do attack wild varieties of *P. lunatus* in Costa Rica. After the introduction of *P. lunatus* in USA and Europe, the geneticists succeeded in creating varieties with few or no traces of phaseolunatin, in order to use this plant as forage.

In laboratory experiments, we tested 3 varieties of *P. lunatus* (a wild v. and two cultivated ones) against *A. obtectus* in order to examine the post-embryonic development of this bruchid which, in nature, does not use this plant as host, although its origin is from the same ecosystems of Mexico and C. America. The results (Table 3), show that the seeds of the wild variety cause 100% post-embryonic mortality in contrast to the cultivated ones («Togo» and «Jackson wonder») which permit the development of certain larvae but provoke a considerable prolongation of the post-embryonic development and a marked decrease in adult weight (Stamopoulos 1980).

Enzyme inhibitors

Enzyme inhibitors, we consider all those substances which can cause the partial or complete in-

TABLE 3. Post embryonic development of *Acanthoscelides obtectus* in seeds of 3 varieties of *Phaseolus lunatus* (Stamopoulos 1980)*.

Seed species	% L ₁ mortality during penetration (with respect to hatched eggs)	% intracotyledonal mortality (with respect to number of larvae penetrated the seeds)	Mean weight of adults (mg)		Mean larval development (days)
			$\bar{x} \pm \text{SEM}$ males	$\bar{x} \pm \text{SEM}$ females	
<i>Phaseolus vulgaris</i> (control)	20	11	5.6 \pm 0.2 a	6.4 \pm 0.2 a	34 \pm 1 a
<i>Phaseolus lunatus</i> (wild var.)	55	100	—	—	—
<i>Phaseolus lunatus</i> (v. Jackson Wonder)	44	93	3.2 \pm 0.6 b	3.4 \pm 0.6 b	75 \pm 5 b
<i>Phaseolus lunatus</i> (v. Togo)	40	34	1.9 \pm 0.2 c	2.8 \pm 0.3 c	49 \pm 4 c

*Means not followed by the same letter are significantly different at $P = 0.05$ (z criterion).

hibition of those enzymes that are involved in the metabolic functions of an organism. Trypsin and chymotrypsin inhibitors were found in the seeds of *A. hypogaea*, *Glycine max*, *Ph. lunatus* and *Vigna chinensis*, while in the seeds of *Ph. vulgaris*, an inhibitor of pancreatic amylase with high in vitro activity has been isolated. Pancreatic amylase inhibitory activities have also been recorded with inhibitors isolated from the seeds of *L. esculenta*, *V. chinensis* and *Cicer arietinum*. No inhibition of the plant's own amylase was obtained with the *Ph. vulgaris* inhibitor. According to Bell (1978), this finding excludes the possibility that the inhibitor has a regulatory role in carbohydrate metabolism of the plant and suggests a protective function.

Applebaum (1964) studied the proteolytic activity of larvae of *C. chinensis* and *A. obtectus* and found that it is very low. The addition of the trypsin inhibitor in the artificial diet of *C. chinensis* at a concentration of 0.2% (Applebaum 1964) as well as to the artificial diet of *A. obtectus* at 0.5% (Stamopoulos 1980) did not have detrimental effects on the larvae of these two insects. Roy and Bhat (1975), who studied the tripsin inhibitor of *Lathyrus sativus*, sustain that this inhibitor in the dormant seeds does not impart protection to the seeds against insect infestation. Their data show that as trypsin inhibitor concentration increases, infestation rate also increases. If we examine Bell's above suggestion, and given that the leguminous seeds are attacked almost exclusively by bruchids with low proteolytic activity, we may conclude that these insects achieve survival by using the available peptides of the seeds and by supplementing the plant proteases with their low protease activity (Applebaum 1964).

Polysaccharides

The seeds of *Ph. vulgaris* contain a heteropolysaccharide consisting of xylose, arabinose, rhamnose, glucose and galactose which according to Applebaum et al. (1970) imparts resistance to the larvae of *C. chinensis* while on the contrary it has no adverse physiological effects on the larvae of *A. obtectus*. The authors suggest that this observed difference in sensitivity is due to the ability of the larvae of *A. obtectus* to hydrolyse this compound to simple assimilative sugars while the larvae of *C. chinensis* with a non appropriate pH in their midgut are not capable of doing so. This example, reinforces the hypothesis of the adaptive role SPS can play, acting as the main agents of the observed bruchids' extreme host-specificity.

Non-protein amino acids

A great number of non-protein amino acids are

structural analogs of protein amino acids and so can substitute them during the process of protein formation, resulting in the synthesis of compounds that can act as anti-metabolites and can provoke, in many cases, the death of the organism in which these SPS are introduced. From this point of view, the non protein amino acids occurring in plants can be considered as a well adapted defence mechanism because only a small number of herbivores can detoxify them. Despite the relative abundance of these substances in leguminous seeds, the exact role at either the plant or the insect level, is relatively unknown.

Janzen et al. (1977) have examined the toxic action of some non protein amino acids against *C. maculatus* but they do not give more detailed information about how this toxic action is expressed. The only example of how a bruchid can detoxify a non protein amino acid is that of *Cariedes brasiliensis* fed on the seeds of *Dioclea megacarpa* in which no other insect can feed because of the presence of L-canavanin at high levels (13%). This non-protein amino acid, is analogous to the L-arginine and is known to be incorporated in place of this amino acid into the protein of a number of species. Rosenthal et al. (1977) have shown that the larvae of *C. brasiliensis* possess two mechanisms, one to detoxify this SPS and another that permits the use of this toxic compound as a nitrogen source. In fact, the larvae have an arginyl-tRNA synthetase which is able to discriminate against canavanine and thus prevent its incorporation into protein and can also degrade this compound to canaline and urea which in turn is degraded with urease to ammonia, enabling it to enter the nitrogen pool of the larva.

Lignins

Lignins are phenolic heteropolymers with a molecular weight greater than 5.000 that are formed by the oxidative condensation of cinnamyl alcohols and occur in mature cell walls of vascular plants (Swain 1979). Their presence in plant tissues provides protection against pathogenic attack and consumption by herbivores. In fact, lignins have an adverse effect on the nutrition of ruminants by reducing the availability of both carbohydrates and protein, in much the same way as do tannins.

The biological action of lignins against the bruchids was studied by Stamopoulos (1987) who tested against *A. obtectus* the lignin extracted from the seed coat of *P. vulgaris*. The experiments showed that this compound provokes high mortality in the larvae and the calculated LC50, in a bean cotyledon diet, is of the order of 0.26%. From preliminary results, it appears that the females of *A.*

obtectus prefer to lay their eggs on cultivars with a low content of intracotyledonal lignin. The total number of emerged adults from the varieties with the lower intracotyledonal lignin (0.18% and 0.21%) was about four times greater than that from a variety with 0.74% lignin. The question which arises from the above results is, how the insect has the ability to discriminate between the different levels of this toxic compound. Further eco-physiological studies are needed to clarify the possible role of lignin as stimulus influencing the host-selection behaviour of this insect.

Conclusions and Discussion

From all the afore mentioned data, we can conclude that the leguminous seeds are, in many cases, well «equipped» with SPS toxic against phytophagous insects. We can also conclude that the Bruchidae are well adapted to the seeds of Leguminosae so that some of its species are the exclusive visitors of seeds rich in SPS. If we admit the plant-herbivore co-evolution theory (Center and Johnson 1974, Janzen 1977a, Rhoades 1979), it is obvious that the natural selection process induces the evolution of defense mechanisms in the leguminous seeds which limit attacks by phytophagous insects and especially by Bruchidae. On the other hand, the latter have evolved their own defense mechanisms based on the avoidance and/or detoxification of the SPS with the aid of the appropriate enzymatic equipment as clearly demonstrated in the case of *C. brasiliensis* and *A. obtectus*. However, as Bell (1978) mentioned, the presence of toxic compounds in the plants does not itself prove that all these compounds have a defensive or offensive role and also does not prove that such compounds have been favored by natural selection; on the other hand it is obviously impossible to go backwards in time to study the effects of past selectionary pressures on the ancestors of the modern plants.

A detailed study of such phenomena is very difficult to carry out by using modern cultivated varieties of Leguminosae, because the selection made by man, led in many cases to the diminution or the elimination of the defensive mechanisms and especially those of SPS. So, it is imperative that we use wild or semi-wild varieties in this type of experiment in order to screen all the SPS produced by plants that will be used, as a data base, for the selection or creation of varieties resistant to herbivores. In fact, as Labeyrie (1980) pointed out, the selection and amelioration at the plant level, allowed the creation of leguminous varieties of high yield, without hard fibrous tissues but deprived

them of some chemical defensive substances, making them more susceptible to attacks from herbivores and favouring the explosive increase of such specialist herbivores as the Bruchidae.

A detailed study of the leguminous SPS as well as the study of the genetic mechanisms involved in their synthesis, must be carried out in order to select those seeds with highly specific SPS-mechanisms to defend themselves from one or another species of Bruchidae. Solving the problem in this way is not easy, because various species of Bruchidae are not equally susceptible to a given SPS and we must consider the possibility that these insects, after long exposure to a very toxic compound, will be able finally to detoxify it and in this case we will be confronted with a highly-specialized phytophagous species.

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KEY WORDS: Secondary plant substances, Leguminosae, Bruchidae, Tannins, Lectins, Alkaloids, Enzyme Inhibitors, Non protein amino acids, Toxic glycosides, Polysaccharides, Lignins, Plant-herbivore interactions, Plant defense systems

Επίδραση των Δευτερευουσών Ουσιών των Leguminosae στην Οικολογία και Βιολογία των Bruchidae

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ΠΕΡΙΛΗΨΗ

Η παρουσία δευτερευουσών ουσιών στους σπόρους των Leguminosae θεωρείται ως ο κυριότερος αμυντικός μηχανισμός που διαθέτουν τα φυτά αυτά για να αποφεύγουν την προσβολή από είδη της οικογένειας των Bruchidae. Από την άλλη μεριά τα έντομα αυτά, ανέπτυξαν τους δικούς τους μηχανισμούς και τις δικές τους στρατηγικές ώστε να μπορούν να αποφεύγουν ή/και να εξουδετερώνουν τις τοξικές αυτές ουσίες και φαίνεται ότι από αυτή την άποψη είναι αρκετά καλά προσαρμοσμένα στους σπόρους των διαφόρων ειδών της οικογένειας αυτής. Οι αλληλεπιδράσεις μεταξύ φυτών και εντόμων που προαναφέρθηκαν, με κύριο άξονα τις δευτερευουσες ουσίες, έχουν ως αποτέλεσμα την εμφάνιση «αποκλεινόντων» ή «συγκλινόντων» μηχανισμών άμυνας σε επίπεδο φυτού ενώ σε επίπεδο εντόμου την εμφάνιση «εξειδικευμένων» ή «μη εξειδικευμένων» ειδών.

Από τις κυριότερες δευτερευουσες ουσίες που απαντώνται στα Leguminosae και που δρουν ως αμυντικά συστήματα απέναντι στα Bruchidae, εξετάζονται στην παρούσα εργασία οι: ταννίνες, λεκτίνες ή φυτοαιμαγλουτινίνες, αλκαλοειδή, διάφοροι γλυκοζίτες, αναστολείς ενζύμων, πολυσακχαρίτες, μη πρωτεϊνικά αμινοξέα και οι λιγνίνες.