Обзор / Review

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Food as a factor determining the physiological state of populations of the phytopagous pests of agricultural crops

ABSTRACT

Relevance. Trophic relationships along with competition and mutualism are the most basic and significant interactions in ecosystems. To develop, survive, and multiply, insects need to consume a certain amount of nutrients at a certain ratio. Food products are complex mixes of nutrients and non-nutritive substances (sometimes toxic ones): macronutrients (proteins, carbohydrates, and lipids), micronutrients (vitamins and minerals), and water. Some nutrients are essential; insects lack the ability to synthesize them in their bodies and must obtain them from their diet or through symbiosis with beneficial organisms. Identification mechanisms being well developed in the system "phytophagous insect – plant" allow insects to successfully spread, multiply, and feed on certain plant species. The complex of hydrolytic enzymes in the insect intestine is one of the main targets for plant defense responses because these enzymes determine the availability of structural compounds for phytophagous insects. For this reason, enzymes in the insect intestine play a key role in the adaptation of insects to the pest resistance of fodder plants. For instance, when proteinase inhibitors are synthesized in a fodder plant as the result of induced insect resistance the complex of enzymes in an insect intestine might change negating the effect of these inhibitors. The development of co-adaptations due to interactions among species in food chains depends on a complicated constellation of conflicting relationships between consumers and food objects. The mechanisms of this influence may be rooted in the allelochemical interactions in the system "phytophagous insect – plant recipient". Allelopathic interactions are among the most complex interactions because they are constituted by direct and indirect effects. Plants when damaged by phytophagous insects activate defense responses, which incorporate several mechanisms, including an increase in the concentration of secondary metabolites, many of which are phenolic compounds.
The aim of the work is to describe the mechanisms of relationships in the system "phytophage-plant".
Conclusion. Management of processes of intra-water divergence of insect-phytophages in agrobiocoenoses in order to prevent the emergence of races and populations of pests adapted to live on initially resistant to them plant forms is possible in compliance with the transition to a targeted selection of agricultural crops for resistance to a complex of pests.

KEYWORDS:
phytophagous insect, plant, food, agroecosystem, digestive enzymes, allelopathic interactions, coevolution, coadaptation

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Пища как фактор, определяющий физиологическое состояние популяций фитофагов-вредителей сельскохозяйственных культур

РЕЗЮМЕ

Актуальность. Трофические отношения, наряду с конкуренцией и мутуализмом, являются наиболее общими и значимыми в экосистемах. Для развития, выживания и выведения потомства насекомым необходимо получать определенные количества и соотношения питательных веществ. Продукты питания насекомых представляют собой сложные смеси питательных и непитательных (иногда токсичных) соединений: макроэлементы (белки, углеводы и липиды), микроэлементы (витамины и минералы) и воду. Некоторые из питательных веществ являются незаменимыми, насекомые лишены способности синтезировать их самостоятельно и должны получать их с пищей или из полезных симбионтов. В системе «фитофаг-растение» хорошо развиты механизмы распознавания, позволяющие насекомым успешно расселяться, размножаться и питаться на конкретных видах растений. Комплекс гидролитических ферментов кишечника насекомых является одной из основных мишеней для действия защитных реакций растения, т.к. именно этими ферментами определяется доступность структурных веществ для фитофагов. Поэтому ферменты кишечника фитофагов играют одну из ведущих ролей в механизмах адаптации насекомых к энтоморезистентности кормовых растений. В частности, при синтезе в кормовых растениях ингибиторов протеиназ в результате индуцированной энтоморезистентности, в кишечнике насекомого может изменяться состав ферментов, что приводит к уходу от действия этих ингибиторов. При взаимодействии видов в пищевых цепях возникновение комплекса взаимоприспособлений находится в зависимости от сложной констелляции противоречивых отношений, связывающих потребителей и пищевые объекты. Механизмы такого влияния могут лежать в области аллелохимических взаимоотношений в системе «фитофаг – растение-реципиент». Аллелопатические взаимоотношения – одни из наиболее сложных, так как в данной форме тесно переплетаются прямое и опосредствованное влияние. Растения при повреждении фитофагами активируют защитные реакции, которые состоят из нескольких механизмов, включая увеличение концентрации вторичных метаболитов, многие из которых являются фенольными соединениями.
Целью работы является описание механизмов взаимоотношений в системе «фитофаг-растение».
Заключение. Управление процессами внутривидовой дивергенции насекомых-фитофагов в агробиоценозах в целях предотвращения появления рас и популяций вредителей, адаптированных к обитанию на первоначально устойчивых к ним формах растений возможно при соблюдении перехода к целенаправленной селекции сельскохозяйственных культур на устойчивость к комплексу вредителей.

КЛЮЧЕВЫЕ СЛОВА:
фитофаг, растение, пища, агроэкосистема, пищеварительные ферменты, аллелопатическое взаимодействие, коэволюция, коадаптация

Introduction

The phytosanitary destabilization of the Russian agriculture, which began in the 1990s, has become long-term and systemic and been contributing greatly to yield losses. Due to the deterioration of the phytosanitary conditions, millions of tons of grain, potato, and root vegetables are lost every year. Failures to comply with the technologies for crop cultivation and to maintain agroecosystem structures are among the main causes of such high losses. The phytosanitary destabilization of agricultural lands are especially noticeable when the structure of these lands is disrupted [1]. A decrease in the number of rotations and crops used, and even more so the total neglect of crop rotation lead to an unacceptable level of phytosanitary destabilization in agroecosystems. In these conditions, the outbreaks of some pest arthropods, plant pathogens, and weeds become more frequent. These species have high ecological plasticity, are optimally adapted to an anthropogenically transformed environment, and have the status of dominant and super-dominant harmful objects, such as Acridoidea pests, the Colorado potato beetle, the Sunn pest, the beet webworm, the European corn borer, and the pathogenic agents of brown rust, potato blight, etc. [2]. It is known that the synergetic effect of the combined adverse impact of diseases, pests, and weeds leads to a significant yield loss worldwide, which may amount to 50% in particular years [1]. Additionally, the cost efficiency of plant protection products has been rapidly increasing due to the more intensive and well-balanced application of fertilizers and the employment of new innovative agricultural techniques, which could improve the yield of the main agricultural crops. Growing resistant varieties is one of these techniques. A high number of studies were dedicated to the influence of resistant varieties on insect pests. This paper reviews several of these studies.

1. Plant immunity to phytophagous insects

The system “phytophagous pest – plant recipient” is viewed by modern science as a result of the co-adaptation and co-evolution of phytophagous animals and fodder plants [3]. An important characteristic of the evolution of these systems is the ability of phytophagous insects to actively and intentionally search for optimal feeding and reproductive conditions [4]. In particular, many insect species are adapted to feeding and reproduction on certain plant organs and tissues at certain stage of their ontogeny. Searching for suitable fodder plants, feeding on plant tissues, digesting, absorbing hydrolyzed food have a significant metabolic cost [5]. Thus, plant recipients acquired a number of specific (morphological, physiological, etc.) traits, which prevent phytophagous insects from colonizing plant tissues [6]. Nowadays the term “plant immunity” or “phytoimmunity” means the development and expression of plant protective properties against consumers [7]. The first classification of the plant barrier properties that prevent heterotrophs from feeding on plants was suggested by N.I. Vavilov in his work “Problems of the immunity of cultivated plants” [8]. Plant immunologists distinguish two forms of innate immunity – passive and active immunity. Passive immunity is inherent in plants irrespective of pathogens, active immunity is induced by virus entry. Anatomical-morphological and physiological-biochemical properties of plants constitute the basis of passive immunity. Active immunity is comprised by the plant protective properties that are brought into action by the entry of an infectious agent or the damage caused by a pest. They are aimed at localizing and eliminating infections such as cicatrisation, wounding, hypersensitive response, the synthesis of phytoalexins, and etc. According to phytoimmunologist B.A. Rubin, the main idea of phytoimmunity is that immunity cannot be considered an individual isolated chemical or a single physical or morphological trait of an organism. Numerous studies have demonstrated that the ability of plants to respond to damage in a certain way serves as the expression of the dynamic properties of protoplasts, cells, organs, and organism as a whole [9].

There are several conventionally distinguished forms of plant responses to phytophagous insects:

- Antixenosis — negative responses resulting in the inability of phytophagous insects to use plants for feeding and/ or reproduction [10].
- Antibiosis – an adverse effect produced by a fodder plant on a phytophagous insect during feeding. Antibiosis is attributed to the damaging effect of physiologically active compounds in plants or to the inability of phytophagous insects to digest and absorb food polymers from plant hosts due to the lack of necessary digestive enzymes [11].
- Plant tolerance to the pathogenic impact of an animal agent is expressed as the ability of a given plant to preserve its biological productivity (yield) without a significant loss when there is no adverse effect on the pathogen [12].

A number of researchers have established that plants have constitutional and induced immunogenetic barriers [13,14,15]. The constitutional barriers are the protective barriers conditioned by the specificity of the morphological constitution that provides plant immunity (external and internal structure of plants and the characteristics of the

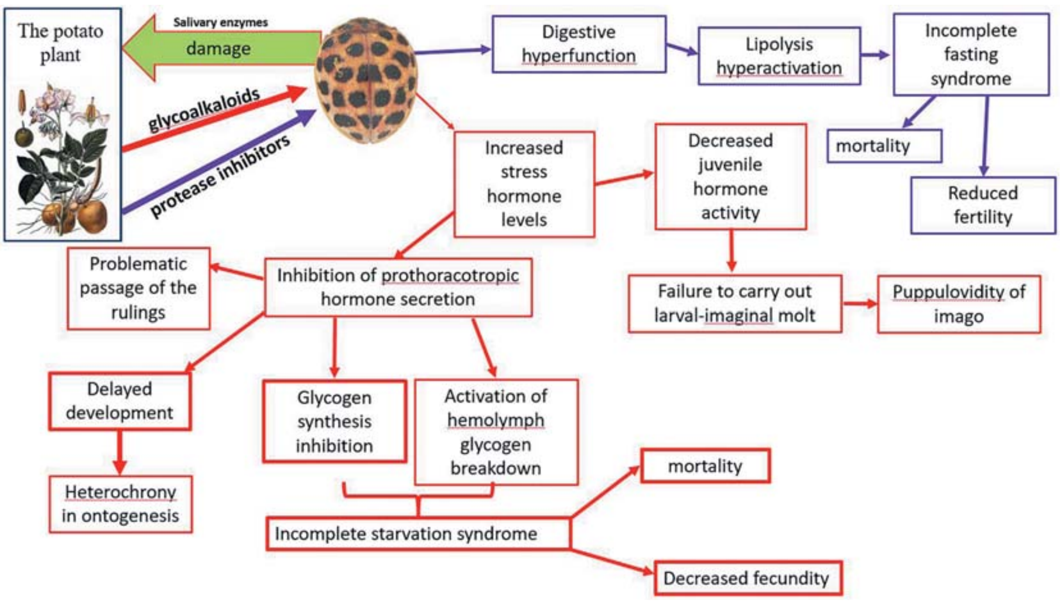

Рис. Схема взаимодействия «фитофаг-растение»
Fig. Scheme of phytophage-plant interaction

metabolism and vital functioning that influence the ontogeny and morphogenesis of insects). This category of barriers includes atretic, morphological, growth, physiological, metabolic, and ontogenetic barriers [16].

The atretic (depolymerizing) barrier is determined by structural differences in plant proteins, lipids, and carbohydrates and reduces their susceptibility to and destruction by the enzymes of phytophagous insects (the insufficient depth and rate of the depolimerization of proteins, lipids, and carbohydrates are a significant immunity factor [17]. The basis of this effect lies in the molecular incompatibility between the enzymes of phytophagous insects and the plant biopolymers targeted by them. This barrier is a property of immune plant varieties. When a phytophagous insect feeds on such plants its nutritional and energy needs are not completely satisfied, which leads to dystrophy – malnutrition and even death (because the energy costs of the search for food, feeding, and the digestion and absorption of food are not fully covered) [18]. The morphological barrier depends on the genetic differences in the differentiation and constitution of plant organs, tissues, and cells. These differences might make it difficult and even impossible for phytophagous insects to use plants as a food source and habitat [19]. The growth barrier is conditioned by differences in the growth rates of vegetative and reproductive plant organs and plant organisms as a whole. This barrier plays an important role because the high growth rates of various plant parts can hinder the normal development of eggs laid by phytophagous insects on rapidly growing plant organs and reduce the contact between their larvae and plant tissues (substrate) thus facilitating the natural cleaning of the latter [20]. The physiological-metabolic barrier depends on the differences between immune and non-immune plants in terms of physiological parameters and the characteristics of metabolism [21]. The ontogenetic barrier is conditioned by differences in the life cycle of immune and non-immune plants and discrepancies in the timing of the diachronic parameters of their individual development (periods, stages, and phases) [22]. The constitutional barriers of phytoimmunity are aimed at thoroughly and consistently protecting plants against harmful organisms at all levels from molecular to organismal one [23]. The induced barriers of phytoimmunity are activated when a plant is damaged. The aim of induced barriers is to localize harmful agents, isolate them from well-functioning unharmed tissues, and subsequently eliminate the pathogenic objects with the withering of damaged tissues. Induced barriers include necrogenic, repairing, gall-forming, oxidative, and inhibitory ones [24]. The necrogenic barrier, which is especially effective against some leaf-miner and sucking phytophagous insects, is manifested as the death of individual cells, cell complexes, tissues, and individual organs induced by injuries and leading to the spatial isolation of phytophagous insects from non-damaged plant parts and thus hindering their feeding on host plants [25]. The repairing barrier is the formation of new homologous organs that morphologically and functionally replace the damaged and destroyed ones (for example, the replacement of one shoot with another or several leaves with newly formed ones, etc.) [26]. The gall-forming and teratogenic barriers are manifested as pathological neoplasms – galls and parasitic teratomorphs – in plant hosts [27]. The oxidative barrier is the oxidation of secondary metabolites occurring when phytophagous insects damage plant tissues. This leads to an increase in the toxicity of secondary metabolites or to the synthesis of compounds interfering with the normal functioning of insects and even causing their death [28]. The inhibitory barrier is the synthesis of compounds with inhibitory functions, which suppress the activity of hydrolytic (amylases, proteases, etc.) and other enzymes, in the plant recipients damaged by phytophagous insects [29,30,31].

Thus, the reviewed immunological barriers developed in plant recipients in the course of their evolution to counteract the adaptation of various phytophagous insects [32,33,34].

2. Influence of food quality on the physiological state of phytophagous insects

Despite the well-developed morphological, physiological, and behavioral mechanisms allowing phytophagous insects to consume adequate nutrition, they still have to face some challenges such as fluctuations in the external supply of plant nutrition over time and in space (the quantity, balance, and availability of nutrients) [35]. Moreover, the nutritional needs of insects are not constant and change depending on what stage of growth, development, and reproduction they are at. If a phytophagous insect cannot respond to the challenge of balancing the ever-changing proportion of what it needs to what fodder plants provide, the insect has to suffer the consequences such as arrested development, a decrease in fecundity, and even premature death. Therefore, studying the compensatory mechanisms used by insects to balance this proportion plays a key role in understanding the relationships between insects and plants. This is also important for pest management and relevant to the optimal foraging theory [36].

In its turn, the nutritional value of plant recipients deeply influences the ecology, behavior, and physiology of phytophagous insects and is determined by numerous factors such as the quantity and quality of different nutrients, leaf roughness, the water content, and the composition of secondary metabolites [37]. Plants differ considerably in the composition and concentration of nutrients. Proteins and carbohydrates are the two macronutrients that are the most often referred to in scientific papers on the feeding ecology of phytophagous insects with special attention paid to their influence on the productiveness and selection of feed [38, 39]. It has been suggested that the recipient selection models used by phytophagous insects might have affected the content of macronutrients in their host plants in the process similar to the coevolution of insects with the defense allelochemical compounds generated by plants [40, 41]. The concentration of nutrients in proportion to unused mass such as cellulose is a component of variability in feeding and plays a certain role in the process [42,43]. It has been reported that phytophagous insects sometimes avoid plant parts containing a high dose of structural compounds [44, 45]. However, there is no definitive interpretation because the structural compounds might affect not only the concentration of nutrients but also the roughness of leaves [46]. Additionally, the experiments that differentiated the mechanical effect from the effect of diluting the volumetric components of plants by prescribing artificial diets showed that phytophagous insects were able to compensate for the dilution of nutrients by increasing the amount of digested food [36]. The same was observed for plant tissues [47]. In general, insects need to obtain a certain quantity of nutrients at a certain ratio to develop, survive, and multiply [48]. It might be challenging to find and gain access to the right combination of nutrients in the wild because food recourses often differ significantly in their chemical and nutritional profiles and do not provide a reliable nutritional profile, which could satisfy the needs of an insect completely [49].

Insects, which cannot change the nutritional content of identified food recourses, compensate the differences in the chemical composition by relying on diversity. For example, it is well known that the floral diversity provides the constant availability of resources allowing insects to regularly digest a great quantity of food and to increase the amount of accumulated food resources [50]. The diversity can improve the nutritional value of food (for example, by diluting toxic plant compounds [51, 52]. However, a large number of plant recipients does not automatically mean high food quality [50], because an important role is also played by the composition. A diet with the ideal composition of nutrients can be the most easily found in an environment with a high diversity of resources. In these conditions, animals can feed on various plant species with a different content of nutrients as have been shown by Trinkl et al. [54]. The authors have analyzed the nutritional composition of the larval feed obtained from bee colonies located in various environments with floral diversity. They have shown that the proportion of beneficial fatty acids and the proportion P:L increase with the improvement of plant species abundance both in the larval feed and in the environments. These results have pointed out the importance of biological diversity in an environment for the adaptability and survival of many phytophagous insect species.

Insects are the main food source for some higher trophic levels (for example, birds), and the advantages offered by the diversity of resources on a lower trophic levels might lead to an increase in the population size of species on higher trophic levels. It is well known that insects choose food depending on the quality content of nutrients. For instance, Grund-Mueller et al. [55] have shown that adding protein and amino acids to a sucrose diet is not sufficient to extend the lifespan and to ensure the reproduction of adult bumblebees (*B. terrestris*). To maintain physiological functioning, other nutrients are required (such as lipids and microelements). Additionally, a number of studies have demonstrated that species specific proportions of micro- and macronutrients are crucial for the health and adaptability of animals in general [56] and insects in particular [57]. However, there are no extensive data on the food needs and the levels of tolerance to differences in the optimal intake of nutrients for the majority of insect species. It has not been conclusively studied how trophic interactions, social organization, and changes in the environment affect the desired ratio of nutrients.

Morimoto and Lihoreau [58] and Crumиre et al. [59] have highlighted the importance of the further development of existing concepts in studies on nutrition such as the geometric framework for nutrition [60]. The latter came to be an extremely useful instrument for evaluating the influence on the proportion of nutrients (for example, P:L) in insects in particular and animals in general. Morimoto and Lihoreau [58] propose open access to GFN data as the basis for the development of comparative analyses and provide a template for structuring these data to simplify meta-analyzes employing quantitative methods [58].

The observed variance in the chemical composition of resources requires the insects that consume these resources to be able to evaluate their chemical/ nutritional profiles (for instance, by tasting) and make appropriate decisions on feeding. Numerous behavioral studies have shown that [61] underlying physiological and neural mechanisms are not sufficiently studied especially the ability to distinguish non-sugar macronutrients (for example, oil or protein). It has been recently shown that bumblebees (*B. terrestris*) can sense all the amino acids that have the polar functional group in addition to the amino- and carboxyl groups specific to aminoacids [56]. Additionally, bees distinguish not only different aminoacids but also different concentrations of the same amino acid [56]. Interestingly, bumblebees do not distinguish pure pollen and the pollen enriched with amino acids [61]. This indicates that their decisions on pollen gathering can be influenced by nutritional compounds other than amino acids. In fact, enriching pollen with fatty acids (instead of amino acids) allowes bumblebees to distinguish between the pure pollen and the supplemented one [62]. This means both amino and fatty acids are important but the signal of fatty acids is prioritized. The priority of fatty acids over aminoacids has been also confirmed by Vaudo et al. [63] who have shown that Bombus impatiens prefers to feed on plants with pollen rich in protein and oil. The prioritized sensitivity to a crucial food component not only increases the chance of survival and therefore the chance of reproduction but also reduces the energy cost. This is a part of a complicated strategy adopted by generalist species for an effective use of various resources by rapidly evaluating the food quality at a low energy cost. This strategy allows insects to maximize the benefits of diversity.

Thus, the food recourses of insects are complex mixes of nutritional and non-nutritive (sometimes toxic) compounds. Usually these compounds include macronutrients (proteins, carbohydrates, and lipids), microelements (vitamins and minerals), and water, all of which directly participate in the physiological functioning of insects [64]. Some nutrients are essential and insects lack the ability to synthesize them in their bodies and must obtain them from food or through symbiosis with beneficial organisms. Others such as nutritional additives (stabilizers, preservatives, and dry compounds) and token stimulators (secondary plant metabolites) do not have a nutritional function.

3. Evolutionary relationships between phytophagous insects and plants

The tritrophic system “plant – phytophagous insect – entomophagous animal” is one of the most significant subsystems within an agroecosystem [65]. Analyzing this three-element system allows us to distinguish the main components in the chain of organisms interacting with each other. These components facilitate the main flow of energy, matter, and information. Phytophagous insects are divided into several categories based on their feeding specialization [66]: 1) host specificity resulting in the ability of insects to survive and normally function only on plant recipients from certain systemic groups; 2) topical specificity affecting the ability of species to normally develop only on specific parts of plant recipients; 3) ontogenetic specificity limiting insects to develop only on plant organs at specific growth stages and in a certain morphological and physiological state [65](Vilkova and Ivashchenko). According to N.A. Vilkova et al. [67], the adaptability of arthropod species to intraspecific forms of fodder plants (varieties, hybrids, and lines) should also be distinguished within the host specificity. The main doctrine of ecology states there is an interaction between a given system and its environment and this interaction is determined by the responses of its inner components to external conditions. The reported phenomena of plant resistance to consumers assigned to different taxonomic ranks allow researchers to review and broadly characterize the immunogenetic system of plants [68].

There are profound differences in the interactions of micro- and macroorganisms with fodder plants [69]. These differences influence many aspects of the vital functioning of organisms. Most notably, they manifest in how arthropod pests actively choose fodder plants compared to microorganisms. Most phytophagous insects live autonomously and come into contact with plants at certain ontogenetic stages. Among invertebrates, insects achieved the highest level of anatomical development, and first of all, the development of the organs of senses and movement. The advanced sensory system of insects allows them to perceive and decode information from the environment and respond accordingly. The ability of insects to choose fodder plants actively depends on this factor [70]. Today the term “plant immunity” or phytoimmunity is used to denote the manifestation of plant defense mechanisms against consumers [71].

Trophic relationships along with competition and mutualism are the most basic and significant interactions in ecosystems. The patterns of the formation and maintenance of trophic relationships in insect communities within ecosystems are one of the most important fundamental problems in agroecology [72]. The characteristics of insects facilitating their rapid spread, reproduction, and adaptation to new environmental conditions create the possibility of numerous trophic interactions both within a given insect community and with other groups of organisms, with plants in particular. Agroecosystems do not have the same stability as natural ecosystems, the ecological groups and their interactions with each other change constantly; new trophic relationships develop. Phytophagous pests and entomophagous generalists establish such relationships most actively [73]. Both phytophagous pests and entomophagous generalists expand the population size by expanding their fodder resources. The nutritional needs of a phytophagous insect is the basis for the interactions between this insect and fodder plants. These needs are reflected in the unique feeding specialization and adaptation of insects allowing them to use plant food most effectively. The feeding specialization of phytophagous insects is determined by the physiological and biochemical characteristics of both plant recipients and phytophagous insects themselves [74]. Plant resistance to phytophagous insects depends primarily on specific factors of plant immunity that play the role of barriers limiting the number of plant species and plant organs and tissues suitable for the feeding of insects and mites. In contrast to animals, the phylogeny of plant immunogenetic system has not been thoroughly studied. The factors that determine plant resistance to arthropod pests have been researched the least. Modern science views the system "phytophagous insect – plant recipient" as a result of the coadaptation and coevolution of phytophagous animals and fodder plants [75]. An important evolutionary characteristic of these systems is the ability of phytophagous insects to actively and intentionally search for optimal conditions for feeding and reproduction (Burov et al., 2005). In particular, many insects are adapted to feeding and reproduction on certain plant organs and tissues at certain ontogenetic stages. Identification mechanisms are well developed in the system "phytophagous insect – plant" and allow insects to successfully spread, multiply, and feed on suitable plant species. Searching for fodder plants, feeding on and digesting their tissues, absorbing hydrolyzed food have a significant metabolic cost [71]. Thus, plant recipients possess a number of specific traits (morphological, physiological, etc.) that prevent phytophagous insects from colonizing plant tissues. An act of insect feeding is a process with a high metabolic cost, a chain of consecutive actions in the process of nutrition-seeking activity [76]. The complex of hydrolytic enzymes in the insect intestine is one of the main targets for plant defense responses because these enzymes determine the availability of structural compounds (proteins, sugars, and lipids) for phytophagous insects. For this reason, the digestive enzymes of phytophagous insects play a key role in the adaptation of insects to the pest resistance of fodder plants. For instance, the synthesis of proteinase inhibitors in fodder plants as a result of induced pest resistance might change the composition of enzymes in the insect intestine. This terminates the effect of the inhibitors. For example, feeding Colorado potato beetles the potato leaves that were treated with jasmonic acid (the imitation of induced resistance to insects) increases the expression of cysteine proteinases in the intestines of the beetles. Asparagine proteinase inhibitors were synthesized in the treated leaves [77]. Plant xenobiotics are transformed in insect bodies primarily by the detoxification system [78]. For example, the activity of esterases increases in the intestines of Myzus persicae when these insects feed on tobacco plants with a high content of niacin compared to feeding on pepper plants [79]. Esterase activity increases in Spodoptera litura when fodder plants are rich in phenols [80]. An increase in GST activity (an enzyme of the detoxification system) was detected in the intestines of *Spodoptera frugiperda* and *Trichoplusia ni* when they fed on a substrate with glucosinolates [81]. Glucose oxidase from the saliva of *Helicoverpa zea* larvae reduces the synthesis rate of nicotine in *Nicotiana tabacum* plants as a response to the acceleration of the nicotine synthesis induced by insect damage [82]. In our opinion, the causes of the development of feeding specialization in phytophagous insect species are a question for discussion. It is necessary to re-examine the needs of phytophagous insects as first-order consumers because they define the character of their interactions with fodder plants and to determine the factors that correct these relationships. From the ecological perspective, the feeding specialization of phytophagous insects can be viewed as a means of preserving and maintaining the stability of the system "producer – consumer". The complex of coadaptations forms between species in food chains in dependence to a complicated constellation of antagonistic relationships between consumers and food objects [83]. For example, we observed that food resources had different effect on the potato ladybird beetle populations depending on the genotype of the potato variety [84]. The mechanisms of this influence are based on allelochemical interactions in the system "phytophagous insect – plant recipient" [85]. Releasing metabolic products into the environment is the characteristic of any living organism. The main biological principle (in both ontogeny and phylogeny) is the consistent adaptation of one species to the metabolic products released by other species into the mutual environment. Each individual in an ecosystem releases different metabolic products into the environment and thus creates specific environmental conditions, which might be toxic, favorable or neutral for nearby plants, phytophagous insects, and microorganisms [86]. In 1996, the International Allelopathy Society expanded its definition of allelochemical interactions by including any processes with the secondary metabolites produced by plants, microorganisms, viruses, and fungi and influencing the growth and development of agricultural and biological systems [87]. Allelopathic interactions are one of the most complex interactions because both direct and indirect effects are intertwined in this form. The direct influence is determined by the metabolites released by plants and the indirect influence is connected to the activity of insects, microorganisms, and fungi. The allelopathic influence can be not only negative but also positive because plant and microbial discharge were found out to contain all the discovered natural organic compounds [88]. The plants damaged by phytophagous insects activate defense mechanisms, which are constituted by several components, such as an increase in the concentration of secondary metabolites, including phenols. An infected plant having a higher concentration of phenolic compounds might demonstrate a higher allelopathic activity when these compounds are released into the environment. An increase in the concentrations of allelochemicals due to the damage caused by insects to plants may also affect the synchronicity of the development of insects and their predators [89]. In other words, it is supposed there are combinations of allelochemicals that might seriously harm insects but be beneficial for their predators at the same time. Although the biosynthesis, accumulation, and release of secondary metabolites, including allelochemicals, are often organized through interpreting a signal by target plants and the subsequent cascade of transduction, the new role of allelopthy is the transduction of signals. This occurs when compounds of indirect effect are released into the environment because allelochemicals have a signal nature (referred to as semiochemical or chemical signals) in relation to acceptor plants [90]. A host plant can release these chemicals as volatile compounds and root exudates not only from damaged organs but also systemically from non-damaged ones, which are activated at early stages of the signal cascade [91]. A secondary plant metabolite is an allelochemical if it can directly or indirectly affect target plant species, and the effect is allelopathic in this case [92].

Conclusion

To get an idea of the intraspecific structure, researchers can study geographical and biotope populations within the habitat range of species. From the evolutionary and ecological perspective, the diversification of population could be viewed as the process aimed at the most effective adaptation to local conditions and resulting in the development of ecological, genetic, and phenetic differences among them [93]. For this reason, the agroecological monitoring of the consequences of ever-increasing anthropological impact on agroecosystems should be an essential element of modern technologies for crop production. The monitoring should include the analysis of changes in species, intraspecific, and intrapopulation biodiversity of all-level consumers in agroecosystems and, first of all, in the diversity of dominant and superdominant pests. These species can serve as test objects (bioindicators) for identifying the consequences of the anthropological transformation of agroecosystems. The results of the monitoring should be considered when developing zonal systems for phytosanitary management in agroecosystems to achieve the high efficiency of plant protection measures by hindering the adaptation of consumers to plant protection products and other specific factors of agricultural production.

Management of processes of intra-water divergence of insect-phytophages in agrobiocoenoses in order to prevent the emergence of races and populations of pests adapted to live on initially resistant to them plant forms is possible in compliance with the transition to a targeted selection of agricultural crops for resistance to a complex of pests.

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