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Synopsis

Current Trends in the Studies of Allelochemicals for Their Application in Practice

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Abstract. The allelochemicals have been largely used in agriculture, forestry, landscape design and ornamental plant growing for many decades. However, there is a lack of the comprehensive studies, where existing publications are analyzed and synthesized with regards to the theoretic aspects for such usage. The objective of this paper was to systemize the advances in the research on allelochemicals' application in practice. Numerous novel methodological propositions have risen recently. We classified them into the physical, chemical, biological, biotechnological and crop-growing approaches. The allelochemicals consist of the wide diversity of the substances according to their chemical nature. Among these substances we outlined, firstly, the unidentified plant exudates and the products of green manuring, secondly, the chemically characterized or purified substances, which include alcohols, organic acids, aliphatic compounds, aromatic, alicyclic and nitrogen-contain organic compounds. Several groups of the biotic sources of allelochemicals were described: dicotyledonous and monocotyledonous plants, particularly under their colonization by non-pathogenic strains of *Fusarium oxysporum*, marine flora and fungi, which exhibit the herbicidal activity. Different targets of the allelochemical application were listed in the paper and they were categorized into several groups: higher flora, animals, unicellular and multi-cellular fungi. We concluded that there is lack of the modern multifaceted knowledge bases for the information about the allelochemical application. Those knowledge bases must be useful in order to choose the appropriate biological method for solving each particular problem of plant cultivation. To that end we systemized the results of current investigation about the usage of allelochemicals in practice.

Key words: allelochemical, crop-growing, crop protection, donor, mechanism of action, organic farming, pathogen control.

Introduction

The allelopathy, since its formation, has evolved from the pure theoretical science into the sphere of knowledge, which is practically beneficial for the humanity. Nowadays the allelopathical researches, directed on the solving of applied tasks, are progressing rapidly. The evaluation of the economical effects, which depend on the presence or the absence of the allelochemicals, is the significant aspect of these researches, but not unique one. The scientific basis is the indispensable prerequisite for such evaluation. It mostly has to do concern with the methodological principles for the management of the applied studies, the knowledge about the chemical properties and the origin, finally the targets and the effects for the impact of the allelochemicals. The comprehension of these effects will be rather incomplete, if the mechanisms of the realization of the allelopathical processes remain unknown. This review especially focuses on the procedures of crop protection. Here the benefit from the allelopathic processes is proposed to be considered as the alternative for the pesticide application, with its harmful consequences.

Primary term 'allelochemicals' meant the out-organism regulators for the biological processes, which are formed with the direct or indirect participation of the plants (GRÜMMER, 1955). However in world scientific fiction the allelochemicals also have been traditionally considered as the compounds, which are synthesized by plants and associated microbiota in order to manage the various biological processes.

Novel methodological achievements in studies on allelochemicals

There exists the modern interpretation of the allelopathy – the multidisciplinary science, where ecologists, chemists, soil scientists, agronomists, biologists, plant physiologists and molecular biologists offer their skills to give an overall view of the complex interactions occurring in a certain ecosystem (MACÍAS *et al*., 2007).

Jack bean *Canavalia ensiformis* (L.) DC. is known to be slightly vulnerable to diseases. This observation may be considered to be a significant methodological question. That is why this species was proposed to be used as the model object in the allelopathical investigations (SANTOS *et al*., 2010).

In the following brief analysis of the recent methodological propositions for the allelopathy we grouped them into several directions: physical, chemical, biological and related with the manufacturing – the crop-growing one.

The novel methods, based on the physical principles:

- electrospray time-of-flight mass spectrometry – ESI-TOFMS (BONNINGTON *et al*., 2003);

- methods of high resolution, such as the UV-analysis, the mass-spectrometry, and the NMR, which are applied to identify the chemical structure of the substance, e.g. myrigalone A (POPOVICI *et al*., 2011).

The novel methods, based on the chemical principles:

- solid-phase microextraction, which provides the detection of the traces of substances, e.g. 1,8-cineole, camphor, coumarin, menthol, and carveol, also the last one is not up-taken by tomato *Lycopersicon esculentum* (LOI *et al*., 2008);

- HPLC (LING *et al*., 2013), and HPLC, combined with the collection of the extractions on the matrix XAD-4 (KURTZ & SHOUTEN, 2009);

- sequential two-steps cation-exchange chromatography for the extraction the protein from the latex (DE FREITAS *et al*., 2011);

- capillary electrophoresis (SANTOS *et al*., 2010);

- optimization of the concentration and the time of the exposition in the course of the extraction of aquatic macroflora with the ethyl-acetate (WU *et al*., 2013).

The novel methods, based on the biological principles:

- combination of the following conditions: Hoagland nutrient medium (pH 6,0); 25°C, 12/12 h light/dark photoperiod, irradiance of 280 mcmol/(m^2 s) for 24 or 48 h for the examination of the plant responds on the exogenous treatment with the allelochemicals were tried (DOS SANTOS *et al*., 2008);

- disc diffusion method (VU *et al*., 2012).

The biotechnological approaches:

- *in vitro* conditions (WU *et al*., 2009);

- cloning of the genomes of the investigated objects for their subsequent sequenation (YANG *et al*., 2013);

- knock-out of genes, that control the biosynthesis of the certain plant-toxic metabolite: this technique was successfully demonstrated through the example of terpene synthases (OsCPS4 and OsKSL4), responding for the momilactone formation (XU *et al*., 2012).

Methodological discoveries in crop-growing:

- demonstration of the amplification of the effect of certain allelochemicals and herbicides on plants due to their combination (FAROOQ *et al*., 2011);

- induction of the resistance for the wilt by means of non-pathogenic form of *Fusarium oxysporum*; here it was confirmed that the diagnostic attributes, important for the detection of this effect, were: a) rapid spore germination; b) orientation in response to root exudate; c) active penetration in roots; d) passive conidia transport in stem; e) enough lag period between induction and challenge inoculation (MANDEEL, 2006);

- prevention of the wilt during the Japanese bunching onion *Allium fistulosum* seeds germination by means of the treatment with the freeze-dried root exudates from shallot *Allium cepa* Aggregatum group (VU *et al.*, 2012);

- suppression of the algae blooms due to the application of the plant extracts without increasing the release of cyanotoxin (WU *et al.*, 2013);

- recirculating hydroponic culture system, developed for continuous trapping of the root exudates (LING *et al.*, 2013).

Chemical nature of allelochemicals

The range of allelochemicals is very diverse in sense of their chemical nature. Many of them are applied on practice. It is reasonable to divide them into two groups of the agents: 1) the materials without accurate chemical identification; 2) the substances or the groups of substances, which are more or less chemically characterized or purified at least.

The first of these groups, particularly, includes the volatile and gaseous exudates of the belowground part of the young stone fruit trees (AFIFI *et al.*, 1977), and the gaseous exudates from the germinating seeds of corn *Zea mays* L. and lentil *Lens culinaris* Medicus (CASTKA & VANCURA, 1980). This group must be also enlarged by the products from the plant decomposing residues, leachates and crude homogenates, which come in the root-containing soil horizons. Listed materials may serve for the nematode control. Elaborated crop-rotation system, intercropping, usage the rapid-growing crops with the responding allelopathic properties provide the enrichment of the rhizosphere with the mentioned products. Same effect may be achieved under the green manuring with such plants (HALBRENDT, 1996). It sounds interesting, but unordinary that the plant pathogenic fungi are allelopathically affected by the pollen and in greater measure by the propolis, originated from five Turkish regions (OZCAN *et al.*, 2004). The allelopathic analyses involve volatiles from the crushed leaves (ZHANG *et al.*, 2008). The resins from the sweet potato *Ipomoea batatas* (L.) Lam., and the residues of the semi-tropical leguminous plants have been tested as insecticides (DUKE *et al.*, 2003). The metabolites from the marine flora have been several times reported to act both as antifeedants and as allelochemicals within recent years. Nevertheless there are few studies on the role of these substances in the suppression of the competitive plants (see the final part of this article) (SIEG & KUBANEK, 2013).

In the second group there exist the compounds, which are made by explorers with a certain purposes. Some of them have completely uncharacterized chemical nature. Thus BARAZANI & FRIEDMAN (2001) proposed to yield two herbicidal preparations (phosphinothricin and bialaphos) on the basis of three active ingredients, which were the phytotoxins: geldanamycin, nigericin and hydanthocidin. These substances were produced by the plant pathogenic fungi.

The researches on the allelochemicals have been related with the identification of the organic substances with the different structural complexity. These could be, particularly, the mixture of ethanol and methanol with acetaldehyde (CASTKA & VANCURA, 1980); organic acids (their effect has been tried together with saccharides) (KRAVCHENKO *et al.*, 2003); aliphatic organic substances and carboxylic acids (TADDEI *et al.*, 2002), including propanedioic acid (JU *et al.*, 2002). The above-mentioned agents have been examined mostly within the root exudations.

The number of substances, being in the solutions, act as low-molecular carboxylic acids. These are saccharides (TADDEI *et al.*, 2002; KRAVCHENKO *et al.*, 2003); saponins from ginseng *Panax ginseng* C.A.Meyer – ginsenosides (YOUSEF & BERNARDS, 2006); saponin chitosan and also 2-deoxy-*D*-glucose (DUKE *et al.*, 2003). Alkanes, fatty acids, and esters (LI *et al.*, 2009; 2013a) present the allelochemicals with more remote properties.

Traditionally the experts in the allelopathy have shown the significant interest in substances, which include the phenolic fragments, aryl groups. The studies on the phenolic derivates provide the advantages for the human practical activities. The list of the most investigated simple aryl substances includes: resorcinol, derived from the seedlings of the aquatic macrophytes (SÜTFELD *et al.*, 1996), acting as an important regulator of the relations between macrophytes and other aquatic inhabitants; soybean-produced phthalic (JU *et al.*, 2002) and benzoic (WU *et al.*, 2009) acids. The last one served for the artificial simulation of the allelopathic impact. The larger number of the researches deals with more complex aryl derivates – the aromatic structures, bound with the aliphatic tails. The aromatic substances in the root exudates from cornflag *Gladiolus communis* L. (TADDEI *et al.*, 2002); caffeic, cinnamic, and chlorogenic acids from the cucurbits crops (LING *et al.*, 2013) have been examined. Also the mechanisms of the action of ferulic acid (DOS SANTOS *et al.*, 2008) and coumarin (LOI *et al.*, 2008) on the plant organisms, myrigalone A from the fruits and leaves of myrtle *Myrica gale* L. on knotweed *Fallopia* × *bohemica* (Chrtek & Chrtková) J. P. Bailey, which had invaded in the North American habitats (POPOVICI *et al.*, 2011), as well as cinnamic, *p*-coumaric, ferulic, syringic, and vanilic acids on the pathogens of wilt (WU *et al.*, 2010) have been diligently clarified.

Sorgoleone has been known as a major component of the hydrophobic root exudates from *Sorghum bicolour* (Moench) L. It can serve as a demonstrative example of the aryl groups, coupled with bulky linear aliphatic structures. In South Korea this substance was utilized for the formulation of the preparation, which is a wettable powder (4.6 WP) (UDDIN *et al.*, 2014).

Among the traditionally depicted allelochemicals there are not only the compounds, containing the aromatic cycles, but along with them there are also alicyclic substances. The latter may be classified into several groups. The non-terpenic structure resides in coffein (ASHIHARA *et al.*, 2008), camphor, carveol, and menthol (LOI *et al.*, 2008), myrigalone A (additionally to its aromatic residue) (POPOVICI *et al.*, 2011), as well as in momilactones A and B, which are common for the roots of rice *Oryza sativa* L. (KATO-NOGUCHI, 2011; XU *et al.*, 2012). These are the agents form the first group. Monoterpenes (e.g. 1,8-cineol), diterpenes (labdane- and casbane-type (SHMELZ *et al.*, 2014)), and sesquiterpenes (eremorhilane-, eudesmane- (GARSIA *et al.*, 2003), and β-macrocarpene-derived (SHMELZ *et al.*, 2014)) can be believed the following three groups of the alicyclic allelochemicals. It is supposed that the metabolites, listed in the second and third groups, could act as phytoalexins.

The great number of the allelochemicals is presented by the nitrogen-containing organic substances. Non-polymeric ones include 2,4-dihydroxy-1,4(2H)-benzoxazin-3-one (DIBOA), 2(3H)-benzoxazolinone (BOA), and 2,2'-oxo-1,1'-azobenzene (AZOB), which were found in rye *Secale cereale* L. (CHASE *et al.*, 1991). 2,4-Dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) was discovered to support the defence of the live organisms against aluminium (POSCHENRIEDER *et al.*, 2005). The polymeric nitrogen-containing compounds include reported about the number of proteins, particularly containing in the plant latex: CpLP from Sodom apple *Calotropis procera* (Aiton) R.Br, PrLP from templetree (Pagoda tree; frangipani) *Plumeria rubra* L., P1G10 from mountain papaya *Carica candamarcensis* Hook.f., and also EtLP from aveloz *Euphorbia tirucalli* L. Their antifungal activity was compared with the same property of cysteine proteinase CMS2MS2 from *Carica candamarcensis*, papain (EC 3.4.22.2) and cysteine proteinase from papaya *Carica papaya* L., trypsin (EC 3.4.21.4) and chymotrypsin (EC 3.4.21.1), two serine proteases (SOUZA *et al.*, 2011). The similar action against plant pathogenic organisms was described for osmotin- and thaumatin-like proteins from *Calotropis procera* latex (DE FREITAS *et al.*, 2011).

Biotic sources of allelochemicals

It is reasonable to consider the sources of allelochemicals, which are mentioned in the publications. First of all it needs to be said, that the allelochimicals mean not only the metabolites themselves, but also the diverse preparations, which are applied for the artificial simulation of the physiological effects, taking place in the interspecific relationships.

Wishing to present better the knowledge about the allelochemicals' donors in this article, we divided them in following way: firstly, into crops and uncultivated plants, secondly, into monocotyledons, dicotyledons and the plants of other taxonomic groups.

The most investigated allelopathic donors among the monocotyledonous crops have been *Secale cereale* (CHASE *et al*., 1991), corn (CASTKA & VANCURA, 1980; POSCHENRIEDER *et al*., 2005), barley *Hordeum vulgare* (LANOUE *et al*., 2010a; 2010b), *Oryza sativa* (KATO-NOGUCHI, 2011; XU *et al*., 2012), and also several vegetable crops, such as garlic *Allium sativum* L. (cv. Caijiapo та Cangshan) (ZHOU *et al*., 2011), *Allium cepa* group Aggregatum (VU *et al*., 2012), Chinese anion *Allium chinense* G.Don (YANG *et al*., 2013), which excrete biological active substances through the root system.

The non-pathogenic strain *Fusarium oxysporum* Fo162 endophytically colonizes the bananas *Musa* × *paradisiaca* L. It evokes the plants' the system responds. Particularly the chemical content of the root exudates alters (KURTZ & SCHOUTEN, 2009).

Momilactones A and B have previously been reported to be found out in *Oryza sativa* and moss *Hypnum plumaeforme* Wilson only. Meanwhile these specific metabolites have been known to act as the allelochemicals and the phytoalexins. H. KATO-NOGUCHI (2011) proposed to spread taxonomic screening of the plant diversity for presence of the momilactones and for analysis of their functional role. The flora of the Earth is well-known to be not restricted by two abovementioned species. The author dwelt on the analysis of the evolutional processes in the plant world by means of the mentioned biosynthesis products.

The dicotyledonous crops were studied as well. It was tested the potential of the green manure with rapeseed for the nematode control (HALBRENDT, 1996) and the herbicidal abilities of the sorghum root exudates (UDDIN *et al*., 2014). The new possibilities of the natural control of pests and pathogenic fungi were discovered concerning chili pepper *Capsicum frutescens* L., *Ipomoea batatas*, and the residues of the semi-tropical leguminous plants (DUKE *et al*., 2003). The anti-fungal properties of *Lens culinaris* (CASTKA & VANCURA, 1980), *Lycopersicon esculentum* (ZHANG *et al*., 2008) (particularly under fungal microsymbiont colonization (SCHEFFKECHT *et al*., 2006)), ginseng *Panax ginseng* C.A.Meyer (YOUSEF & BERNARDS, 2006), the germinating seeds and the roots of the seedlings of apricot *Prunus armeniaca* L. (AFIFI, 1977), the root exudates of *Lycopersicon esculentum* (KRAVCHENKO *et al*., 2003), soybean *Glycine max* Moench (HAN *et al*., 2005), seven year melon *Cucurbita ficifolia* Bouche (HUANG *et al*., 2007) were found out. Also the natural mechanisms of the chemical defense and allelopathic properties of some species of *Camellia* L., *Coffea* L., *Theobroma* L., and *Ilex* L. genera were described (ASHIHARA *et al*., 2008). The biochemical distinctions of genetically modified (GM) insect-resistant cotton *Gosypium hirsutum* L. comparing to the parental lines were characterized. In the both cases the similar types of substances were revealed, but the unsimilar content of the metabolites in separate types and the unsimilar quantitative ratios between the different types of compounds were observed. E.g., the type and content of the fatty acids and esters were significantly reduced, whereas some alkanes were increased in the root exudates of the GM *Gosypium hirsutum*. By the way some specific components were revealed among these esters (LI *et al*., 2009; 2013a).

It was assumed, that the specifics in the content of the root exudates of the susceptible (Ganhua-5) and mid-resistant (Quanhua-7) cultivars of peanut *Arachis hypogaea* L. took part in the formation of the mechanisms of the plant resistance for infection with plant pathogens from the rhizosphere soil (LI *et al.*, 2013b).

LING *et al.* (2013) revealed the discrepancy in the content of root exudates of watermelon *Cucurbita citrullus* L., grafting onto bottle gourd *Lagenaria siceraria* (Molina) Standl., comparing with the own-watermelon and own-bottle gourd exudates. Salicylic acid was identified in all three root exudates, but chlorogenic, caffeic and cinnamic acids were abundant only in separate variant of exudates.

Speaking about the uncultivated plants, first of all the studies, conducted on the aquatic plants: on the marine flora (authors didn't define its specific content) (SIEG & KUBANEK, 2013); on the fresh-water macophytes (namely on the exudates of yellow water-lily *Nuphar lutea* (L.) SM.) (SÜTFELD *et al.*, 1996); on water lettuce *Pistia stratioles* L. (WU *et al.*, 2013) as well as on fresh-water and marine cyanobacteria (BERRY *et al.*, 2008) must be mentioned.

Meanwhile the vast range of the cases of the allelopathy, displayed by the terrestrial uncultivated plants, was studied.

Studying allelopathic properties of neem *Azadirachta indica* A.Juss, the researchers obtained azadirachtin. To this end they used the alcohol extraction of the seeds from this plant. The researchers (GOPAL *et al.*, 2007) observed the series of the indices of the functioning of the micro- and macroflora, related with plants and soil, under impact of the granulated 10 % azadirachtin. The other works pertained the testing of the properties of the laticifer plants (*Calotropis procera*, *Plumeria rubra*, *Carica candamarcensis*, *Euphorbia tirucalli*) to control plant pathogens as well as the possibilities of the fruit and leaves of *Myrica gale* to control weeds (POPOVICI *et al.*, 2011).

Whitetop weed *Parthenium hysterophorus* L. drastically reduces harvest of crops in America, Asia, Africa, and Australia. However PATEL (2011) described the range of the benefits from the utilization of this species. The plant may serve for the removal of heavy metals and dyes from the environment, the eradication of aquatic weeds, the usage as substrate for commercial enzyme production, as additives in cattle manure for biogas production, as biopesticide, as green manure and compost. The compounds, responsible for hazardous properties, were reported to be present in this species.

A number of researches investigate the anti-fungal potential of the plants. Contrastingly some of the studies focused on the herbicidal activity of the fungi: *Streptomyces hygroscopicus* and *S. viridochromogenes* (BARAZANI & FRIEDMAN, 2001).

Target objects for practical application of allelochemicals

The sense of allelopathy can be formulated as one of the forms of the interactions between the organisms, mediated by means of substances, commonly called chemical interactions. Allelopathy is distinguished from the inter-organism interactions by the participation of plants. The latest can act as donors, acceptors, sometimes even as modifiers of BAS. This opinion makes us consider the targets and the effects of the action of the allelochemicals to be one of the most important issues for the applied studies in allelopathy in the last part of the article.

For the purposes of discussion these targets can be divided into plants and other representatives of biota: microbiota, mycobiota and animals (mostly invertebrates). There are the favorable and antagonistic, the beneficial and deleterious organisms among these objects. The pathogenic fungi occupy the lion part of the unfavorable organisms.

For example, the Agricultural Research Service of the USDA set the goal of searching the molecular mechanisms of the action of the insecticides and the fungicides, which are obtained from the natural sources (DUKE *et al.*, 2003). In this research authors revealed several novel molecular sites for the action of the tested substances. The sites responded the asparagine synthetase and the fructose-1,6-bisphosphate aldolase. The genes for polyketide synthases involved in production of pesticide polyketide compounds in fungi were discovered. It may serve as the new clue for the pesticide application.

The novel way of the utilization of bacterial BAS to control algae, noxious plants and pests, particularly in the aquatic environments, was proposed in the similar, but later work (BERRY *et al*., 2008).

Higher flora as targets

Substances with the allelopathic properties act on the vast range of the higher plants, as it follows from the investigations. Some of them were proposed to be used as the model objects. Particularly we have already mentioned *Canavalia ensiformis* as one of the models (SANTOS *et al*., 2010). The seeds of lettuce *Lactuca sativa* L. cv Blackseeded Simpson and barnyardgrass *Echinochloa crus-galli* (L.) Beauv cv Kudiraivali were ascertained to serve as indicators in the studying of the physiological properties of momilactone (XU *et al*., 2012). At the same time the allelopathic properties of the mature plant: *Allium chinense* were indicated with *Cucumis sativa* (YANG *et al*., 2013). The latest study treated the stimulation of test seedlings by the root exudates of donor plants.

Cress *Lepidium sativum* L., *Echinochloa crus-galli*, cucumber *Cucumis sativus* L. and snap bean *Phaseolus vulgaris* L. were used as indicators in the examinations of the action of the hydroxamic allelochemicals on the test plants. AZOB, BOA and DIBOA were all applied singly at 50, 100, and 200 ppm and in two- and three-way combinations, where the total concentrations reached 200 ppm. The treatment with 100 and 200 ppm AZOB inhibited plants worse (38-49 %) comparing with the treatment with DIBOA. The three-way combination, contained 100 ppm AZOB + 50 ppm BOA + 50 ppm DIBOA, depressed plants more considerably (54-90%), than BOA+DIBOA mixture. Under the examination of the joint action of the hydroxamic acids allelochemicals on the germination and growth barnyard grass plants exhibited the slight antagonistic response, cress – the synergetic ones, while snap beans and cucumber – the both types of the response (CHASE *et al*., 1991).

Two species from the Cryptophytaceae completely eliminate the presence of resorcinol in the aquatic ecosystems with the concomitant increase of the size of starch granule enclosures. Futhermore, this substance depresses the model object, which belongs to animals – daphnia. However, SÜTFELD *et al*. (1996) observed no effects on Cyanophyceae and Chlorophyceae.

BARAZANI & FRIEDMAN (2001) demonstrated that sometimes the higher plants under the allelopathic influence of bacteria exhibited the distinctions even on the levels of subspecies and cultivar. This was proved on *Lactuca sativa* and wheat.

LOI *et al*. (2008) showed the fact of the uptake of the BAS by common radweed *Artemisia annuifolia* L., *Lycopersicon esculentum*, and purslane *Portulaca oleracea* L. These scholars emphasize on the pivotal importance of this phenomena in the allelopathical studies. There is a lack of methods to measure allelochemical uptake in the natural conditions. So the idea about the activity of these substances may be judged on the basis of their observed toxicity. The authors stated that the elaboration of the solid-phase microextraction (see above: the part 'Novel methodological achievements in studies with allelochemicals') provided the new possibilities for the extraction for the observation on the transport of compounds inside the target plants.

Myrigalone A is considered to be effective environmental unthreatening herbicide with the potential to mitigate the *Fallopia* × *bohemica* invasion (POPOVICI *et al*., 2011).

The treatment of the lettuce seeds with the root extractions of *Allium sativum* in 10- and 5-fold dilutions improved the germination and the growth of the lettuce. Vice versa, these processes were suppressed by the higher (40% and 60%) concentrations of the extractions, especially obtained from cv. Caijapo. Thus, the lettuce exhibited the two-phase respond, depending on the concentration of the allelochemical (ZHOU *et al*., 2011).

The broadleaf weeds were more susceptible than grass species to sorgoleone according with the seed germination and shoot growth. At the concentration 0.2 g/l (a.i.) sorgoleone the inhibition of the germination and the growth of the broadleaf species were achieved in a growth chamber study reached 100%. The growth of the weeds was supressed 20-25 % greater under the post-emergence application of sorgoleone comparing to the pre-emergence one in the greenhouse experiments. The developed preparation inhibited the growth more than 90 % of the analysed broadleaf species in all experimental conditions. Japanese sorrel *Rumex japonicus* Houtt. as well as Chinese plantain *Plantago asiatica* L. were completely suppressed under 0.4 kg(a.i.)/ha sorgoleone. The crops proved to be less susceptible to sorgoleone even under 0.4 kg(a.i.)/ha, that was the highest of the tested dose, exhibiting only 30 % diminishing of the growth. Thus, the impact of wettable powder (4,6WP) of sorgoleone on the weeds specifically distincted from the same impact on the crops (UDDIN *et al.*, 2014).

Unicellular organisms and multi-cellular fungi as targets

The Canadian scientists focused on the range of the allelopathic effects of *Panax ginseng* on the soil microbiota (YOUSEF & BERNARDS, 2006). The article of BERRY *et al.* (2008) was devoted to the influence of the BAS from cyanobacteria on the microorganisms and the water macrophytes.

GOPAL *et al.* (2007) quantified the amount of the various representatives of microbocenosis, including fungi, as well as the dehydrogenase, phosphatase activity and respiration of the soil under the impact of azadirachtin. The listed indices were estimated fifthly: simultaneously and on the 15th, 30th, 60th and 90th day after the treatment of the sandy loam soil, collected from the field, with azadirachtin. It was found that the preparation inhibited actinomycetes, fungi and bacteria, including nitrifiers, and the intensity of the soil respiration, but didn't acted on *Azotobacter* sp. The listed observations were the most severe in the first 15 days. The populations of bacteria, actinomycetes, the respiration, and the phosphatase activity were recovered after the 60th day, in contrast to the fungi and the nitrifiers. Very high biocidal effects were achieved at the two- and five-times doses of the tested substance.

The anti-algal effect of water lettuce root exudations on the algae *Microcystis aeruginosa* and the excretion of microcystin-LR by the cells of this alga were registered. The lowest concentration of this allelochemical, enabling the strongest anti-algal half-effect, equaled 65 mg/l. The allelochemicals, extracted with the solvent – ethyl acetate, exhibited the strongest inhibitory effect on the growth of algae when used within a dose range of 60-100 mg/l. The relative inhibitory ratio reached 50-90%, the reduction of chlorophyll a content – 50-70%. However the intensity of the microcystin-LR excretion into the environment left stable (WU *et al.*, 2013).

The root exudates of *Allium cepa* increased the population and improved some species of bacteria, actinomycetes, and improved the structure of their communities in the rhizosphere soils, on the one hand, but decreased the fungal community, including the plant pathogen *Fusarium* sp., on the other hand. These effects were most significantly caused by onion cv. L-06 with the high allelopathic activity (YANG *et al.*, 2013).

The root exudates of *Lycopersicon esculentum* influence on the growth and anti-fungal activity of the pseudomonade strains, stimulating the plant growth. KRAVCHENKO *et al.* (2003) believed saccharides and organic acids to enhance this effect.

We find it reasonable to dwell on the numerous researches, which study how the plant metabolites of the various origin and chemical nature influence on the plant pathogenic fungi. First of all the *Fusarium* sp. are to be mentioned (e. g. VU *et al.*, 2012).

Some plant metabolites of the germinating seeds and the roots of the apricot became known to provide the mechanism of the virulence of *F. solani* through the enhancing the mycelium growth and the conidia germination of the plant pathogen (AFIFI, 1977). Likewise the volatile exudates from the lentil cultivar, which is susceptible to the series of the agent of the root diseases, promoted the germination of the *Botrytis cinerea, Mucor racemosus, Trichoderma viride, Virticillium dahliae*, and especially *Fusarium oxysporum* spores. However the analogous exudates of the less susceptible cultivar restrain this process (CASTKA & VANCURA, 1980).

The continuous cropping of *Glycine max* leads to the accumulation of the infectious agents in soil. The laboratory experiments, the sand and water cultures were used to investigate this problem. The promotion of the growth of *F. oxysporum*, *Gliocladium roseum*, and especially *F. semitectum* were registered under the continuous cropping, but not under the control variant – the rotation system. The root exudates in lower concentrations stimulated the growth rather than in higher ones. Moreover, the continuous *Glycine max* cropping exhibited this effect stronger comparing with the control variant. The significant and the especially significant levels of the suppression of the three above-mentioned pathogens were reached under the high concentration of phthalic acid and propanedioic acids. *F. semitectum* exhibited the greatest decline. Nevertheless the low concentration of these acids led to the considerable stimulations of all three pathogens (JU *et al*., 2002).

Gladiolus communis cv. White Prosperity is more resistant to *F. oxysporum* f. sp. *gladioli* than susceptible cv. Spic Span. Probably the increased content of the aromatic compounds within the root exudates induces the exhibition of anti-fungal properties of gladiolus cv. White Prosperity (TADDEI *et al*., 2002).

The extract from the propolis inhibit *F. oxysporum* f. sp. *meloni* stronger comparing with *Alternaria alternata* (OZCAN *et al*., 2004).

HAN *et al*. (2005) reported about the following distinctions, which were exhibited by plant pathogens, tested for the interaction with *Glycine max* roots (Table 1).

Table 1. Effects of the different fractions of root exudation on the plant pathogens

<table>
<tr><th rowspan="3">Infestant</th><th colspan="4">Fraction of root exudations and genotype of Glycine max</th></tr>
<tr><th>water-soluble carbohydrates</th><th colspan="2">water-soluble amino acids</th><th>organic acids</th></tr>
<tr><th>both genotypes</th><th>9536</th><th>Jilin 30</th><th>both genotypes</th></tr>
<tr><td>Fusarium oxysporum</td><td rowspan="2">stimulation at low and suppression at high concentrations</td><td rowspan="3">significant suppression at mid and high con-centrations</td><td rowspan="3">mostly stimulation at mid and high con-centrations</td><td rowspan="3">significant suppression (concentrations aren't pointed)</td></tr>
<tr><td>Fusarium semitectum</td></tr>
<tr><td>Gliocladium roseum</td><td>no effect</td></tr>
</table>

Consequently the various genotypes of *Glycine max* can have different potential to suppress the agents of root rots.

The properties of the arbuscular mycorrhiza are suggested to be inconstant. The increment of the level of root colonization with symbiotic fungus results in the promotion of microconidia germination. The investigation of the mutualistic pair of *Lycopersicon esculentum*–*Glomus mossea* testifies that the exudates of mycorrhiza facilitated the germination of the *F. oxysporum* f. sp. *lycopersici* conidia. The tests with the different phosphorus levels allow concluding, that the improving of the phosphorus status of plants doesn't cause the enhancing of microconidia germination (SCHEFFKNECHT *et al*., 2006).

The volatiles, emitted from *Lycopersicon esculentum*, decrease their inhibitory efficiency on the spore germination and mycelia growth of *F. oxysporum* and *Botrytis cinerea* in the following order: plants in anthesis stage>10-leaf>2-leaf plants. It was noted that the first above-mentioned pathogen was more susceptible to the exudates of *Lycopersicon esculentum*, than the second one (ZHANG *et al*., 2008).

Exogenously supplied ferulic acid induced premature cessation of root growth, with disintegration of the root cap, compression of cells in the quiescent centre, increase of the vascular cylinder diameter, earlier lignification of the metaxylem, as well as the reduction of the activity of cinnamyl alcohol dehydrogenase (EC 1.1.1.195) with the concomitant increased peroxide level, activity of the anionic isoform of peroxidase (EC 1.11.1.7) and lignin content in roots. Piperonylic (heliotropic) acid (an inhibitor of the cinnamate 4-hydroxylase), being applied jointly with the feruloyl-CoA, promoted the lignin content (DOS SANTOS *et al*., 2008).

Benzoic acid stimulates some factors of the virulence of *F. oxysporum* f. sp. *niveum*, although it suppresses the growth of mycelium (83-96 %), the sporulation, and the conidia germination under the application in 0.2 ‰ concentration (WU *et al*., 2009).

Gosypium hirsutum can acquire the chemical properties, which enhance its resistance to *F. oxysporum* due to the genetic modification (LI *et al*., 2009; 2013a).

The inoculation of barley *Hordeum vulgare* with *F. graminearum* led to the significant increase of the pools of *trans*-cinnamic, *p*-coumaric, ferulic, syringic and vanilic acids in the root exudates within 2 days. The biosynthesis of *trans*-cinnamic acid occurred simultaneously. The biochemical alternations, caused by the inoculation, inhibited the germination of the *F. graminearum* macroconidia. The exudation of this metabolite from the roots accompanied with its accumulation in roots. The natural mechanism of the barley resistance to plant pathogens may be the result of the de novo biosynthesis and exudation of the substances with anti-pathogenic properties (LANOUE *et al*., 2010a). It was supposed that wild or less domesticated varieties exhibited the described mechanism more strongly, than the domesticated cultivars (LANOUE *et al*., 2010b).

Gallic acid has been known as allelochemical and its application at 0.08 % concentration (1250-fold dilution) inhibited the growth and the conidia germination of *F. oxysporum* f. sp. *niveum* on 9.5 % and 52.3 % respectively. This treatment furthered the sporulation and the synthesis of mycotoxin by this fungus. The gradual increment of gallic acid level was accompanied with the alternations of pectinase and protease activities. The both activities initially rose and then declined. Thus gallic acid has potential for the usage as environment friendly remedy, which enables to control the mentioned plant pathogens (WU *et al*., 2010).

The proteins from the plant latex can suppress *F. solani*. IC_{50} for CpLP was quantified as 2.07×10^{-2} ‰ and for P1G10 – 2.53×10^{-2} ‰. Both the thermal inactivation and the proteolysis eliminated this suppression, suggesting, that these are proteins, which respond for the inhibition. The reducing agent dithiothreitol improved the antifungal properties of CpLP and P1G10. However, the pre-treatment with iodoacetamide drastically reduced endogenous proteolytic activities and partially abrogated antifungal activity. The antifungal property could be directly regulated by the proteases, presenting in plant latex, because the vast range of the purified enzymes from the respective plants adversely influenced on the spores. The numerous proteases induced the effects, which were quite similar to those, observed for CpLP and P1G10. Papain, CpLP and CMS2MS2 enhanced the ROS generation and consequently oxidative stress in the spores of *F. solani*. The latex proteins seemed to be one of the factors of plant defense from the fungal disease (SOUZA *et al*., 2011). Likewise DE FREITAS *et al*. (2011) quantified IC_{50} for osmotin (the protein, purified from latex) as 6.7×10^{-2} ‰ regarding *F. solani*, 3.21×10^{-2} ‰ regarding *Colleotrichum gloesporoides*, and 5.75×10^{-2} ‰ regarding *Neurispora* sp.

The suppression of the spore germination and the mycelial growth of *F. oxysporum* directly depended on the concentration of the root exudates of *Allium sativum* with different resistance for the plant pathogen. *F. oxysporum* f. sp. *cucumerinum* exhibited greater susceptibility for the impact of these preparation, than *F. oxysporum* f. sp. *niveum* (ZHOU *et al*., 2011).

Caffeic and chlorogenic acids were suggested to enhance the wilt-resistance of watermelon onto bottle gourd rootstock. The inverse dependence of the spore germination and the conidial growth intensities on the doses of the both phenolic acids was determined with stronger inhibitory effect, was observed for chlorogenic acid (LING *et al*., 2013).

The processes of spore germination, sporulation, mycelia growth of such soil-borne plant pathogens as *F. oxysporum* and *F. solani* directly depend on the concentration of the root exudates from two cultivars of *Arachis hypogaea* L. One of them is susceptible and the other is mid-resistant for the wilt (LI *et al*., 2013b).

Animals as targets

The possibility to control the population of American dagger nematode *Xiphinema americanum sensu lato* by means of the green manuring was discovered due to the experiments in temperate orchards (HALBRENDT, 1996).

Sesquiterpenes are often considered as the allelochemicals. Their administration to red flour beetle *Tribolium castaneum* larvae evoked the morphological, chemical alternations and great lengthening in the duration of the pupal stage (GARSIA *et al*., 2003).

The plant nematodes slighter colonize the bananas roots under the symbiosis with one of the non-pathogenic strains of *F. oxysporum*. KURTZ & SHOUTEN (2009) ascertain that the chemical content of the extractions slightly modifies the inoculation of the bananas with this strain, excepting few compounds.

The relationship between the presence of the allelochemicals in plants and the behavior of their herbivores was critically reviewed (GLINWOOD *et al*., 2011).

The shredding and the chemical degradation of the detritus by animals and microorganisms, which belong to the detritivores, can be avoided due to the presence of the allelochemicals. Currently this phenomenon is considered to be a mechanism for the chemical defence of the marine flora. It results in the delaying the time before the plant matter enters the microbial loop (SIEG & KUBANEK, 2013).

Conclusion

The recent research trends reflect the present state of the allelopathy. Today this subject field adopts the approaches and the methods from the diverse branches of science extensively, increases the diversity of the examined objects (both in the taxonomical and ecological senses), as well as involves additional hierarchical levels for the observation of the allelopathic phenomena. These all don't only promote a better cognitive understanding, but also serve for the application of allelochemicals in the human practical activity. Particularly the results of the modern allelopathic studies meet the demands of crop protection, including the withstanding the pathogens – this can be concluded on the basis of the reviewed sources. It is arguable to predict, that the enhancement of the management of the wide spectrum of the natural phenomena will get better. It is important for the durable relationships between the human and the biosphere.

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