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review

Allelopathic interactions between plants. Multi site action of allelochemicals

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Abstract

Allelopathy is defined as mechanism of plant-plant, plant-microorganisms, plant-virus, plant-insect, and plant-soil-plant interactions mediated by plant- or microorganism-produced chemicals released to the environment. The majority of allelochemicals are secondary metabolites and among others belong to terpenoids, phenolic compounds, organic cyanides and longchain fatty acids. The action of allelochemicals in target plant is diverse and affects a large number of biochemical reactions resulting in modifications of different physiological functions. Thus the results of allelochemical action can be detected at different levels of plant organization: molecular, structural, biochemical, physiological and ecological. Enzyme activities, cell division and ultrastructure, membrane permeability, ion uptake and as a consequence plant growth and development are modified by allelochemicals. Significant effects on photosynthesis and respiration are the best-characterized results of allelopathic interactions. Moreover allelopathic compounds seem to induce a secondary oxidative stress expressed as enhanced free radical production and induction of cellular antioxidant system. Plant survival under allelopathy stress conditions depends on plant defense leading to allelochemical detoxication, the process which may go on in parallel to cell defense reaction to oxidative stress.

The article presents some aspects of the current knowledge regarding mechanisms of the allelopathy phenomenon. The allelopathy is a complex problem, thus comprehensive understanding of allelochemical mode of action requires further investigation and still remains an open question.

List of abbreviations:
BOA - 2(3H)-benzoxazolinone, CAT - catalase, GDH - glutamate dehydrogenase, DHZ - dehydrozaluzanin, DIBOA - 2,4-dihydroxy-1,4-benzoxazin-3(4H)-one, DIMBOA - 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3(4H)-one, GD6PDH - glucose-6-phosphate dehydrogenase, GS - glutamine synthetase, HPPD - hydroxyphenyl-pyruvate dioxygenase, ICL - isocitrate lyase, MBOA - 6-methoxy-2-benzoxazolinone, MDA – malondialdehyde, OPPP – oxidative penthose phosphate pathway, PSI - photosystem I, PSII - photosystem II, QA - plastoquinone A, QB - plastoquinone B, ROS - reactive oxygen species.

Introduction

Allelopathy phenomenon was defined for the first time in the late 1930s by Hans Molisch as the influence of one plant on another through releasing of chemicals into the environment (Molish 1937). It was later explained as any direct or indirect harmful or beneficial effect of one plant (including microorganisms) on another through the production of chemical compounds that are released into the environment (Rice 1984). Since this description was criticized as meaningless, International Allelopathy Society in 1998 confirmed the nowadays working definition: *"any process involving secondary me-*

tabolites produced by plants, algae, bacteria and viruses that influence the growth and development of agricultural and biological systems; a study of the function of secondary metabolites, their significance in biological organization, their evolutionary origin and elucidation of the mechanisms involving plant-plant, plant-microorganisms, plant-virus, plant-insect, plant-soil-plant interactions" (Mallik and Inderjit 2002). Although the definition of allelopathy includes both positive and negative aspect of allelochemical action, most observations suggest rather harmful effect of allelopathic compound on target plant.

The answer to the questions which compounds may be regarded as allelochemicals is difficult. Do allelochemicals include only secondary metabolites or also primary metabolites? Are they products of degradation of non-allelopathic compounds? Do they influence the growth of neighboring plants in certain mixtures and in certain concentrations? These problems are still unresolved, although great progress in allelopathy research has recently been done. Numerous allelochemicals were identified, but most studies on allelopathy deal with plant extracts containing unknown compounds. In the majority, allelochemicals are secondary plant metabolites, belonging to: terpenoids, phenolic compounds, long chain fatty acids, organic cyanides, alkaloids and others (Macias *et al*. 2001 and references therein, Oleszek and Stochmal 2002). Almost every class of secondary plant products has been implicated to take part in allelopathic interference (Weston and Duke 2003 and references therein). The term "allelochemical" relates to the role the compound plays, but not to the actual chemical identity, since depending on an organism or specific environmental parameters, the same compound may sometimes acts as an allelochemical and at other times or places can share other roles (Inderjit and Duke 2003). Allelochemicals are released into the environment as exudates, volatiles and/or residues of decomposition. Their toxicity in the environment is a function of concentration, flux rates, age and physiological stage of the plant, climate, season and environmental conditions. A large number of isolated allelochemicals exhibit their bioactivity at low (10^{-5} - 10^{-6} M) or even extremely low concentrations of 10^{-10} M (Macias *et al*. 2001 and references therein). For example, juglone - an allelochemical produced by black walnut (*Juglans nigra*) exerted its allelopathic effect at concentration of 10^{-3} - 10^{-7} M, while its concentration in a field as high as 2 x 10^{-5} M was reported (Jose 2002). To have a direct effect, allelochemicals must be taken up by a target plant. There is extremely little literature demonstrating mechanisms of allelochemicals uptake by plants. There are some hypotheses that allelochemicals are directly transferred to target plants by cell-cell contact, or that physical contact of the roots with allelopathic compound is more important than uptake (Inderjit and Duke 2003 and references therein).

Although allelopathy has been discussed for many years, it has been finally accepted as a legitimate area of research. Olofsdotter *et al*. (2002) suggested protocol to demonstrate allelopathy and summarized the criteria for allelopathy screening:

· a pattern of inhibition of one plant by another must be shown;
· the donor plant must produce chemical or chemicals;
· the chemical(s) from the donor plant must be released into the environment;
· the chemical(s) must be available through transport or accumulation in the environment in bioactive concentrations;
· the target plant must have some means for uptake of the chemical;
· the observed pattern in nature should not be solely explained by other mechanisms of interference, especially resource competition.

Most assessments of allelopathy involve bioassays of plant or soil extracts based on seed germination or seedling growth. Biological observations include also seed viability, root and shoot morphology, measurement of length and weight of certain plant parts. Allelochemicals can indirectly affect many physiological processes and a phenotypic response to the specific compound may mainly be the result of secondary effects, rather than the primary mechanism of its action (Dayan *et al*. 2000). Modifications in plants growth and development in response to allelopathics can be explained by alterations of cell molecular biology, ultrastructure as well as

biochemical and physiological processes. The knowledge of primary molecular target site of allelochemicals may be the most important step in developing methods of agroecology applicable to agronomy and sustainable crop production.

During the last few years many articles describing plant reactions to allelochemicals were published (Jose and Gillespie 1998, Czarnota *et al.* 2001, Abenavoli *et al.* 2003, Bais *et al*. 2003, Burgos *et al.* 2004, Hejl and Koster 2004). A general review on ecophysiological aspects of allelopathy was done by Inderjit and Duke (2003), some of biochemical and physiological mechanisms mediated by allelochemicals were discussed by Dayan *et al*. (2000), Politycka and Wójcik-Wójtkowiak (2001), Singh *et al*. (2003), Bertin *et al.* (2003), Weston and Duke (2003), Weir *et al.* (2004).

In this paper we describe and summarize the variety of plant reactions in response to allelopathic compounds. Allelochemical mode of action on molecular and cell ultrastructure level is also presented.

Seed germination

Potential of allelopathic compounds is often verified by testing their influence on seed germinability and seed viability. Inhibition or delay of seed germination and radicle growth by allelochemicals from many species *e.g.* sorghum (*Sorghum bicolor*), wheat (*Triticum aestivum*), sunflower (*Helianthus annuus*), rye (*Secale cereale*) were reported and reviewed (Wu *et al.* 1999, Inderjit and Duke 2003, Inderjit and Callaway 2003, Weston and Duke 2003).

Germination of cereals depends on α-amylase activity that regulates starch breakdown, necessary for supplying substrates to respiratory metabolism. Eucalyptus *(Eucaliptus globosus)* leaf leachates decreased α-amylase activity in seeds of fingermilet (*Eleusine coracanta),* resulting in inhibition of germination (Padhy *et al.* 2000). Similar data were obtained in the case of cress (*Lepidium sativum*) seeds in the presence of 6-methoxy-2-benzoxazolinone (MBOA), commonly occurring in cereals (Kato-Naguchi and Macias 2004). Moreover, in radicle of bean (*Phaseolus vulgaris*) seeds treated by extracts of leaves and stems of *Callicarpa accuminata* an enhanced expression of 11.3 kDa protein, similar to α-amylase inhibitor was detected (Cruz-Ortega *et al*. 2002).

During germination of fat-storing seeds, the glyoxylate cycle plays a key role in the mobilization of triacylglycerides. During early stages of germination enzymes of glyoxylate cycle such as isocitrate lyase (ICL), increase their activity due to maximum lipid metabolism in the storage tissue of germinating seeds (McLaughlin and Smith 1994). Inhibition in lipid mobilisation in the presence of ferulic and *p*-coumaric acids was detected during canola (*Brassica napus)* seed germination (Baleroni *et al*. 2000), as well as in sunflower (*Heliantus annus*) seeds germinating in the presence of alkaloids from thorn-apple (*Datura stramonium)* (Levitt *et al*. 1984). Electron microscopy data showed that cells of radicle of treated seeds contained greater quantities of lipids than non-stressed ones. The suppression of lipid mobilization accompanied by decreased ICL activity was observed in mustard (*Sinapis alba*) seeds treated by *H. annuus* leaf extract (Kupidłowska and Bogatek 2003, Bogatek and Stepień 2003). Germination of cucumber (*Cucumis sativus*) seeds was inhibited by benzoic acids with methoxy–ring substituents (Maffei *et al.* 1999). Incubation of cucumber seeds with 3,4-dimethoxybenzoic and vanilic acids lowered ICL activity accompanied by the disappearance of ICL protein from extracts of young seedlings. Data obtained by Maffei *et al.* (1999) suggest the influence of allelopathic compounds not only on activity of ICL but also on ICL gene expression. Thus, ICL seems to be one of the most sensitive enzymes in reaction to allelopathy stress and its decreased activity may result in inhibition or delay of seed germination.

Phenolic compounds extracted from soils covered by beech (*Fagus sylvatica)* and pine (*Pinus laricio* spp. Calabria) markedly inhibited germination of pine seeds (Muscolo *et al.* 2001). Tested phenolic compounds lowered the activity of glucose-6-phosphate dehydrogenase (G6PDH), glucose-phosphate isomerase and aldolase – enzymes involved in glycolysis and oxidative pentose phosphate pathway (OPPP), which ensure the seed supply with sufficient level of reducing power, ATP

and carbon skeletons for biosynthesis. Additionaly, it was suggested that the observed decrease in enzymatic activity is a secondary effect of allelochemicals, related to protein damage (Muscolo *et al.* 2001).

Therefore, effects of allelochemicals on seed germination appear to be mediated through a disruption of normal cellular metabolism rather than through damage of organelles. Reserve mobilisation, a process which usually takes place rapidly during early stages of seed germination seems to be delayed or decreased under allelopathy stress conditions**.**

Photosynthesis and respiration

Disturbances of photosynthesis are one of the most frequently observed physiological effects of many allelochemicals. Due to this action of allelopathic compounds they possess perspectives to be commonly used in organic agriculture e.g. in sustainable weed management as natural herbicides.

Sorgoleone - lipophilic benzoquinone compound from root exudates of *S. bicolor* is an inhibitor of photosynthesis (Einhellig *et al*. 1993, González *et al*. 1997, Rimando *et al*. 1998, Czarnota *et al.* 2001). It acts in a similar way to triazine herbicides such as atrazine. Studies with oxygen–evolving spinach (*Spinacia oleracea*) tylakoid membranes containing plastoquinones (Q_A and Q_B) electron acceptors of PSII showed that sorgoleone is a potential inhibitor of photosynthetic electron transport acting on photosystem II (PSII) (Nimbal *et al*. 1996). Furthermore, sorgoleone does not inhibit photosystem I (PSI) reactions. The site of inhibition for this allelochemical within PSII complex involve specifically the Q_B site of D_1 protein (Nimbal *et al*. 1996). 2,4-dihydroxy-7-methoxy-1,4--benzoxazin-3(4H)-one (DIMBOA) inhibited photosynthesis by affecting chloroplast ATPase (CF1) activity in spinach leaves, probably due to its reaction with sulfhydryl groups of the enzyme (Queirolo *et al.* 1983). Decreased chlorophyll content, accompanied by reduction of carotenoid concentration was detected in lettuce (*Lactuca sativa*) seedlings treated by artemisinin and some of its sesquiterpene analogs (Dayan *et al*. 1999a). Meazza *et al*. (2002) showed that juglone, sorgoleone and some other allelochemicals belonging to benzoquinones, napthoquinones and triketones inhibit key enzyme for plastoquinone synthesis p-hydroksyphenylpyruvate dioxygenase (HPPD). Inhibition of this enzyme disrupts the biosynthesis of carotenoids and results in foliar bleaching. Lowered chlorophyll content was detected also in duckweed (*Lemna minor*) grown in the presence of juglone. However, there was no alterations in chlorophyll a:b ratio (Hejl *et al.* 1993). Juglone dependent chlorophyll degradation related to the decrease in net photosynthetic rate was detected in maize (*Zea mays*), soybean (*Glycine max*) (Jose and Gullespie 1998, Jose 2002) and *L. minor* (Hejl *et al.* 1993). On the other hand reduced photosynthesis rate in leaves of mustard (*S. alba*) plants exposed to *H. annuus* allelochemicals corresponded with reduction in transpiration rate suggesting limited CO_2 diffusion into chloroplast due to stomata closing (Bernat *et al*. 2004a).

One of the suggested explanation for disruption of seedling growth and development during allelopathy stress is modification in mitochondrial respiration leading to decreased supply of ATP for all energy demanding processes. Coumarins decreased mitochondrial respiration rate in onion (*Allium cepa*) root cells (Kupidłowska *et al*. 1994a). Takahashi *et al.* (1998) investigated the inhibitory effect of quercetin and its glycoside – rutin on isolated mitochondria from *G. max* hypocotyls. Quercetin affected respiratory activity of isolated mitochondria by three modes of action: inhibition of substrate oxidation due to direct action on electron transfer chain, inhibition of phosphate uptake and uncoupling of oxidative phosphorylation. It was suggested that quercetin may act on an electron transfer steps between quinone pool and oxygen. Quercetin at 0.5 mM concentration caused increase in the basal respiration accompanied by the decrease in respiration coupled to ATP synthesis (Takahashi *et al.* 1998).

Monoterpenes are allelochemicals found in Umbellifereae and Pinaceae families which diminished the mitochondrial respiration by increasing the rates of electron transport through an alternative pathway (Peñuelas *et al.* 1996). α-Pinene and cinnamic acid also decreased the oxygen consumption in *G. max* cotyledons and increased relative

partitioning of electrons to the alternative pathway (Peňuelas *et al.* 1996). Abrahim *et al.* (2000) demonstrated that reduced respiratory activity of *Z. mays* primary root mitochondria by monoterpenes led to a complete repression of respiratory control. It was suggested that those compounds may act as uncouplers of oxidative phosphorylation. Similar effect of allelochemicals from maize pollen on respiration was observed in isolated mitochondria from watermelon (*Citrulus lanatus*) hypocotyls (Cruz-Ortega *et al.* 1988). DIMBOA isolated from maize seedlings reduced electron transport in maize mitochondria and also inhibited oxidative phosphorylation. Addition of 10 mM succinate to the medium prevented this effect, therefore it was suggested that DIMBOA inhibited electron transport from NADH to O_2 in maize mitochondria (Massardo *et al.* 1994).

Most of effects of allelochemicals on respiration are examined on isolated mitochondria, since measurement of allelopathy influence on respiration of intact plant may be disturbed by photorespiration. Inhibitory effect on O_2 uptake of such allelochemicals as monoterpenes, hydroxamic acids or coumarins may depend on their ability to penetrate plant tissue. On the other hand allelopathic extract from *H. annuus* leaves, which inhibited mustard seed germination (Bernat *et al.* 2004b, Ciarka *et al.* 2004, Bogatek *et al.* 2005), lowered seed respiration rate during 3 first days of germination (Bogatek, unpublished results). This suggests correlation between inhibition of dark respiration and delay of germination in the presence of allelopathic compounds.

Other energy demanding processes - ion uptake and growth

The effect of allelochemicals on respiration and photosynthesis, resulting in decreased ATP production, may alter other cell processes which are energy demanding. A great decrease in ATP/ADP level and energy charge was detected in *S. alba* seeds treated by sunflower leaf allelochemicals (Bogatek *et al.* 2002b). Ion uptake and growth are the most energy consuming processes in plant cells (Van der Werf *et al.* 1988). Inhibition of seedling growth in allelopathy stress conditions may be therefore a result of decreased ion uptake. A root is the first organ to come into contact with allelochemicals in the rhizosphere, thus the effect of allelochemicals on ion uptake is particularly important. Root exudates of *C. sativus* inhibited ion (NO_3^-, K^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, BO_3^{3-}) uptake by cucumber seedlings (Yu and Matsui 1997). An inhibitory effect of *p*-hydroxycinnamic, vanillic and ferulic acids on the uptake of $H_2PO_4^-$ by cucumber roots was also detected (Lyu *et al*. 1990). A gradual decrease in uptake of both ^{32}P and ^{65}Zn was observed in three *T. aestivum* varieties exposed to extracts of stem and roots of different weeds: tropical whiteweed (*Ageratum conyzoides),* small melitot *(Melilotus indicans*), Santa Maria fewerfew *(Parthenium hysterophorus*) (Saxena *et al.* 2003). Cells from carrot (*Daucus carota*) suspension culture treated with coumarins took up ammonium preferentially to nitrate ions (Abenavoli *et al.* 2003), probably due to lower energy cost associated with ammonium assimilation (Salsac *et al.* 1987). Therefore, influence of allelochemicals on ion uptake may be a result of the decreased respiration rate and insufficient amount of ATP synthesized in root cells.

There is also much data on the effect of allelochemicals on membrane bound enzymes *e.g.* proton pumping ATPase localized in plasma membrane (H^+-ATPase). H^+-ATPase is responsible for generation of proton electrochemical gradient (Michelet and Boutry 1995) and thereby providing the driving force for the uptake and efflux of ions and metabolites across the plasma membrane (Palmgren 2001). H^+-ATPase inhibition results in reduction in mineral and water uptake by roots and as a consequence leads to strong effect on essential plant functions such as photosynthesis, respiration or protein synthesis leading finally to reduction of growth. The decrease in H^+-ATPase activity was correlated with an increasing juglone concentration in root microsomal membrane fraction of maize and soybean (Hejl and Kostel 2004). Incubation of *L. sativa* seedling with polygodial – allelopathic compound from knot-grass (*Polygonum hydropiper*) also resulted in inhibition of H^+-ATPase activity (Fujita and Kubo 2003). Additionaly *S. cereale* allelochemicals: BOA and DIBOA lowered the activity of plasma membrane H^+-ATPase from

roots of oat (*Avena sativa*) and vetch (*Vicia faba*) (Friebe *et al.* 1997). The localization of this enzyme in plasma membrane implies its early interactions with absorbed allelochemicals. Additionaly it was proven that allelopathic action of DIBOA and BOA on plasma membrane H^+-ATPase activity was closely related to their effect on root and shoot elongation. This corresponds to the suggestion that allelochemical potential of those compounds is connected with their auxin-inhibiting activity (Hasegawa *et al.* 1992). On the other hand 3,4-dihydroxybenzoic acid at high concentration inhibited root growth of tobacco (*Nicotiana tabacum*) plants, while at low concentration enhanced callus formation (Mucciarelli *et al.* 2000). This effect was explained by allelochemical action as an auxin analog, stimulating ethylene synthesis and thus influencing plant growth in concentration dependent manner. Additionally, phenolic compounds were reported to have auxin-protecting activity leading to accumulation of auxins. It was suggested that these allelochemicals act by inhibition of auxin oxidation (Mato *et al.* 1994, Cvikrova *et al*. 1996).

The inhibitory effect of DIMBOA on oat (*Avena sativa*) coleoptile elongational growth was explained by its influence on the cell wall peroxidase activity (González *et al.* 1999). DIMBOA enhanced the rate of NADH oxidation by oat cell wall peroxidases (González *et al.* 1999), or horseradish peroxidase (Rojas *et al.* 1997) leading also to increased generation of hydrogen peroxide (H_2O_2).

Alterations in cell growth were detected in the presence of coumarins, as well. Coumarins inhibited growth of carrot (*Daucus carota*) cells suspension culture in the concentration dependent manner. Abenavoli *et al*. (2003) detected a reduction of carrot cell enlargement leading to a visibly spherical shape of the coumarin treated cells. Cells appeared to have lost their ability to establish growth polarity, which is essential for allowing cell elongation. Promotion of radial growth and reduction of longitudinal extensibility of the cell wall after coumarin treatment was observed also in *A. cepa* root cells (Kupidłowska *et al*. 1994b). It was suggested that an inhibitory effect of those allelochemicals consists in suppression of the exponential growth phase prior to the stationary phase (Podbielkowska *et al*. 1994).

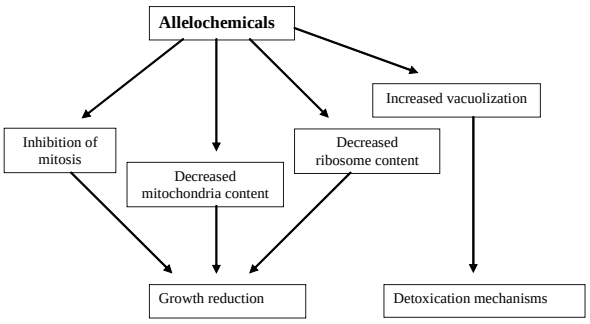

Fig. 1. Mode of action of allelochemicals at the subcellular level.

Cell ultrastructure

It is often proposed that reduction of plant growth in the presence of allelochemicals is associated with the strong inhibition of mitosis or/and disruption of the structure of organelles *e.g*. nuclei and mitochondria (Fig. 1). Analysis of mitotic index is one of methods used to study the allelopathic effect of one plant on another. Additional microscopic observations are helpful in detection of abnormalities in mitotic arrangement or atypical cell wall formation and can suggest a disruption of microtubule organizing centres or alterations in cell wall biosynthesis respectively.

Z. *mays* pollen allelochemicals decreased mitotic activity in radicle meristematic cells of the dark grown watermelon (*Citrullus lanatus*), as well as induced the rise of irregular and pycnotic nuclei (Cruz-Ortega *et al.* 1988). Similarly, leachates of aerial parts (leaves and stems) of *Mirabilis jalapa* affected cell division in germinating seeds of different crops: *T. aestivum, Z. mays*, pea (*Pisum sativum*) and weeds: pigweed (*Amaranthus leucocarpus*), pursley *(Portulaca oleracea)*, cockspur-grass (*Echinochloa crus-galli*), morning-glory (*Ipomea purpurea*). Those allelochemicals reduced the mitotic index by about 31 % but did not change length of the cell cycle. As the result of treatment seed-

lings showed an increase in the root diameter and hypertrophy of root cap (Anaya and Pelayo-Benavides 1997). Mitosis inhibition was detected also in *A. cepa* root tips influenced by quassinoids (Dayan *et al*. 1999b). It was not accompanied by aberrant mitotic conformations, evident in cells treated with sesquiterpene endoperoxide lactones (Dayan *et al*. 1999a). Light microscopic observations of *P. vulgaris* root tips affected by aqueous leachates of *Sicyous deppei* showed that cells around quiescent center appeared compressed (Cruz-Ortega *et al*. 1998). Cell ultrastructure was disorganized and lacked evident symptoms of cell differentiation. Root cap cells showed amorphous and inactivated (nondividing) nuclei. Increased invaginations of vacuoles were detected, some of which contained cellular components (Cruz-Ortega *et al.* 1998). Other allelochemicals: 2(3H)-benzoxazolinone (BOA) and 2,4-dihydroxy-1,4-benzoxazin-3(4H)-one (DIBOA) reduced the regeneration of *C. sativus* root cap cells and increased the width of cortical cells resulting in increased root diameter. Additionally, BOA and DIBOA increased cytoplasmic vacuolisation, reduced ribosome and dictiosome density, decreased number of mitochondria (Burgos *et al*. 2004). Authors proposed that enlargement of vacuoles may be due to their lytic function, helping in toxin degradation.

Separation of the plasma membrane from the cell wall, similar to the symptom of plasmolysis was detected in cells of cucumber cotyledons in the presence of dehydrozaluzianin (DHZ). It was not accompanied by any disturbances in chloroplasts or any other organellar structures, except for slightly distended cristae of mitochondria (Galindo *et al*. 1999). More evident changes in the structure of mitochondria in cells of apical *A. cepa* root meristem were induced by coumarins (Kupidłowska *et al.* 1994a). Most of mitochondria became condensed with electron dense matrix and extended intracristal spaces. In some organelles protrusions containing fragments of membranes were formed as the result of hypertrophy of mitochondrial membranes. It was suggested that disturbances of cell membranes by coumarins were associated with the ability of these compounds to react with membrane lipids or proteins, resulting in changes of membrane permeability and finally in modification of energy production (Kupidłowska *et al*. 1994a).

There are also some data on the effect of allelochemicals on biosynthesis and metabolism of amino acids and proteins (Romero-Romero *et al*. 2002, Abenavoli *et al*. 2003, Pawar and Chavan 2004) as well as on DNA and RNA synthesis (Baziramakenga *et al*. 1997).

All of the observed alterations in plant cell ultrastructure, mentioned above were detected in laboratory conducted tests with isolated allelochemicals or plant extracts. In those experiments the involvement of field conditions: presence of soil microorganisms and interactions with other abiotic stresses were omitted. Additionally, the physiological or anatomical response observed in isolated organelles, cells or tissues may not be an equivalent to relations occurring between plants in their natural environment.

Oxidative stress

One of the effects of allelochemicals on target plant is uncontrolled production and accumulation of reactive oxygen species (ROS). It is accompanied by activation of cellular antioxidant system, involving both enhanced activity of antioxidant enzymes as well as increased synthesis of molecular antioxidants: glutathione, ascorbate, tocopherole.

(-)-Catechin, the allelochemical from root exudates of spotted cnapweed (*Centaurea maculosa*), that inhibited germination and growth of Idaho fescue (*Festuca idahoensis*), crested hair-grass (*Koeleria micrantha*) and *Arabidopsis thaliana* enhanced production of ROS (Bais *et al*. 2003). A burst of ROS in susceptible plant roots and the kinetics of ROS induction was similar to the patterns of cell death induced by (-)-catechin. Antioxidant (ascorbic acid) added with (-)-catechin blocked increase in ROS level. A large number of genes induced after (-)-catechin treatment was related to oxidative stress and phenylopropanoid and terpenoid pathways (Bais *et al.* 2003). Activation of antioxidant system enzymes in response to coumarin treatment was reported in *T. aestivum* seedlings (Abenavoli *et al.* 2001). Similarly aqueous extract of leaves and stems of beauty-berry *(Callicarpa accuminata)* in-

creased free radicals level, catalase activity and oxidative membrane damage in roots of tomato (*Lycopersicon esculentum*) plants. The enhanced synthesis of protein which showed close similarity to glutatione-S-transferase was also detected (Cruz-Ortega *et al*. 2002), indicating an involvement of detoxication mechanism. The exposure of *C. sativus* roots to ferulic and *p*-coumaric acids increased both H_2O_2 level and peroxidase activity (Politycka *et al.* 2004). Moreover aqueous root extracts of cucumber increased catalase (CAT), superoxide dismutase (SOD) and peroxidase (POD) activity in cucumber roots (Yu *et al*. 2003). The induction of oxidative stress by *H. annuus* allelopathics was observed during germination of *S. alba* seeds (Bogatek *et al.* 2002a). Water extract of sunflower leaves stimulated H_2O_2 production and CAT activity. Western blott analysis showed that enhancement of CAT activity was associated with synthesis of CAT 5 isoform. An increased CAT activity in response to allelochemicals was detected also in germinating cucumber seeds treated by different benzoic acids (Maffei *et al.* 1999). An activation of antioxidant enzymes system was accompanied by a severe membrane injury. This may be due to membrane lipid peroxidation since the increase in malondialdehyde (MDA) concentration in allelopathy stressed plants was detected (Bogatek *et al.* 2005, Politycka 1996, Yu *et al*. 2003). Dehydrozaluzianin C (DHZ), natural sequiterpenolide from roots of many of Compositae families (Macias *et al*. 1999) caused a rapid plasma membrane leakage in cucumber cotyledone discs (Galindo *et al*. 1999). The complete reversion of the ion leakage effect was obtained when DHZ-treated tissue was incubated in the presence of antioxidant - glutathione. However tocopherol, a radical scavenger does not reverse the electrolyte leakage caused by DHZ, indicating that the loss of membrane integrity may be not only due to peroxidative damage (Galindo *et al.* 1999).

An oxidative burst in plant cells in response to allelochemicals shows some similarities with reaction to pathogen infection (Mc Dowel and Dangl 2000, Huckelhoven and Kogel 2003) as well as reaction to abiotic stresses (Van Breusegem *et al*. 2001). This is questionable if increased ROS production is only a primary effect of allelochemicals leading to activation of antioxidant system. ROS may also act as signal molecules in plant transduction cascade. Some allelochemicals, *e.g*. quinones undergo reactions leading to formation of free radicals, which can cause oxidative damage in cells structures themselves. On the other hand we can imagine that ROS activate detoxication or antioxidant mechanisms leading finally to plant resistance to allelochemicals. The involvement of the first or latter pathway in reaction to allelochemicals may be crucial for plant death or survival.

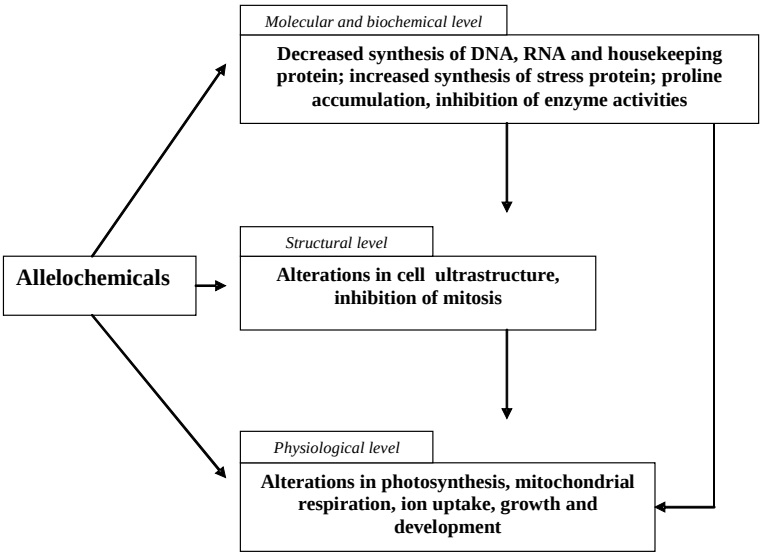

Fig. 2. Multi site action of allelochemicals

Conclusions

For many years allelopathy was an area of interest reserved mainly for botanists and agronomists and focused on allelopathic cover crops, intercropping and application of crude plant extracts to study the effect on crop yields and weed suppression under field conditions (Vyvyan 2002). Current allelopathy research is interdisciplinary and requires the contribution of chemists, soil scientists, ecologists and molecular biologists to make significant progress. Most of the allelochemicals are characterized as multi- site active com-

pounds that may interfere with various physiological processes of a target plant (Fig. 2). Therefore, the activity of allelochemicals can not be explained by just a single mode of action. The majority of effects, such as reduction in seed germinability and seedling growth, chlorosis, decreased ion uptake and other physiological, morfological and anatomical abnormalities are caused by a variety of more specific interactions between allelochemicals and cellular or molecular systems. In the last few years researchers approached different allelochemical mode of action *e.g*. sorgoleone, BOA, (-)-catechin (Czarnota *et al.* 2001, Reigosa *et al.* 2004, Bais *et al.* 2003) applying biochemical, cytological, physiological and molecular techniques. Using microarray technique to study the early changes in DNA expression pattern, more than 200 genes significantly up or down-regulated as a result of BOA action were observed (Reigosa *et al*. 2004). The expression of several stress proteins was proven by 2D electrophoresis. Additionally other effects of allelochemicals: membrane peroxidation, changes in energy generation, and changes in water status were noted. It was suggested also that some of the detected symptoms may be due to induction of secondary, oxidative stress. Plant survival in allelopathy stress depends on resistant mechanisms leading to detoxication: conjugation, sequestration and oxidation of allelopathics which may be switched on parallely to oxidative stress (Fig. 3). Therefore, Reigosa *et al.* 2004 proposed that detoxication process could be the first target and most important effect of allelochemicals. On the other hand, Weir *et al.* (2004) reviewing biochemical and physiological mechanisms mediated by allelochemicals concluded that specific plant response to allelochemicals is to activate a cell death cascade in susceptible plants. They suggested that allelochemicals are not very toxic in themselves but they rather induce toxic responses.

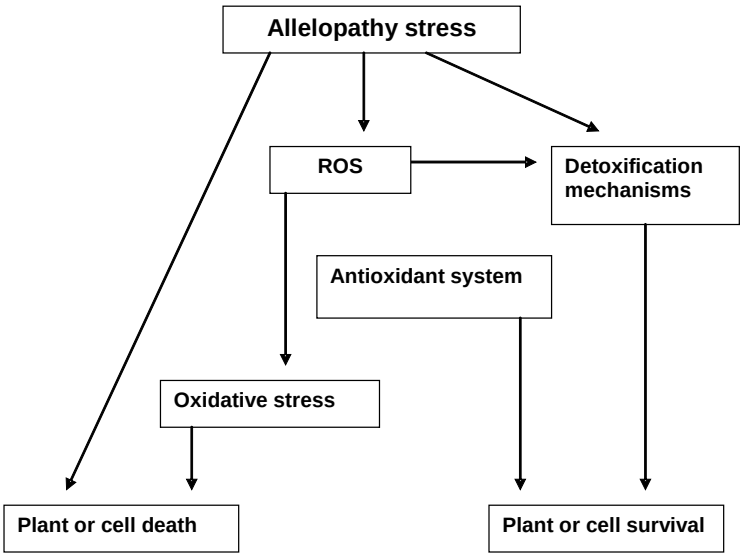

Fig. 3. First reactions to allelopathy stress which decide about plant/cell death or survival.

Interdisciplinary approach to allelopathy may make the story even more complicated but at the same time more fascinating and surprising. There is some new data indicating that allelochemicals may influence signal transduction pathway, since allelopathics from *Flourensia cernua* interacted with bovine brain CaM (calmoduline) (Mata *et al*. 2003). This example illustrates a complication and complexity of allelopathy phenomenon, being much more sophisticated than simple negative interactions between tomato and radish evident to every gardener.

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