

IOBC/wprs Bulletin, Vol. 44, 2009

Working Group "Induced Resistance in Plants Against Insects and Diseases",
Proceedings of the meeting at Heraklion, Crete (Greece), 27-29 April, 2006.
Edited by: Annegret Schmitt, Brigitte Mauch-Mani, Nicholas Birch & Marcel Dicke
ISBN 978-92-9067-218-0 [xii + 154 pp.].

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Mechanisms involved in inducible and constitutive resistance to pests and diseases

Priming as a mechanism behind induced resistance against pathogens, insects and abiotic stress

Jurriaan Ton, Sjoerd van der Ent, Marieke van Hulten, Maria Pozo, Vivian van Oosten, L.C. van Loon, Brigitte Mauch-Mani, Ted C. J. Turlings, Corné M.J. Pieterse

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Abstract: Upon treatment with a resistance-inducing agent, plants acquire an enhanced defensive capacity that results in a faster and/or stronger defence reaction at the moment the plant is exposed to biotic or abiotic stress. This phenomenon is commonly known as priming and has been associated with different forms of induced resistance. Priming accelerates and increases the plant's ability to activate the defence that is best adapted to resist the stress situation encountered. Under conditions of disease pressure, primed plants exhibit a higher fitness than non-primed plants or defence-expressing plants. Hence, the benefits of priming outweigh its costs in environments where disease occurs. Although priming has been known to occur in plants for decades, most progress in the understanding of this phenomenon has been made over the past few years. Recent insights in the mechanisms behind systemic acquired resistance (SAR), β -amino-butyric acid-induced resistance (BABA-IR), rhizobacteria-mediated induced systemic resistance (ISR), and volatile organic compound-induced resistance (VOC-IR) against insects have revealed various priming mechanisms that protect against different stresses. Whereas SAR and BABA-IR are associated with priming for salicylate (SA)-dependent defence that acts against biotrophic pathogens, ISR and VOC-IR seem to function through priming for jasmonate (JA)-dependent defence against pathogens and insects. Expression of BABA-IR and ISR against pathogenic fungi and oomycetes is also associated with an augmented formation of callose-rich papillae. This priming response depends on a largely unknown defence pathway, which involves abscisic acid (ABA) and phosphoinositide (PI) signalling, and is thought to target the cellular secretory pathway. Induction of the primed state may be mediated by an enhanced accumulation of signalling compounds, such as transcription factors (TFs) that remain inactive until the plant is exposed to stress. A Q-PCR-based transcription profiling of ~2.200 TF genes in *Arabidopsis* has revealed consistent changes in the expression of certain TF genes directly upon activation of ISR and BABA-IR. We are currently investigating the contribution of these transcription factors to the various priming responses.

Priming in induced disease resistance of plants

Gerold J. M. Beckers, Uwe Conrath

15-18

Abstract: Infection of plants by necrotizing pathogens or colonization of plant roots with selected rhizobacteria often induces an enhanced resistance to further pathogen attack. The resistance can also be induced upon treatment with certain chemicals or by introducing genetic modifications. In the state of induced resistance (IR) plants are primed for quicker and more effective activation of defense responses upon further pathogen contact. Although the phenomenon has been known for decades, most progress in the understanding of priming has been made over the past few years. Here we summarize the present knowledge of priming in some selected IR phenomena of plants.

An extract of *Penicillium chrysogenum* induces resistance in *Arabidopsis* independently of known signalling pathways and elicits early defense-related responses

Barbara Thürig, Georg Felix, Andres Binder, Thomas Boller, and Lucius Tamm

19-24

Abstract: An aqueous extract of the dry mycelium of *Penicillium chrysogenum* (further called 'Pen'), previously shown to protect various crop plants against several diseases (Thuerig et al. 2006), protected *Arabidopsis thaliana* against *Hyaloperonospora parasitica*, *Botrytis cinerea*, *Alternaria brassicicola* and *Pseudomonas syringae* pv. *tomato* DC3000 without having a direct antimicrobial activity. Various mutants of *A. thaliana* were used to test whether Pen induces resistance on one of the known signalling pathways. Pen was still fully protective against *B. cinerea* in transgenes or mutants impaired in the salicylic acid (*NahG*, *npr1*), jasmonic acid (*coi1-1*), and ethylene (*ein2-1*) signalling pathway. Similarly, Pen-mediated resistance against *H. parasitica* was not affected in the mutants *npr1*, *coi1-1* or *ein2-1*. However, its efficacy was reduced in *NahG* plants.

Pen induced early defense-related responses such as an extracellular alkalinisation in cell cultures and ethylene production in leaf slices of numerous mono- and dicotyledonous plant species, including *A. thaliana*, tomato, tobacco and rice. The Pen-elicitor was sensitive to protease digestion but insensitive to other enzymes, suggesting that the elicitor-active region is a protein or a peptide.

From our data on cell cultures and on *A. thaliana* we conclude that Pen contains an unidentified elicitor, most likely a protein or a glycoprotein, inducing resistance via signal transduction pathways different from classical SA/NPR1- or JA/ethylene-dependent pathways.

The identification of *PAD2* as glutamylcysteine synthetase highlights the importance of glutathione in plant disease resistance

Vincent Parisy, Benoit Poinssot, Lucas Owsianowski, Antony Buchala, Jane Glazebrook, and Felix Mauch 25

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Using Q-RT-PCR to determine a defence-related signal signature of maize

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Extracellular factors of early basal resistance induced against bacteria

Eszter Besenyei, Ágnes Szatmári, Zoltán Bozsó, Erika Szabó, Éva Kondorosi, Katalin F. Medzihradzky, Attila Csorba, and Péter G. Ott 27-30

Abstract: Early basal resistance (EBR) is a response of plants to general bacterial constituents (elicitors), amounting in suppression of the hypersensitive and partial suppression of the susceptible reaction. The quickness of EBR raises the possibility that plants have a non-specific system for inhibition of bacterial activity, for example to prevent deployment of pathogenicity factors. As bacterial pathogens remain outside living plant cells, cell wall proteins and/or structural modifications are likely to be involved in the above EBR effects. Using genomic and proteomic approaches in tobacco, *Medicago truncatula* and pepper, several general elicitor-inducible plant extracellular factors were found to be associated with EBR, including chitinases, peroxidases, proteases as well as structural proteins. Their roles in generating a harmful environment for bacteria may include direct enzymatic damage, nutrient, water and osmotic adjustment and mechanical barrier formation.

Cytological aspects of oligosaccharide-induced resistance against *Plasmopara viticola* in grapevine

S. Trouvelot, M. Allègre, J.-M. Joubert, A. Pugin, X. Daire 31-36

Abstract: Under greenhouse conditions an oligosaccharide (OS) was shown to induce resistance in grapevine (*Vitis vinifera*) against *Plasmopara viticola* (downy mildew). A spray application reduced the severity of the disease by 60-80 %. Following OS application, foliar tissues underwent significant ultrastructural and biochemical modifications, detectable only after the pathogen inoculation. This included H₂O₂ production at the infection site, the deposition of phenolic-enriched material, the restriction of pathogen development in foliar tissues and the inhibition of its sporulation. Moreover our observations suggested that OS, in grapevine, acted like a priming agent.

BABA induced resistance in grapevine

Ana Slaughter, Mollah Md. Hamiduzzaman, Gabor Jakab, Brigitte Mauch-Mani, and Jean-Marc Neuhaus 37-41

Abstract: Grapevine (*Vitis vinifera*) is a major fruit crop worldwide and is affected by many diseases. Downy mildew, caused by the oomycete *Plasmopara viticola* leads to great damage and yield losses in grapevine if no protective measures are taken. The majority of the traditional cultivars that are planted are susceptible to this disease, necessitating the intensive use of chemicals to limit the damage in vineyards. One possible solution would be the activation of a plant's own defense system, known as induced resistance. β -Aminobutyric acid (BABA) has previously been shown to induce resistance against many oomycetes. It was observed that the protective effect of BABA in *Arabidopsis* was due to the potentiation of natural defense mechanisms against biotic stresses, a phenomenon referred to as priming. Priming is the capacity of a plant to express a faster and stronger basal defense response upon pathogen infection. BABA was used to induce resistance in grapevine. The resistance depended to a large extent on the deposition of callose. A strong reduction of mycelial growth and sporulation in the susceptible cultivar Chasselas was observed. Initial expression profile by microarray of BABA-treated Chasselas will be discussed.

Does BABA prime early signalling events in grapevine defence during elicitation and *Plasmopara viticola* infection?

R. Dubresson, C. Dubreuil, B. Poinssot, J.-M. Neuhaus, A. Pugin, and B. Mauch-Mani 43-47

Abstract: Elicitor treatments or pathogen attack induce early signalling pathways in plants and cell suspensions. β -aminobutyric acid (BABA) has been shown to prime specific defence pathways in plant upon exposure to biotic or abiotic stress. Here we report that BABA priming of grapevine cell suspensions and/or plants treated with elicitors or pathogens did not induce the entire early signalling pathways. BABA primed the production of active oxygen species (AOS) in both cell suspensions and leaves but did not affect nitric oxide (NO) or Ca^{2+} levels in cell suspensions.

Studying constitutive and inducible defence of Bt oilseed rape grown under elevated atmospheric CO₂ and ozone concentrations

Sari Himanen, Anne-Marja Nerg, Anne Nissinen, Guy M. Poppy, C. Neal Stewart Jr., and Jarmo K. Holopainen 49-52

Abstract: Cruciferous plants have distinctive secondary defence against generalist herbivores by glucosinolates and indirect defence, which targets also specialist herbivores. Transgenic Bt plants are the first commercial GM applications conferring specific pest resistance. A transgene coding for Lepidopteran specific *CryIAC* Bt toxin was inserted into oilseed rape (*Brassica napus* ssp. *oleifera*) genome, and we are studying if this transformation can result in any changes for the secondary defence of oilseed rape. Concentrations of atmospheric CO₂ and tropospheric ozone, as components of global climate change, are continuously increasing and in the future, this can influence crop productivity and plant-insect interactions. Therefore, we are also investigating if the secondary defence of Bt oilseed rape is changed under elevated CO₂ and O₃, compared to the parent line.

Activation of plant defence response contributes to the antiviral activity of Dioicin 2 from *Phytolacca dioica*

Franco Faoro, Barbara Conforto, Antimo Di Maro, Augusto Parente, and Marcello Iriti 53-57

Abstract: Using the patosystems *Nicotiana tabacum*, cv. Samsun NN - tobacco mosaic virus (TMV) and *Phaseolus vulgaris* - tobacco necrosis virus (TNV), we demonstrated that Dioicin 2 (D2), a type-1 ribosome-inactivating protein (RIP), possesses a strong antiviral activity, expressed only *in vivo*, when both RIP and virus were contemporaneously inoculated in the same leaf (either in the same surface, or separately in the adaxial and abaxial surfaces), but not in the upper leaves. This suggests that D2 cannot translocate into the phloem, nor induce SAR signals. Moreover, D2 alone induced localized H₂O₂ accumulation in treated tissues but not cell death, which was instead elicited by the concomitant presence of the virus. In that case, some ultrastructural features, such as mitochondrial swelling and nuclear disorganization seem to indicate that programmed cell death phenomena were undergoing. In D2 treated leaves, virus replication still occurred, but was restricted to very few cells and virus lesions remained invisible. Thus, it is likely that D2 antiviral activity is the result of the combined effect of its deadenylation properties on cell and viral nucleic acid and the activation of plant own defense response.

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Evolutionary and ecological aspects of plant resistance / deployment strategies for durable resistance within integrated crop management

Linking aboveground and belowground inducible plant resistance

T. Martijn Bezemer 65-71

Abstract: Induced resistance of plants against pests and diseases via plant defense responses is well documented and can occur aboveground, in the leaves, and belowground in the roots. A number of recent studies have shown that soil-borne pests can also induce plant resistance aboveground and *vice versa*. Since plants are frequently exposed to aboveground and belowground pests simultaneously, interactions between induced plant defense responses in the foliage and in the roots can have major implications for induced resistance. On the one hand, induction in one plant part may result in systemically induced resistance in the other part. On the other hand, simultaneously occurring aboveground and belowground induced plant defenses may interfere, for example, when the activities of root feeders alter the effectiveness of induced resistance against foliar herbivores. Such aboveground-belowground interactions can also potentially influence tritrophic interactions between plants, herbivores and their natural enemies such as parasitoids or predators.

Inducible defenses in food webs: models and experimental data

Irene van der Stap, Matthijs Vos, and Wolf M. Mooij 72

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Exploring the barley-Magnaporthe pathosystem

Nina Zellerhoff, Marcus Jansen, and Ulrich Schaffrath 73-76

Abstract: *Magnaporthe oryzae* is a major pathogen of rice (*Oryza sativa* L.) but is also able to infect other grasses including barley (*Hordeum vulgare* L.). Recently, we discovered that barley genotypes expressing a high degree of resistance against powdery mildew are hypersusceptible against *M. oryzae*. To our knowledge, this was the first example showing that manipulation of the defence potential of a plant which confers resistance against a particular pathogen may favour the development of other diseases. This manuscript is written to give a short survey on research work from our group on the interaction of barley with different species of the *Magnaporthe* species complex, thereby highlighting mechanisms of the basal defence machinery of barley.

Identification and expression of genes related to herbivory

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- Communicating plants: Ecological consequences of induced responses to herbivory
André Kessler 83-92
Abstract: The study of plant-insect interactions is exemplary among the integrative biological research fields and succeeds by unifying the research efforts on the cellular and organismal level with those on the whole plant and community level. This integrative research approach will help to understand the mechanisms of plant-insect interactions and will thus allow the utilization of the plants' natural defenses in agriculture. Here, I highlight studies of herbivore-induced responses of the wild tobacco plant *Nicotiana attenuata* and emphasize both, the role of using chemical and molecular tools in ecological research and the importance of a profound knowledge of the natural history of species when studying plant-insect interactions. In particular I will focus on recent results on the role of herbivore-induced volatile organic compound emission in mediating organism interactions in nature and the potential value of indirect plant defenses for modern agriculture.
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- Factors influencing root colonization by the beneficial strain *Pseudomonas chlororaphis* O6
Anne Anderson, and Y-C Kim 97-100
Abstract: *Pseudomonas chlororaphis* O6 (PcO6) is an aggressive colonizer of plant roots under laboratory and field conditions. Root colonization is beneficial to the plant, inducing systemic protection against bacterial, fungal and viral pathogens. Antimicrobial phenazines and hydrogen cyanide are produced by PcO6 under GacS-dependent acyl homoserine lactone regulation. Phenazines are produced predominantly in the seed zone of a colonized barley seedling. Mutations in *dctA*, encoding a transporter for carboxylic acids and in *edd*, eliminating catabolism of sugars through the Entner-Doudoroff pathway and reduces colonization early and later in colonization. These findings suggest to us that both organic acids and sugars are used during colonization. Reduced colonization in both *dctA* and *edd* mutants correlated with lessened ability to induce systemic resistance to the soft rot pathogen. Systemic protection against soft rot also is correlated with production of butanediol, a presumed product of fermentation. Butanediol production correlated with increased leaf surface production and induced resistance and is dependent on *gacS* activity. GacS regulates negatively the production of IAA from tryptophan and the shift in phenotype to a highly hydrophobic cell variant that is effective in generating

biofilms in minimal medium conditions. These observations illustrate several ways in which the Gac system in *P. chlororaphis* O6 regulates important ecological features in this bacterium.

Changes in free amino acids induced in cucumber plants by spider mites and plant growth promoting rhizobacteria (PGPR)

Anna Tomczyk 101-104

Abstract: The experiment was conducted on glasshouse cucumber cv. Corona. Plants were cultivated either in the presence of *Pseudomonas fluorescens* (PGPR) or without these bacteria. Half of the bacterized, as well as non-bacterized plants were infested with *Tetranychus cinnabarinus* Boisd. In all groups of plants, free amino acids were identified and their content was estimated. The total content of free amino acids strongly increased in both spider mite- damaged and PGPR treated plants. Spider mite feeding on bacteria-treated plants caused a lower increase in free amino acids as compared to untreated plants, however the density of the spider mite population was also lower on bacterized plants as compared to non-bacterized. Amounts of all free protein amino acids strongly increased as a result of spider mite feeding on the leaves of non-bacterized plants as compared to bacterized, while content of non-protein amino acids was decreased in mite-infested as well as in bacteria-treated plants. A high increase of aromatic amino acids was observed in mite-infested plants, however this was less evident when mites fed on bacteria-treated plants. Significant differences in the concentration of proline were found between spider mite-damaged and control as well as bacteria-treated plants.

Changes in phenolic acids of cucumber, induced by plant growth promoting rhizobacteria (PGPR) in relation to infestation with spider mites

Anna Tomczyk 105-108

Abstract: The influence of plant growth promoting rhizobacteria (PGPR), developing in root system of glasshouse cucumber on phenolic acid concentrations in the leaves, important in interaction between host plant and spider mites was studied. Seeds of cucumber plants were inoculated with *Pseudomonas fluorescens*, known as an inducer of plant resistance to some diseases, insects and spider mites. The increase in phenolic acids content was observed in mite and bacteria treated plants as compared to control plants. It was more expressed in young leaves. The plant response was connected with induction of cucumber resistance to spider mites. Changes in the level of phenolic compounds in cucumber leaves, induced by PGPR, can be responsible for the decrease in mite population observed in the previous studies conducted by the author. They can be of some importance in spider mite – cucumber plant interactions.

Host spruce quality and its effect on spruce spider mite (*Oligonychus ununguis*

Jacobi, Acari: Tetranychidae) biology

Malgorzata Kielkiewicz, Ewa Puchalska, and Barbara Czajkowska 109-118

Abstract: Comparative studies on chemical composition of needles of Serbian spruce (*Picea omorika*), white spruce (*P. glauca* ‘Conica’) and blue spruce (*P. pungens*) and the effect of host quality on the spruce spider mite (*Oligonychus ununguis*) was carried out. It was stated that fecundity of *O. ununguis* was positively correlated with concentration of reducing sugars, and negatively with concentration of total soluble phenolics in needles of the investigated species of spruce. To the contrary, mortality of the mites was positively correlated with concentration of the total phenols and negatively with concentration of reducing sugars.

The lowest total amount of essential oils was found in needles of *P. omorika*, whereas the one in needles of *P. pungens* and *P. glauca* ‘Conica’ was twice and five times higher, respectively. There were also marked differences in quantities of particular single components of essential oil mixtures among spruces. Needles of *P. glauca* ‘Conica’, being attractive food for *O. ununguis*, distinguished themselves by the highest quantities of camphor, limonene and β -myrcene. Thus, these three monoterpenes may play an important role in spruce spider mite success on white spruce. Needles of *P. omorika*, reluctantly populated and attacked by *O. ununguis*, did not show the presence of camphor and of three other monoterpenes (sabinene, γ -terpinene, *p*-cymene) found in needles of spruces readily accepted by the mite. Moreover, the percent contribution of bornyl acetate, borneol, β -pinene, methyl salicylate, citronellol, geranyl acetate and linalool in the total amount of oil of *P. omorika* was significantly higher than in total amount of oils of the remaining two spruces. Results obtained in these studies indicate that inadequate host spruce quality affects *O. ununguis* bionomy and its abundance reported elsewhere.

Types of resistance important for plant breeders and possible contribution of inducible resistance

Breeding for inducible resistance against insects – applied plant breeding aspects

Inger Åhman 121-130

Abstract: Many of the pre-requisites necessary for breeding plants with inducible resistance to pests are no different from breeding for constitutive resistance. In both cases it is necessary to have resistance genes giving high enough yield gains from pest protection, efficient selection methods and means of introducing resistance genes into agronomically acceptable plant material. In addition, insect resistance traits need to be neutral or positive to non-target organisms. In inducible resistance, there is also the need for proper timing and specificity of induction. Tentatively the ideal inducible resistance is triggered by specific cues which rapidly induce specific resistance traits with long duration relative to the sensitive period of the crop and which give a systemic plant response. It takes knowledge to develop appropriate selection methods for resistance and in the case of inducible resistance we also need knowledge about how the inducing factors are operating. Inducing cues may come from insect activities on the plant (e.g. feeding, oviposition), from neighbouring plants or from manmade chemical formulations of elicitors. Plant selections can be based on plant damage levels, insect numbers, insect responses, plant resistance traits and/or molecular characteristics of the plant genome.

Breeding for insect-inducible resistance to insects has been applied in the form of rapidly induced highly specific resistance in insect–crop combinations where there are gene-for-gene relationships, such as with the Hessian fly and the Russian wheat aphid in wheat. To my knowledge there are no examples of traditional breeding where less specific types of resistance; induced by insects, by neighbouring plants or by chemical formulations; have been deliberately bred into commercial cultivars. It is likely that the accumulating knowledge about the mechanisms of induced resistance will find applications in cultivars produced by genetic engineering.

Deployment strategies for crops with inducible resistance

Adrian Newton, Gary Lyon, Graham Begg, Jiasui Zhan, David Guy, Dale Walters

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Abstract: In the field induced resistance in current varieties of crop plants is a normal defence component but it can be further exploited either by a) treating with a resistance elicitor, b) using genotypes which possess a stronger inducible response, or c) selectively encouraging pathotypes that induce it.

Characteristically, resistance elicitors are unreliable as unknown environmental factors sometimes cause substantial loss of efficacy. Furthermore, different crop genotypes, such as cereal varieties, express differential degrees of inducible resistance with given elicitors. As elicitors may act via different receptors it seems advisable to use a combination of elicitors to combine different modes of action to improve efficacy, although trial data to validate this is lacking. However, gene expression data from field-grown plants indicates considerable activation of defence-related pathways so opportunities for further specific pathway induction may be limited.

Growing mixed genotypes of plants would be the norm in many natural ecosystems, but is uncommon in most crops grown as high input monocultures. Nevertheless, there is considerable evidence that cultivar mixtures reduce disease, increase yield, and deliver stability in yield and quality. This is through the spatial effects of dilution of susceptible plants and barriers of resistance plants, and through induced resistance. The latter is achieved through cross-over of spores virulent on one component but avirulent on another, and is thus most effective for pathogens with a 'simple' and specific race structure such as some obligate biotrophs on cereals where its contribution has been estimated. However, mixtures are effective against hemi-biotrophic pathogens with little race-specificity too, and critical to all mixture efficacy is component number, proportions and spatial deployment strategy. For example, a multi-component 'patchy' mixture is likely to be more efficacious than just two or three components in a homogeneous mixture. The scale and degree of patchiness must be a compromise between the parameters required for individual pathogen species control and resource exploitation, the former being determined by pathogen dispersal gradient.

The stability of disease control through exploitation of induced resistance is dependent on its costs, both to the pathogen and to the plant. Modelling demonstrated how the balance can be tipped towards disease control through spatial resistance deployment strategies in mixtures. It can be argued that resistance elicitors will not select for pathotypes that will erode their efficacy as they do not act directly against the pathogen, although experimental evidence indicates this may not always be the case.

- Response of *Solanum stoloniferum* to infestation by the green peach aphid: Induced resistance and gene expression
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Abstract: Treatment of *Arabidopsis* plants with yeast suspension increases phytoalexin accumulation, PR gene expression and resistance against a subsequent infection with *Pseudomonas syringae* and *Botrytis cinerea*. This protection effect of yeast against *P. syringae* was not detectable in mutants in the salicylic acid pathway indicating that this pathway is important for the protection. In contrast, the increased resistance against *B. cinerea* was present in mutants in the salicylic acid pathway, jasmonic acid pathway or camalexin biosynthesis. This suggests that none of the pathways tested is indispensable for the yeast-mediated protection against this fungus.
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Impact of transgenic cucumbers expressing the thaumatin II gene on the occurrence of arthropod fauna

Malgorzata Kielkiewicz, Janina Gajc-Wolska, Maria Szwacka, and Stefan Malepszy 149-153

Abstract: The present study report on the impact of genetically modified cucumbers expressing the thaumatin II gene on the occurrence of arthropod fauna. Four lines of transgenic cucumbers (T224, T225, T212, T210) derived from the inbred line of *Cucumis sativus* L. cv. Borszczagowski (line B) and exhibiting relatively high/low level of thaumatin II protein in the leaf were weekly evaluated under field conditions on insect and mite pests, and their natural enemies abundance. Fewer onion thrips (*Thrips tabaci*), cotton aphids (*Aphis gossypii*) and two-spotted spider mites (*Tetranychus urticae*) settled and developed on transgenic lines than on the control, line B. More leaves damaged by tarnished plant bug (*Lygus rugulipennis*) were recorded on non-transgenic than transgenic plants. The coexistence of herbivores and their natural enemies as *Coccinella septempunctata*, *Aphidoletes* sp., *Chrysoperla* sp., *Aeolothrips intermedius* and *Orius minutus* on studied cucumber lines was observed. Our results indicate that transgenic cucumber plants expressing the thaumatin II gene affect the abundance of piercing-sucking pests. However, there was no clear relationship between herbivores density and leaf thaumatin level.

Transgenic plantlets of grapevine (*Vitis* spec.) provide a look insight of host-pathogen interaction

T. Seibicke, and H.-H. Kassemeyer 154

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