Literatuuroverzicht Plantweerbaarheid

Om inzicht te verkrijgen hoe plantweerbaarheid tot stand komt
en de rol van het metaboloom en microbioom daarin

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Referaat
De maatschappij (consumenten, producenten, retail en overheden) zijn zich steeds meer bewust van de eventuele negatieve bijwerkingen die gewasbeschermingsmiddelen kunnen hebben op de gezondheid van mens, dier en leefomgeving. Dit heeft er toe geleid dat het middelenpakket door Europese en nationale regelgeving is ingeperkt en in de toekomst verder zal worden gereduceerd, mede onder druk door van eisen die worden gesteld door retail en consument. Alternatieven zijn voorhanden in de vorm van biologische middelen en middelen van natuurlijke oorsprong (extracten, stoffen), waarvan verwacht wordt dat de negatieve gevolgen op gezondheid en milieu afwezig, of zeer gering zijn. Echter, er zijn vragen vanuit de praktijk of deze middelen voor alle gewassen effectief zullen zijn en onder welke omstandigheden ze werkzaam zijn. Deze kennis is voor telers belangrijk om een juiste keuze te kunnen maken om ziekten en plagen te beheersen in hun gewassen. Echter, het blijkt dat fundamentele kennis ontbreekt om aan te geven hoe deze middelen ingrijpen op de inhoudsstoffen en het microbioom van de plant, die een belangrijke rol spelen in de weerbaarheid tegen biotische stress factoren.
De rest van dit referaat na de laatste Bijlage

Abstract
Consumers, retail and governments are increasingly aware of the possible negative side effects that crop protection products can have on human and animal health and on our living environment. This results in an increasing limitation of the availability of pesticides due to European and national regulations and due to requirements set by retail and consumers. Plant resilience, the natural ability of a plant to defend itself against diseases and pests, is an important part of an integrated approach to prevent and/or control diseases and pests in a residue-free manner. In this literature review, we show the potential of activating the plant's natural defenses based on results obtained in model crops, such as Arabidopsis and tomato, and show what has already been translated into practice.
The end of this Abstract will follows on the inside backcover

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Inhoud

Samenvatting

Consumenten, retail en overheden zijn zich steeds meer bewust van de eventuele negatieve nevenwerkingen die gewasbeschermingsmiddelen kunnen hebben op de gezondheid van mens en dier en op onze leefomgeving. Dit zorgt voor een toenemende beperking van het middelenpakket door Europese en nationale regelgeving en door eisen die gesteld worden door retail en consument. Plantweerbaarheid, het natuurlijke vermogen van een plant om zich te verdedigen tegen ziekten en plagen, is een belangrijk onderdeel van een geintegreerde aanpak om ziekten en plagen te voorkomen en/of te bestrijden op een residue-vrije manier. In dit literatuuroverzicht laten we zien wat het potentieel is van het aanschakelen van de natuurlijke afweer van de plant op basis van resultaten behaald in modelgewassen, zoals arabidopsis en tomaat, en laten we zien wat hiervan al vertaald is naar de praktijk.

Het aanschakelen van de natuurlijke afweer wordt geïnitieerd door een elicitor. Dit is een stof die de plant herkend en daarop deze reageert door het verhogen van de plantweerbaarheid. Dit kunnen chemische stoffen zijn of stoffen van natuurlijke oorsprong. Twee belangrijke groepen zijn: 1. Analogen van de planthormonen jasmonzuur en salicylzuur; 2. Polysaccharides: afbraakproducten van chitine, pectine of cellulose. Ook fungeren sommige micro-organismen als elicitor, omdat de plant het micro-organisme zelf of een stof die deze uitscheidt herkend. De vier belangrijkste geslachten waarin stammen met elicitor-functie voorkomen zijn: 1.Trichoderma spp.; 2.Arbuscular mycorrhizal fungi; 3 Pseudomonas spp.; 4. Bacillus spp. Van elk van de genoemde elicitors worden voorbeelden uit de literatuur gegeven en wordt aangegeven in welke commerciële product deze aanwezig zijn.

Plantweerbaarheid, plantinhoudsstoffen en het microbioom (de micro-organismen in en vlakbij de plant) zijn drie factoren die niet los van elkaar kunnen gezien worden. Verhoging van de plantweerbaarheid heeft gevolgen voor de samenstelling van de plantinhoudstoffen en het microbioom, maar ook andersom: veranderingen in microbioom of plantinhoudsstoffen resulteren in veranderingen in de plantweerbaarheid.

Het zijn meestal secundaire metabolieten die ervoor zorgen dat ziekten en/of plagen zich minder snel kunnen vermenigvuldigen op de plant, waardoor de infectie wordt vertraagd. Belangrijke groepen metabolieten wat betreft plantweerbaarheid zijn terpenoiden, carotenoiden, alkaloiden, glucosinolaten and polyfenolen. Welke stoffen binnen deze groepen verantwoordelijk zijn voor het verhogen van de plantweerbaarheid verschilt per gewas en zelfs per ras. Op basis van onderzoek tot nu toe lijken de veranderingen in de samenstelling van het metaboloom in verschillende gewassen hetzelfde patroon te volgen, maar er is meer onderzoek nodig, vooral in niet-modelgewassen, om te weten hoe breed deze patronen aanwezig zijn in het plantenrijk.

Micro-organismen in een microbiële gemeenschappen zijn met elkaar in evenwicht. Micro-organismen met elicitor-werking kunnen zich alleen vestigen als deze onderdeel worden van dit evenwicht. Het toevoegen ‘goede’ micro-organismen is dus alleen succesvol onder specifieke omstandigheden. Over dit evenwicht en zijn relatie met plantweerbaarheid is nog weinig bekend.

1 Introduction

1.1 Need for this review

At the European level the admittance of chemically synthesized plant protection products to the market is strongly regulated. In addition, there is an increasing demand by society for residue-free products. Therefore, in crop production a shift is taking place from curative chemical to non-chemical preventive control of pests and diseases. Growers need alternative strategies for plant health issues. Plant resilience is the natural potential of a plant to defend itself against pests and diseases. Stimulating the plant's natural defense potential instead of directly acting on pests/pathogens is an important alternative reducing the necessity of intervention with chemical pesticides. In this regard the application of chemical and microbial elicitors, amongst others biostimulants, may become essential, promoting plant growth in general as well as specifically activating natural plant defenses.

1.2 Biostimulants: types and effects

Plant biostimulants contain organic or inorganic compounds(s) and/or micro-organisms whose function when applied to plants or the rhizosphere is to stimulate natural processes to enhance/benefit nutrient uptake, nutrient efficiency, tolerance to (a)biotic stress, and crop quality (EBIC definition). Commercialized biostimulants or promising candidates are of very different natures, including humic and fulvic acids, proteins and amino acids, biopolymers such as chitosan and chitin, plant and algal extracts, inorganic compounds, and beneficial microorganisms (du Jardin, 2015).

Many of these products have in common to act through the stimulation of biological processes at the soil and/or plant level. Thus, rather than intervening directly on an external biotic stress such as pest and disease attack, many products act indirectly through the plant, stimulating natural plant defense and/or better absorption of nutrients. They, therefore, are claimed to have a very wide range of effects such as increased relative abundances of beneficial microorganisms on plants and roots, higher organic matter soil content and better soil structure, increased plant nutrient availability and efficiency, enhanced physiological plant responses, such as flowering as well as a better plant root development and higher plant production.

Biostimulants can be applied on many crops and soil types by soil drenches, seed coating, foliar spraying, or post-harvest treatments. They are used in different agricultural sectors such as arable field crops, fruits, vegetables, ornamental shrubs, flowers, and bulbs as well as pastures. Besides the agricultural context they are used for lawns and sport fields.

Despite all the qualities biostimulants are claimed to have, their effect on plant resilience does not seem to be consistent (IFOAM EU, Definition of and discussion of Biostimulants). Most of the knowledge gained on plant resilience, has been obtained under controlled conditions from *Arabidopsis thaliana*, a model research plant. Clearly, this is not representative for an agri- and horticultural environment. Therefore, some bioproducts now on the market have shown no effects under laboratory conditions or field conditions. There is thus a mismatch between the producers claims, the user's expectations and the real effect of the product.

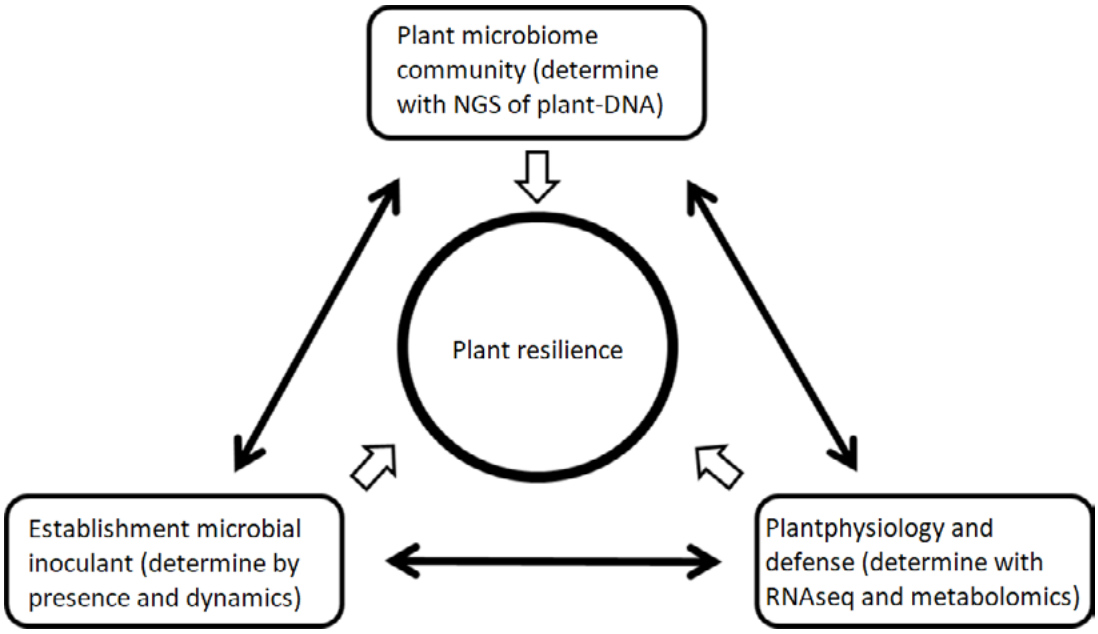
1.3 Determination of effectiveness by metabolome and microbiome shifts

Resilience can be stimulated by the application of elicitors, such as biostimulants. These can work as elicitors in two different ways.

The first way is elicitation of the plant defenses resulting in the (elevated) production of specific secondary metabolites. Secondary plant metabolites are substances that are not directly needed for plant growth, development or reproduction, but to defend the plant against pests and diseases. These metabolites ensure that pests or pathogens attacking the plant are weakened or disrupted, so that their development and/or damage is limited.

The second way is through the interaction of the plant with beneficial microorganisms. Numerous and diverse microorganisms live in very close interaction with plants. The total of the microbial community within the plant or surrounding it forms the microbiome. Most of the microbiome lives in some form of dependence with the plant. For these microorganisms it is important that the plant, as their host, survives pest and disease attacks. They, therefore, have a direct interest in protection of their plant hosts. Microorganisms can have a direct effect on pests and diseases by producing toxic substances, competition for nutrients and interruption of communication between different groups of the microbiome (quorum sensing). They can also act as elicitors negatively affecting pests and pathogens via the plant by influencing the production of secondary metabolites.

In most of the current scientific literature both these two ways are described independently from each other. Their interaction and its impact on plant resilience is largely unknown. However, the metabolome of a plant and the microbiome are closely interrelated (Fig. 1). Biochemical changes of the plant will give rise to other types of microorganisms colonizing the plant. On the other hand, changes in the microbiome may lead to the production of different secondary metabolites.



Figuur 1 *The interaction between plant metabolome and plant microbiome and its effects on plant resilience.*

1.4 Knowledge gaps

Practical knowledge gaps: when, where and how to apply elicitors
The choice of the right treatment location and circumstances as well as the timing of application play an important role in achieving robust effects of biostimulants/elicitors. Lack of knowledge of these factors is the main reason for reported biostimulant's inefficiency.

The right moment: In which developmental plant stages are the secondary metabolites and beneficial microorganisms needed for plant resilience and when should they thus be added? There may be large differences in effectiveness by application to seeds, cuttings, seedlings, vegetative or generative plants. The question is also whether a single administration is sufficient or whether it should be administered repeatedly.

The right place: In order to be able to be efficient the secondary metabolites and beneficial microorganisms must be present at the right place. In some cases, the microorganisms are endophytic, they colonize the interior of the plant, in other cases they are residents of the rhizosphere where the microorganisms colonize the exterior of the root. The question is where the microorganisms thrive best and how they can best colonize that niche. Applications can thus be administered as soil/substrate or plant treatments. Alternatively, treatments can be passed on to the young plant via seed or cutting treatments. Also, treatments of parent plant may be transferred to the next generation through cuttings.

The right circumstances: Secondary metabolites involved in plant resilience can be increased in susceptible plants by targeted management of environmental factors such as light quantity and quality. Microorganisms, however, need a substrate to grow, and are dependent on environmental factors such as acidity, moisture, and temperature. After administration of microorganisms there is usually a strong decrease in population densities due to changes in these environmental factors. In addition, competition with endemic microorganisms may play a role. One of the important questions in the proposed research is how to get a grip on these circumstances. How much inoculum is needed for a successful microorganism establishment? How much inoculum is needed to achieve activation of plant resilience? How can an actively growing population of beneficial microorganisms within and around plants be ensured?

In the right composition: Each secondary metabolite as well as microorganism has its own function and niche by which they can increase plant resilience. By increasing different secondary metabolites or by administering a mixture of beneficial microorganisms a potentially more robust protection of plants may be obtained. Which types of organic or inorganic compounds should be present simultaneously to achieve additive and/or synergistic effects on plant resilience? Which types of microorganisms can be combined to achieve additive and/or synergistic effects on plant resilience? Can compounds and microorganisms be combined to achieve additive and/or synergistic effects on plant resilience?

Theoretical knowledge gaps: Interaction between plant metabolome and microbiome
Most of the studies on plant resilience are focusing either on the plant metabolome or the plant microbiome but not on their interaction and its underlying mechanisms. While in metabolomics as well as microbiome studies a beginning has been made to use untargeted analysis to enable analysis of a wide array of different metabolite and microorganism groups genomic studies of both are often restricted to one of few specific sets of target genes.

2 Scientific principles

2.1 The natural immune system of plants

Manipulating the plant's own immune system is seen as an important strategy for triggering plant defense systems in a natural way increasing plant resilience. Previous research has shown that various elicitors can induce resistance (Derkx *et al.* 2012). Induced resistance can directly lead to the activation of defense mechanisms but can also sharpen plants to respond more strongly to an attack of a pest or disease. This increased state of readiness, also known as 'potentiation' or 'priming', only mobilizes immune responses when there is actual danger and ensures that a plant is, as it were, immunized. Induced defenses often spread systemically throughout the plant, protecting the plant against future attacks by pests and diseases. An interesting side effect is that this form of resistance not only works against the original attacker but has a broad spectrum of action.

2.1.1 Induced defense: signal transduction routes

The immune system of plants is an extremely complex biological system and consists of a network of different defense mechanisms that is triggered by molecular pest and disease recognition patterns which activate specific plant hormones. With the help of these signal hormones, plants can then coordinate their defense very precisely against the relevant attackers. the following plant hormones appear to play a major role in the regulation of plant defense: salicylic acid (SA) and jasmonic acid (JA) and to a lesser extent ethylene (ET). The involvement of these specific hormones determines the type of defense that is ultimately formed and bring different metabolic cascades into play.

Via the salicylic acid route, a plant builds up an increased resistance to attackers who live exclusively on living material, the so-called biotrophic pathogens, such as mildew. Jasmonic acid, on the other hand, often initiates defense mechanisms against necrotrophic pathogens, like Botrytis, living on dead material, as well as against herbivorous insects. These defense components often appear to be conserved in different plant families and play an important role in the generic defense processes of plants (Kogel & Langen, 2005). The main mechanisms in induced resistance involved are the induced systemic resistance (ISR) and the systemic acquired resistance (SAR) (Choudhary *et al.* 2007).

2.1.2 Systemic resistance

Systemic acquired resistance (SAR) can be caused by pathogens and is accompanied by a hypersensitivity reaction, the hypersensitive response, followed by the development of necrotic lesions (French & Telgen). A local infection can then generate a systemic signal that not only defends the damaged cells or leaf, but the entire plant. SAR is characterized by accumulation of the plant hormone SA as well as the accumulation of pathogen-related proteins (PR proteins) that can inhibit the growth of pathogens (Edreva, 2005). These proteins are non-pathogen-specific and can be divided into many different classes including glucanases, chitinases, proteinases and peroxidases.

A similar mechanism, phenotypically like SAR, can be triggered by certain non-pathogenic, root- colonizing bacteria, and is referred to as induced systemic resistance (ISR). ISR differs from SAR in that it does not cause necrotic lesions in the plant. Resistance to insects and necrotrophic pathogens is mainly observed after induction of ISR. This is based on various signal transduction systems. Unlike SAR, ISR is not associated with the induction of PR proteins (Durant & Dong, 2004) and is independent of SA. The signal transduction of ISR is dependent on the hormones JA and ET. Although there are indications that SAR and ISR can be switched on simultaneously to enhance the resistance response (van Wees *et al.* 2000; Durant & Dong, 2004), these two mechanisms seem to be antagonistic in most cases counteracting each other.

2.2 Chemical induction of resistance mechanisms

One of the first applications of chemical elicitors to enhance plant resilience is from 1974, describing a polyacrylic derivative generating resistance to both the tobacco mosaic virus (TMV) and the tobacco necrosis virus (TNV) by activating the PR1 gene (Bektas & Eulgem, 2015). Many compounds are known to activate the intrinsic resilience of the plant. These so-called elicitors can be both natural and synthetic. In Table 2 an overview of chemical elicitors activating systemic induced plant defenses is given. They comprise functional analogues of plant hormones, polysaccharides, organic acids, vitamins, and inorganic components such as phosphate and silicate. Below the main three groups comprising of JA and SA analogues as well as polysaccharides are described providing examples of increased resilience for different agri- and horticultural crops.

Elicitors are applied as soil drenches or by plant sprays. Treatment of seed has the advantage that only a small volume of the active substance needs to be used. Tree injections represent another form of applied target precision (Berger & Laurent, 2019). In addition, elicitors are used as post-harvest treatments to promote shelf life (Huang *et al.* 2000; Chen *et al.* 2017) preventing fruit rot (Terry & Joyce, 2004; Romanazzi *et al.* 2016).

2.2.1 Salicylic acid analogues

Salicylic acid plays an important role in SAR (Grant and Lamb, 2006). The disadvantage of SA is that application is often accompanied by concentration-dependent phytotoxicity. The clear majority of known synthetic elicitors are derived structural analogs that induce the SA signal molecule (Annex 1 Table 2A). Well known SA derivatives include acetyl salicylic acid (ASA: aspirin), halogenated derivatives (Conrath *et al.* 1995; Silverman *et al.* 2005), imprenatin and glycoconjugates (Cui *et al.* 2014). However, the glycoconjugate SA hydrazine does not appear to induce the expression of PR- as SAR marker genes but the expression of JA-marker genes (Cui *et al.* 2014). In addition to SA agonists, which mimic SA at the molecular level, there are other synthetic elicitors that can trigger transcriptional and physiological responses that are independent of SA accumulation.

Thiadiazole, isothiazole and pyrazole derivatives
Benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester (BTH) also known asacibenzolar-S-methyl (ASM) belongs to the chemical group benzothiadiazole. ASM is a functional analogue of SA and is known as the commercial formulations Actigard®, Bion®, Blockade®, Insimmo® or Boost®. This chemical is one of the most described elicitors with numerous publications describing its use in a wide range of plant species against fungal, bacterial and viral diseases as well as against some insects and nematodes (Bektas & Eulgem, 2015; Zhou & Wang, 2018). Induced defenses have been evaluated in more than 120 pathogen systems, mostly in the form of leaf sprays but also as soil drenches (Francis *et al.* 2009) and seed treatments (Buzi *et al.* 2004; Toksoz *et al.* 2009; Ramasamy *et al.* 2015). Treatment of melon seeds with BTH offered seedling protection against the fungal pathogen *Didymella bryoniae* (Buzi *et al.* 2004), but it appeared that spraying of melon leaves was ineffective (Ishii *et al.* 1999). Interestingly, the use of ASM as a leaf spray in broad bean or pea also offered protection against the root parasitic plant *Orobanche crenata* (Pérez-de-Luque *et al.* 2004; Sillero *et al.* 2012).

Another well-known synthetic elicitor is Probenazole (PBZ). This elicitor is commercially available under the name Oryzemate and has been used in the field for more than 30 years to protect against fungal disease such as rice blast (*Magnaporthe oryzae)* and corn leaf blight (*Cochliobolus heterostrophus)*. Probenazole as well as the active metabolite 1.2 benzothiadiazole-1.1 dioxide (BIT) induce SAR by increasing the activity of defense-related enzymes such as peroxidase, polyphenol oxidase and PAL (Iwata *et al.* 2001; Yoshioka *et al.* 2001). In the search for isodiazole derivatives, besides the well- known acibenzolar S-methyl, second generation substances have also been commercialized, including Tiadinil (V-GET® in Japan) and isotianil (Stout® in Japan and China) against rice blast. In addition to rice, isotianil has also been reported to protect wheat and pumpkin against powdery mildew, as well as cucumber and strawberry against anthracnose, Chinese cabbage against Alternaria, and peach against shot hole disease (Ogawa *et al.* 2011). The underlying mechanisms of action are not yet clear (Maienfisch & Edmunds, 2017). Structure-activity relationship studies are conducted with chlorine-substituted derivatives of SA and fluorine-containing BTH molecules both potent SAR inducers (Conrath *et al.* 1995; Fan *et al.* 2009; Du *et al.* 2011; Chang *et al.* 2017; Shi *et al.* 2019).

Isonicotinic acid derivatives

Isonicotinic acid (INA) was identified as an elicitor inducing resistance to the fungus *Colletotrichum lagenarium* in cucumber (Metraux *et al.* 1991). INA is considered a functional analogue of SA (Delaney *et al.* 1994; Vernooij *et al.* 1995). Like SA, INA can inhibit the activity of the enzymes catalase (CAT) and ascorbate peroxidase (APX) and induces the accumulation of reactive oxygen species (ROS) accumulation. Although INA has not been placed on the market due to its high phytotoxicity (Oostendorp *et al.* 2001), it is considered a useful tool to study mechanisms of induced resistance. INA induces resistance to pathogens in various host plants, including Arabidopsis, tobacco, pear, pepper, rice, cucumber and beans.

2.2.2 Jasmonic acid analogues

While SA mediates defenses against biotrophic pathogens jasmonates mainly activate defenses against necrotrophic pathogens and herbivorous insects (Campos *et al.* 2014; Wasternack & Hause, 2013). JA can either be metabolized to its airborne methylester, methyl-jasmonate (MeJA), or conjugated to L- isoleucine producing the biologically active form JA-isoleucine (JA-Ile) (Pieterse *et al.* 2012). Treating plants with synthetic jasmonic acid (JA) induces a defensive response similar to herbivore attack and is a potential strategy for integrated pest management (Annex 1 Table 2B). It has been suggested that the coordinated activation of the metabolic pathways mediated by JAs provides resistance to biotic stress conditions. JA is an important class of elicitors which is regarded as an integral signal for the biosynthesis of many secondary plant metabolites including alkaloids (Haider *et al.* 2000; Wasternack & Hause, 2013; Memelink *et al.* 2001), flavonoids (Fliegmann *et al.* 2003), terpenoids and phenylpropanoids (Thakur *et al.* 2019). In addition to inducing direct defenses, JA is also capable of regulating the expression of indirect induced defenses attracting predator and parasitoids of insect herbivores (Kappers *et al.* 2011). The bacterial phytotoxin coronatine produced by Pseudomonas spp. is a natural structural and functional mimic of JA-Ile and elicits similar responses as JA, which facilitates growth of the bacterium by weakening the plant host (Uppalapati *et al.* 2005). A more potent mimic of coronatine, coronalon was shown to induce various stress-responsive genes as well as the synthesis and accumulation of secondary metabolites, including defense-related compounds (Schuler *et al.* 2004). In addition, several other synthetic mimics have been studied and shown to induce JA signaling and defense responses in (Svoboda & Boland, 2010).

2.2.3 Polysaccharides: chitin, pectin and cellulose derivatives

Poly- or oligosaccharides from cell walls induce resistance through chemical and mechanical barriers, whereby oligomers are often more effective than polymers (Abouraïcha *et al.* 2015). Polysaccharides from seaweeds, including ulvans, alginates, fucans, laminarin and carrageenan and their derived oligosaccharides, cause the activation of SA, JA and/or ET. Table 2C (Annex 1) mainly focuses on chitosan and champost induced resistance. The activation of these signaling hormones leads to an increase in the expression of PR proteins with antifungal and antibacterial activities as well as an increased expression of immune enzymes that participate in the synthesis of phenylpropanoid compounds, terpenes, terpenoids and alkaloids. All these secondary metabolites are known for their negative effects against insects and pathogens (Vera *et al.* 2011). Polysaccharides for induction of the plant immune system are also commercially produced from seashells. A much-described and extensively investigated elicitor is chitosan. A combination of oligochitosan and oligopectate (COS-OGA) is commercially used as FADO® as a fungicide against powdery mildew in field and under glass ornamentals.

The addition of suppressive compost as a bio-formulation is widely used for controlling plant diseases (Aviles *et al.* 2011). Among such compost amendments are spent mushroom substrates (Champost). Spent mushroom compost is the primary residual compost waste generated by the mushroom production industry and, therefore, perfectly fits in a bio-based economy. Interestingly, their use has not only been associated with reductions in soil-borne diseases but may also prove to be effective against foliar diseases (Yohalem *et al.* 1994). The majority of studies emphasize the exploitation of antibiotic producing microorganisms present in soil mushroom substrates upon compost application (Yohalem *et al.* 1994, Cronin *et al.* 1996, Viji *et al.* 2003, Choi *et al.* 2007). Other putative mechanisms of suppression of such composts are (1) improving plant nutrition; (2) enhancement of beneficial micro- organisms; (3) parasitism by micro-organisms and (4) induced resistance by elicitors (Hadar & Papadopoulou 2012). Mycelia of mushrooms are abundant sources of elicitors, which, upon recognition by a plant, may enhance resistance to pathogen attack by inducing SAR.

2.3 Microbial induction of resistance mechanisms

Microorganisms, next to their direct effect on plant pests and diseases can also function as elicitors for the activation of plant defense. In Annex 1 Table 3 an overview of microbial elicitors activating systemic induced plant defenses is given. Below the main four groups consisting of Trichoderma, Pseudomonas and Bacillus are described providing examples of increased resilience for different agri- and horticultural crops.

2.3.1 Trichoderma spp.

Trichoderma spp are fungi present in a wide range of soil types (Nusaibah & Musah, 2019). They colonize the roots of most plant species to establish a symbiotic relationship with the host plant. Most of them are known to enhance plant production but also to protect plants against a wide range of pathogens such as *Pythium spp., Rhizoctonia spp., Fusarium spp., Sclerotinia*, powdery mildew and *Botrytis cinerea* amongst others. This can be a direct effect through synthesizing antibiotic compounds or cell wall degrading enzymes. Indirectly, *Trichoderma spp.* acts through activation of the induced systemic resistance involving both JA/ET and SA without production of PR-related proteins (Vinale *et al.* 2007; Tucci *et al.* 2010). Amongst Trichoderma species *Trichoderma harzianum T22*, is a strain widely used for improving plant nutrition and plant resistance to biotic stresses. This strain is commercially available as Trianum G® and Trianum P®.

2.3.2 Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi are ubiquitously found in soils and are obligate symbionts colonizing plant roots. More than 80% of all the plants on earth, including the majority of crops, form a symbiosis with those fungi. They provide plants with an enhanced uptake of nutrients and as well as resistance against various biotic and abiotic stresses in exchange of plant carbohydrates and lipids. Arbuscular mycorrhizal fungi induce plant defense in aboveground plant tissues against necrotrophic pathogens and generalist chewing insects (Pozo *et al.* 2008). Mycorrhiza-induced resistance is mainly based on priming. Arbuscular mycorrhizal fungi have been shown to be efficient against apple cancer *Neonectria ditissima* (Berdeni *et al. 2018),* white head disease (*Gaeumannomyces graminis* var. *tritici*) in barley (Castellanos-Morales *et al.* 2011) as well as the nematodes *Radopholus similis* and *Pratylenchus coffeae* in banana (Elsen *et al.* 2018*)*. Arbuscular mycorrhizal fungi are commercialized as Symbivit®, Ectovit®, and Rhodvit® amongst others.

2.3.3 Pseudomonas spp.

Beneficial *Pseudomonas* bacteria are rhizobacteria promoting plant growth and defending plants against pathogens too. Compared to pathogenic strains of *Pseudomonas*, beneficial ones can circumvent plant defense mechanisms to colonize plant roots (Stringlis *et al.* 2018a). *Pseudomonas simiae* WCS417*,* a widely used strain to study induced plant defense, was initially isolated from the rhizosphere of wheat. This rhizobacteria has a direct effect on soil borne pathogens through competition for space and nutrients, especially iron. In addition, root colonization with *P. simiae* triggers plant defense priming, activating SA independent defence signalling through ISR. This leads to an accelerated defense response in the case of pest or pathogen attack. Induced defense after treatment with *P. simiae* has been shown against *Fusarium oxysporum* and downy mildew (*Hyaloperonospora arabidopsidis)* in tomato, *Fusarium* wilt disease in carnation, as well as against *Botrytis cinerea* and the herbivore *Mamestra brassicae* in *Arabidopsis*. *Pseudomonas syringae*, a pathogenic Pseudomonas bacterium, when applied in low non-pathogenic concentrations induced resistance against western flower thrips in tomato increased production of the JA analogue coronatine leading to an accumulation of secondary phenolic metabolites (Chen *et al.* 2018).

2.3.4 Bacillus spp.

The genus Bacillus contains very diverse bacteria that can be pathogens or plant growth promoting rhizobacteria colonizing the root surface of many plants. These bacteria form spores that can survive in the soil for a long period. Within this genus, *B. amoliquefaciens, B. anthracis, B. cereus, B. pumilus and*

B. subtilis are known to be beneficial for plants. As such they can act directly against pathogens through synthesis of antibiotic compounds, cell wall degrading enzymes or antioxidants. Indirectly they act through induction of plant defense (Hashem *et al.* 2019). *Bacillus subtilis* strains for example induce SA and JA defense related responses, and as such the synthesis of phenols, enzymes and PR proteins. Bacillus spp. have been shown to be efficient against Potato blight (*Phytophthora infestans*) (Caulier *et al.* 2018)*,* powdery mildew in melons *(*García-Gutiérrez *et al.* 2013) and root-knot nematodes activity in tomato (Adam *et al.* 2014). Bacillus spp. is used as a commercial fungicides such as Serenade® ASO.

2.4 Plant resilience and metabolomics

Secondary metabolites are substances that are often formed via complex metabolic pathways in plant leaves, fruits and roots. Their total number is estimated at 200,000. Secondary plant metabolites are substances that are not directly needed for its growth, development or reproduction, but play important roles in improvement of disease and herbivore resistance. This chemical form of defense can be constitutively present or induced after pest or pathogen attack. They can be chemically classified into different families such as terpenoids, carotenoids, alkaloids, glucosinolates and polyphenols. Secondary metabolites represent a large and varied reservoir of plant compounds. They can have a direct effect on pests and pathogens acute toxicity but, may also affect them through physiological and behavioural sublethal effects such as reduced fecundity, malformations and delayed development (Mouden *et al.* 2017).

Enhancement of phenolic metabolism of plants has been often connected with induced resistance and may, in addition to defenses, enhance the quality and suitability of plant food storage for post-harvest application. One of the most studied classes in this regard are the phenylpropanoid-derived metabolites are flavonoids which may have many complex roles in plant-insect interactions (Harborne, 2001; Simmonds, 2001). Phenols were involved in plant resistance to western flower thrips in chrysanthemum (Leiss *et al.* 2009) and carrot (Leiss *et al.* 2013) while terpenes and alkaloids were involved in tomato (Escobar-Bravo *et al.* 2017; Mirnezhad *et al.* 2010). Genetic markers of thrips damage partly based on terpene volatiles were identified in tomato (Bac-Molenaar *et al.* 2019). Treatments with UV-B (Escobar-Bravo *et al.* 2018; 2019) as well as *Pseudomonas syringae* (Chen *et al.* 2018) led to increased production of phenols resulting in significant decreases of thrips damage. Induction of plant secondary metabolite accumulation is not limited to certain types of metabolites, but includes a wide variety including terpenoids, flavonoids, glucosinolates, alkaloids, and phenylpropanoids plus many other types of secondary metabolites in most plants (Zhao *et al.* 2005; Thakur *et al.* 2019).

Elicitors are well known modulators of plant defense responses and often share very similar defense profiles at the metabolic level, suggesting that defense mechanisms follow the principles of parsimony (Mayer *et al.* 2004). Consequently, metabolite profile patterns can provide a holistic signature of the physiological state under study as well as deeper knowledge of specific biochemical processes. Most researchers studying environmental or genetic effects on secondary metabolite production however, tend to focus on a class of compounds for practical reasons. Analyzing several groups of secondary compounds of various chemical properties is often time-consuming and requires the use of different extraction procedures and chromatographic methods. Therefore, the study of chemical host plant resistance has for technical reasons been restricted to the identification of single compounds, applying specific chemical analyses adapted to the compound in question. Recent developments in the research of plant metabolomes makes it possible to get a more complete overview of the secondary metabolite present in a plant. As such metabolomics allows the simultaneous detection of a wide array different chemical compound groups related to plant defense (Leiss *et al.* 2011; Macel *et al.* 2010).

While induced plant defense mechanisms are conserved among plan families secondary plant metabolites for plant defense can be specific to certain taxonomic plant families (Table 1). For instance, glucosinolates are characteristic secondary metabolites found in the Brassicaceae family. They are toxic compounds against insect herbivorous pests which can be induced by insect attacks. The Rosaceae family is relatively rich in a class of inducible disease resistance proteins called nucleotide binding site leucine-rich repeats (*NBS-LRR*). In the Solanaceae, many defense related miRNA are conserved and have conserved target genes amongst potato, tomato and pepper. In addition, systemin, a polypeptide possessing hormone-like activity that amplifies the jasmonic acid signal, is characteristic of the Solanaceae. Sesquiterpene lactones can be found in Cactaceae, Solanaceae, Araceae, and the Euphorbiaceae but in terms of quantity and diversity they are the most prevalent in the Asteraceae. They are defensive secondary metabolites regulated by JA serving as antifeedants against herbivore but also display antimicrobial activity. However, some secondary metabolites for plant defence are conserved amongst families: for instance, within the phenylalanine derived phytoalexins, pisatin, gliceollin I and medicarpin are found in the Fabaceae while sakuranetin and 3-deoxyanthocyanidin are found in the Poaceae. Within the anthranilate-derived secondary metabolites, indole and benzoxazinone glucosides are found in the Poaceae while indol-3-ylmethyl glucosinolate and 4-methoxy-I3G are found in the Brassicaceae.

2.5 Plant resilience and the microbiome

During their life cycle, plants coexist and interact with a multitude of microorganisms, the microbiome. The microorganisms are present within the plant organs like the endophytes, or on the plant or root surface. The microbiome is involved in plant germination development, growth and productivity. It allows the plant to adapt to various abiotic and biotic stresses and, therefore, plays a crucial role in plant resistance to pests and diseases. The microorganisms constituting the plant microbiome can be grouped into three categories: "The good": microorganisms beneficial for the plant, making it more resilient to attackers, improving plant nutrition, and stimulating plant growth. "The Evil": pathogenic microorganisms parasitizing the plant and finally "the Ugly": microorganisms constituting a health hazard for humans or animals. Metabarcoding and next generation sequencing techniques allow to explore and identify the different components of the plant microbiome. At the phylum level the microbiome mainly comprises of the bacteria Proteobacteria, Actinobacteria, Bacteroidetes and Firmicutes, while the Ascomycota and Basidiomycota constitute the major fungal components. Most of the beneficial microorganisms of the microbiome belong to the bacterial genera Bacillus, Pseudomonas and Rhizobium and to the fungal genera Trichoderma and Mycorrhiza.

The structure of the plant microbiome is mostly dependent on the plant genotype, the root system, the soil type and seasonal changes (Liu *et al.* 2019). At the root level, plant exudates constitute a major nutrient source for the microbiome. Those exudates attract both surrounding beneficial microorganisms as well as pathogens. Infection by pathogens and non-pathogens occurs often simultaneously. However, the plant is able to recognize and react to both types of microorganisms. Infection of a plant by a pathogen or non-pathogen microorganism activates the induced defense pathways ISR and SAR, leading to enhancement of various secondary metabolites in the plant and its rhizosphere. This can in turn affect the plant microbiome composition. Scopoletin, released as a root exudate by Arabidopsis, upon activation of induced plant defenses, had a negative effect on the fungal pathogens *Fusarium oxysporum* and *Verticillium dahliae in-vitro* but had only little or no effects on the growth of the beneficial bacteria

P. simiae WCS417 and *Pseudomonas capeferrum* WCS358. A resilient plant producing exudates in response to the activation of the JA and SA pathway has thus the ability to shape its own microbiome (Sasse *et al.* 2018) Mendes *et al.* (2018), showed that common bean cultivars displaying a higher resistance to *Fusarium oxysporum* contained a higher relative abundance of beneficial microorganisms in its microbiome. Also cotton cultivars resistant to *Verticillium dahliae* (Wei *et al.* 2019) and sugar beets infected with *Rhizocotonia solani* (Chapelle *et al.* 2016) showed a higher number of beneficial microorganisms. Berendsen *et al.* (2018), reported that Arabidopsis with infected downy mildew leaves actively recruited three bacterial taxa in the rhizosphere: Microbacterium, Stenotrophomonas, and Xanthomonas spp. These had a direct effect against the downy mildew but also induced plant defense mechanism.

As stated by Rolfe *et al.* (2019), the plant is "crying for help": when under attack by a pest or pathogen plant induced defense mechanisms are activated, leading to a change of metabolic compounds with a negative effect on pathogenic- but no or a positive effect on beneficial microorganisms. There is thus a close interaction between plant microbiome, plant metabolome and plant resilience. This could be used for enhancement of natural plant defense crop protection increasing the relative abundance of beneficial microorganisms. This could be achieved via inoculation or by creating a favourable plant and root environment for colonization.

3 Conclusions

1. The mechanism of action of induced defences to biotic stress is mainly studied in detail in Arabidopsis, tomato and rice, but in many other crops from different plant families it is shown that the same plant hormones play a role in plant resilience

2. Analogues of the plant hormones jasmonic acid and salicylic acid and several polysaccharides are important elicitors that prime resistance mechanisms against biotic stress.

3. Microbes can also have an elicitor function. The four main genera containing strains with elicitor function are: 1.Trichoderma spp.; 2.Arbuscular mycorrhizal fungi; 3 Pseudomonas spp.; 4. Bacillus spp.

4. Important groups of metabolites with regard to plant resilience are terpenoids, carotenoids, alkaloids, glucosinolates and polyphenols.

5. Plant resilience, plant metabolites and the microbiome (the micro-organisms in and near the plant) are three factors that cannot be seen in isolation from each other. Increasing plant resistance has consequences for the composition of the plant components and the microbiome, but also vice versa: changes in the microbiome or plant components result in changes in plant resistance.

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Bijlage 1 Chemical elicitors – Salicylic acid analogs

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
Alliaceae									
	Onion (Allium cepa)	leaf blight (Xanthomonas axonopodi	ASM	Foliar spray	Field	four weekly applications of acibenzolar-S-methyl reduced severity of Xanthomonas leaf blight	ns		Gent and Schwartz, 2005
	Onion (Allium cepa)	Leaf blight (Stemphylium vesicarium)	Salicylic acid 2 mM		Greenhouse	reduction in disease severity	Increased activity in peroxidase and polyphenoloxidase and increased total phenol and SA content		Abo elyousr et al., 2009
	Onion (Allium cepa)	Leaf blight (Xanthomonas axonopodis pv. Allii)	Actigard 50WG	ASM applied at 26.3 g a.i./ha	greenhouse and field	reduce Xanthomonas leaf blight severity (measured as relative area under the disease progress curve) Bulb yield not affected	NS		Lang et al., 2007
	Onion (Allium cepa)	Leaf blight (Stemphylium vesicarium)	Bion	Spray (50 ml/ seedling)	Greenhouse	Disease severity reduced up to 15 days after application	No direct induction of PO, PPO, PAL but priming effect. Treated plant inoculated show increase in enzyme activities	No direct induction of phenols but treated plant inoculated show increase total phenol content	Kamal et al., 2008
	Onion (Allium cepa)	Purple blotch (Alternaria porri)	BTH (BION)	foliar application and seedling root dipping method using 125 ppm BTH	Greenhouse	Reduction of disease severity by both application methods	Bion inoculated with the pathogen showed higher PAL, PO, PPO activity, and phenolic contents (= priming of defenes)	Bion inoculated with the pathogen showed higher phenolic contents (= priming of defenes)	Mansha et al., 2019

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
Asteracea									
	Sunflower (Helianthus annuus)	Rust (Puccinia helianthi)	BTH 100 µg/ ml, INA and BABA	foliar (5 or 25 mL), soil drench and root dip (5 ml; 24 hours)	Greenhouse	Foliar spay with 200 µg/ml BTH provided 33% protection. Foliar spay with 200 µg/ml INA provided 35% protection	ns		Amzalek and Cohen 2007
	Sunflower (Helianthus annuus)	Downey mildew (Plasmopara halstedii)	BTH (BION)	seedling dip 200 mg dm-3 for 12 hours	Growth chamber	ns	Direct induction: BTH-treated sunflower seedlings showed increased peroxidase and chitinase activities.		Roldan Serrano et al., 2007
	Sunflower (Helianthus annuus)	Downey mildew (Plasmopara halstedii	Chitosan	5% chitosan seed treatment	greenhouse and field	Decrease severit and provided >40% protection	Priming: Enhanced activation of catalase (CAT) and phenylalanine ammonia lyase (PAL), peroxidase (POX), polyphenol oxidase (PPO) and chitinase (CHI) post-inoculation		Nandeesh-kumar et al., 2008
	Lettuce (Lactuca sativa)	Bacterial leaf spot (Xanthomonas campestris pv. Vitians)	ASM; Bion 50 WG	Foliar spray seedling (200 µl of 0,2 mg/ ml ASM) (cv. Arizona RZ)	Greenhouse	severity of disease and bacterial growth reduced	PR protein activity chitinase showed remarkable increase in inoculated plants		Yigit, 2011
	Lettuce (Lactuca sativa)	Root knot nematode (Meloidogyne javanica)	Bion 500®, Syngenta	Seedling treatment shoot spray at 0.5 g ai/L	Greenhouse	> 60% decrease in M. javanica population. No negative effect on vegetative growth	ns		Hernandes et al., 2017

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Lettuce (Lactuca sativa)	Fusarium wilt (Fusarium oxysporum spp.)	Bion 50WG	Pre-planting spray application	Greenhouse	3 treatments of ASM provided 59.9% efficacy. Disease reduction accompanied with high fresh yield	ns		Gilardi et al., 2016
Amaranthaceae									
	Beet (Beta vulgaris)	Cercospora leaf spot (C. beticola)	Bion	Foliar spray 25 mg/L ASM	Greenhouse conditions	Reduction leaf spot severity by 91%	PR activation: ASM promoted the accumulation of peroxidases and β-1,3 glucanases in beet leaves		Felipini & Piero, 2013;
	Beet (Beta vulgaris)	Cercospora leaf spot (C. beticola)	Bion		greenhouse	ASM (50 mg/L) resulted in enhanced disease control.	ASM increased peroxidase and glucanase activities		Felipini et al., 2015
	Spinach (ƒspinacia oleracea) —™ —	White rust (Albugo occidentalis)	Actigard 50WG (acibenzolar-S-methyl) at 26.25 g a.i./ ha	Foliar application using CO2 spray two weekly application	Field study	% infected leaf area lower and disease progression over time lower than in control. No phytotoxicity (chlorosis) and no yield loss	ns		Leskovar and Kolenda, 2001
Brassicaceae									
	Arabidopsis thaliana	Pseudomonas syringae pv. tomato DC 3000 and Peronospora parasitica	Probenazole (Oryzemate) and its active metabolite BIT (1,2-benzi-sothiazole-1,1-dioxide)	Foliar spray 2 mM BIT	Growth chamber	BIT treatment reduced growth of bacterial pathogen pseudomona and reduced disease symptoms by oomycete pathogen	Icreased expression of PR1, PR2 and PR5 and levels of total salicylic		Yoshioka et al., 2001

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	White cabbage (B. oleracea)	downy mildew (Peronospora parasitica)	INA/ / SA/ BTH	leaf treatment, seed treatment, young plants		Infection area assayed. INA significantly reduced downy mildew symptoms after seed treatment, but, BTH and SA did not	Induction of SAR markers by INA. expression of chitinase and 1,3-beta-d-glucanase activity as markers for SAR was increased after increasing periods of exposure		Wolf, van der 2012
	Canola (Brassica napus)	cabbage aphid (Brevicoryne brassicae)	SA	Leaf spray at 1 mM containing 0,1% (v/v) aq. TWEEN		net reproductive rate, intrinsic rate of increase and finite rate of increase	total glucosinolate, total phenolic content and total flavonoid content increased in aphid infested leaves treated with SA		Khosh-farman-Borji et al., 2020
	Cauliflower (Brassica oleracea var botrytis)	downy mildew (Peronospora parasitica)	BTH (CGA 245704)	Drop and spray treatments	Greenhouse	Disease rating demonstrated that treated seedlings (8 day old) and 30-day old plants were more often classified as resistant . However dose-dependent growth reduction	NA		Godard et al., 1999
	Cauliflower (Brassica oleracea var botrytis)	downy mildew (Peronospora parasitica)	ASM	foliar spray (0·015 or 0·075 mg a.i. mL−1 ASM) applied to 7-day-old seedlings (susceptible cultivar Billabong)	Glasshouse	Dose dependent efficacy in % of protection. 50% protection already 1 day after treatment	ASM significantly induced β-1,3 glucanase activity but not chitinase		Ziadi et al., 2001

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Cauliflower (Brassica oleracea s)	downy mildew (Peronospora parasitica)	BABA (20 mM) and ASM (as positive control indluded)	foliar spray applied to 7-day-old seedlings		Reduction disease severity	accumulation of the pathogenesis-related protein PR-2		Silué and Cohen, 2002
	winter oilseed rape, brussel sprouts	light leaf spot (Pyrenopeziza brassicae), clubroot (Plasmodiophora brassicae)	Bion (0.175 a.i. g/L)	Foliar application, root drench and seed soak	field trial (multiple years) and greenhouse	Reduction of light leaf spot (LLS) in winter oilseed rape by Bion. Root drench or seed soak Bion® reduced symptom development of the soil-borne brassica disease clubroot	Foliar spray and soil drench increase transcript levels of PR1 days after treatment with Bion®	ns	McGrann et al., 2017
	Brocolli	Head rot (Brassica oleracea italica)	ASM	Brocolli heads sprayed until run-off using ASM (0.23 mM AI)	Greenhouse	Treated non-excised brocolli heads are protected by ASM and BABA. Lower disease index (less browning symptoms)	ns		Pajot & Silué, 2005
Curcubitaceae									
	Cucumber (Cucumis sativus)	Pythium ultimum	BTH, CGA 245704)	Foliar spray at 1.5 mm BTH	glasshouse	Histological examination shows that BTH treated plants have less fungal colonization		Phenolic deposition and accumulation of β-glucoside residues	Benhamou & Belanger 1998

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Cucumber (Cucumis sativus)	powdery mildew (Podosphaera xanthii) downy mildew (Pseudo-peronospora cubensis)	ASM	Spray, seed soaking , soil amendment, micro-encapsulated formulations 50% (a.i.) water-dispersible granular (WG) or 2% granular (G) formulation	Pot and greenhouse experiment	Lowered disease severity	not specified. Assumed that ASM-induced SAR		Ishii et al., 2019
	Cucumber (Cucumis sativus)	Colletotrichum orbiculare	ASM	Leaf dipping (5s) with ASM at 500 or 100 uM	Greenhouse	Reduction lesion nr	Systemic induction POX and PR1-1a. Priming of PAL		Cools and Ishii, 2002
	Cucumber (Cucumis sativus)	Scab (Cladosporium cucumerinum)	BTH	Leaf dipping in 0.5 mM	Greenhouse	Reduction of disease severity	ASM-mediated SAR is associated with an increase in the enzyme activity Systemic expression of peroxidase and chitinase genes. Induction gene expression of b-1,3-glucanase (GLU) only locally on treated leaf		Narusaka et al., 1999

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Cucumber (Cucumis sativus)	Anthracnose fungus (Colletotrichum orbiculare), scab fungus (Cladosporium cucumerinum) and Corynespora leaf spot fungus (Corynespora cassiicola)	ASM	Leaf dipping in 100 ppm ASM suspension	Greenhouse	Local and systemic reduction of disease severity		No induction of phytoalexin -like phenolics	Lin et al., 2009
	cucumber (Cucumis sativus)	Powdery mildew (Sphaerotheca fuligin)	Bion (ASM)	Seed imbibition 75 ug a.i. ml_1 ASM for 12 h	Detached leaf assay	Severity of powdery mildew reduced in cucumber cotyledon-disc assays	seed treatment with ASM increased the activities of pathogenesis-related (PR) proteins and correlated with increased resistance		Ramasamy et al., 2015
	Squash (Cucurbita pepo)	Phytophthora blight (Phytophthora capsici)	ASM (Actigard 50 WG)	Seedling spray at at concen-trations of 36, 18, and 9 µg/ml in greenhouse followed by foliar spray at 17.5, 8.8, and 4.4 g a.i. ha−1 in field experiment	Field conditions	Field experiment: reduction area under the disease progress curve (AUDPC) values but not Phytophthora blight incidences. ASM at all three concentrations increased marketable yield (kg/h)	ns		Ji et al., 2011
	Squash (Cucurbita pepo)	Phytophthora blight (Phytophthora capsici)	ASM, Actigard 50WG, Saver (SA), BABA, INA	Soil drench 25 ml of solution at 25 or 50 µg ml/1 into each seedling pot followed by 3 foliar applications	greenhouse	All compounds reduced disease severity with no signs of phytotoxicity	ns		Kone et al., 2009

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Melon (Cucumis melo)	gummy stem blight (Didymella bryoniae) and white mould disease (Sclerotinia sclerotiorum)	acibenzolar-S-methyl (BTH) 50 µg/ml and 5 mm SA	Seed treatment		Protection of seedlings against S. sclerotiorum, and, to a less extent, against D. bryoniae. Reduction in percentage of necrotic lesions.4 SA showed a limited effect at the tested concentration on the containment of S. sclerotiorum and D. bryoniae infection.			Buzi et al., 2004
	Muskmelon (Cucumis melo L.)	Fruit decay (Trichothecium roseum)	BTH	Post-harvest fruit dipping at 100 mg/L for 10 min	NA	Reduction of fruit lesion area	Enhancement of cell membrane integrity. Decrease in oxygen radicals. increased enzyme activities associated with ROS production (Induction of NADPH oxidase (NOX), superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR))		Ren et al., 2012

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Muskmelon (Cucumis melo L.)	Alternaria rot (Alternaria alternata) and Fusarium rot (Fusarium spp.)	ASM	Preharvest treatment 100 mg/L a.i. sprayed with droplets of ASM (approximately 20 mL plant−1)	Open Field	ASM treatments effectively controlled latent infection and improved postharvest qualities of muskmelon fruit	Increases in defense-related enzyme activities of peroxidase, phenylalanine ammonia lyase, β-1,3-glucanase and chitinase. Enhancement of the levels of lignification and suberization of cell walls.	accumulation of phenolic compounds, lignin and flavonoids	Zhang et al., 2011
	Cantaloupe (Cucumis melo) (melon)	C. lagenarium and Cucumber mosaic virus (CMV)	ASM (Actigard)	One-week-old seedlings (cv. Durango) were sprayed with 10, 20 or 40 µg/ml ASM. In field experiment foliar application at a rate of 37.5-50 or 100 µg/ml until run-off at 2 or 3 week interval	greenhouse en field	Complete protection against fungal pathogen and fungal virus. delayed the spread of CMV in greenhouse setting	Accumulation of chitinase. higher than 50 µg/ml caused phytotoxicy		Smith-Beckers, 2003
Solanaceae									
	Tomato	bacterial spot (Xanthomonas campestris pv. vesicatoria) early blight (Alternaria solani), leaf mold (Fulvia fulva) leafminer (Liriomyza spp.).	BTH (Actigard)	Four rounds of exogenous foliar application every 3 weeks. [1.85 g ai (active ingredient)/3.8 liter water]	Field study and laboratory trials	Cross resistance by BTH; 33-40% reduction leaf miner density. lower incidence, bacterial spot, early blight and leaf mold.	Foliar induction of PR genes and defensive proteins (peroxidase, chitinase, β-1,3-glucanase and lysozyme)		Inbar et al., 1998

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Tomato	Grey mould (Botrytis cinerea)	ASM (Bion)	ASM 0.3 mM solution	Growth chamber	restricted B. cinerea infection/ Reduced infection development	Disease resistance correlated with enhanced ROS generation as well as the increase in peroxidase (PO) activity		Małole-psza, 2006
	Tomato	bacterial canker (Clavibacter michiganensis)	ASM; Bion 50 WG	Tomato seedlings sprayed with 200 ul of 0.2 mg ml−1	Greenhouse	Reduction severity disease symptoms. The disease index was reduced by 75% in ASM-treated seedlings 7 dai, and this was maintained at the same level until 14 dai	increase in activity of both oxidative and antioxidative protection systems in planta. Enhanced levels of peroxidase (POX) and glutathione peroxidase (GPX)		Soyly et al., 2003
	Tomato	Bacterial wilt (Ralstonia solanacearum)	Salicylic acid	0.01% concentration SA and 0.1% CHT added to media	Growth chamber hydroponics culture	Provided resistance against Ralstonia solanacearum. Less vascular browning and wiltin (indexing)	Increased lignin deposition in cell walls of roots, accumulation of phenolics, increase in the activity of enzymes PAL, POD, polyphenol oxidase, cinnamyl alcohol dehydrogenase, and catalase.		Mandal et al., 2013
	Tomato	Bacterial spot	ASM	soil applications and foliar sprays	Growth chamber and field studies	Weekly ASM soil application of at 10 mg/l reduced final disease severity and disease progress.	Induction of PR1a and PR1b		Huang and Vallad, 2018

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Tobacco (Nicotiana tabacum)	Pseudomonas syringae pv. Tabaci tobacco mosaic virus Powdery mildew (Odium spp)	Probenazole, BIT (1,2-benziso-thiazole-1,1-dioxide), SA	Leaf treatment using 2 mm PBZ, 2 mM BIT, 0.2 mM BTH Soil drench 2.5 mg/pot BIT	growth chamber	enhanced resistance to the viral pathogen tobacco mosaic virus (TMV; reduced lesion size by PBZ, BIT and BTH). BIT treatment enhances resistance to TMV, the bacterial pathogen Pseudomonas syringae pv. tabaci (Pst), and the fungal pathogen Oidium sp	SA accumulation upon BIT treatment. Induction SAR marker genes PR1, PR2 and PR5		Nakashita et al., 2002,a
	Tobacco (Nicotiana tabacum)	Pseudomonas syringae pv. Tabaci tobacco mosaic virus and powdery mildew (Odium lycopersici)	NCI, BTH and BIT	Soil drench application and foliar spray	Growth chamber	50% reduction of lesion size caused by powdery mildew	NCI induced PR gene expression. SA-independent		Nakashita et al., 2002
	Potato (Solanum tuberosum)	late blight (Phytophthora infestans) early blight (Alternaria solani)	INA	Foliar spray of INA at 50.0 and 100 mM	greenhouse and field	Individual INA reduced the late and early diseases by 82.1% and enhanced tuber yield	increase in activity of both ß-1,3-glucanase and chitinase		El-Gamal et al., 2007
	Potato (Solanum tuberosum)	Verticulum wilt (Verticillium dahliae)	Acibenzolar-S-methyl (ASM) and Chitosan	foliar spray on potato seedlings at concentration 100 mug a.i./ plant;	'in vitro' and greenhouse conditions.	Reduction disease severity and increased tubers fresh weights, but ASM was more effective than chitosan	NS		Amini, 2015

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Potato (Solanum tuberosum)	early blight (Alternaria solani) and powdery mildew (Erysiphe cichoracearum) dry rot fungus (Fusarium semitectum	Benzo-thiadiazole (BTH), as Bion WG50	Foliar spray BTH at 50- 100 mg a.i. L−1	field and glasshouse	50 mg a.i./ L of BTH gave full control of foliar diseases: reduced disease infection (%leaf area). BTH (100 mg a.i./L reduced dry rot severity in field experiment	BTH treatment increased β-1,3-glucanase activity in leaves up to 45 days post-treatment		Bokshi et al., 2003
	Potato (Solanum tuberosum)	Brown leaf spot (Alternaria alternata)	Acibenzolar-S-methyl (ASM) and Acetyl Salicylic Acid (ASA)	Foliage and tuber spray until runoff	Field and laboratory experiment (detached potato leaves)	Reduced disease index and impoved tuber yield. In field experiments ASA has no effect on disease index	ns		Soleimani and Kirk,2012
	Potato (Solanum tuberosum)	Fungal dry rot (Fusarium sulphureum	BTH	BTH post harvest treatment	NA	Reduced weight loss and disease index.	BTH induced lignin and suberin accumulation and enhanced firmness of healing tissues. ncreased activities of phenylalanine ammonia-lyase, cinnamate-4-hydroxylase, 4-coumaryl-CoA ligase and cinnamyl alcohol dehydrogenase.	Elevated metabolism of phenylpropanoid pathway. Phenol and lignin content increased. cinnamic, caffeic and ferulic acids	Jiang et al., 2019
	Pepper (capsicum annuum)	bacterial spot (Xanthomonas axonopodis pv. Vesicatori) bacterial wilt (Ralstonia solanacearum) & Cucumber mosaic virus d	BTH	0.5 mM BTH	Greenhouse/ field	Reduced symptom development at 0.5 mM but also reduction in seedling growth. Inhibtion of pst bacterial growth	Increased expression of pepper defense genes CaTin1, CaPR4, and CaPR1		Yi et al., 2013 Yi et al., 2012

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Pepper (capsicum annuum)	Pepper golden mosaic virus	BTH	300 mg/L foliar spray	Greenhouse experiment	Reduced the percentage of infected plant. less severe symptoms. Reduction in the multiplication of TMV in the locally-infected leaves, while a 4-day delay was observed in the multiplication of TMV in systemically infected leaves Productivity of BTH-treated plants is not affected.	Induction of PR-1 gene expression by BTH treatment		Trejo-Saavedra et al., 2013
	Pepper (capsicum annuum)	blight disease (Phytophthora capsici)	Bion (ASM)	Spray 0.2 cm3 per seedling	Greenhouse	ASM-treated plants have 45% lower mean disease index (less severe wilting)	rapid and transient induction of L-phenylalanine ammonia-lyase (PAL), increase in total phenol content and activities of chitinase and β-1,3-glucanase.		Baysal et al., 2005

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Pepper (Capsicum annuum)	Bacterial spot disease (Xanthomonas campestris pv. Vesicatoria)	ASM (CGA 245704) and acibenzolar-S-methyl acid derivative (CGA 210007)	Foliar spray basal leaves: ASM at 300 µM (64 µg ml−1 a.i.) and CGA 210007 (55 µg ml−1 a.i.)	Growth chamber and open field conditions	Growth chamber: systemic reduction in degree of infection, spot diameter and in planta bacterial growth Field experiment: four sprays 1,25- 5 g ai/h reduced % of infected area by >96% However in open field trial conducted in 1990 control efficacy of ASM was lower (16-51% reduction infected leaf area)	NS Speculative SAR inducer		Buonaurio et al., 2002
	Eggplant (Solanum melongena)	Fusarium oxysporum	ASM	Seedling spray at 0.2 mg mL−1 ASM	Growth chamber	NA	biochemical activities +histochemical analysis (callose)		Altinok and Bikilitas, 2014
	Eggplant (Solanum melongena)	Bacterial wilt (Ralstonia solanacearum)	Salicylic acid, chitosan, methyl salicylate, and methyl jasmonate	Root immersion	Field	Provided resistance against Ralstonia solanacearum/ not truly measured but speculation based on antioxidant increases	Increased lignin deposition in cell walls of roots, accumulation of phenolics, increase in the activity of enzymes PAL, POD, polyphenol oxidase, cinnamyl alcohol dehydrogenase, and catalase.		Mandal, 2010
	Eggplant (Solanum melongena)	Wilt disease (Verticillium dahliae)	Salicylic acid	pre-sowing seed treatment (0.2- 0.5 and 1 mM SA)	greenhouse conditions	Reduction of disease incidence at 0.5 mM (39.25% vs untreated control 97.5%)	SA increased plant growth parameters and defense-related enzymes chitinase and β-1,3-glucanse		Mahesh et al., 2017

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
Fabaceae									
	Chick pea (Cicer arietinum)	chickpea blight (Didymella rabiei)	Bion Sandoz, 50%WP BTH	Seed soaking and foliar spray of seedlings (100 ppm i.e. BTH 50 ppm) Commercial product Bion (50% ai, Sandoz) was used at a concentration of 100 ppm.	Greenhouse and field experiment	Seed soaking and multiple foliar applications effectively managed the disease under economic threshold levels. repeated BTH sprays have yield penalties in chickpea.	not specified		Sharma et al., 2011
	Cow pea (Vigna unguiculata)	anthracnose fungus Colletotrichum destructivum	BTH (CGA 245704)	Seed treatment (24 h at 25 ppm)	Laboratory experiment (incubator)	Reduction host penetration and infection (i.e. anthracnose lesion size)	Increase in phenylalanine ammonia-lyase (PAL) and chalcone isomerase (CHI). Accumulation of PR proteins	accelerated accumulation of the isoflavonoid phytoalexins kievitone and phaseollidin in treated hypocotyls.	Dada and Lucas, 2001

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Faba bean (Vicia faba)	rust (Uromyces viciae-fabae), ascochyta blight (Ascochyta fabae), broomrape (Orobanche crenata)	Bion 50 (50% a.i.) and SA	Paint brush application using solution with BTH (0.05, 0.5, 5 and 50 mM) or SA (0.1, 1 and 10 mM)	Growth chamber and field conditions	Sstemic belowground protection> 50% protection against rust fungus. Under field conditions 2,5 mM BTH reduced disease severity by 44-66% in susceptible and moderately resistant cultivars. Foliar necrosis indicating phytotoxicity was observed with BTH 50 mMS. SA reduced infection frequency of U. viciae-fabae on faba bean seedlings. 1 mM SA provided >50% protection. 5 MM application in field reduces disease severity.	not specified		Sillero et al., 2012
	Pea (Pisum sativum)	rust (Uromyces pisi)	BTH (Bion 50 WG (50% active ingredient) from Syngenta AG)	Foliar application 10 mM for BTH and 50 mM for BABA	Growth chamber experiment	reduced infection frequency : 1–10mM BTH provided a 30–40% reduction in rust infection on treated leaves.	BTH treatment primed the activity of pathogenesis related-proteins such as β-1,3-glucanase, chitinase and peroxidase.		Barilli et al., 2010a

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Pea (Pisum sativum)	rust (Uromyces pisi)	BTH (Bion 50 WG (50% active ingredient) from Syngenta AG	Droplets (45 ul) on leaflet at the first node from the base. Solution prepared as 10 mM and 50 mM for BTH and BABA	Growth chamber experiment	Reducted infection type and disease severity	BTH acting as a more potent inducer of defense-related proteins than BABA	Plants reduce their metabolism and enhance the production of defense-related proteins Enzymes from isoflavonoid pathways were significantly increased with BABA induce	Barilli et al., 2010b
	Pea (Pisum sativum)	rust (Uromyces pisi)	BTH (Bion 50 WG (50% active ingredient) from Syngenta AG)	Droplets (45 ul) on leaflet at the first node from the base. Solution prepared as 10 mM and 50 mM for BTH and BABA	Growth chamber experiment	reduce rust penetration		Cell wall reinforcement: increase in scopoletin, pisatin and medicarpin contents. Coumarin only induced in resistant var.	Barrili et al., 2015
	Soybean	Soybean looper (Chrysodeixis includens)	Actigard 50WG (acibenzolar-S-methyl) at 70 - 210 g/ha)	Exogenous foliar spray (2 days before laboratory assay)	Field study with laboratory assays	Adverse effects on developmental time, defoliation, and pupal weight No negative effect on seed production	ns		Chen et al., 2018
	Soybean	white mold (Sclerotinia sclerotioru)	2,6-dichloro-isonicotinic acid (INA/ CGA 41396)	Multiple (3-4x) foliar application 25% a.i. in a wettable powder	Field and greenhouse study	reduce fungal disease incidence and severity by 20–70%	ns		Dann et al., 1998

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
Rosaceae									
	Rosa hybrida	NA	SA and BTH	Post harvest vase application	NA	Extended vase life of cut-rose flowers.	BTH significantly increased the levels of phenols but had negative effect on stem due impaired water uptake		Cocetta et al., 2017
	Rosa hybrida	NA	SA	Vase application of SA at 0.5; 1.0; 1.5 and 2.0 mM	NA	Improved quality cut roses in post-harvest, with reduced mass loss, neck bending, wilting and petal darkening. Increased shelf life	Increased total protein content and phenylalanine ammonia-lyase (PAL) probably reduce senescence		Mazaro et al., 2018
	Rosa hybrida	Black spot (Diplocarpon rosae)	Bion	Spray preharvest (50 µmol/L BTH)	In-vitro propagated plants	Not specified: speculative role in restricting the development of disease symptoms on the rose leaves infected with D. rosae	increased β-1,3-glucanase and chitinase activities. Induction and accumulation of a set of extracellular proteins (PR-1, PR-2, PR-3 and PR-5)		Suo and Leung, 2001; 2002
	(Rosa spp.)	Rose powdery mildew (Podosphaera pannosa)	Bion (ASM)	10 ml Spray and watering at concentration 0,05 -0,1 mg/ ml	Pot experiments (cv Pink Monte Rosa) in greenhouse	Reduction disease severity	ns		Luz-Herrero et al., 2012

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Apple ((Malus domestica)	Blue mold Penicillium expansum and grey mould (Botrytis cinerea)	ulvans and oligoulvan	Post harvest fruit dip using 20 ul of 5 mg ml/1 solution	post harvest	Oligomer more efficient than polymer in reducing decay index and lesion diameter	increase hydrogen peroxide (H2O2), catalase (CAT), superoxide dismutase (SOD) phenylalanine ammonialyase (PAL), peroxidase (POD) and polyphenoloxydase (PPO). Increase lignin content and total phenolics	Increase total phenolics	Abouraïcha et al., 2015
	Apple	Glomerella leaf spot (Glomerella cingulata)	SA solution	Foliar spray of three-year-old apple trees (uniform size selected) 0.1, 0.2, 0.5, 1.0 mM concentrations	Greenhouse	SA treated leaves (0.1–1.0 mM) show significant reduction in lesion numbers and disease index to varying degree	Exogenous SA induces resistance against GLS in a highly susceptible apple cultivar. SA increased defence-related enzymes activities of CAT, POD, SOD, PAL and PPO. Exogenous SA markedly up-regulated the expression of five pathogenesis-related genes.		Zhang et al., 2016
	Apple	Fire blight (Erwinia amylovora)	ASM (Actigard)	100 and 200 mg/	Greenhouse and orchards	In greenhouse experiment 100 and 200 mg/L reduced % of infected seedlings. Reduction of infected shoots in scions reduced infected clusters in trees	Increase of peroxidases and β-1,3-glucanases in seedlings (local and systemic)		Brisset et al., 2000

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Apple	Fire blight (Erwinia amylovora)	ASM/ potassium phosphites (PH)	Trunk injection (vascular transport: xylum uptake)	Field experiment	fire blight symptom suppression	SAR: induction of PR-1, PR-2, and PR-8 protein genes		Aćimović *et al.* (2015)
	Apple	Fire blight (Erwinia amylovora)	ASM, Actigard	Spray spurs and shoots	Field experiment	six ASM sprays (75 mg/L) provided 50% of shoot blight control	SAR: induction of PR-1, PR-2, and PR-8 protein genes		(Maxson-Stein et al., 2002)
	Apple	Fire blight (Erwinia amylovora)	ASM (Actigard 50W)	trunk paint, root drench, or foliar spray treatments with ASM	Greenhouse	% suppression of fire blight canker rootdrench, trunk paint, foliar spray 36%, 43, 34 respectively	Increased epression of pathogenesis-related (PR) genes PR-1 and -2 only observed in trunk paint not in root drench		Johnsen and Temple, 2016
	Apple	Fire blight (Erwinia amylovora)	Bion 50 WG & lamanarin	Seedling spray until run-off (0,4 g/L)	Greenhouse	protection rate ranging from >70%	PR-proteins, terpenoid biosynthetic enzymes, and salicylic acid-related markers were strongly upregulated		Dugé de Bernonville et al., 2014
	Apple	Fire blight (Erwinia amylovora)	Bion (ASM)	0.05% ASM sprayed on apple rootstock/ plants	greenhouse conditions and field trials	Greenhouse: Reduction disease development by 82% correlated with reduction of the growth of the pathogen within host plants up to 64%. In field trials ASM provided 21% protection	Eenhanced activities of PR-proteins (chitinase and β-1, 3-glucanase)		Abo-elyousr et al., 2009

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Apple	Apple scab (Venturia inaequalis) and frogeye leaf spot or black rot (Botryosphaeria obtusa)	Actigard and SA	Two applications of trunk injection Actigard (100 mg) or spray treatment (0.1 g/L Actigard) at flower bud development and late pink bloom stage.	Field study (orchard)	Reduced scan infection on foliage but not on fruit. No effect on frogeye infection	ns		Abbasi et al., 2019
			SA	Two applications of Trunk injection salicylic acid (200 mg) Spray treatments (1 mM SA)		Reduced foliage scab but not on fruit. Fruits from SA treated trees have less black rot infections	ns		
	Apple	apple scab (Venturia inaequal)	ASM (Bion WG 50 at 200 ppm (w/v)	Application of seedlings on adaxial side until run-off	Growth chamber	reduced the scab severity score. Reduction of germinated conidia	Upregulation of PR proteins, PR1 and PR8		Bengtsson et al., 2009
	Apple	apple scab (Venturia inaequal)	ASM (Bion, 50 WG)	Seedling, scions and trees treated with 0.4 g/L ASM combined with IPM practices	Field (orchard) and greenhouse assays	decrease of disease incidence when combined with IPM practices. Single ASM treatment of seedlings 3 or 10 days before inoculation provided protection rate of roughly 60% and 35%, respectively.	ASM primed induced defense expression of PR2, PR4, and CSL locally and systemically		Marolleau et al., 2017

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Apple	blue mold (Penicillium expansum)	ASM 500µg a.i.ml−1.	pre-storage fruit dip	Post harvest	partial reduction in grey mould severity /lesion diameter at room temperature (23 °C)	ns		Sparado et al., 2004
	Apple	L eaf blotch (Alternaria mali)	BTH and INA	Foliar application (run-off) in potted plants (cv. Red Delicious) at 50, 100 and 200 ppm	Greenhouse trials	Dose-dependent reduction in disease intensity	ns		Sofi et al., 2012
	Pear/Pyrus pyrifolia	Alternaria rot/ mold Alternaria alternata)	SA	Post harvest dip at 0.5 mM (pH 3.6)	NA	reduction in disease incidence	enhance defense related enzyme activities: β-1,3-glucanase, phenylalanine ammonia lyase, peroxidase, and polyphenol oxidase		Tian *et al.* (2006)
	Japanese pear	Scab (Venturia nashicola)	ASM	Foliar spray of potted trees using 100 µg ml−1 ASM	Greenhouse experiment	two applications of ASM at 100 µg ml−1 reduced percentage of diseased leaves	Upon treatment and inoculation polygalacturonase-inhibiting protein (PGIP) transcripts, PAL activity and SA levels and expression of PR-1, chitinase, and PR-10 were enhanced		Faize et al., 2004

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Yali pear (Pyrus bretsch-neideri)	blue mould (Penicillium expansum)		Post harvest dip of fruit 0.5 mM at 20°C		Reduction lesion diameter	No direct induction but priming of defence and antioxidant enzymes. Increase of PAL, chitinase, SOD and CAT upon inoculation	Priming of metabolites upon inoculation of ASM treated fruits: Increase total phenolics and flavonoids	Cao et al., 2005
	Yali pear (Pyrus bretsch-neideri)	blue mould (Penicillium expansum) and Alternaria rot Alternaria alternata)	ASM, CGA245704	Pre harvest spray of trees (five liters of 75 mg/L per trea)	NA	Inhibition of post harvest decay. Lower disease incidence and lesion diameter in mature pears 3x ASM spray	Activities of PAL, chitinase and β-1,3-glucanase in mature fruit from ASM-treated trees were 84.3, 84.8 and 96.6%, respectively, higher than in control fruit In young pear fruit activities of POD, PPO, PAL, chitinase and β-1,3-glucanase are increased		Cao and Jiang, 2006
	Nuango pear (Pyrus ussuriensis)	(Blue mold (Penicillium expansum is)	ASM (syngenta)	10 minute fruit immersion in 100 mg/L ASM	Post harvest	decreased lesion development	influence on energy metabolism. Higher levels of ATPase, CCO and SDH activities in pear fruit, which played important roles in increasing energy status and providing energy to defence reaction		Ge et al., 2017

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Peach (prunus persica)	Blue mold (Penicillium expansum)	BTH	Post harvest fruit dip 5 min in 200 mg/ dm3 BTH		Control of blue mold decay. Reduction in lesion area and disease-incidence without altering fruit quality	Direct induction: chitinase and -1,3-glucanase activities enhanced. Primed resistance: Inoculated BTH fruyit show enhanced the activities of phenylalanine ammonialyase (PAL), polyphenoloxidase (PPO), peroxidase (POD), hydrogen peroxide (H2O2) and superoxide dismutase (SOD)	Total phenolcs, chlorogenic acid and lignin increased	Liu et al., 2005a,b;
	Strawberry	Powdery mildew (Podosphaera aphanis)	Bion (BTH)	Root application at BTH (0.1, 1.0 and 10 g L-1) and foliar spray basal leaves	greenhouse/ tunnel	Reduction disease severity (lower percentage of leaf surface covered by fungus) and area under the disease progress curve (AUDPC). At 0,1 and 1 g/L bion soil and foliar application provide same disease control. Root aplication > 10 g L-1 BTH phytotoxic.	na		Pertot et al., 2008

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Strawberry	Fragaria × ananassa Fruit decay	BTH	Fruit immersion in a solution of 0.2 g/l BTH for 5 min. Foliar application of basal leaves	NA	decay index of BTH-treated fruit reduced by 70.8% after 10 days of storage at 1 °C	Increase the disease resistance by enhancing their antioxidant systems free radical-scavenging capabilities. enhanced antioxidant enzyme activities , including superoxide dismutase, ascorbate peroxidase, and glutathione reductase.	Increase in phenolic and anthocyanin content	Cao et al., 2011
	strawberry ((Fragaria × ananassa)	Powdery mildew (Sphaerotheca macularis)	BTH (Bion 50WG, Syngenta)	0.4 g L-1 of active BTH in distilled water until runoff (ca. 5 mL per plant)	greenhouse	Improved resistance measured by reduction in nr and size of patches. Foliage yield reduced by 17%.		BTH-induced resistance to powdery mildew results from enhanced accumulation of phenolics ellagic acid deoxyhexose, three agrimoniin-like ellagitannins, sanguiin H-10- and lambertianin C-like ellagitannins in the leaves, ellagic acid, p-coumaric acid, gallic acid, and kaempferol hexose and kaempferol malonylglucoside	Hukkanen et al, 2007

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	strawberry ((Fragaria ananassa)	Grey mould (Botrytis cinerea)	Bion	multiple pre-harvest foliar treatment: Pre-harvest spray 4 wk old plants (cv Adana & Elsanta) were sprayed sprayed weekly for 9 times using solutions of 0.25–2.0 mg AI /ml until run-off (10 ml/ plant)	glasshouse	Delay in grey mold disease development corresponds to15-20% increase of storage life	ns		Terry and Joyce, 2000
	strawberry ((Fragaria × ananassa)	Grey mould (Botrytis cinerea)	Bion 500WG	5x biweekly pre-harvest ASM applications at dose of 0.0005 kg−1	Greenhouse	Reduction of rea under the progress curve, aborted flower% and % of fruits with rot. reducing leaf blight and grey mould	increase in phenylalanine ammonia-lyase activity and total phenol production		Tomazeli et al., 2016
	strawberry ((Fragaria × ananassa)	Grey mould (Botrytis cinerea)	BTH (Bion)	Post-harvest application: fruit dip in 0.05, 0.20 or 0.50 g l−1 BTH for 5 min	post-harvest	Fruit decay incidence reducted at 0,2 g/L BTH. Less bacterial, yeast and mold counts	Increase chitinase and ß-1,3-glucanase activity	ns	Cao et al., 2010a, b

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	strawberry (Fragaria × ananassa)	NA	BTH (Bion)	Fruit immersion (BTH) at 0.2 g L–	post-harvest	ns	BTH increases anthocyanin and activity of activities of glucose-6-phosphate dehydrogenase (G6PDH, EC), shikimate dehydrogenase (SKDH), tyrosine ammonia lyase (TAL), phenylalanine ammonia lyase (PAL, EC 4.3.1.5), cinnamate-4-hydroxylase (C4H) and dihydroflavonol 4-reductase (DFR9).	BTH induces enzyme activities related to anthocyanin metabolism in strawberry fruit after harvest	Cao et al., 2010b
	strawberry (Fragaria × ananassa)	Grey mould (Botrytis cinerea)	BTH (Bion)	Fruit immersion immersed in a solution of 0.2 g/l BTH for 5 min	post-harvest	decreased the development of decay. Lower % decay index	enhanced the activities of antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), and glutathione reductase (GR). Enhanced radical-scavenging capacity	increased the contents of phenolic and anthocyanin	Cao et al., 2011
	strawberry ((Fragaria × ananassa)	Powdery mildew (Sphaerotheca macularis)	BTH	Spray leaves until run off 3x with BTH (0.6 – 1.2 g/l) using cv. Jonsok (greenhouse) and cv. Bounty (farm)	Greenhouse and field condition	Provided protection for 3 weeks. Reduction infected leaf surface area	0,05 and 0,2 g/L BTH increased chitinase activity	BTH indued phenolics ellagic tannin, gallic acid, quercetin and kaempfero. In berries the flavonols quercetin and kaempferol quercetin and kaempferol conjugates were increased	Karjalainen et al., 2002

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
Liliaceae									
	Lily (Lilium spp)	Leaf and blossom blight (Botrytis elliptica)	SA	rhizosphere drench at 0.4 mmol/kg potting mix (cv. Star Gazer)	Laboratory	Reduced lesion development	Accumulation of β-1,3-glucan polymer (callose). Increase stomatal closure. Accumulation of LsGRP1-related transcript	ns	Lu and Chen, 2005
	Lily (Lilium spp)	Leaf and blossom blight (Botrytis elliptica)	Probenazole	rhizosphere drench at 40 mg/ kgg soil(cv. Star Gazer)	Lab and Field	Reduction nr of lesions. No growth retarding effect Reduction of conidial germination ofand fungal penetration rate	Folair stomatal closure, callose deposition. No increase in SA content	ns	Lu and Chen, 1998 Lu et al., 2007
Poaceae									
	Sugar cane (Saccharum officinarum)	red rot disease (Colletotrichum falcatu)	CGA-245704 (50% WP, Novartis) and SA	Soildrench using various concentations 1- 100 ug/ml (500 ml/pot)	Greenhouse conditions	Reduction lesion development inssuceptible but not in resistant cultivar. At 100 ug/ml BTH supressed pathogen growth. SA appeared to be phytotoxic at conc above 100 ug/ml.	Increased phenolic content and accumulation of pathogenesis-related (PR) proteins, viz., chitinase, il1,3-glucanase and thaumatin-like protein (PR-5), were observed in sugarcane plants treated with acibenzolar-S-methyl.		Ramesh-Sundar et al.,2001

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Sugar cane (Saccharum officinarum)	red rot disease (Colletotrichum falcatu)	Bion500WG and SA at 250 uM	Drench	field conditions	Pathogen growth arrested and reduction of disease severity in the pathogen-inoculated canes	induction of defense-related enzymes like phenylalanine ammonia-lyase (PAL), peroxidase (POX), polyphenol oxidase (PPO) and accumulation of phenolics in systemically protected sugarcane stalks	ns	Sundar et al., 2009
	Wheat (Triticum aestivum)	Leaf rust (Puccinia triticina)	BTH and SA	3x foliar application 4 mM BTH and 1 g/L SA	Field experiment	Both elicitors reduced disease severity and symptoms	Reactive oxygen species superoxide and hydrogenperoxide increased as well as antioxidant enxymes CAT, POX and PPO upon infection of SA and BTH treated plants (presumably priming)	ns	Hafez et al., 2014; 2017
	Wheat (Triticum aestivum)	Wheat blast (Pyricularia oryza)	ASM (BION) at 300 mg/L	Foliar spray	greenhouse	lower nr of lesions and blast progress	Only increase in LOX activity		Rios et al., 2014

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	Secondary metabolites	Reference
	Wheat (Triticum aestivum)	NA	BTH, MeJA, Thiamine, Robiflavin and DCPA	50 mM thiamine, 0.5 mM riboflavin, 0.7 mM 2,6-dichloro-pyridine-4 carboxylic acid (DCPCA), 1 mM benzo(1,2,3) thiadiazole-7-carbothioic acid S-methyl ester (BTH), 44 mM methyl jasmonate, and 50 mM sodium salicylate (SS	greenhouse	not evaluated	Increase in total phenolics.B1, DCPCA, BTH, and SS, significantly increased TPC by 18, 28, 34, and 23%		Ramos et al., 2017
	Wheat (Triticum aestivum)	NA	BTH (Bion, Novartis)		greenhouse	not evaluated	Increased gene expression lipoxygenase, pathogenesis-related genes (PR1a/1b, 2, B1) and (WCI2, WCI1, WCI4 and WCI5),		Pasquet et al., 2005
	spring barley (Hordeum vulgare)	Rhynchosporium commune and powdery mildew (Blumeria graminis)	ASM (Bion) 1 mM BABA (1mM) cis-jasmone CJ (0.625 g/l)	Foliar spray of elicitor cocktai	glasshouse and field	reductions in R. commune infection, with Bion® reducing infection by 64- 70%	Direct induction and priming of defenses: increases in expression of PR1b before and after inoculation		Walters et al., 2014
	Barley (Hordeum vulgare)	powdery mildew (Blumeria graminis)	chitosan and BTH	foliar spray	Laboratory	Reduction of powdery mildew ifection by 55% by CTH and 68.9% by BTH			Faoro et al., 2008

Bijlage 2 Chemical elicitors – Jasmonic acids analogs

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
Asteracea									
	Gerbera jamesonii,	spider mite Tetranychus urtica	JA	Petiole dip in 15 ml of 2uM meJA	greenhouse	attraction of predatory mite Phytoseiulus persimilis	Indirect resistance	Enhanced odour blend of terpenoids (E)-4,8-dimethyl-1,3,7-nonatriene, (E)--ocimene and linalool	Gold et al., 1999
	Lettuce (Lactuca sativa)	pill-bugs (Armadillidium vulgare)	MeJA	Weekly foliar application MeJA (10 µM and 100 µM)	Growth chamber/ greenhouse	Reduced percentage of plant mortality. 10 mM more effective than 100 mM	Induce hydrogen peroxide (H2O2	Increase phenolics and flavonoids content	Tierrane-gra-García et al., 2011
	Chrysan-themum × morifolium	Western flower thrips	JA	Foliar application at 3 mM JA	Laboratory (growth chamber)	Reduction silver damage symptoms	Local induction of PPO	Untargeted metabolomics: local induction of sugars, phenylpropanoids, flavonoids and some amino acids	Chen et al., 2020
Amaranthaceae									
	Sugar beet (Beta vulgaris	Beet Mosaic Virus (BtMV)	MeJA	Foliar spray with 3.0 µg/ml MeJA	Greenhouse	Augmented resistance; reduced leaf symptoms	increased polyamines (PAs), soluble ornithine decarboxylase (ODC) and polyamine oxidize (PAO) and accumulation of peroxidase, chitinase, polyphenoloxidase and phenols	increases in levels of free and conjugated putrescine, spermidin and spermine	Haggag et al., 2010

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Amaranth (Amaranthus hypo-chondriacus)	Phloem feeders/ chewing insects and parasitoid predators	JA	Foliar application at low (0.5 mM JA) and high dose (1,5 mM JA)	Field conditions	Inconsistent effect on aphids dependent on time and year. In 2000 lower damage by phloemfeeders and chewing insects	Accumulation of foliar trypsin and α-amylase inhibitors	ns	Délano-Frier et al., 2004
	spinach (Spinacia oleracea)	dark-winged fungus gnat (Bradysia impatiens)	MeJA	Aqueous root drench at 45 mM MeJA	Laboratory	Less root damage. Reduced establishment		induction of 20-hydroxyecdyson	Schmelz et al., 2002
Brassicaceae									
	Arabidopsis Thaliana	NA	COR	NA	Laboratory	NA	Accumulation of anthocyanin and Coronatine and MeJA also induced the systemic appearance of proteinase inhibitor activity		Bent et al., 1992; Feys et al., 1994
	Arabidopsis thaliana	Alternaria brassicicola. Botrytis cinerea or Plectosphaerella cucumerina	MeJA	Exogenous application	Laboratory growth chamber	Reduced average lesion diameter	Induction of PDF 1.2, PR1 andPR-4	ns	Thomma *et al.* 1998, 2000
	Arabidopsis and Chinese cabbage (Brassica rapa)	Western flower thrips	50 µM JA	Chamber exposure	Laboratory	Reduction feeding scars, nr of adults, nr of larvae and nr of eggs	ns	ns	Abe et al., 2019
	broccoli (Brassica oleracea subsp. italica L.)	cabbage root fly (Delia radicum)	JA	Root application (JA, 500 µg/plant)	Greenhouse	JA root treatment reduced herbivore larval performance (% pupation rate) whereas in turnips it was enhanced	ns	JA induced changes in glucosinolate and sugar content	Pierre et al., 2012

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Brussel sprouts	NA	MeJA	MeJA (50, 100, 200 and 300 µM) sprayed on sprouts	post-harvest	NA	ns	accumulation of vitamin C, flavonoids and glucosinolates.	Pérez-Balibrea et al., 2011
	Brassica oleracea	Mamestra brassicae and the specialist Pieris rapae.		Root and shoot application using 500 µg per plant	greenhouse	M. brassicae larvae grew significantly slower on JA-induced	ns	Shoot-induction increased indole glucosinolates, whereas root-induction induced aliphatic glucosinolates in the leaves	van Dam and Oomen, 2008
	Oilseed rape (Brassica napus)	diamondback moth, Plutella xylostella	JA	Foliar application		Reduction of digested food, relative consumption rate, and relative growth rate of P. xylostella	Systemic defenses. Induction proteinase inhibitors	Induction glucosinolates	
	oilseed rape Brasica napus	NA	MEJA	Spray or vapour (1,5-150 mg/L MeJA)	glasshouse	ns	ns	Accumulation of indolyl glucosinolates (3-indolylmethyl- and 1-methoxy-3-indolylmethyl-glucosinolates)	Doughty et al., 2005
	oilseed rape (Brassica rapa)	NA	MeJA	Seedlings sprayed with 5 ml of MeJA at 1 mg/mL	Laboratory (growth chamber)		NA	Induced production of indolyl glucosinolates 4-OH-glucobrassicin, glucobrassicin and 4-methoxyglu-cobrassicin and volatile organic compounds (VOC) omoterpene (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT)	Loivamäki et al., 2004

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Cabbage (Brassica oleracea)	abbage loopers and tobacco hornworms	MeJA	Gaseous exposure to MeJA using cotton balls	Laboratory	Reduced feeding of lepidopteran larvae	increased lipoxygenase activity	elevated production of volatile C_6-aldehydes (hexanal and E-2-hexenal)	Avdiushko et al., 1997
Curcubitaceae									
	Cucumber (Cucumis sativa)	downy mildew (Pseudo-peronospora cubensis)	MEJA, SA and chitosan	Foliar treatment at 10-5 , 5x10-5 and 10-4 M	Field conditions	Reduced disease severity in two seasons by ~60%	Leaf structural changes: increase midrib thickness	No induction of total soluble phenols	Farouk et al., 2008
	Melon (Cucumis melo)	gummy stem blight (Didymella bryoniae) and white mould disease (Sclerotinia sclerotiorum)	MeJA	MeJa 45 uM Seed treatment (12 h soak)	Laboratory	Protection of seedlings against soil-borne fungal pathogens . Reduction in percentage of necrotic lesions	Increase lipoxygenase activity. The chitinases, peroxidases and lipoxygenase were upregulated	ns	Buzi et al., 2004
	Melon (Cucumis melo)	NA	JA	Cell suspension with 0.5, 5 and 10 µmol JA	Laboratory cell suspension	NA	at 10 uM JA Increases CAT, (ascorbate) peroxidase and oxidase, gluthathion reductase, PAL,PPO	reprogramming the primary and secondary metabolism. Increase total flavonoids	Nafie et al., 2011
Fabaceae									
	Lima Bean (Phaseolus lunatus)	Spider mites (Tetranychus urticae)	JA and MeJA	Petiole dip with 0.1 and 1 mM JA and gaseous exposure to MeJA (1 ul/100 ul EtOH)	Glasshouse	attraction of predatory mite Phytoseiulus persimilis	Indirect resistance	Induced volatile blend: (E)-4,8-dimethyl-1,3,7-nonatriene and the phenolic methyl salicylate	Dicke et al., 1999 and Gols et al., 2003

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Lima Bean (Phaseolus lunatus)	Mexican bean beetles (Epilachna varivestis)		Foliar application (0.001, 0.01, 0.1, and 1.0 mmol L−1)	Greenhouse	JA induced leaves have have lower consumption area and are less preferred	enhanced release of gaseous hydrogen cyanide via the induction of β-glucosidase activity	ns	Kautz et al., 2014
	Bean ((Phaseolus vulgaris)	Spider mites (Tetranychus urticae)	MeJA	Foliar spray with 10-5 M MeJA, after infestation	Field experiment	Control of spider mite infestation, improved plant growth and bean yield	Alteres leaf anatomical characteristics	ns	Farouk et al., 2011
	Ground nut ((Arachis hypogaea)	Cotton bollworm (Helicoverpa armigera)	JA	Foliar spray using 1 mM JA until runoff	Laboratory	Pretreatment JA reduced larval survival	Priming of defenses: enhanced oxidative enzymes [peroxidase (POD) and polyphenol oxidase (PPO)] and the amounts of other host plant defense components [total phenols, hydrogen peroxide (H2O2), malondialdehyde (MDA), and protein content] in JA-treated plants upon infestation	ns	War et al., 2011
	Soybean	Soybean looper, Chrysodeixis includens	MeJA	Exogenous foliar spray (2 days before laboratory assay)	Field study with laboratory assays	MeJA reduced pupal weight by 6.8% and delayed larval development by 14.3%.		ns	Chen et al., 2018
Solanaceae									
	Eggplant (Solanum melongena)	Ralstonia solanacearum	MeJA (and chitosan, SA and methyl salicylate)	Root immersion	NA	Speculative: resistance provided against Ralstonia solanacearum	Increased lignin deposition, increase of enzymes	Accumulation of total phenolics	Mandal et al., 2010

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Tomato	Western Flower Thrips (Frankliniella occidentalis)	MeJA	Foliar spray at 7,5 mM	Laboratory growth chamber	Reduction feeding damage	Increase glandular trichome density and WIPI-II expression	Increased in terpene production: α-pinene, p-cymene, myrcene, δ-carene, α-phellandrene, terpenoline, α-terpinene, limonene, β-phellandrene, trans-β-Ocimene	Escobar-Bravo et al., 2017
	Tomato	Western Flower Thrips (Frankliniella occidentalis)	Coronatine	Leaf injection 5 µM COR	Laboratory growth chamber	Lower preference of MeJA treated leaf discs	Increase PPO,WIPI-II and PR-P6	NMR metabolomics: Increase in aspartic acid, GABA, ethanolamide, fumaric acid and rutin	Chen et al., 2018
	Tomato	Grey mould disease (Botrytis cinerea) and root knot nematode (Meloidogyne incognita)	JA	Foliar spray seedlings	Growth chamber and bioassays	Cultivar dependent effect of enhanced resistanc. JA reduced mean lesion diameter. Durability up to 3 weeks protection after treatment. No effect on root knot nematode.	ns		Bruce et al., 2017
	Tomato	whitefly Bemisia tabaci	MeJA	Three applications of foliar spray at 7,5 mM MeJA	Glasshouse	hanced resistance to whiteflies. Reduction virus transmission	60% increase in type-IV trichome density. Enhanced expression of genes invovled in acylsugar biosynthesis	Increase in phenolics and acylsucrose production	Escobar-Bravo e tal., 2016

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Tomato	Botrytis cinerae	MeJA (and BABA)	Seed imbibition (7 days), seedling spray and soil application	Laboratory growth chamber	extended seed treatment with 0.1 mM reduced lesion diameter more efficient than seedling treatment. 1 mM BABA reduced lesion diameter	ns	ns	Luna et al., 2016
	Tomato	Fusarium oxysporum	MeJA	1 hour seed soaking (cv. Beta) 0.01, 0.1 and 1 mM MeJA	Growth chamber	inhibition of Fusarium development	Priming of defenses: Up-regulation of phenylalanine ammonia-lyase (PAL5) and benzoic acid/salicylic acid carboxyl methyltransferase (BSMT) genes	increased accumulation of the flavonols quercetin and kaempferol	Krol et al.,2015
	Tomato	Alternaria porri f. sp. solani	MeJA	Seed soaking and fumigating seedling treatment at 0,1 - 0.1 & 1 mM	Growth chamber	0.01 and 0.1 mM JA reduce severity index	Increase in phenylalanine ammonia-lyase activity (PAL)	Increase total phenols and anthocyanin	Kęp-czyńska & Król, 2012
	Tomato	red spider mite (Tetranychus urticae) , caterpillars aphics Botrytic cinerea	JA	seed soaking at 3 mM	Glasshouse and bioassays	Priming of defences, up to 8 weeks protection. Cultivar dependent effect of JA. JA reduced lesion area of Botrytis cinerea	Enhanced gene expression: AOS2. PINII and		Worrall et al., 2012
	Tomato	Leaf miner (Tuta absoluta)	MeJA	Seed soaking (24 h) in 0,8 mM MeJA	Growth chamber and detached leaf assay	Increase developmental time (from larvae to pupae) and decrease in pupal weight	Upon herbivory in MeJA seed treated plants more volatile emission. Attraction to predator Chrysoperla externa	Enhanced volatile emission	Strapasson et al., 2014

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Tomato	tomato fruit worm (Helicoverpa zea)	MeJA	Seed soaking (cv. Micro-Tom) in 0,05 - 0,4 mM MeJA	Greenhouse and herbivore assays	JA seed treatment enhances plant resistance in vegetative, flowering and fruiting stage by reducing larval growth. 1 mM MeJA is associated with costs (lower germination%, plant height, nr of fruits and fruit ripening time)	MeJA enhanced polyphenol oxidase (PPO) activity	ns	Paudel e tal., 2014
	Tomato	Frankliniella occidentalis Pergrande (thrips), Spodoptera exigua and Trichoplusia ni Hubner (noctuid caterpillars), Epitrix hirtipennis Melsheimer (flea beetles), and Macrosiphum euphorbiae Thomas, and Myzuspersicae Sulzer (aphids)	MeJA and JA	Vapour (cotton) and foliar spray until run-off	Field and laboratory	Reduced preference, performance and abundance	induction of proteinase inhibitors and polyphenol oxidase	ns	Thaler et al., 1996 and 19999
	Tomato	red spider mite (Tetranychus urticae)	JA	Seed soaking (24 h) in 3 mM JA	Growth chamber/ bioassay	Cultivar dependent effect. Seed soaking in Carousel reduced nr of eggs and survival of T. urticae	JA enhanced volatile production of TMTT and methyl salicylate (MeSA). This, in turn atttracts, the natural predator Phytoseiulus persimilis	Enhanced volatile emission	smart et al., 2013

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Tomato	root-knot nematode (Meloidogyne incognita)	MeJA	Foliar treatment at 0.5 mM using atomizer	Greenhouse	MeJA at 0.5 mM or higher reduced the infection of RKN. Effect lasted for about 1 week.	Induction of proteinase inhibitors (PIs) and multicystatin (MC)	ns	Fujimoto et al., 2011
	Tomato	Potato aphid (Macrosiphum euphorbiae	JA	Foliar application at 1,5 mM	Growth chamber	Ja spray reduced aphid longevity (i.e. life expectancy), survival, reproduction (fecundity)	ns	ns	Cooper and Goggin, 2005
	Potato and tomato	Phytophthora infestans	Meja and JA	Foliar spray 20 to 1000 ug/ml	Greenhouse	Induced resistance reduces infection	ns	No phytoalexin induction	Cohen et al., 1993
Rosaceae									
	Loquat	Anthracnose rot (Colletotrichum acutatum)	MeJA	Fruit treatment in sealed chamber at 10 μmol l−1 MeJA	Post-harvest	MeJA treatment induced disease resistance in postharvest loquat fruit.	MeJA induced disease resistance due to the increased polyamines and ATP. Enhanced H2O2 generation, but lower PAL, PPO and POD.	MeJA treated fruit manifested higher contents of polyamines (putrescine, spermidine and spermine).	Cao et al., 2008a, b; 2014
	Rose hybrida	Grey mould, caused by Botrytis cinerea	MeJA	Pulsing flowers -post harvest	Laboratory experiment	MeJA enhanced disease index by sypressing rot symptoms but is cultivar and concentration dependent. Min application 300 uM Meja	ns		Meir et al., 1998

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Sweet cherry (Prunus avivum)	Brown rot (Monilinia fructicola)	MeJA and SA	Pre and post harvest treatments (foliar spray and 2 min fruit dip, respectively) at 0.2 mM MeJA and 2 mM SA	Field (Orchard)	Pre and post harvest reduce disease incidence. Pre-harvest treatment is more effective in reducing lesion diameter	Pre-harvest MeJA induced β-1,3-glucanase, phenylalanine ammonia-lyase (PAL) and peroxidase (POD)	ns	Yao and Tian 2005
	Peach (prunus persica)	Blue mould decay (Penicillium expansum) grey mould decay (Botrytis cinerea) and soft rot (Rhizopus stolonifer)		Fruit dip 1 μmol L−1 MeJA	Post harvest	Reduction fruit decay: 12 hr immersion reduced disease incidence and lesion diameter for all pathogens	Increase in defence enzyme activities including chitinase, β-1,3-glucanase, phenylalanine ammonia-lyase, polyphenol oxidase and peroxidase. Higher level of hydrogen peroxide (H2O2) upon inoculation (= priming of defenses)	ns	Jin et al., 2009
	Acacia holosericea	NA	SA and JA	Postharvest application (i.e. ase solution) of salicylic and jasmonic acid.	post-harvest	SA at 0.5, 1.5, and 2.5 mM gave ~1.3- to 1.5-fold vase life extensions. JA at 0.5 mM in vase solutions also prolonged vase lifeCut A. holosericea foliage stems treated with SA and JA exhibited higher relative fresh weight (RFW)		MeJA treated fruits have higher total phenolics	Chen et al., 2017

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Strawberry	two-spotted spider mite (Tetranychus urticae)	MeJA	Spray until run-off using 0.1% JA-Me in 0.05% Triton X-100 (wetting agent).	Glasshouse	MeJA negatively affects population growth: lower nr of mites and lower oviposition. Application of the exogenous JA-Me increased the resistance of both the Aga and Kent strawberry cultivars to T. urticae.	ns	Antibiosis or non-preference mechanism: increase of the level of phenolic compounds like chlorogenic acid and rutin	Warabieda et al., 2005 amd 2010
	Strawberry (Fragaria x ananassas	Fungal disease	MeJA		post-harvest	Reduction of fungal decay improved overall quality index	Meja increased antioxidant capacity,	Increase in total phenolics, and anthocyanins. MeJA in combination with ethanol increased volatile emission of ethyl hexanoate, methyl acetate, and butyl acetate	Ayala-Zavala et al., 2005
	Chilean strawberry (Fragaria chiloensis)	gray mold decay (Botrytis cinerea)	MeJA	Pre-harvest foliar application at three stages. Post harvest application on fruits using 250 µmol·L−1 MeJA	Field (Orchard)	Preharvest treatment has a long lasting effect Fruits exhibited lower incidence of B. cinerea infection	upregulation of the FcBG2-1, FcBG2-3, FcPGIP1, and FcPGIP2. Induction of PR and PGIP gene expressio		Saavedra et al., 2017
	raspberry fruits (Rubus spp)	fungal diseases	MeJA	Methyl Jasmonate (MJ) fumigation	post harvest		Reduced decay incidence enhances post harvest life	higher antioxidant capacity and total anthocyanins	Ghasem-nezhad and Javaher-dashti, 2008

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Apple	NA	MeJA	Fruit immersion 2 min in 0,224-2,24 g/L MeJA	post harvest		Photoprotection; enhanced coloration	enhanced anthocyanins and phenolics : chlorogenic acid, cyanidin, quercetin and phloretin glycosides	Rudell et al., 2002
	Apple	two-spotted spider mite (Tetranychus urticae)	MeJA	Spray until run-off using 0.1% JA-Me in 0.05% Triton X-100 (wetting agent).	Glasshouse	Negative influence of JA on performance. Of the two varieties of apple trees, the negative impact of JA-Me plant treatments on the development of the spider mite population were found only in the case of the Close cultivar.	ns	Higher level of phenolic compounds on leaves treated with JA-Me	Warabieda et al.,2003 and 2010
Poaceae									
	Oats (Avena sativa)	Root lesion nematode (Pratylenchus neglectus), cereal cyst nematode (Heterodera avenae), and stem nematode (Ditylenchus dipsaci)	MeJA		Laboratory with bio-assays	methanolic extracts containing induced flavonesimpaired nematode invasion and development		three flavone-C-glycosides, O-methylapigenin-C-hexoside-O-deoxyhexoside, apigenin-C-hexoside-Opentoside, and luteolin-C-hexoside-O-pentoside	Soriano et al., 2004

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Barley (Hordeum vulgare	powdery mildew (Blumeria graminis f. sp. hordei)	MeJA	20 mM MeJA gaseous vapour in camber	Laboratory	Reduction in powdery mildew (Blumeria graminis f. sp. hordei) infection	increased activities plant defence-related enzymes, phenylalanine ammonia lyase (PAL) and peroxidase and of soluble ornithine decarboxylase (ODC), soluble and particulate arginine decarboxylase (ADC), S-adenosyl-methionine decarboxylase (AdoMetDC) and increased activities of soluble ornithine decarboxylase (ODC), soluble and particulate arginine decarboxylase (ADC) and diamine oxidase (DAO) ,S-adenosyl-methionine decarboxylase (AdoMetDC)	Altered polyamine metabolism: increases in levels of free putrescine, spermidine and spermine.	Walters et al., 2002
	Barley (Hordeum vulgare)	powdery mildew (Wrysiphe graminis f.sp. hordei.)	JA	Topical spray application on seedlings (30 ug/plant)		Local protection	Induction PR proteins		Schweizer et al., 1993
	rice (Oryza sativa)	rice water weevil (RWW) Lissorhoptrus oryzophilus	MeJA	2,5 and 5 mM MeJA seed treatment (soaking in 250 mL excess solution). cv. 'Cheniere'	Greenhouse and field experiments	MJ seed treatments induced resistance to RWW, although this effect decayed over time	NA	NA	Kraus et al., 2019

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	rice (Oryza sativa)	rice water weevil, Lissorhoptrus oryzophilus and fall armyworm, Spodoptera frugiperda	JA	sprayed until run-off with 100 ml of 1 mM or 5 mM JA solutions	Greenhouse	JA reduced nr of Lissorhoptrus oryzophilus eggs and larvae		Emission of volatime ocmpounds	Hamm et al.,2010
	rice (Oryza sativa)	fall armyworm, Spodoptera frugiperda	JA	Spray seedlings 2 mM JA until runn-off	greenhouse	Lower relative growth rates and weight gein of armyworm across all five varieties	ns	ns	Stout et al., 2009
	rice (Oryza sativa)	brown planthopper (Nilaparvata lugens)	JA	Foliar application JA 2,5 mM and 5 mM	greenhouse	Negative effect on surviership: Reduced the longevity and egg hatchability and at 5 mM reduction of percentage of nymphs surviving to maturity	ns	ns	Haggag et al., 2010
	Sugar Cane	Diatraea saccharalis and Spodoptera frugiperda	JA	spray (10 ml of 1 mM JA)	Greenhouse	Mock-treated plants are preferred by both insects	Direct and indirect resistance	Indirect resistance for natural enemy recruitment: emission of a volatile blend (mainly sesquiterpenes) attractive tosugarcane borer parasitoid C. flavipes	Sanches et al., 2017

Bijlage 3 Chemical elicitors – Polysaccharides

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
Asteracea									
	Sunflower (Helianthus annuus)	Downey mildew (Plasmopara halstedii)	Chitosan	5% chitosan seed treatment	greenhouse and field	Decrease severit and provided >40% protection	Priming: Enhanced activation of catalase (CAT) and phenylalanine ammonia lyase (PAL), peroxidase (POX), polyphenol oxidase (PPO) and chitinase (CHI) post-inoculation		Nandeesh-kumar et al., 2008
Amaranthaceae									
	Beet (Beta vulgaris)	Cercospora leaf spot (C. beticola)	Chitosan	Foliar spray uising suspension of chitosan with 85% deacetylation	Greenhouse conditions	Reduction leaf spot severity by 80%			Felipini & Piero, 2013;
	Beet (Beta vulgaris)	Cercospora leaf spot (C. beticola)	Chitosan CHT (1.0 mg/mL)		greenhouse	CHT (1.0 mg/mL) significantly reduced CLS severity			Felipini et al., 2015
Brassicaceae									
	Arabidopsis	Botritis cinerea	chitosan oligomers (COS) and quaternized COS	Spray (twice) 200 µg/mL COS, 200 µg/ mL QCOS	Laboratory	QCOS reduced lesion area	QCOS triggers callose deposition of callose and H2O2. Upregulation of PAD3 (indepdent of SA)		Feng et al., 2015
	Arabidopsis	Tobacco mosaic virus	chitosan oligo-saccharide (COS)	Rosettes sprayed with 25-100 mg/L	Laboratory	Pretreatment reduces TMV-intensity and disease incidence	chitosan induced resistance is SA dependent. COS treatment increases NO		Jia et al.,2016

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Oilseed Rape (Brassica napus)	Sclerotinia Sclerotiorum	chitosan oligo-saccharide (COS)	Foliar application at 50-µg-mL−1 COS	grreenhouse	reduced the disease symptoms up to 48%	jasmonic acid (JA) synthase (2-oxophyto-dienoate-10,11-reductase) gene, a JA-mediated defense required kinase ATMPK4-homolog gene, an ethylene receptor gene, COS induced bursts of cytosolic Ca2+, nitric oxide (NO), and hydrogen peroxide (H2O2).		Yin et al., 2006; Yin et al.,2013
	Brussel sprouts	NA	Chitosan (crab shell derived)	50 mM chitosan sprayed on sprouts	post-harvest	NA	ns	accumulation of vitamin C, flavonoids and glucosinolates	Pérez-Balibrea et al., 2011
Curcubitaceae									
	cucumber (Cucumis sativus	Powdery mildew (Sphaerotheca fuliginea)	COS-OGA	Five foliar sprays at 25 g in 500 l/ha	Greenhouse and field trials	ns	Enhanced expression of PR1,PR2 and PR3		Van Aubel et a., 2013
	cucumber (Cucumis sativus	gray mould (Botrytis cinerea)	Chitin oligomer and chitosan	Foliar spray 0.1% (w/v) chitosan or chitin oligomer mixture	Laboratory	Chitosan decreased gray mould by 52%	elicited chitosanase and peroxidase activity		Ben-Shalom et al., 2003
	Cucumber (Cucumber sativus)	Phytophthora drechsleri	Leached spent mushroom compost (SMC)	soil amendment containing SMC rates of 15%, 25%, 35% and 45	greenhouse	Pathogen suppressed (i.e. lower disease severity) only when non-sterilized SMC was used. In-vitro: reduced mycellium growth	ns		Goonani et al., 2011

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Cucumber (Cucumber sativus)	anthracnose (Colletotrichum orbiculare)	Spent mushroom substrate (SMS) and water extract	Foliar spray (water extract) and soil amendment		Cucumber plants treated with water-extract from SMS are protected from anthracnose. Significantly reduced necrotic lesions	SAR: Priming of defense: water extract and pathogen inoculation icreased expression of chitinase and β-1,3-glucanase genes		Parada et al., 2011
	Cucumber (Cucumber sativus)	Pythium aphanidermatum	Spent blewit mushroom compos	Substrate	Greenhouse	suppression of Pythium damping-off	NA		Chen et al., 2015
Fabaceae									
	Bean (Phaseolus vulgaris)	Tobacco necrosis virus (TNV)	Chitosan	Foliar spray seedlings 0.15% CHT	Field	reduction of TNV lesion size	activation of priming mechanisms		Iriti et al., 2010
	Soy bean	NA	chitin and Chitosan	Foliar spray on seedlings	Laboratory	NA	Increase activation of key enzymes of phenylpropanoid biosynthessis : Phenylalanine ammonia-lyase (PAL) and tyrosine ammonia-lyase (TAL)	Increase total phenolics	Khan et al., 2003
Solanaceae									
	Tomato	Fusarium Crown and Root rot (Fusarium oxysporum)	chitosan	seed treatment 0.1 - 1 mg/ml	growth chamber	Patogen growth and development halted-delay symptom development		Production of B-1,3 glucans, phenols and likninlike comoiunds	Benhamou et al., 1994
	Tomato	Fusarium oxysporum	(oligo)-glucuronan and (oligo)-ulvans	Seedlings (cv. Super Red) internodal injection of 20 µl		reduced wilt development by 45-55%	SAR: stimulation of PAL activity was accompanied by an increase of phenolic compounds content and an induction of salicylic acid	Increase in total phenolic content	El Modafer et al, 2012

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Tomato	Bacterial wilt (Ralstonia solanacearum)	chitosan	0.01% concentration SA and 0.1% CHT added to media	Growth chamber hydroponics culture	Provided resistance against Ralstonia solanacearum. Less vascular browning and wiltin (indexing)	Increased lignin deposition in cell walls of roots, accumulation of phenolics, increase in the activity of enzymes PAL, POD, polyphenol oxidase, cinnamyl alcohol dehydrogenase, and catalase.		Mandal et al., 2013
	Tomato	Crown and root rot (Fusarium oxysporum)	chitosan	soil amendment	greenhouse	Lower mortality of plants	Morphological barriers: fungal growth was restricted to the epidermis and the cortex		Lafontaine and Ben-hamou, 1996
	Tomato	Early blight (Alternaria solani) and bacterial spot/blight (Xanthomonas vesicatoria)	chitosan extract (Armour-Zen)	Foliar spray applications at 0.05% v/v concentration at 20 mL per plant.	Greenhouse and field	Reduction disease percentage	Elevated levels of defence enzymes (Chi, Glu, PO, PAL and PPO) and upregulation of the PIN II marker gene		Ram-kissoon et al.,2016
	Potato (Solanum tuberosum)	Fusarium sulphureum	Chitosan		post harvest	reduced the lesion diameter	0.25% chitosan increased the activities of peroxidase and polyphenoloxidase, and the contents of flavonoid compounds and lignin in tissues		Viacava et al., 2018
	Potato	Colorado potato beetle (Leptinotarsa decemlineata)	spent mushroom compost (SMC)	Soil amendment	Field	No significant effects on the density of Colorado potato beetle small larvae, large larvae, or defoliation ratings			Stoner et al.,1996

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Potato	Verticillium dahliae	Spent mushroom substrate	soil amendment					LaMondia et al., 1999
	Tomato	Phytophthora nicotianae and Fusarium oxysporum	Spent mushroom compost	compost amendments	Laboratory	Supress soil boirne P. nicotianae and foliar pathogen S. lycopersici	ns		Ntougias et al., 2008
Rosaceae									
	Apple (Malus domestica)	Fire blight (Erwinia amylovora)	Iodus 2 (Laminarin 4,5% w/v)	Seedling spray until run-off (7,5 ml/L)		protection rate ranging from <10%. Despite transient activation of defenses compound D did not confer a significant protection against E. amylovora	PR-proteins, terpenoid biosynthetic enzymes, and salicylic acid-related markers were strongly upregulated		Dugé de Bernonville et al., 2014
	Apple (Malus domestica)	Penicillium expansum and Botrytis cinerea	Ulvan and Oligoulvan			Reduced disease incidence. Oligo-ulvan inhibited blue and grey mold decays completely	Accumulation of accumulation of hydrogen peroxide (H_2O_2), catalase (CAT) and superoxide dismutase (SOD), phenylalanine ammonialyase (PAL), peroxydase. (POD) and polyphenoloxydase (PPO	Increase lignin and phenolic compound	Abouraïcha et al., -2015

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Apricots (Prunus armeniaca)	Alternaria alternata	Chitosan and Salicylic acid	preharvest spray with 0.05 % chitosan oligochitosan (COS) or/ and 1 mmol L_{-1} salicylic acid of trees. Repeated twice 7d and 2 days before harvest	Field	Inhibited decay rate	OS + SA treatment remarkably activated the activity of defense enzymes (PPO, POD, PAL)	COS + SA treatment improved phenol metabolism. Ascorbic acid, total phenol content, total flavonoid content, phenol compounds	Ciu et al., 2020
	Peach (prunus persica)	brown rot caused (Monilinia fructicola)	chitosan and oligochitosan	post harvest fruit dip10 min in 0.5 and 5 g/L	postharvest	Enhanced resistance against brown rot by reducing decay incidence >50%. Delay fruit softening and scenesence	enhanced antioxidant and defense-related enzymes, such as catalase (CAT), peroxidase (POD), β-1,3-glucanase (GLU) and chitinase (CHI), and they also stimulated the transcript expression of POD and GLU. crease antioxidant and defense-related enzymes activitie		Ma et al., 2013
	Raspberry	Fungal post harvest diseases	Chitosan	Pre and post harvest sprat of fruits at 1 or 2% chitosan	Laboratory	Control decay index and weight loss. 1 or 2% post harvest	Reduced transpiratation to preserve water		Tezotto-Uliana et al., 2014

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	strawberry ((Fragaria × ananassa)	gray mold decay (Botrytis cinerea)	Chitosan	Preharvest treatment spray of fruits using 2, 4, and 6 g/l chitosan	Greenhouse	Postharvest evaluation: Reduction of incidence of decay. Two sprays improve storage at higher temperature	ns		Reddy et al., 2000
	strawberry ((Fragaria × ananassa)	gray mold decay (Botrytis cinerea) and rhizopus rot (Rhizopus stolonifer)	chitosan (Chito Plant, 1%, w/v), oligosacch-arides (Algition)	10 sec fruit immersion	postharvest	Reduced % of decay and disease severity indexing	ns		Romanazzi et al., 2013
	strawberry ((Fragaria × ananassa)	gray mold decay (Botrytis cinerea)	Chitosan (Chito plant)	Fruit immersion (30s) in 1% chitosan	postharvest	NA	Promoted the expression of key phenylpropanoid pathway genes, for synthesis of lignin and flavonoids; only those associated with flavonoid metabolism were upregulated		Landi et al., 2014
	strawberry ((Fragaria × ananassa)	gray mold decay (Botrytis cinerea) and rhizopus rot (Rhizopus stolonifer)	chitosan and laminarin	Preharvest spray every 5 days from flowering to ripening	Field	0,5 and 1 % chitosan reduced decay incidence with 36 and 29%, respectively	NA		Feliziani et al., 2015
				BTH					

Plant family	Plant species	pathogen/pest	Elicitor	Application	Test conditions	Response measured	Resistance mechanism	secondary metabolites	Reference
	Chilean strawberry (Fragaria chiloensis)	gray mold decay (Botrytis cinerea)	Chitosan	Pre-harvest foliar application at three stages. Post harvest application on fruits using1.5% (w/v) chitosan	Field (Orchard)	Preharvest treatment has a long lasting effect Fruits exhibited lower incidence of B. cinerea infection	upregulation of the FcBG2-1, FcBG2-3, FcPGIP1, and FcPGIP2. Induction of PR and PGIP gene expressio		Saavedra et al., 2017
Poaceae									
	Barley (Hordeum vulgare)	powdery mildew (Blumeria graminis)	chitosan and BTH	foliar spray		Reduction of powdery mildew ifection by 55% by CTH and 68.9% by BTH	ns	ns	Faoro et al., 2008
	Ryegrass (Lolium perenne)	Gray leaf spot (Pyricularia grisea)	Spent mushroom substrate	soil amendment	Laboratory and greenhouse	In-vitro inhibition by pathogen insolates present in SMS and in-vivo supression of grey leaf spot	ns	ns	Viji et al., 2003
	Wheat	Fusarium graminearum		seed treatment	Laboratory	Seed and primary root infection by F. graminearum was reduced to >50%		Increase in precursors of lignin such as p-coumaric, ferulic, and sinapic acids and phenolic acids having antimicrobial activity such as benzoic, p-coumaric, caffeic, protocatechuic, chlorogenic, ferulic, and gallic acids	Bhaskara Reddy et al.,1999

Bijlage 4 Microbial elicitors

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
Asteraceae								
	Lactuca sativa	Botrytis cinerea	Trichoderma harzianum T39	greenhouse	Induced resistance mechanisms	NA	application at sites spatially separated from the B. cinerea inoculation resulted in a 25–100% reduction of grey mould symptoms	de Meyer et al, 1998
Brassicaceae								
	Raphanus sativus L.	Fusarium oxysporum f. sp. raphani	P. fluorescens strains WCS374 and WCS417	greenhouse	Induced systemic resistance	Salicylic acid	dependant on iron availability	Leeman *et al.* 1996
	Raphanus sativus	Fusarium oxysporum raphani	Pseudomonas simiae WCS417r and WCS374	greenhouse	Induced systemic resistance	O-antigenic chain of outer membrane lipopolysaccharides		Leeman *et al.* 1995
	Arabidopsis thaliana	Alternaria brassicicola	Bacillus amyloliquefaciens (UCMB5113)	on plate in growth chamber	Jasmonic-acid pathway		ISR through jasmonic-acid-dependent host responses, interactions with catalases	Asari *et al.* 2017
	Arabidopsis thaliana	ns	Pseudomonas simiae WCS417	on plate in growth chamber	Jasmonic-acid pathway	flagellin flg22 417		Stringlis *et al.* 2018

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Arabidopsis thaliana	Pseudomonas syringae (pv. tomato DC3000)	Cladosporium sp., Ampelomyces sp.	hydroponic culture system	Induced systemic resistance: both the SA-and JA-signaling pathways	M-cresol volatile	m-cresol induced the SA-inducible marker genes PR1 and PR2, confirming that the volatile lowered disease severity by inducing systemic resistance mainly through the SA-signal transduction pathway. JA-inducible gene PDF1.2 was expressed by treating plants with m-cresol	Nazrin *et al.* 2014
	Arabidopsis thaliana	Pseudomonas syringae pv. maculicola ES4326	Paenibacillus polymyxa E681	greenhouse	transcriptional expression of the salicylic acid, jasmonic acid, and ethylene signaling marker genes	C13 hydrocarbon, tridecane		Lee *et al.* 2012
	Arabidopsis thaliana	Pseudomonas syringae pv. tomato DC3000	Saccharothrix yanglingensis Hhs.015	growth chamber	Induced systemic resistance: both the SA-and JA-signaling pathways	Protein Elicitor BAR11	BAR11 may modulate plant immune responses by perturbing H2O2 homeostasis	Zhang *et al.* 2018

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Arabidopsis thaliana	Pseudomonas syringae pv. tomato DC3000	Bacillus cereus AR156	growth chamber	Induced systemic resistance	NA	ISR through stimulation of the transcription of WRKY70, but suppressed that of WRKY11	Jiang *et al.* 2016
	Arabidopsis thaliana ecotype Columbia-0 (Col-0, N1092)	Xanthomonas translucens pv. translucens	Rhizobium radiobacter F4	growth chamber	Jasmonic acid pathway	NA		Glaeser *et al.* 2016
	Arabidopsis thaliana	Erwinia carotovora subsp. carotovora	Bacillus subtilis strain GB03	growth chamber	Induced systemic resistance	2,3-butanediol		Ryu *et al.* 2003
Curcubitaceae								
	Cucumis sativus	Phytophthora melonis and glomus mossae	Trichoderma harzianum Rifai (Bioplus)	greenhouse	SA-and JA-signaling pathways	NA	increase in polyphenol oxydase activity, in peroxydase activity, increased expression of Lox, Cupi4, Pal and Gal genes, could involved both JA and SA pathway	Sabbagh *et al.* 2017
Solanaceae								
	Solanum lycopersicum	herbivorous arthropods	pathovars of P. syringae, including alisalensis, atropurpurea, glycinea, maculicola, morsprunorum, porri, and tomato		Jasmonic acid pathway	Coronatine		Geng *et al.* 2014

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Solanum lycopersicum	Xanthomonas gardneri	Lactobacillus plantarium	greenhouse	Jasmonic acid-dependent signaling pathway	Exopolysaccharides		Blainski *et al.* 2018
	Solanum lycopersicum	Fusarium oxysporum	Pseudomonas aeruginosa PM12	greenhouse	Salicylic acid pathway	3-Hydroxy-5-methoxy benzene methanol (HMB)	Levels of salicylic acid were significantly upregulated in all the treatments in comparison to the untreated control. Plants treated with the elicitor and the pathogen showed increased levels of phenylalanine	Fatima and Anjum , 2017
	Solanum lycopersicum	Meloidogyne incognita	Bacillus subtilis isolates Sb4-23, Mc5-Re2, and Mc2-Re2	greenhouse	Induced systemic resistance	supernatant		Adam *et al.* 2014
	Solanum lycopersicum	Fusarium wilt disease	Bacillus fortis IAGS162	greenhouse	Induced systemic resistance through phenyl-propanoid precursors	phenylacetic acid (PAA)		Akram et al, 2016

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Solanum lycopersicum	Alternaria solani Sorauer	AMF Funneliformis mosseae	growth chamber	Jasmonic acid pathway	NA	priming systemic defense response using JA: AMF pre-inoculation led to significant increases in activities of β-1,3-glucanase, chitinase, phenylalanine ammonia-lyase (PAL) and lipoxygenase (LOX) in tomato leaves upon pathogen inoculation, higher induction of defense-related genes and enzymes	Song *et al.* 2015
	Solanum lycopersicum	Cucumber mosaic virus	Trichoderma harzianum T-22	growth chamber	Salicylic acid pathway	NA	mit-SOD activity highest in plants treated only with T22, increase in the leaf and root ABA content when T22 inoculated alone, T22 led to a significant increase of SA when the plants were treated before or simultaneously with CMV	Vitti *et al.* 2016

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Solanum lycopersicum Mill, pepper, Nicotiana tabacum L. Capsicum annuum L.	Botrytis cinerea	Trichoderma harzianum T39	greenhouse	Induced resistance mechanisms	NA	application at sites spatially separated from the B. cinerea inoculation resulted in a 25–100% reduction of grey mould symptoms	de Meyer et al, 1998
	Solanum lycopersicum	B. cinerea CECT2100	Trichoderma harzianum T-78	greenhouse	Jasmonic acid, Salicylic acid and abscisic acid	NA	Trichoderma harzianum-Induced Systemic Resistance is Dependent on the Phytohormones JA, SA, and ABA	Martinez-Medina *et al.* 2013

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Solanum lycopersicum	Botrytis cinerea	Trichoderma harzianum T22 and T. atroviride P1	growth chamber	Jasmonic acid pathway	NA	in the absence of pathogen infection, a preventative treatment of the plant with Trichoderma, as typically used in agriculture, induces an increase in the expression PR genes (SAR markers PR1b1 and PR-P2) indicative of a priming of the defence reaction; when plants are challenged by B. cinerea, pretreatment with Trichoderma might mitigate the SA-dependent gene expression; soon after infection, expression of PINI, PINII, TomLoxA and TomLoxC is enhanced, possibly as a consequence of the priming effect, which results in an increased systemic resistance, probably caused by promotion of the JA-mediated response.	Tucci *et al.* 2011

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Solanum lycopersicum	Botrytis cinerea	Micromonospora spp.	greenhouse	Jasmonic acid pathway	NA	LoxA and PinII are upregulated in presence of B. cinnerewa and Micromonospora spp.	Martínez-Hidalgo *et al.* 2015
	Solanum lycopersicum	Botrytis cinerea	Bacillus subtilis S499	greenhouse	induced systemic resistance	surfactins & fengycins		Ongena *et al.* 2007
	Solanum lycopersicum	Pythium splendens	Rhizobacterium Pseudomonas aeruginosa 7NSK2	greenhouse	Salicylic acid pathway	Salicylic Acid	SA and maybe also pyochelin are responsible for ISR induction	Buysens *et al.* 1996
	Solanum lycopersicum	Alternaria solani, Botrytis cinerea, Pseudomonas syringae pv. tomato (Pst DC3000)	Trichoderma virens and T. atroviride	greenhouse	Salicylic acid and/or Jasmonic acid pathways	Sm1 and Epl1 proteins	Induction of ISR could be more important in this case than the SAR signal to counteract pathogens	Salas-Marina et al., 2015
	Capsicum annuum L.	Rhizoctonia solani	Bacillus subtillis SL-44	growth chamber	Jasmonic acid pathway	flagellin flg22		Wu *et al.* 2019
Fabaceae								
	Phaseolus vulgaris L.	Botrytis cinerea	Trichoderma harzianum T39	greenhouse	Induced resistance mechanisms	NA	application at sites spatially separated from the B. cinerea inoculation resulted in a 25–100% reduction of grey mould symptoms	de Meyer et al, 1998
	Phaseolus vulgaris	Botrytis cinerea	Bacillus subtilis S499	greenhouse	induced systemic resistance	surfactins & fengycins		Ongena *et al.* 2007
	Phaseolus vulgaris	Botrytis cinerea	Pseudomonas aeruginosa 7NSK2	greenhouse	Salicylic acid pathway	Salicylic Acid		De Meyer and Höfte, 1997

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	Phaseolus vulgaris	Botrytis cinerea	Pseudomonas putida BTP1	growth chamber	induced systemic resistance	N-alkylated benzylamine		Ongena *et al.* 2005
Rosaceae								
	Malus domestica	Valsa mali strain 03-8	Saccharothrix yanglingensis Hhs.015	leaf assay	Induced systemic resistance: both the SA-and JA-signaling pathways	Protein Elicitor BAR11	BAR11 may modulate plant immune responses by perturbing H2O2 homeostasis	Zhang *et al.* 2018
Poaceae								
	Zea mays	Bipolaris maydis	Bacillus subtilis DZSY21	Field plot experiment	Induced systemic resistance: both the SA-and JA-signaling pathways	surfactin A, surfactin B, and fengycin	defense-related genes PR1 and LOX were concurrently expressed	Ding *et al.* 2017
	Oryza sativa	Cochliobolus miyabeanus	Pseudomonas protegens CHAO	greenhouse	Jasmonic acid pathway potentially	orfamide	abscisic acid signaling, the transcriptional activator OsWRKY4 and pathogenesis-related protein PR1b are triggered by orfamide A	Ma *et al.* 2017
	Zea mays	Fusarium moniliforme	Bacillus amyloliquefaciens, Bacillus subtilis	on plate	system acquired resistance	Iturin A, Fengycin, Bacillomycin	induction of pathogenesis-related genes, including PR-1 and PR-4	Gond *et al.* 2015

Plant family	Plant species	Pathogen/ pest	Microbial strain	Test conditions	Defense pathway triggered in plants	Molecule triggering the defense pathway	Mechanisms	Reference
	wheat cv. Bobwhite	Xanthomonas translucens pv. translucens	Rhizobium radiobacter F4	growth chamber	Jasmonic acid pathway	NA		Glaeser *et al.* 2016
In vitro testing								
			Xanthomonas campestris pv. phormiicolai		Jasmonic acid pathway	COR-analogs		Mitchell, 1991
			Lasiodiplodia theobromae strain 2334		Jasmonic acid pathway	Jasmonic acid		Eng *et al.* 2016
		Macrophomina phaseolina, Fusarium udum, Fusarium oxysporum, Bipolaris oryzae, Pyricularia oryzae, Alternaria alternata and Curvularia lunata	Bacillus licheniformis MML2501	on plate	ns	Salicylic Acid		Shanmugam and Narayanasam 2008
		Botrytis cinerea, Colletotrichum coccodes, C. gleospoiroides, Rhizoctonia solani, and Sclerotia sclerotiorum	Pseudomonas sp. PRGB06	on plate	ns	Salicylic Acid		Indiragandhi *et al.* 2008

Vervolg van de referaat op de binnenzijde cover

Plantweerbaarheid is het natuurlijke vermogen van een plant om zich te verdedigen tegen ziekten en plagen. De plant zelf heeft verdedigingsmechanismen om zich te kunnen weren tegen vraat en aantasting, vergelijkbaar met het immuunsysteem van mens en dier, en deze eigenschappen zijn vastgelegd in het genoom van de plant. Vaak zijn deze eigenschappen niet bekend en door selectieve veredeling op specifieke kwaliteitsmerkers kan het zijn dat een deel van deze eigenschappen verloren zijn gegaan. Vanuit fundamenteel onderzoek in *Arabidopsis thaliana* (zandraket) is gebleken dat er planthormoon-gereguleerde routes zijn die weerbaarheid aanschakelen. Bepaalde onderdelen van belagende schimmels, bacteriën of insecten schakelen deze routes aan en wordt er vervolgens een scala aan genen aangeschakeld in de plant die er voor zorgen dat aantasting wordt beperkt. Het zijn meestal secundaire metabolieten, zoals afweerstoffen, die ervoor zorgen dat ziekten en/of plagen zich minder snel kunnen vermenigvuldigen op de plant, waardoor de infectie wordt vertraagd. Belangrijke groepen metabolieten wat betreft plantweerbaarheid zijn terpenoiden, alkaloiden, glucosinolaten and fenolen. Welke stoffen binnen deze groepen verantwoordelijk zijn voor het verhogen van de plantweerbaarheid verschilt per gewas. Zandraket behoort tot de familie van de koolachtige planten en het zou kunnen zijn dat alle koolachtige gewassen vergelijkbare routes hebben om weerbaarheid aan te schakelen. Maar, in de landbouw worden ook gewassen van andere plantenfamilies geteeld en het is nog onvoldoende bekend of deze gewassen, die niet tot de familie van koolachtige planten behoren, ook dezelfde routes hebben om weerbaarheid tegen ziekte en plaagveroorzakers te induceren. De vertaalslag van fundamenteel onderzoek (lees onderzoek in zandraket) naar de belangrijkste gewassen die geteeld worden in de praktijk moet nog worden gemaakt. Als deze routes bekend zijn, is het duidelijk te maken op welke wijze biologische middelen ingrijpen op de weerbaarheid van deze planten. Vertaalslag van fundamenteel onderzoek naar de vragen vanuit de praktijk moet nog worden gemaakt. Weerbaarheid is op dit moment nog een abstract begrip voor telers, terwijl er in de praktijk behoefte bestaat om weerbaarheid te kunnen regelen, bijvoorbeeld door bepaalde teeltmaatregelen, cultivarkeuze of plantbehandelingen.

Voor het aanschakelen van weerbaarheid zijn dus stoffen nodig die planten herkennen als een ‘aanval door ziekte of plaagveroorzakers’, zoals afbraakproducten van chitine, pectine of cellulose. Deze stoffen worden elicitors genoemd. Daarnaast kunnen het ook de planthormonen zelf zijn die de weerbaarheidsroutes aanschakelen zoals jasmonzuur en salicylzuur, of stoffen die chemisch erg veel lijken op deze planthormonen, de zogenaamde analogen. Dergelijke stoffen zijn aanwezig in stoffen en extracten van natuurlijke oorsprong. Daarnaast kunnen ook micro-organismen stoffen produceren en uitscheiden die plantweerbaarheid stimuleren. Onder deze groepen van micro-organismen zijn soorten die dikwijls in de praktijk al als biologische bestrijders worden ingezet, zoals bepaalde schimmelsoorten die behoren tot de groepen van *Trichoderma* soorten en Arbusculaire mycorrhiza schimmels, maar ook bacteriesoorten zoals behorend tot de geslachten van *Pseudomonas* en *Bacillus*. Om kennis te kunnen vertalen vanuit het fundamentele onderzoek, gedaan op zandraket, naar praktijkkennis met gangbare teeltgewassen zijn deze stoffen, extracten en micro-organismen belangrijk om vast te kunnen stellen op welke wijze weerbaarheid wordt geïnduceerd in deze gewassen.

Dan is er nog het plantmicrobioom dat een rol speelt bij weerbaarheid tegen biotisch stressfactoren. Tot het plantmicrobioom behoren micro-organismen die samenleven met planten. Deze micro-organismen leven op bladeren (epifyten) of in wortels, stengels en bladeren (endofyten) en in de overgangszone van bodem en wortel, in de zogenaamde rhizosfeer. Micro-organismen uit de bodem komen via de rhizosfeer in contact met planten en veel soorten die leven als endofyt in planten komen uit de bodem. Daarnaast zijn er ook soorten die niet van buitenaf komen, maar via het zaad worden overgedragen naar de volgende generaties van planten.

De bodem speelt een belangrijke rol als reservoir van micro-organismen die uiteindelijk het plantmicrobioom gaan vormen. Vandaar dat bodem en plantmicrobiomen door microbiologen vaak als één doorlopend geheel wordt gezien. Het plantmicrobioom moet worden gezien als een verdedigingsschild tegen binnenkomende pathogenen, vaak schimmels, oömyceten en bacteriën. Hoe veelzijdiger dit schild, des te lastiger het voor deze ziekteverwekkers wordt om binnen te dringen. Een grote microbiële diversiteit in bodem en plant wordt dikwijls als 'gunstig' geïnterpreteerd door onderzoekers in weerbaarheid tegen biotische stressfactoren. Echter, er is nog veel onbekend over de microbiële levensgemeenschappen in bodems en planten. Een één op één vertaalslag van bodem en plant microbiële diversiteit naar weerbaarheid is op dit moment nog niet te maken. De plant kan 'zijn' microbioom aanpassen. Dit gebeurt via uitscheiding van eenvoudige stoffen zoals suikers, aminozuren en organische zuren via de wortels, wortelexudatie genoemd. Micro-organismen uit de bodem worden aangetrokken door wortelexudaten en gebruiken deze stoffen om te groeien in de rhizosfeer en zich te vestigen op of in de wortel. Wanneer een plant wordt aangevallen door een belager, dan verandert de plant de samenstelling van het wortelexudaat, waardoor de plant kan sturen op 'nuttige' micro-organismen uit de bodem die de plant ondersteunen bij weerbaarheid.
In de interacties tussen micro-organismen en planten speelt de genetica van de plant een belangrijke rol. Planten bezitten overerfbare eigenschappen die belangrijk zijn voor de samenwerking met micro-organismen. Dit is ook de reden dat verschillende cultivars van hetzelfde gewas anders kunnen reageren op micro-organismen. Deze eigenschappen zijn nog nauwelijks onderzocht, maar zouden voor telers een belangrijk handvat kunnen zijn om weerbaarheid, op basis van microbioomsamenstelling, te kunnen sturen. Om effectief te zijn in weerbaarheid tegen biotische stressfactoren moet het microbioom in kunnen grijpen in de verschillende routes voor weerbaarheid die aanwezig zijn in planten. Om deze reden veronderstellen wij dat het microbioom ingrijpt in metabole processen in planten, maar andersom ook, dat de metabole samenstelling van planten bepalend zijn voor de samenstelling van het microbioom. Het microbioom en metaboloom van iedere plant is dus aan elkaar verbonden.

Onderzoek naar de microbiële en metabole samenstelling van planten is de laatste jaren sterk verbeterd door nieuwe, snelle en grootschalige doorstroom technologieën. Hierdoor zijn wetenschappers beter in staat om complexe analyses op planten te verrichten. Naar verwachting zullen deze technologieën tot grote doorbraken leiden in de opheldering van biologische en chemische processen in planten. Inzet van deze moderne technologieën zullen daarom zeker tot nieuwe inzichten kunnen leiden in de weerbaarheid tegen biotische stressfactoren in planten.

Samengevat zijn de belangrijkste punten uit dit verslag:
- Er is veel fundamentele kennis over weerbaarheid tegen biotische stressfactoren bij de modelplant zandraket (Arabidopsis), maar de vertaalslag naar landbouwgewassen moet nog worden gemaakt.
- De mechanismen van weerbaarheid zal binnen een plantengroep (bijvoorbeeld koolachtige gewassen) veel op elkaar lijken, maar dat hoeft niet het geval te zijn voor gewassen die buiten deze groep vallen.
- Metabole routes in planten die leiden tot verhoogde weerbaarheid kan worden aangeschakeld door stoffen die aanwezig zijn in plantengroei-bevorderende middelen, zoals stoffen en extracten van natuurlijke oorsprong en bepaalde groepen van micro-organismen.
- Het microbioom van de plant ondersteund weerbaarheid, maar werkingsmechanismen zijn op dit moment nog nauwelijks bekend.

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Consumers, retail and governments are increasingly aware of the possible negative side effects that crop protection products can have on human and animal health and on our living environment. This results in an increasing limitation of the availability of pesticides due to European and national regulations and due to requirements set by retail and consumers. Plant resilience, the natural ability of a plant to defend itself against diseases and pests, is an important part of an integrated approach to prevent and/or control diseases and pests in a residue-free manner. In this literature review, we show the potential of activating the plant's natural defenses based on results obtained in model crops, such as Arabidopsis and tomato, and show what has already been translated into practice.

The activation of the natural defenses is initiated by an elicitor. This is a substance that the plant recognizes and responds to by increasing plant resilience. These can be chemical substances or substances of natural origin. Two important groups are: 1. Analogues of the plant hormones jasmonic acid and salicylic acid; 2. Polysaccharides: breakdown products of chitin, pectin or cellulose. Also, some micro-organisms act as elicitors, because the plant recognizes the micro-organism itself or a substance that it secretes. The four main genera containing strains with elicitor function are: 1.Trichoderma spp.; 2.Arbuscular mycorrhizal fungi; 3 Pseudomonas spp.; 4. Bacillus spp. Examples from the literature are given of each of the mentioned elicitors and it is indicated in which commercial product they are present.

Plant resilience, plant metabolites and the microbiome (the micro-organisms in and near the plant) are three factors that cannot be seen in isolation from each other. Increasing plant resistance has consequences for the composition of the plant components and the microbiome, but also vice versa: changes in the microbiome or plant components result in changes in plant resistance.

Usually secondary metabolites slow down the spread of diseases and/or pests in the crop. Important groups of metabolites with regard to plant resistance are terpenoids, carotenoids, alkaloids, glucosinolates and polyphenols. Which substances within these groups are responsible for increasing plant resistance differs per crop and even per variety. Based on research to date, changes in metabolome composition in different crops appear to follow the same pattern, but more research is needed, especially in non-model crops, to understand how wide these patterns are across the plant kingdom.

Microorganisms in a microbial community are in equilibrium with each other. Microorganisms with elicitor action can only settle if they become part of this equilibrium. Adding 'good' micro-organisms is therefore only successful under specific circumstances. Little is known about this balance and its relationship with plant resistance.

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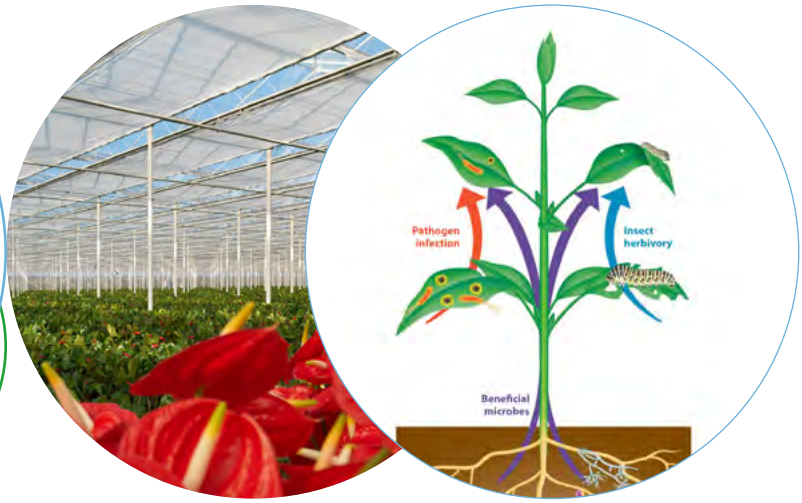

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