PLANT–MICROBE–INSECT INTERACTIONS

Beneficial microbes in a changing environment: are they always helping plants to deal with insects?

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Summary

1. Plants have a complex immune system that defends them against attackers (e.g. herbivores and microbial pathogens) but that also regulates the interactions with mutualistic organisms (e.g. mycorrhizal fungi and plant growth-promoting rhizobacteria). Plants have to respond to multiple environmental challenges, so they need to integrate both signals associated with biotic and abiotic stresses in the most appropriate response to survive.

2. Beneficial microbes such as rhizobacteria and mycorrhizal fungi can help plants to 'deal' with pathogens and herbivorous insects as well as to tolerate abiotic stress. Therefore, beneficial microbes may play an important role in a changing environment, where abiotic and biotic stresses on plants are expected to increase. The effects of beneficial microbes on herbivores are highly context-dependent, but little is known on what is driving such dependency. Recent evidence shows that abiotic stresses such as changes in soil nutrients, drought and salt stress, as well as ozone can modify the outcome of plant–microbe–insect interactions.

3. Here, we review how abiotic stress can affect plant–microbe, plant–insect and plant–microbe–insect interactions, and the role of the network of plant signal-transduction pathways in regulating such interactions.

4. Most of the studies on the effects of abiotic stress on plant–microbe–insect interactions show that the effects of microbes on herbivores (positive or negative) are strengthened under stressful conditions. We propose that, at least in part, this is due to the crosstalk of the different plant signalling pathways triggered by each stress individually. By understanding the cross-regulation mechanisms we may be able to predict the possible outcomes of plant-microbe–insect interactions under particular abiotic stress conditions. We also propose that microbes can help plants to deal with insects mainly under conditions that compromise efficient activation of plant defences.

5. In the context of global change, it is crucial to understand how abiotic stresses will affect species interactions, especially those interactions that are beneficial for plants. The final aim of this review is to stimulate studies unravelling when these 'beneficial' microbes really benefit a plant.

Key-words: abiotic stress, abscisic acid, below- and above-ground interactions, climate change, cross-talk, induced systemic resistance, microbial symbiosis, mycorrhiza, plant growth promoting rhizobacteria, plant signalling

Introduction

Plants live in complex environments where they interact with multiple detrimental organisms such as herbivorous insects and microbial pathogens, but also with beneficial organisms, such as carnivorous insects that reduce herbivore pressure and beneficial fungi and rhizobacteria (Pieterse & Dicke 2007; Dicke, van Loon & Soler 2009; Pineda *et al.* 2010). Additionally, plants in nature are exposed to multiple abiotic stress factors (e.g. nutrient deficiency,

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extreme temperatures and drought), some of which are predicted to increase in severity with global environmental change (Fig. 1). A large body of research has demonstrated how abiotic factors can affect population size, community dynamics and the physiology of different organisms, from herbivorous insects to beneficial microbes. However, an emerging new issue is how environmental changes will affect the interactions between plants and multiple organisms (Tylianakis *et al.* 2008; van der Putten, Macel & Visser 2010), such as microbe–plant, plant–insect and plant–microbe–insect interactions.

The symbioses of plants with beneficial microbes (e.g. endophytes, mycorrhizal fungi, and plant growth-promoting rhizobacteria) are mostly mutualistic and can be considered as nutritional and/or defensive mutualisms depending on whether the plant receives nutrients or protection against attackers in exchange for offering shelter or food to its partner. Most groups of beneficial microbes are located in the rhizosphere, although there are also fungal and bacterial endophytes that colonize the phyllosphere. Several of these beneficial microbes are able to promote plant growth and to enhance tolerance to abiotic stress (Berendsen, Pieterse & Bakker 2012). Additionally, they can suppress pathogens locally and induce systemic resistance (ISR) against a broad range of diseases and herbivorous insects (Sanchez *et al.* 2005; Pozo & Azcon-Aguilar 2007; van Wees, van der Ent & Pieterse 2008; van der Ent, van Wees & Pieterse 2009b; Pineda *et al.* 2010; Partida-Martinez & Heil 2011; Zamioudis & Pieterse 2012). However, it is recognized that the interactions of plants with 'beneficial' microbes may range along a continuum from mutualism to parasitism (Hoeksema *et al.* 2010), that is

with positive or negative effects on plant growth. This continuum is also evident in plant–microbe–insect interactions, where a range of positive and negative plant-mediated effects of microbes on herbivores can be observed (Gehring & Bennett 2009; Koricheva, Gange & Jones 2009; Pineda *et al.* 2010). A major question is what the reasons are for these conditional outcomes (Koricheva, Gange & Jones 2009; Partida-Martinez & Heil 2011), and clearly both biotic (e.g. plant and microbe genotype, insect feeding guild, degree of insect specialization) and abiotic factors are modulating the final plant-mediated effects of microbes on herbivores (Pineda *et al.* 2010). The knowledge of what is driving this context-dependency is crucial if we want to be able to predict the outcome of a certain interaction, and here, we aim to highlight the role of abiotic factors in such dependency.

Interestingly, the plant interactions with beneficial and detrimental organisms, as well as the plant responses to abiotic stresses, are all finely regulated through a complex network of signal-transduction pathways (Fujita *et al.* 2006; Pieterse *et al.* 2012). Exciting recent advances highlight that signalling pathways that regulate the plant responses to biotic and abiotic stresses have common regulators (Fujita *et al.* 2006; Atkinson & Urwin 2012; Lee & Luan 2012) that may allow the plant to prioritize the different responses when the plant is facing multiple simultaneous stresses. By understanding how biotic and abiotic factors affect the plant signal-transduction pathways and the responses they regulate, we may be able to predict how plant–microbe, plant–insect and plant–microbe–insect interactions will respond to a changing environment.
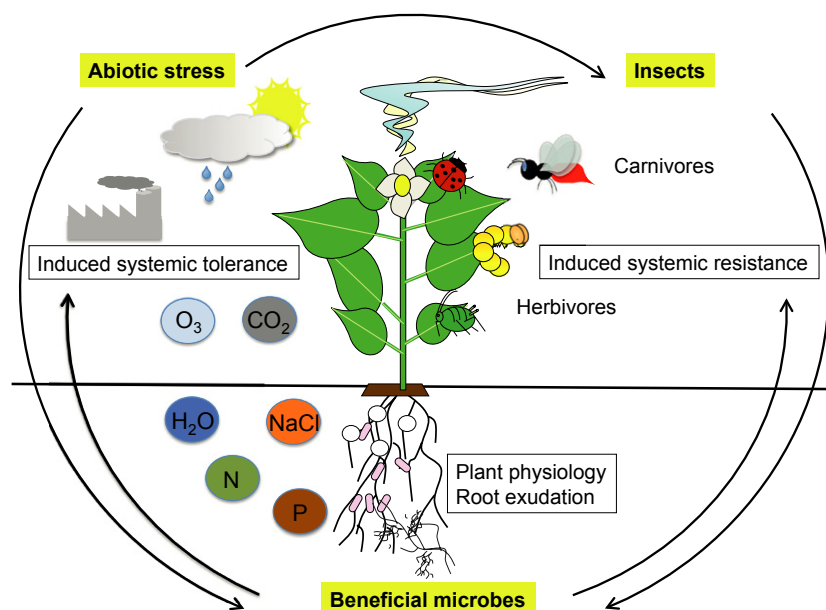

Fig. 1. Plant-mediated interactions between beneficial microbes, insects and abiotic stress. Beneficial microbes can induce systemic resistance against herbivorous insects and tolerance to abiotic stress. Both biotic and abiotic factors can also affect microbial symbiosis via changes in plant physiology and root exudation. How well a plant integrates the response to protect itself from both types of stresses and to accommodate the symbiont microbes will determine its success in a changing environment. Adapted from Pineda *et al.* (2010).

Signal-transduction pathways regulating plant responses to biotic and abiotic stresses

To protect themselves against biotic and abiotic stresses while accommodating beneficial interactions, plants have evolved a highly sophisticated network of signal-transduction pathways that are regulated by different phytohormones (Pieterse *et al.* 2012). It is well established that plant responses to biotic stresses such as herbivory and pathogen attack are mainly regulated by the phytohormones jasmonic acid (JA) and salicylic acid (SA). The SA-dependent pathway is induced by (and mainly effective against) biotrophic pathogens and phloem-feeding insects, whereas the JA-dependent pathway is mainly induced by necrotrophic pathogens and chewing insects (Walling 2000; Glazebrook 2005; Pozo, Van Loon & Pieterse 2005; de Vos *et al.* 2005; Pieterse *et al.* 2012). Additionally, these hormones also regulate interactions of plants with beneficial organisms such as the herbivore-induced attraction of parasitoids (Girling *et al.* 2008; Snoeren, Van Poecke & Dicke 2009) or the symbiosis with microbes (Pozo &Azcon-Aguilar 2007; Gutjahr & Paszkowski 2009; Hause & Schaarschmidt 2009), and even the plant-mediated effect of soil microbes on parasitoid attraction above-ground (Pineda *et al.* 2012a). In general, the JA- and SA-signalling pathways are considered mutually antagonistic (Pieterse *et al.* 2012; Thaler, Humphrey & Whiteman 2012). In contrast, plant responses to abiotic stress, especially the osmotic stress that is imposed by drought and salinity, are mainly regulated by the phytohormone abscisic acid (ABA) (Christmann *et al.* 2006). However, there is an increasing awareness that JA and SA play an important role in responses to abiotic stress too (Peleg & Blumwald 2011). Indeed, whereas the JA-signalling pathway contributes to plant tolerance to drought and salinity (Seo *et al.* 2011; Ismail, Riemann & Nick 2012), SA has also been recognized as a regulatory signal mediating plant responses to drought and osmotic stress (Borsani, Valpuesta & Botella 2001), chilling (Kang & Saltveit 2002) and heat stress (Larkindale *et al.* 2005).

Now, we know that the regulation of stress responses is far more complex. Plants use pathways regulated by other phytohormones such as ethylene (ET), auxins, gibberellins, cytokinins and brassinosteroids to shape distinct response patterns through complex positive and negative interactions (Koornneef & Pieterse 2008; Robert-Seilaniantz, Grant & Jones 2011; Erb, Meldau & Howe 2012; Pieterse *et al.* 2012). Indeed, ABA, besides its role as major regulator of abiotic stress responses, plays a major role in the regulation of plant defences against pathogens (Mauch-Mani & Mauch 2005; Ton, Flors & Mauch-Mani 2009; Beattie 2011; Sánchez-Vallet *et al.* 2012) and herbivorous insects (Thaler & Bostock 2004; Bodenhausen & Reymond 2007; Erb *et al.* 2009, 2011; Verhage 2011; Pineda *et al.* 2012b), possibly by interfering with other signalling pathways (Fujita *et al.* 2006; Atkinson & Urwin 2012). For example, in Arabidopsis, the JA-signalling pathway has two main branches, one effective against herbivorous insects and the other against necrotrophic pathogens, differentially regulated by the transcription factors MYC2 and ERF1, respectively (Anderson *et al.* 2004; Lorenzo *et al.* 2004). Interestingly, whereas ABA is a positive regulator of the MYC2 branch, ET is a positive regulator of the ERF1 branch. Exciting advances have recently shown that after herbivory by leaf chewers, there is an ABA induction that activates the MYC2-branch and represses genes in the ERF-branch (Bodenhausen & Reymond 2007; Verhage 2011), the MYC2 branch being more effective at repelling the chewing herbivore (Verhage *et al.* 2011). Furthermore, ABA may be crucial for the interactions of plants with mutualistic microbes. A functional ABA-signalling pathway has been shown to be required in tomato for a successful mycorrhization (Martín-Rodríguez *et al.* 2011). Additionally, rhizobacteria-mediated ISR against pathogens requires functional expression of different regulators related to ABA signalling such as the transcription factors MYC2 and OCP3 (Pozo *et al.* 2008; Ramirez *et al.* 2010) or the ABA synthase *ABA1/IBS3* (van der Ent *et al.* 2009a) as well as limited watering (pers. obs.), known to trigger ABA accumulation.

As depicted in Fig. 2, the response to different stresses shares common regulatory elements, among them the signalling pathways regulated by defence-related phytohormones. Through synergistic and antagonistic effects, the so-called phytohormone crosstalk allows the plant to prioritize the responses in the case of simultaneous stresses. Crosstalk is considered to provide a plant a powerful regulatory system to meet with the different threats that it faces during its life (Spoel, Johnson & Dong 2007; Koornneef & Pieterse 2008). Thus, crosstalk at the plant-signalling level may have ecological consequences for plant tolerance to multiple stresses and may constitute a driving force for the dynamics of insect and microbial populations. After perceiving a first attack, plants modify several molecular and chemical traits that, via crosstalk, may alter plant response to subsequent attackers leading to induced resistance or induced susceptibility (de Vos *et al.* 2006; Spoel, Johnson & Dong 2007; Poelman *et al.* 2008; Zhang *et al.* 2009; Soler *et al.* 2012). It may, therefore, be expected that after experiencing a certain abiotic stress, the plant activates signalling pathways that will interact with those triggered by herbivores and microbes. The ABA-signalling pathway is an excellent candidate to be mediating such effects. Integrating all this information will be needed to predict the impact of environmental changes on phytohormone homoeostasis and, finally, on the interaction of plants with microbes, insects or in the plant-mediated effects of microbes on insects.

Beneficial microbes can alter plant responses to multiple stresses

The symbioses of the plant with beneficial microorganisms result in important changes in the plant physiology that
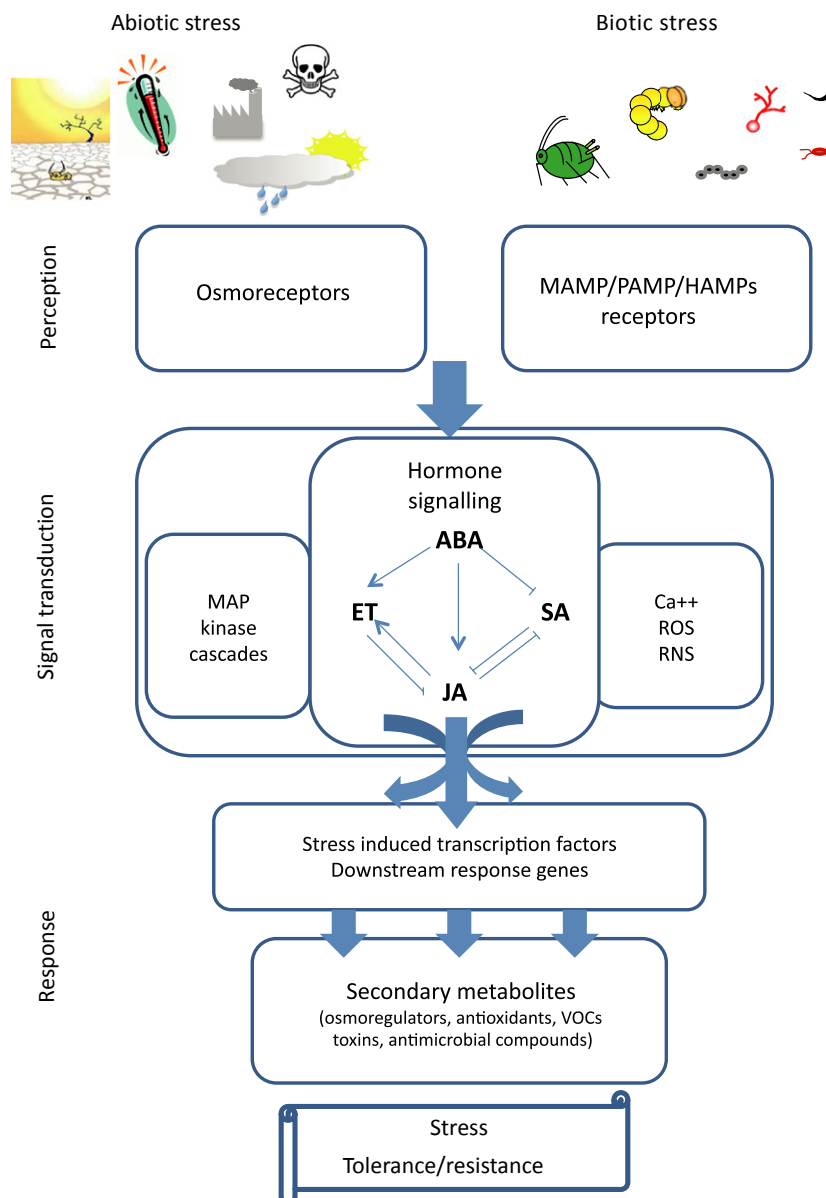
Fig. 2. Signalling events in plants triggered upon perception of abiotic or biotic (attackers and beneficial microbes) stress signals. These stresses are perceived by specific cellular receptors, and then overlapping signalling cascades are activated to regulate the appropriate defence response, finally leading to plant tolerance or resistance to abiotic or biotic stress. (MAMP/PAMP/HAMP, microbe/pathogen/herbivore associated molecular patterns; Ca++, calcium ions; ROS, reactive oxygen species; RNS, reactive nitrogen species; VOC, volatile organic compounds).

are frequently related to plant growth and development, but they also have an important impact on the plant's ability to cope with stress. In fact the induction of tolerance/resistance to stresses may explain the perpetuation of plant–microbe symbioses in conditions where there are no nutritional benefits for the plant (Smith *et al.* 2009).

BENEFICIAL MICROBES CAN INDUCE RESISTANCE OR SUSCEPTIBILITY TO HERBIVORES

In addition to locally suppressing pathogens via competition or via the production of antibiotics and siderophores,

beneficial soilborne microbes can enhance plant resistance against a wide range of pathogens and herbivores in systemic plant tissues. The mechanisms regulating the plant interaction with beneficial microbes, and those underlying the effect of these interactions on organisms deleterious for the plant, are shared by taxonomically different groups of beneficial microbes (van Wees, van der Ent & Pieterse 2008; van der Ent, van Wees & Pieterse 2009b; Pineda *et al.* 2010; Partida-Martinez & Heil 2011; Zamioudis & Pieterse 2012). The best-studied example of the induction of resistance by beneficial soil microbes is that triggered by plant growth-promoting rhizobacteria in

Arabidopsis thaliana. ISR has been mainly studied against microbial pathogens, and it is characterized by priming of the plant for a more efficient activation of defence responses regulated by the JA/ET-signalling pathways (Pozo *et al.* 2008; van der Ent, van Wees & Pieterse 2009b). Priming is a phenomenon that can be elicited by beneficial microbes, but also by pathogens, herbivores and selected synthetic compounds and that provides plants with an enhanced capacity for rapid and effective activation of cellular defence responses to combat pathogen or insect attack (Conrath *et al.* 2006; Pastor *et al.* 2012). Typically, priming is characterized by accelerated defence-related gene expression only once primed plants are attacked by a pathogen or an insect, and as a consequence, priming is less costly for the plant than the expression of constitutive and, to a lesser extent, induced defences (van Hulten *et al.* 2006). Although the mechanisms of ISR against herbivores also involve priming of JA-dependent responses (van Oosten *et al.* 2008; Pineda *et al.* 2012b), other, yet unknown, mechanisms are important as well (Valenzuela-Soto *et al.* 2010). It has been proposed that the priming of plant defences by beneficial micro-organisms is a consequence of the modulation of the plant immune system associated with the establishment of the symbiosis that implies changes in defence-related signalling (Pozo & Azcon-Aguilar 2007; Zamioudis & Pieterse 2012). These changes may have a significant impact on plant–insect interactions. Thus, an integrative approach is needed to understand the plant–microbe–insect interactions, where the mechanism by which the microbe interacts with the plant will subsequently affect the plant–insect interaction.

It is important to note that the outcome of the interactions with beneficial microbes may not always be beneficial for the plant if the cost of maintaining the symbiosis outweighs its benefits (Hoeksema *et al.* 2010). In the context of plant–microbe–insect interactions, the outcome of the plant-mediated interaction between soilborne microbes and herbivores may be positive for the herbivore (Gehring & Bennett 2009; Koricheva, Gange & Jones 2009; Pineda *et al.* 2010), even when higher trophic levels are considered (Pineda *et al.* 2012a). The best-known effect of beneficial microbes is the promotion of plant growth and the improvement of the nutritional status of plants. Therefore, the effect of a certain microbe on herbivore performance will be the result of a balance between a positive effect via the improved quality and quantity of their host plant, and a negative effect of the induction of resistance mechanisms (Bennett, Alers-Garcia & Bever 2006; Gehring & Bennett 2009; Koricheva, Gange & Jones 2009; Pineda *et al.* 2010). The final outcome will then depend on several biotic factors such as microbial identity or plant genotype, but also on the abiotic environment (Pineda *et al.* 2010).

A general pattern has been proposed for effects of mycorrhizal associations under ecological settings, based on the feeding behaviour and degree of specialization of the herbivorous insect (Gehring & Bennett 2009; Koricheva, Gange & Jones 2009). Mycorrhizal fungi generally have a negative effect on generalist leaf chewers and neutral or positive effect on specialist leaf chewers and phloem feeders. This pattern seems to correlate with the spectrum of action of the plant defence response (Pozo & Azcon-Aguilar 2007). Potentially, induced resistance is mediated by an induction of secondary metabolites that are toxic for generalist herbivores, while not negatively affecting specialist herbivores. Additionally, whereas leaf chewers ingest and promote the toxicity of certain metabolites during cell rupture, phloem feeders avoid cell damage and feed on phloem sap, which contains lower levels of toxic compounds.

Interestingly, our studies with the plant growth-promoting rhizobacteria *Pseudomonas fluorescens* and the model plant *Arabidopsis thaliana* confirm the pattern described previously for mycorrhiza–plant–insect interactions in ecological systems. Rhizobacterial colonization induces systemic resistance against the generalist caterpillar *Spodoptera exigua*, whereas it does not affect the growth of the specialist *Pieris rapae* (van Oosten *et al.* 2008). ISR was associated with priming for an enhanced expression of genes regulated by the JA/ET-signalling pathway (van Oosten *et al.* 2008). In contrast, rhizobacterial colonization did not affect the performance of the specialist aphid *Brevicoryne brassicae*, whereas it enhanced the intrinsic growth rate of the generalist aphid *Myzus persicae* (Pineda *et al.* 2012b). Interestingly, this positive effect on the generalist aphid species occurred even though priming for an enhanced expression of the JA-biosynthesis gene *LOX2* was observed in rhizobacteria-colonized plants. Aphid feeding imposes water stress on the host (Cabrera *et al.* 1995), and accordingly, the expression of the ABA biosynthetic gene *ABA1* was induced upon *M. persicae* herbivory. However, plants that were previously colonized by rhizobacteria did not show such activation (Pineda *et al.* 2012b), which may suggest that these plants are less affected by water stress. This result highlights the importance of considering both microbially induced resistance to biotic stress and induced tolerance to abiotic stress when evaluating the effects of beneficial microbes on plant–insect interactions.

BENEFICIAL MICROBES INDUCE TOLERANCE TO ABIOTIC STRESS

Beneficial microbes may also induce host tolerance to abiotic stresses in the soil, such as the presence of heavy metals, the lack of nutrients, drought and salinity (Auge 2001; Dimkpa, Weinand & Asch 2009; Yang, Kloepper & Ryu 2009; Aroca *et al.* 2013; Ruiz-Lozano *et al.* 2012), as well as to above-ground abiotic stresses such as high CO_2, heat or light stress (Compant, van der Heijden & Sessitsch 2010; Davitt, Stansberry & Rudgers 2010). It is noteworthy that the environmental conditions in the natural habitat of particular plants may influence whether a mutualism increases tolerance to abiotic stress or not (Compant, van der Heijden & Sessitsch 2010). For instance, colonization

by the endophyte *Neotyphodium* increased regrowth after drought in a *Lolium perenne* genotype from a dry area, but not in a genotype from a wet area (Hesse *et al.* 2004). Thus, when searching for microbial strains to induce tolerance to abiotic stress, it is important to search under the conditions where both plant and microbe are naturally experiencing the stress of interest.

One clear effect of the beneficial soil microbiota is the increase in root growth and the alteration of root architecture. The improvement of the root system may enhance tolerance to nutrient deficiencies and drought (Yang, Kloepper & Ryu 2009) by increasing the volume of soil to be explored in the search for nutrients and water. Interestingly, these root modifications are partly mediated by changes in phytohormone levels associated with the microbial colonization. Altered hormone levels may explain the differential response of symbiotic plants to stress. For example, mycorrhizal plants usually have altered ABA levels, and ABA is essential for the enhanced tolerance to abiotic stress that is induced by mycorrhizal fungi (Aroca *et al.* 2008). Rhizobacteria may also alter phytohormone levels under stress conditions. For example, ET production increases under some abiotic stresses such as drought, reducing plant growth. Under drought stress rhizobacteria can produce ACC deaminases that degrade the ET precursor ACC, thereby decreasing ET content and restoring normal plant growth (Glick *et al.* 2007).

Plant interactions with insects and microbes in a changing environment

Previously, we have summarized how beneficial microbes may modify the outcome of plant–insect interactions and impact plant tolerance/resistance to different stresses. In this section, we discuss the interactions in the opposite direction: how abiotic stresses can affect plant–microbe and plant–insect interactions, and ultimately, how abiotic stresses can alter the plant-mediated effect of the microbe on the insect.

PLANT-BENEFICIAL MICROBE SYMBIOSES IN A CHANGING ENVIRONMENT

For a beneficial microbe to enhance plant tolerance to a particular stress, the plant–microbe symbiosis needs to be functional under such stress conditions. Abiotic stresses can affect beneficial microbes directly, or indirectly via changes in the host plant physiology and/or root exudation (Compant, van der Heijden & Sessitsch 2010; Aroca *et al.* 2013; Chakraborty, Pangga & Roper 2012). Several studies have recently reviewed the effects of climate change on the interactions of plants with beneficial microbes (Compant, van der Heijden & Sessitsch 2010; Pritchard 2011; Chakraborty, Pangga & Roper 2012). The majority of studies show that elevated CO_2 has a positive influence on the abundance of mycorrhizal fungi, whereas the effects on rhizobacteria and endophytes are more variable (Compant, van der Heijden

& Sessitsch 2010). In contrast, drought and soil salinity seem to decrease the abundance of beneficial microbes (Auge 2001; Juniper & Abbott 2006; Compant, van der Heijden & Sessitsch 2010). The effects of increased temperature are highly variable for all groups of microbes, but for mycorrhizal fungi most studies suggest an increase in their abundance. Soil pH is also an important determinant not only of microbial populations (Rousk *et al.* 2010) but also of microbial activity, affecting, for example, symbiotic efficiency in mycorrhizae (Hayman & Tavares 1985). Collectively, these reviews show that abiotic stresses can modify the abundance and composition of soil microbial communities and, consequently, their effects on the plants.

A well-established symbiosis with mycorrhizal fungi or rhizobacteria is the first prerequisite to observe a beneficial effect of microbes on plants, and in some cases, a threshold of colonization is required (Raaijmakers *et al.* 1995; Cordier *et al.* 1998). Therefore, abiotic stresses that affect the microbial colonization of the roots may impair the microbial induction of ISR. However, a better microbial colonization may not necessarily result in a stronger induced resistance. For instance, a rise in CO_2 increases ryegrass (*Lolium perenne*) colonization by the endophyte *Neotyphodium lolii* but decreases the concentration of alkaloids (Brosi *et al.* 2011), which are the toxic compounds that mediate the resistance conferred by these endophytes. Similarly, we would expect plant fitness to be enhanced when environmental changes lead to an increase in symbiont abundance, but this seems to occur only when the limiting factor for plant growth is the same that the symbiosis is alleviating (Compant, van der Heijden & Sessitsch 2010).

Changes in the microbial community composition will affect herbivores, because combinations of certain strains or species of bacteria and mycorrhiza have synergistic effects whereas others have antagonistic effects (Gange, Brown & Aplin 2003; Saravanakumar *et al.* 2008). The importance of the microbial community composition can also be observed for the interactions of plants with members of the third trophic level, for example parasitoids. For example, depending on the combination of mycorrhizal species colonizing *Leucanthemum vulgare* plants, parasitism of the leaf miner *Chromatomyia syngenesiae* by the parasitoid *Diglyphus isaea* was enhanced or reduced (Gange, Brown & Aplin 2003). Therefore, understanding how environmental conditions affect microbial communities may shed some light on how herbivore communities respond to environmental changes.

PLANT–INSECT INTERACTIONS IN A CHANGING ENVIRONMENT

Recent studies have reviewed the effects of climate change on interactions between plants and herbivorous insects (Massad & Dyer 2010; Thomson, Macfadyen & Hoffmann 2010; Cornelissen 2011; Robinson, Ryan & Newman 2012). Global climate change is expected to lead to an increase in herbivory, particularly by generalist insects

(Massad & Dyer 2010). However, different abiotic stresses have different effects on herbivores probably depending, at least in part, on the changes in the quality of the host plants as food source.

The effects of the best-studied abiotic stresses, that is elevated CO_2 and drought, on herbivorous insects seem to depend on the insect-feeding guild. Drought and high CO_2 generally improve the performance of phloem feeders and decrease the performance of chewing herbivores (Koricheva, Larsson & Haukioja 1998; Khan, Ulrichs & Mewis 2010; Robinson, Ryan & Newman 2012). Exceptions to this pattern are, however, common in the literature, and the factors responsible still need to be elucidated. In the case of drought, the intensity and phenology of the stress seems to be crucial (Huberty & Denno 2004; Mody, Eichenberger & Dorn 2009; Jactel et al. 2012). Changes in carbon, nitrogen and their associated defensive compounds have been proposed to mediate the effects of abiotic stresses on herbivores. For instance, an increase in CO_2 leads to an increase in plants of the C : N ratio and phenolics, which are carbon-based defensive compounds that may negatively affect leaf chewers (Robinson, Ryan & Newman 2012). In contrast, in a CO_2-rich atmosphere the levels of free amino acids in the phloem sap decrease, but aphids compensate for this by ingesting more phloem sap to the extent that aphid growth increases (Sun, Jing & Ge 2009).

Little information is available on whether changes in plant signalling are important for the plant-mediated effects of abiotic stress on herbivores, but some experimental evidence suggest such a role. UV-B radiation reduces thrips damage and oviposition by leaf chewers, and these effects are dependent on a functional JA-signalling pathway (Caputo, Rutitzky & Ballare 2006; Demkura et al. 2010). Similarly, light regulates through JA signalling the secretion of extrafloral nectar, an indirect defence mechanism against herbivores (Radhika et al. 2010). Additionally, changes in JA have been proposed to mediate the increased susceptibility to leaf and root chewers under high CO_2 conditions (Zavala et al. 2008). These first reports should stimulate further studies on the effects of abiotic stress on plant signal-transduction and the consequences for plant–insect interactions.

An additional level of complexity is the influence of abiotic stress on parasitoids and predators of herbivores. For example, caterpillar parasitism decreases when climate variability increases (Stireman et al. 2005). The effects of abiotic stress on the third trophic level can be mediated by changes in the herbivorous hosts, or by changes in the emission of herbivore-induced plant volatiles (HIPV) used by the carnivores as cues to locate their hosts. Abiotic factors such as temperature, drought, nutrients, ozone and CO_2 can alter the emission of HIPV (Gouinguene & Turlings 2002; Holopainen & Gershenzon 2010). As an example, ozone modified the emission of HIPV by cabbage plants infested with the caterpillar *Plutella xylostella*, thereby altering the preference of the parasitoid *Cotesia vestalis* (Pinto, Nerg & Holopainen 2007).

Abiotic factors such as nutrient supply or drought can also determine whether the interaction between two herbivores results in competition or facilitation (Gange & Brown 1989; Staley et al. 2011). Interestingly, this can even occur between herbivores that are located above- and below-ground (Gange & Brown 1989; Staley et al. 2007; Erb et al. 2011). For instance, root feeding in corn by *Diabrotica virgifera* induces resistance against the chewing herbivore *Spodoptera littoralis* above-ground, but only under drought stress conditions (Erb et al. 2011). Interestingly, in this study, water stress enhanced the induction upon above-ground herbivory of defence genes related to the biosynthesis of ABA and the antifeedant DIMBOA. These studies highlight the importance of abiotic factors such as water stress in mediating above-ground and below-ground interactions between herbivores (Masters, Brown & Gange 1993) and support the idea of abiotic factors affecting plant-mediated interactions between mutualistic microbes and herbivores.

PLANT–MICROBE–INSECT INTERACTIONS IN A CHANGING ENVIRONMENT

In the previous sections, we have addressed the effects of abiotic stresses, which are predicted to increase with climate change, on the interactions of plants with microbes and with insects. The next question is whether abiotic factors affect the plant-mediated effects of microbes on herbivores. This research field is still in its infancy and there are only studies on beneficial fungi (i.e. mycorrhizae and other endophytes) while nothing is known for plant growth-promoting rhizobacteria or nodulating rhizobia. However, there is evidence that indeed abiotic stress may strengthen certain microbial effects on plant resistance. Although a few studies have explored how stresses such as salinity (Younginger, Barnouti & Moon 2009), ozone (Manninen et al. 2000), or CO_2 (Marks & Lincoln 1996) affect plant–microbe–insect interactions, to date most of our knowledge on this topic is centred on the effects of nutrient levels and drought.

Soil nutrient content plays an important role in plant–insect interactions with mycorrhizal fungi and fungal endophytes, with contrasting effects between the two groups of microbes. Mycorrhizal fungi can have positive or negative effects on herbivores, but such effects are not observed when the soil is supplemented with phosphorous (Borowicz 1997; Gange, Bower & Brown 1999) or nitrogen (Gange & Nice 1997; Manninen, Holopainen & Holopainen 1998). In contrast to mycorrhizal fungi, the negative effect of fungal endophytes on herbivore performance is strengthened by the addition of nitrogen or an NPK fertilizer, probably by promoting increased synthesis by the endophyte of the nitrogen-based alkaloids that are toxic for the herbivores (Lehtonen, Helander & Saikkonen 2005; Vesterlund et al. 2011).

The relevance of drought as regulator for plant–microbe–insect interactions to date has only been demonstrated

for fungal endophytes (Vidal 1996; Bultman & Bell 2003; Miranda, Omacini & Chaneton 2011; Vesterlund *et al.* 2011; Yule, Woolley & Rudgers 2011). Most of these studies evaluated the effects on phloem feeders (see Bultman & Bell 2003 and Vesterlund *et al.* 2011 for other herbivores), which generally are negatively affected by endophyte infection only under certain level of drought stress (Bultman & Bell 2003). For instance, the negative effect of the endophyte *Neotyphodium coenophialu* on the aphid *Rhopalosiphum padi* was only present when plants recovered from the stress but not when the plants were continuously under water stress (Bultman & Bell 2003). Such effects may be related to the concentration of loline alkaloids, toxic for aphids, which was higher in previously stressed plants (Wilkinson *et al.* 2000). Whether drought affects plant–insect interactions with microbes that do not produce alkaloids, and how herbivores other than phloem feeders would respond remains to be elucidated.

Even less attention has been paid to the modification of multitrophic interactions between microbes, plants, herbivores and their natural enemies by abiotic stresses. To our knowledge, the first study addressing this aspect has been recently published (Yule, Woolley & Rudgers 2011), with the endophyte *Neotyphodium* PauTG-1 colonizing the grass *Poa autumnalis*, and assessing the effects on the aphid *Rhopalosiphum padi* and on its parasitoid *Aphelinus* spp. Under field conditions, a moderate water-stress treatment strengthened the positive effect of endophytes on plant biomass and parasitoid incidence, which was lost under a high-watering regime. Interestingly, the water stress applied did not affect plant biomass of endophyte-free plants. These results suggest that a plant response to a moderate abiotic stress may affect plant–microbe–insect interactions, independently of effects on plant growth.

Are beneficial microbes recruited under unfavourable conditions?

We believe that symbiotic microbes are beneficial for plants mainly when plants need help, and this need will be determined, at least in part, by the occurrence of biotic and abiotic stresses. There is enough evidence that beneficial microbes are initially perceived as hostile organisms, and accordingly, the plant responds as to a potential enemy. Later on, upon mutual recognition, the plant switches off the defence response and a symbiotic program is started (Pozo & Azcon-Aguilar 2007; Zamioudis & Pieterse 2012). Such a switch might be determined by plant needs. It is well documented that several symbionts only benefit their host plants under limiting conditions, where the benefit may outweigh the costs of maintaining the symbiosis (Hoeksema *et al.* 2010). For example, as the main benefit of the mycorrhizal symbiosis is an improved phosphorous acquisition, under low phosphate conditions the plant promotes the interaction and switches on a symbiotic program. In contrast, high phosphate levels inhibit the

activation of symbiotic genes and reduce mycorrhizal colonization (Breuillin *et al.* 2010). As previously discussed, beneficial microbes can also play a crucial role in plant survival and/or fitness by priming defence mechanisms. It is possible then that microbial symbioses are promoted under stressful environmental conditions to improve stress resistance.

Interestingly, studies with disease-suppressive soils have shown that a strong disease outbreak is required for the onset of the suppressiveness (Mendes *et al.* 2011), which may support the idea of beneficial microbes being recruited after attack. There is evidence that upon above-ground herbivory, mycorrhizal colonization can increase (Kula, Hartnett & Wilson 2005), although it may revert after intense herbivory (Gehring & Bennett 2009). Recently, the first proof of rhizobacteria recruitment upon above-ground herbivory has been published (Yang *et al.* 2011; Lee, Lee & Ryu 2012). The mechanisms that explain how the microbe–plant symbiosis is enhanced after the plant perceives a certain stress are only now starting to be uncovered. Exciting advances have shown that plants can 'cry for help' below-ground via the production of compounds that attract enemies of root herbivores (Rasmann *et al.* 2005) or that enhance the root colonization by beneficial microbes (Rudrappa *et al.* 2008; Lopez-Raez, Pozo & Garcia-Garrido 2011; Neal *et al.* 2012). For instance, pathogen attack on *Arabidopsis* leaves increased the root exudation of malic acid and this led to the recruitment of the PGPR *Bacillus subtilis* (Rudrappa *et al.* 2008). Phytohormones may also play a role. For example, an increase in JA after repeated mechanical damage aboveground that partially simulates herbivory damage seems to enhance mycorrhizal colonization of roots in *Medicago truncatula* (Landgraf, Schaarschmidt & Hause 2012).

Help may be also requested under abiotic stress conditions. Exciting research about a new group of plant hormones, strigolactones, showed that plants increase their production under phosphorous-limiting conditions (Lopez-Raez, Pozo & Garcia-Garrido 2011). Interestingly, these hormones have several functions. In the rhizosphere, they are key signalling molecules in the establishment of the mycorrhizal symbiosis, ultimately improving the plant's capacity to acquire phosphorous. Within the plant, they regulate shoot branching and root architecture, which may indirectly affect plant tolerance to abiotic stress (Lopez-Raez, Pozo & Garcia-Garrido 2011). Remarkably, under salt stress, mycorrhizal plants increase the production of strigolactones (Aroca *et al.* 2013). The synthesis of these hormones is regulated by ABA (Lopez-Raez *et al.* 2010); thus, it is tempting to speculate that abiotic stress may increase strigolactone production to promote the mycorrhizal symbiosis and alleviate stress. As plants in nature are simultaneously affected by biotic and abiotic stresses, it would not be surprising if the production of compounds that favour beneficial plant–microbe symbioses are

further enhanced when perceiving both biotic and abiotic stresses.

Future perspectives

Plants are members of complex communities formed by multiple species of insects and microbes that may be detrimental or beneficial for the plant and be located above- or below-ground. Unfortunately, plant–microbe and plant–insect interactions have long been studied in isolation. However, exciting discoveries in the last decade show that plant responses to microbes and insects share important similarities and common regulators, and in recent years, these research fields have been frequently connected (e.g. Pieterse & Dicke 2007). However, the connection of these two research fields has mainly been based on individual microbe and herbivore species. Accordingly, there is still a big gap (Box 1) on how microbes affect insects at the community level, including herbivores from different feeding guilds and insects of higher trophic levels (i.e. carnivores).

Moreover, plants in nature are simultaneously exposed to biotic and abiotic stresses. Again, plant responses to these two types of stresses have traditionally been studied separately, but recent discoveries illustrate that the signalling cascades activated in response to both biotic and abiotic stresses are similar and that they interact through common regulatory nodes, opening a plethora of possible mechanistic interactions (e.g. Atkinson & Urwin 2012). This review was motivated by those recent findings showing how plant responses to biotic and abiotic stresses may interact, with ecological consequences at several trophic levels (e.g. Holopainen & Gershenzon 2010). There is evidence for abiotic stress affecting plant–microbe and plant–insect interactions, but much less explored is the influence of abiotic stress on the plant-mediated effects of microbes on insects. The challenge that climate change is imposing to plant growth in natural and agricultural ecosystems urges for studies of the effects of abiotic stress on two- and three-way interactions between plants, microbes and insects.

A microbial community approach is necessary when addressing plant–microbe–insect interactions. Recent evidence on disease-suppressive soils highlight that plant protection against pathogens is provided by a consortium of bacteria rather than by single strains (Mendes *et al.* 2011; Berendsen, Pieterse & Bakker 2012). The diversity of microbes is enormous and, although it is difficult to visualize, each strain that has been selected in a certain environment should have a particular biological function. Different microbial symbionts have different effects on plants, and it will be fascinating if plants under certain stresses favour those symbiotic relationships that increase their ability to deal with the inducing stress.

As our knowledge on the mechanisms regulating plant responses to biotic and abiotic factors increases, we can increase the complexity of our study systems. By doing so, we will get closer to understand the functioning of natural ecosystems, where plants are exposed to multiple attackers with different invasive strategies, to beneficial organisms such as mutualistic microbes and carnivorous insects, and to abiotic stresses that are predicted to increase in severity with global change. The use of model systems has highly contributed to unravel the underlying mechanisms of all these interactions in the past decade, and in the near future, the rapidly advancing techniques in molecular biology will allow scientists to work with ecological systems, thus expanding our knowledge from the laboratory to the field and from changes in genes to effects on the ecosystem.

Box 1: Future research questions

What are the effects of beneficial microbes on insects in a changing environment?

- What are the plant-mediated effects of microbes on insects (herbivores, carnivores, pollinators) under different abiotic stress conditions?
- How do these microbial effects on herbivores under abiotic stress change in a multitrophic context (when higher trophic levels – i.e. carnivores – are considered)?
- Do the effects of single microbial strains change when they are part of a microbial community?
- Do beneficial microbes modify how abiotic stress affects insect communities in the field (herbivores, carnivores, pollinators)?

What are the mechanisms underlying such effects?

- Can plant defence mechanisms and crosstalk of plant defence-signalling pathways explain the effects?
- Are effects of abiotic stress on plant–microbe–insect interactions related to changes in the microbial abundance/composition?

Recruitment of beneficial micro-organisms

- Does a certain stress favour those symbiotic interactions that protect plants better against such stress?
- Can plants under stress actively recruit beneficial micro-organisms? How?

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