



## Review

# Bacteria and fungi controlling plant growth by manipulating auxin: Balance between development and defense<sup>☆</sup>



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## ARTICLE INFO

## Article history:

Received 18 December 2013  
 Received in revised form 15 January 2014  
 Accepted 17 January 2014

## Keywords:

Auxin homeostasis  
 Auxin signaling  
 Defense  
 Plant disease  
 Resistance

## SUMMARY

Plant diseases cause huge losses by changing the quality and quantity of harvested crops. Many disease symptoms caused by bacteria or fungi rely on the involvement of plant hormones, while other plant hormones act as defense signals in the plant. In this review the role of auxins in these processes will be evaluated. Some growth promoting plant hormones cause disease symptoms. For example auxins stimulate cell division and cell elongation in a healthy plant, but tumor formation after bacterial infection. Thus, control of auxin levels and auxin signaling pathways significantly contribute to the defense network in plants. Auxin can also act directly as defense molecule with antimicrobial activity. Since much research has been done in the recent years on auxin as a pathogenicity factor for many diseases, several examples will be presented to highlight the complexity between normal plant growth, which is regulated by auxin, and processes determining resistance or susceptibility, triggered by the same class of molecules.

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## Introduction

Plant growth and development is controlled by many signaling molecules, the so-called plant hormones, but these are also sometimes signals for defense responses. In their natural environment plants have to cope with a plethora of different organisms by which they are challenged. They have therefore developed many resistance mechanisms, using different cues for the recognition of a diverse range of pathogens. As outlined by [Mausz and Pohnert \(2015\)](#) metabolic properties are relevant for the defense status not only for single cells but also for whole organisms. In many cases the defense response is induced, but on behalf of the fitness of the plant.

*Abbreviations:* IAA, indole-3-acetic acid; IAA-Asp, IAA-Aspartate; IAN, indole-3-acetonitrile; IBA, indole-3-butyric acid; JA, jasmonic acid; NPA, naphthylphthalamic acid; SA, salicylic acid.

<sup>☆</sup> This article is part of a Special Issue entitled: Plant Physiology meets Biodiversity.

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This could be a dilemma, because the balance between defense and beneficial growth responses has to be maintained. Plant hormones can integrate the response to developmental and environmental cues and thus limit defense-associated fitness costs. Many plant hormones, especially those controlling plant growth responses, fit into this category (reviewed in [Denancé et al., 2013](#)), but here auxin will be taken as an example to explain the concept of “balance between benefit and pathogen”. In plant–pathogen interactions the term “race of arms” has been coined to describe the ongoing co-evolution of defense and colonization strategies between the two partners ([Anderson et al., 2010](#)). This term could also be adjusted for the growth promotion (for instance by nitrogen fixation, see [Gresshoff et al., 2015](#)) vs. defense responses. If the hormonal balance is on the plant’s side, then the plant will “win the race”, but when the pathogen can turn the hormonal system to its own advantage, the pathogen is the “winner”. The pathways to be regulated by hormones include direct defense pathways, nutritional aspects, but also cell wall maintenance (reviewed in [López et al., 2008](#)).

Auxins play many different roles in plant growth and development ([Davies, 2010](#)). On the cellular levels they are involved in the

regulation of cell division, cell expansion, cell differentiation and polarity. On the whole plant levels they also contribute to organ development, such as roots (lateral and adventitious), shoots (i.e. apical dominance), leaves, as well as flower organs and fruits. They are also involved in vascular patterning and orientation in the environment (e.g. gravi- and phototropism). These examples indicate their roles in all major developmental processes of a plant. Auxins are also involved in the regulation of changes in different growth processes associated with pathogens and symbionts. While pathogens can alter the auxin response to induce specific disease symptoms during disease development, beneficial microorganisms interfere with the auxin metabolism of the host plant to induce plant growth for their own benefit (for review see Ludwig-Müller, 2014).

Even though auxin has long been recognized as a regulator of plant defense, the molecular mechanisms involved have been only recently taken under investigation. Similar to the signaling pathways of the defense-associated compounds salicylic acid (SA) and jasmonic acid (JA), auxin signaling differentially affects resistance to various pathogen groups (reviewed in Kazan and Manners, 2009). Recent evidence suggested that the auxin and SA pathways act antagonistically during plant defense reactions, whereas auxin and jasmonate pathways have many similarities regarding plant defense responses (Kazan and Manners, 2009). Auxin may also affect disease outcomes indirectly through effects on plant development (Gil et al., 2001). The evolutionary reasons behind the antagonistic interactions between SA and auxin might be that plants divert limited resources to defense-related processes at the expense of plant growth when attacked by a pathogen (Kazan and Manners, 2009). The growth of plants is dependent on energy, mainly from photosynthesis and respiration. SA-mediated induction of PR (pathogenesis related) proteins was dependent on the presence of intact photoreceptors, linking light to defense (Karpinski et al., 2003). A connection between SA and photosynthesis is the protein isochlorismate synthase, which is involved in SA synthesis, but also in the synthesis of phyloquinone, which is incorporated into photosystem I (Szechynska-Hebda and Karpinski, 2013). An excess excitation energy has similar effects on the expression of nuclear genes involved systemic acquired acclimation and systemic acquired resistance, which are both tightly linked to programmed cell death (reviewed in Szechynska-Hebda and Karpinski, 2013). However, recently we have shown that auxin and SA systemically co-increased during infection of *Arabidopsis thaliana* with Cucumber mosaic virus (Likić et al., 2014), so that not in all cases an antagonism of auxin and SA can be anticipated.

When talking about “auxin” the major compounds in plants, indole-3-acetic acid (IAA) is usually meant, but there are some indole and other derivatives with auxin activity (Epstein and Ludwig-Müller, 1993; Ludwig-Müller, 2000; Ludwig-Müller and Cohen, 2002). Also, only the free form of IAA and related compounds is considered to be active, the majority of auxin in a given tissue, however, is conjugated mainly to amino acids and sugars and thereby inactivated (Ludwig-Müller, 2011). Since IAA can be even growth inhibitory at high concentrations, the tight control of auxin homeostasis is essential. Here, several processes are important: (1) biosynthesis, (2) degradation, (3) reversible conjugation, and (4) transport, the latter includes long distance and cell-to-cell movement of auxin, leading to local auxin maxima or auxin gradients (e.g. Smith, 2008). These four main possibilities to control auxin concentrations in a given tissue are connected to transcriptional activation of auxin-inducible genes, which can be growth or defense related (Fig. 1). In the case of expansins the proteins can act in developmental responses, for example cell expansion, or in changing the penetration environment (cell wall) for pathogens.

In addition to developmental processes, IAA has come into focus to play a role in plant defense processes against pathogens, mainly

bacteria and fungi. In some cases the pathogens use the auxin machinery to induce disease symptoms (Fig. 1), such as crown gall disease (Gelwin, 1990) or clubroots (Ludwig-Müller et al., 2009b). In other instances, they hijack the auxin signaling or conjugation pathways in their own favor to manipulate plant defense responses (Figs. 2 and 3). Finally, there are some examples where auxins could be directly inhibitory and thus involved in the defense response of the plant (Fig. 3). These examples show that the benefit for a plant can be turned against it by pathogens, but vice versa the pathogens can be fought off as well (Table 1). Some examples indicative of the above dilemma will be discussed for plant–pathogens from diverse evolutionary groups to demonstrate the use of similar strategies among different organisms, but also how variable such strategies can turn out.

On the other hand there are plant growth promoting soil microbes either producing IAA (Patten and Glick, 2002), or mediating the IAA levels in the plants (Fig. 1). The growth promoting basidiomycete *Piriformospora indica* has been shown to produce auxin in culture (Sirrenberg et al., 2007; Vadassery et al., 2008), but the contribution of IAA to the growth promotion phenotype of colonized plants is still a matter of debate. Only recent work has reported that *P. indica* uses the auxin biosynthesis pathway via tryptamine as an intermediate (Hilbert et al., 2012). It was also shown that a gene encoding one protein from the pathway was expressed during the biotrophic phase of the interaction. However, attenuation of IAA synthesis in a transgenic fungus did not have an effect on growth promotion (Hilbert et al., 2012), confirming earlier results (Vadassery et al., 2008). Addition of low IAA concentrations led to suppression of an oxidative burst in barley, suggesting that the IAA produced by the fungus could interfere/suppress host plant defense (Hilbert et al., 2012, 2013). For arbuscular mycorrhiza it has been shown that two auxin might play a role, IAA and indole-3-butyric acid (IBA) (Ludwig-Müller et al., 1997; Kaldorf and Ludwig-Müller, 2000). Auxin could be involved in the mediation of the root phenotype seen in some species, i.e. more lateral roots in mycorrhized plants of maize (Kaldorf and Ludwig-Müller, 2000). In the rhizobium–legume interaction also some indications have been published that IAA is needed for the initiation of the root nodules as organs, especially the intact auxin transport machinery (Wasson et al., 2006). Also, Campanella et al. (2008) have shown that some members of an auxin conjugate hydrolase family from *Medicago truncatula* were transcriptionally upregulated both during arbuscular mycorrhiza formation and nodulation, which could lead to higher free IAA levels. While these are examples for the beneficial role of auxin in plant–microbe interactions, in the following different strategies of plant–pathogens will be specifically discussed.

## Auxin biosynthesis

Auxin biosynthesis can contribute to the symptoms of certain plant diseases, but is also essential for the normal development of the plant and its orientation in the environment. Either a pathogen hijacks the biosynthetic system of the host plant, or it can produce the auxin itself. One prominent example for the latter is the tumor formation induced by the soil bacterium *Agrobacterium tumefaciens*, where genes for auxin and cytokinin biosynthesis are stably transformed into the plant tissue (Zupan and Zambryski, 1995). Other bacteria, which do not transform their host, are also capable to synthesize IAA via various routes (for review see Spaepen et al., 2007).

Another example is the clubroot disease of Brassicaceae, caused by the obligate biotrophic protist *Plasmodiophora brassicae* (Ludwig-Müller et al., 2009b), where the increased levels of IAA are produced by the plant. Of importance is the conversion

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