



Research article

Local and systemic hormonal responses in pepper leaves during compatible and incompatible pepper-tobamovirus interactions



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ABSTRACT

Phytohormone levels and the expression of genes encoding key enzymes participating in hormone biosynthetic pathways were investigated in pepper leaves inoculated with two different tobamoviruses. *Obuda pepper virus* (ObPV) inoculation led to the development of hypersensitive reaction (incompatible interaction), while *Pepper mild mottle virus* (PMMoV) inoculation resulted in a systemic, compatible interaction. ObPV-inoculation markedly increased not only the levels of salicylic acid (SA) (73-fold) and jasmonic acid (8-fold) but also those of abscisic acid, indole-3-acetic acid, indole-3-butyric acid, *cis*-zeatin, *cis*-zeatin-9-riboside and *trans*-zeatin-9-riboside in the inoculated pepper leaves 3 days post inoculation. PMMoV infection increased only the contents of gibberellic acid and SA. Hormone contents did not change significantly after ObPV or PMMoV infection in non-infected upper leaves 20 days post inoculation. Concentrations of some brassinosteroids (BRs) and progesterone increased both in ObPV- and PMMoV inoculated leaves. ObPV inoculation markedly induced the expression of three phenylalanine ammonia-lyase (*PAL*) and a 1-aminocyclopropane-1-carboxylate oxidase (*ACO*) genes, while that of an isochorismate synthase (*ICS*) gene was not modified. PMMoV inoculation did not alter the expression of *PAL* and *ICS* genes but induced the transcript abundance of *ACO* although later than ObPV. Pre-treatment of pepper leaves with exogenous 24-*epi*-brassinolide (24-*epi*-BR) prior to ObPV-inoculation strongly mitigated the visible symptoms caused by ObPV. In addition, 24-*epi*-BR pre-treatment markedly altered the level of several hormones in pepper leaves following ObPV-inoculation. These data indicate that ObPV- and PMMoV-inoculations lead to intricate but well harmonized hormonal responses that are largely determined by the incompatible or compatible nature of plant-virus interactions.

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1. Introduction

The resistance of plants against phytopathogenic viruses is determined by the timely recognition of the virus and the rapid deployment of efficient antiviral defense reactions. Viruses are generally perceived by intracellular resistance proteins (R-proteins) of host cells. Upon recognition, signals are transmitted to the nucleus leading to the rapid and extensive reprogramming of host gene expression patterns and ultimately to the development of effector-triggered immunity (ETI) in resistant plant genotypes. ETI

is often associated with programmed cell death at sites of infection (hypersensitive response, HR) (Künstler et al., 2016). The reprogramming of the transcriptome is regulated by a complex, multi-layered regulatory network, in which various transcription factors (Gatz, 2013) and defense-related plant hormones (Alazem and Lin, 2015) play critical roles.

It is generally accepted that the plant hormones salicylic acid (SA), jasmonic acid (JA) and ethylene play a key role in plant immunity (Alazem and Lin, 2015). A substantial rise of endogenous SA content was revealed in leaves of resistant tobacco plants following *Tobacco mosaic virus* (TMV) inoculation (Enyedi et al., 1992). SA was shown to induce virus resistance by inhibiting both virus replication and virus movement (Singh et al., 2004). In addition, SA is essential to the development of systemic induced resistance (SAR)

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Nomenclature

| | | | |
|-----------|--|-------|---|
| ABA | abscisic acid | ICS | isochorismate synthase |
| ACO | 1-aminocyclopropane-1-carboxylate oxidase | IPA | N6-isopentenyl-adenine |
| ACS | 1-aminocyclopropane-1-carboxylate synthase | ISTD | internal standard |
| AOC | allene oxide cyclase | JA | jasmonic acid |
| AOS | allene oxide synthase | K | kinetin |
| BR | brassinosteroid | KR | kinetin-9-riboside |
| c-Z | cis-zeatin | NCED | 9-cis-epoxycarotenoide-dioxygenase |
| c-ZR | cis-zeatin-9-riboside | LOX | lipoxygenase |
| dpi | days post inoculation | ObPV | Obuda pepper virus |
| 24-epi-BR | 24-epi-brassinolide | PAL | phenylalanine ammonia-lyase |
| GA1 | gibberellin A1 | PMMoV | Pepper mild mottle virus |
| GA3 | gibberellic acid | SA | salicylic acid |
| GA4 | gibberellin A4 | SAR | systemic induced resistance |
| GA6 | gibberellin A6 | TMV | Tobacco mosaic virus |
| hpi | hours post-inoculation | TSA | transcriptome shotgun assembly |
| IAA | indole-3-acetic acid | t-Z | trans-zeatin |
| IBA | indole-3-butyric acid | t-ZR | trans-zeatin-9-riboside |
| | | UHPLC | ultra performance liquid chromatography |

(Gaffney et al., 1993; Fodor et al., 1997). Exogenously applied SA can effectively induce the expression of numerous defense genes including a suite of pathogenesis-related (PR) genes (Vlot et al., 2009). The biosynthesis of SA can occur by two possible pathways. One pathway is initiated by the transformation of phenylalanine to trans-cinnamic acid catalyzed by phenylalanine ammonia-lyase (PAL, E.C. 4.3.1.5) isoenzymes (Kim and Hwang, 2014). Alternatively, SA can be synthesized from chorismate via the rate-limiting enzyme isochorismate synthase (ICS, E.C. 5.4.4.2) enzyme (Catnot et al., 2008). However, little information is available about which biosynthetic pathway is predominant during the accumulation of SA in virus-infected leaves.

In contrast to SA, JA was shown to negatively regulate the TMV-resistance in tobacco (Oka et al., 2013). The first reaction in the multi-step pathway of jasmonic acid biosynthesis is catalyzed by 13-lipoxygenase (13-LOX, E.C. 1.13.11.12) isoenzymes, which perform the peroxidation of α -linolenic acid to 13-hydroperoxy-linolenic acid (Feussner and Wasternack, 2002). This metabolite is further converted by allene oxide synthase (AOS, E.C. 4.2.1.92) and allene oxide cyclase (AOC, E.C. 5.3.99.6) enzymes to (9S, 13S)-12-oxo-phytodienoic acid (12-OPDA), which is transformed by several further enzymatic steps ultimately to JA (Feussner and Wasternack, 2002).

Ethylene also plays an important role as a highly inducible signal compound in the defense reactions of virus-infected plants (Alazem and Lin, 2015). The massive accumulation of ethylene was observed in various incompatible plant-virus interactions (Barna et al., 2012b) including ObPV-infected pepper (Tóbiás et al., 1989). The last two key steps in the ethylene biosynthetic pathway are catalyzed by the 1-aminocyclopropane-1-carboxylate synthase (ACS, E.C. 4.4.1.14) and the 1-aminocyclopropane-1-carboxylate oxidase (ACO, E.C. 1.14.17.4) enzymes, which are encoded by small gene families in plants (Kim et al., 2003).

These hormones can have synergistic and antagonistic interactions as well. A well known example is the antagonism of SA and JA/ethylene pathways (Koorneef and Pieterse, 2008; Spoel and Dong, 2008). In addition, numerous experimental data have recently demonstrated that abscisic acid (ABA), auxins, brassinosteroids (BRs), cytokinins and gibberellins also play important roles in plant defense responses (Jameson and Clarke, 2002; Denance et al., 2013; Alazem and Lin, 2015). TMV-infection increased the

concentration of both free and bound forms of ABA (Whenham et al., 1986). ABA is also a negative regulator of TMV-resistance (Balázs et al., 1973), although long-term treatments with low ABA concentrations promoted virus resistance (Fraser, 1982). In the multi-step biosynthesis of ABA the 9-cis-epoxycarotenoide-dioxygenase (NCED) isoenzymes play a critical role (Taylor et al., 2000).

BRs are known not only to regulate plant growth and development (Bajguz, 2007), but they have been shown to play substantial roles also in plant disease resistance (Nakashita et al., 2003; Alazem and Lin, 2015). According to our previous results the pre-treatment of oilseed rape cotyledons with a BR substantially decreased the damage caused by *Pseudomonas syringae* inoculation (Skoczowski et al., 2011). Application of BR also lowered the susceptibility of rice to fungal and bacterial diseases, and induced resistance of tobacco to *Tobacco mosaic virus* (TMV), *P. syringae*, and to the powdery mildew fungus *Oidium* sp. (Nakashita et al., 2003). Zhang et al. (2015) proved that high BR concentrations in *Arabidopsis thaliana* are positively correlated with tolerance against *Cucumber mosaic virus* (CMV) infection by manipulating the endogenous BR levels. BR treatment protected the photosystems, increased the activity of antioxidative enzymes and induced the expression of defense-associated genes in CMV infected plants.

Progesterone is one of the mammalian hormones but its presence has already been confirmed in some plants as well (Janeczko, 2012). Our knowledge about the roles of progesterone in plants is very limited. Progesterone has been shown to participate in plant development and abiotic stress responses (Janeczko, 2012; Janeczko et al., 2013a). Contrary to brassinosteroids, progesterone has no hormone status in plants, so every study devoted for the evaluation of its physiological functions in plants will be helpful for the evaluation of its hormonal nature.

To obtain a deeper knowledge about the role of plant hormones in mechanisms of plant-virus interactions, we have investigated the levels of several plant hormones in tobamovirus-infected pepper (*Capsicum annuum* L.) plants. Two different viruses were used. Inoculation of pepper leaves with *Obuda pepper virus* (ObPV) led to the appearance of hypersensitive necrotic lesions (incompatible interaction), while *Pepper mild mottle virus* (PMMoV) caused only very mild chlorotic symptoms (compatible interaction) (Tóbiás et al., 1989; Rys et al., 2014). The massive up-regulation of various 9-LOX genes and a divinyl ether synthase gene was revealed earlier

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