BIOLOGIA PLANTARUM 53 (1): 195-199, 2009

BRIEF COMMUNICATION

# Multiple hormone analysis indicates involvement of jasmonate signalling in the early defence of potato to potato virus $Y^{NTN}$

M. KOVAČ*[1], A. MÜLLER**, D. MILOVANOVIČ JARH*, M. MILAVEC*, P. DÜCHTING** and M. RAVNIKAR*

*Department of Plant Biotechnology and Systems Biology, National Institute of Biology, Večna pot 111, SI-1000 Ljubljana, Slovenia**
*Lehrstuhl fűr Pflanzenphysiologie, Ruhr-Universität Bochum, Universitätsstr. 150, D-44801 Bochum, Germany***

## Abstract

The involvement of plant hormones in the very early response of plants to virus infection was studied in potato plants (*Solanum tuberosum* L.) infected with potato virus $Y^{NTN}$ ($PVY^{NTN}$). Endogenous plant hormones and compounds mediating a stress response (JA - jasmonic acid, OPDA - 12-oxo phytodienoic acid, SA - salicylic acid, IAA - indole-3-acetic acid, ABA - abscisic acid) were simultaneously quantified in susceptible cv. Désirée and resistant cv. Santé, one and three hours after inoculation. Of the hormones analysed, only the contents of endogenous JA and its precursor OPDA changed in a way that could be clearly connected with the early resistant response. In comparison to susceptible cultivar, a much more pronounced increase of JA was detected in virus-inoculated leaves of resistant cultivar at both time points. The same trend of changes was also observed with OPDA. However, there were no significant changes of JA and its precursor in upper intact systemic leaves and roots, at either time point. These findings implicate the jasmonate signalling pathway in a very early local but not systemic resistant defence of potato to $PVY^{NTN}$.

*Additional key words:* abscisic acid, GC-MS/MS; indole-3-acetic acid, jasmonic acid, 12-oxo pytodienoic acid, salicylic acid, *Solanum tuberosum* L.

---

Plant hormones play important roles in the plant defence response to stress. In particular, abscisic acid (ABA), ethylene, jasmonic acid (JA) and salicylic acid (SA) have been shown to be involved in mediating responses to biotic and abiotic stresses (Rojo *et al.* 2003, Maksymiec and Krupa 2007, Mahdavian *et al.* 2008). The roles of the hormones in biotic stress are dependent upon the particular host-pathogen interaction.

Virus infection can cause serious inhibition of plant growth and loss of yield. There is considerable evidence that these changes are controlled in part by virus-induced alterations in plant hormone metabolism (Fraser and Whenham 1982). The ability of viruses to perturb or interfere in signalling pathways involving phytohormones provides the opportunity for them to interfere with host gene expression and affect plant growth and development (Pompe-Novak *et al.* 2006, reviewed in Whitham *et al.* 2006). Jameson and Clarke (2002) demonstrated that the effects of virus infection on the biosynthesis and metabolism of plant hormones are extremely complex. The mode of resistance to a virus by plants of one species may differ from that in another host species and it can use a different mechanism induced by a distinctly different signalling pathway.

In this study the involvement of plant hormones in plant-virus interaction was investigated in potato plants infected with the potato virus $Y^{NTN}$ ($PVY^{NTN}$) that causes the severe potato tuber necrotic ringspot disease. A few days after infection of a susceptible cultivar, the primary symptoms like chlorosis and spot necrosis develop on the infected leaves.

The involvement of plant hormones in potato-$PVY^{NTN}$

---

*Received* 16 July 2008, *accepted* 27 January 2009.
*Abbreviations*: ABA - abscisic acid; hpi - hours post inoculation; IAA - indole-3-acetic acid; JA - jasmonic acid; OPDA - 12-oxo-phytodienoic acid; SA - salicylic acid.
*Acknowledgements*: We thank Mrs. Lidija Matičič for her excellent technical support. This work was funded by the Slovenian Research Agency (P40165).
[1] Corresponding author; fax: (+386) 1 257 38 47, e-mail: maja.kovac@nib.si

interaction has been already indicated in our previous studies. The addition of exogenous 0.1 μM jasmonic acid (JA) to the growth medium reduced the content of $PVY^{NTN}$ in potatoes grown *in vitro*, indicating that JA plays a role in the potato-virus interaction (Petrovič and Ravnikar 1995). The same virus also alters the distribution and concentration of JA in potato plants grown in tissue culture (Petrovič *et al.* 1997). Analysis of endogenous cytokinins in soil-grown $PVY^{NTN}$-susceptible potato plants revealed that, four days after primary infection, the greatest changes occurred in the roots, where a shift in concentrations of biologically active free cytokinins towards the inactive 9-glucosides was observed (Dermastia *et al.* 1995). This shift was not observed in the resistant cultivar. The involvement of salicylic acid in the $PVY^{NTN}$-potato interaction was demonstrated by its induction one day post inoculation and later, when systemic symptoms appeared in a susceptible but not in a resistant cultivar (Krečič-Stres 2005).

In order to better understand the role of plant hormones in $PVY^{NTN}$-potato interaction, we studied the involvement of endogenous plant hormones in the very early responses of susceptible cv. Désirée and resistant cv. Santé to mock and virus inoculation. In infected cv. Désirée the symptoms on inoculated leaves were observed between 5 - 8 d after inoculation while virus titre reached a level detectable by ELISA in 4 - 5 d after inoculation (Mehle *et al.* 2004). In infected cv. Santé, which carries the $Ry_{sto}$ gene from *Solanum stoloniferum* (Hinrichs *et al.* 1998*)*, no symptoms appeared and the virus could not be detected by ELISA or electron microscopy (Mehle *et al.* 2004). We measured absicic acid (ABA), salicylic acid (SA), indole-3-acetic acid (IAA), jasmonic acid (JA) and its precursor 12-oxo-pytodienoic acid (OPDA) simultaneously, 1 and 3 h after inoculation. Although these plant hormones have already been shown to be implicated in some plant-virus interactions (reviewed in Jameson and Clarke 2002), this is the first simultaneous study of their involvement in the very early response of plants with different sensitivity to virus infection.

Potato plants (*Solanum tuberosum* L. susceptible cv. Désirée and resistant cv. Santé) were obtained from stem node tissue culture. The plants were grown in quartz sand in a growth chamber, with irradiance of 21.6 W $m^{-2}$ (*Osram L36W/77* lamps) for a 16-h photoperiod, a relative humidity of 75 ± 2 % and day/night temperature of 20/18 ± 2 °C. Four-week-old plants with 6 to 7 leaves were inoculated with $PVY^{NTN}$ or mock inoculated with the sap of healthy plants as described in Milavec *et al.* (2001). Intact plants were used as control. Plant hormones were analysed in roots and, separately, in three to four lower inoculated leaves and in three to four upper intact leaves. Samples were collected 1 and 3 h post inoculation (hpi) and immediately frozen in liquid nitrogen and stored at -80 °C for analysis. Tissue (0.3 g) was ground to a fine powder in liquid nitrogen, and transferred into reaction vials containing standards: 30 pmol $[^2H]_2$-indole-3-acetic acid, 50 pmol of $[^{13}C]_2$-jasmonic acid, and 100 pmol of $[^2H]_4$-salicylic acid (*Campro Scientific*, Berlin, Germany), and 30 pmol $[^2H]_5$-12-oxophytodienoic acid and 30 pmol $[^2H]_6$-abscisic acid synthesized according to Müller *et al.* (2002). 100 % MeOH (4 $cm^3$) was added and the mix was homogenized for 1 - 2 min using an *Ultra-Turrax* (6000 rpm). The homogenate was filtered (0.22 μm) and evaporated to dryness.

Endogenous contents of IAA, ABA, SA, JA, and OPDA were simultaneously quantified in MeOH extracts pre-cleaned by microscale solid-phase extraction on silica-based aminopropyl matrix (*Varian*, Darmstadt, Germany) using a multiplex GC-MS/MS (*Varian Saturn 200* ion-trap mass spectrometer connected to a *Varian CP-3800* gas chromatograph) as previously described (Müller *et al.* 2002). The endogenous contents of plant hormones quoted are mean values from 4 - 6 extracts of two experiments. The Student *t*-test was used to calculate the significant differences between intact and mock-inoculated plants and between mock- and virus-inoculated plants.

The resistance of cv. Santé to $PVY^{NTN}$ did not correlate with high basal level of plant hormones analysed (Tables 1, 2). Of the five hormones, SA predominated in both cultivars studied. These results are in accordance with the reports that potato contains higher basal level of SA than several other plants and that its high basal level is not related with resistance (Yu *et al.* 1997, Krečič-Stres *et al.* 2005).

To distinguish the processes connected specifically with infection from those associated with the procedure of inoculation, plant hormones were analyzed in intact- and mock-inoculated plants. Significant changes following mock-inoculation were observed only in old leaves. In comparison to intact plants, transient increase of JA was detected at 1 hpi in both cultivars (Tables 1, 2). A similar, but less prominent trend of changes was observed for OPDA, the precursor of JA synthesis. In contrast to cv. Santé, the increase of OPDA in cv. Désirée was even greater at 3 hpi. Unexpectedly, in mock-inoculated leaves, a significant increase of SA content was detected in cv. Santé at 1 hpi and 3 hpi, but in cv. Désirée only at a later time point. A connection of mock-inoculation with the octadecanoid pathway is expected (reviewed in Howe 2004). Mock-inoculation is a kind of mechanical wounding although the damage to the leaves was not so severe; besides, the plants sap, used for mock-inoculation contains a number of biologically active substances. Although SA is not regarded as wound signal, there is mostly indirect evidence of interactions between wounding and SA or JA (Machinandiarena *et al.* 2001, Yamada *et al.* 2004). The role of SA in early response of *Arabidopsis* to mechanical wounding was confirmed recently by Pan *et al*. (2008) who have observed multi-fold increase of endogenous SA in leaves 1 and 6 h after wounding.

Of the hormones analysed, only the contents of endogenous JA and its precursor OPDA changed in a way

Table 1. Contents of JA, OPDA, SA, IAA, ABA [pmol $g^{-1}$(f.m.)] 1 and 3 h post inoculation (hpi) in upper intact and lower inoculated leaves and in roots of resistant cv. Santé. Control is intact plant. Mean ± SE. Student's *t*-test revealed differences between intact and mock-inoculated and mock-inoculated and $PVY^{NTN}$-inoculated plants (* - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$).

| | | control | 1 hpi mock | 1 hpi virus | 3 hpi mock | 3 hpi virus |
|---|---|---|---|---|---|---|
| JA | intact leaves | 23.43 ± 13.56 | 12.09 ± 5.15 | 10.98 ± 4.96 | 31.07 ± 13.30 | 34.70 ± 18.12 |
| | inocul. leaves | 18.58 ± 10.73 | 344.60 ± 39.87*** | 1070.09 ± 156.8*** | 51.34 ± 13.31 | 187.47 ± 35.37* |
| | roots | 46.81 ± 22.54 | 24.77 ± 12.30 | 28.41 ± 17.97 | 33.27 ± 14.38 | 31.69 ± 11.56 |
| OPDA | intact leaves | 53.52 ± 31.50 | 73.19 ± 24.01 | 169.81 ± 62.34 | 46.40 ± 23.87 | 38.96 ± 23.29 |
| | inocul. leaves | 65.30 ± 33.60 | 188.94 ± 40.52* | 369.62 ± 110.94 | 77.43 ± 29.43 | 145.55 ± 25.97 |
| | roots | 88.06 ± 20.60 | 115.01 ± 16.25 | 73.27 ± 19.77 | 30.84 ± 9.67 | 40.35 ± 12.25 |
| SA | intact leaves | 3219.18 ± 1530.7 | 4268.30 ± 1460.7 | 3463.12 ± 1033.2 | 2614.68 ± 881.08 | 1788.07 ± 449.11 |
| | inocul. leaves | 1274.76 ± 318.96 | 3940.08 ± 697.31** | 4169.78 ± 528.20 | 3564.27 ± 869.35* | 4108.00 ± 1302.1 |
| | roots | 416.02 ± 195.92 | 595.77 ± 216.31 | 800.36 ± 312.65 | 330.96 ± 117.40 | 369.84 ± 133.38 |
| IAA | intact leaves | 110.72 ± 21.16 | 98.40 ± 11.30 | 99.10 ± 25.49 | 98.41 ± 13.40 | 106.31 ± 30.10 |
| | inocul. leaves | 26.98 ± 4.71 | 32.00 ± 11.46 | 16.06 ± 1.60 | 16.26 ± 0.73 | 14.06 ± 1.03 |
| | roots | 130.33 ± 19.98 | 108.68 ± 10.62 | 109.51 ± 14.30 | 69.17 ± 8.98 | 103.34 ± 11.03 |
| ABA | intact leaves | 69.93 ± 28.31 | 85.08 ± 33.41 | 87.22 ± 20.08 | 70.44 ± 16.61 | 71.23 ± 19.83 |
| | inocul. leaves | 83.73 ± 25.78 | 69.02 ± 17.04 | 60.17 ± 16.24 | 58.80 ± 12.39 | 50.19 ± 10.36 |
| | roots | 1.88 ± 1.59 | 3.59 ± 3.12 | 0.45 ± 0.45 | 3.06 ± 1.53 | 4.47 ± 1.49 |

Table 2. Contents of JA, OPDA, SA, IAA, ABA [pmol $g^{-1}$(f.m.)] 1 and 3 h post inoculation (hpi) in upper intact and lower inoculated leaves and in roots of susceptible cv. Désiréé. Control is intact plant. Mean ± SE. Student's *t*-test revealed differences between intact and mock-inoculated and mock-inoculated and $PVY^{NTN}$-inoculated plants (* - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$).

| | | control | 1 hpi mock | 1 hpi virus | 3 hpi mock | 3 hpi virus |
|---|---|---|---|---|---|---|
| JA | intact leaves | 87.23 ± 30.43 | 73.72 ± 19.90 | 34.76 ± 8.45 | 100.15 ± 35.77 | 106.54 ± 24.26 |
| | inocul. leaves | 77.04 ± 26.04 | 368.82 ± 42.47*** | 559.82 ± 66.52 | 118.49 ± 28.27 | 102.72 ± 15.22 |
| | roots | 34.33 ± 13.91 | 24.01 ± 17.05 | 37.62 ± 22.22 | 109.30 ± 22.00 | 88.46 ± 37.44 |
| OPDA | intact leaves | 28.04 ± 11.76 | 23.66 ± 4.62 | 36.53 ± 15.03 | 152.54 ± 65.96 | 33.40 ± 13.83 |
| | inocul. leaves | 18.25 ± 5.51 | 60.80 ± 10.03** | 106.81 ± 39.63 | 105.28 ± 26.52* | 95.25 ± 24.81 |
| | roots | 90.82 ± 32.44 | 137.15 ± 79.63 | 61.62 ± 35.02 | 227.53 ± 149.42 | 369.58 ± 211.65 |
| SA | intact leaves | 18968.27 ± 9843.4 | 14750.62 ± 8239.4 | 5680.83 ± 2275.7 | 6162.14 ± 3347.6 | 6678.73 ± 2881.0 |
| | inocul. leaves | 5504.00 ± 532.37 | 7247.40 ± 1184.0 | 5374.00 ± 634.22 | 11852.07 ± 1267.7** | 9391.42 ± 768.11 |
| | roots | 2476.58 ± 1526.2 | 7231.98 ± 4801.1 | 2034.84 ± 925.19 | 1217.93 ± 510.59 | 2017.48 ± 885.89 |
| IAA | intact leaves | 253.62 ± 107.35 | 144.32 ± 38.53 | 168.02 ± 58.54 | 139.51 ± 35.02 | 155.14 ± 61.77 |
| | inocul. leaves | 45.67 ± 8.55 | 59.49 ± 19.54 | 55.19 ± 8.69 | 31.38 ± 7.58 | 77.32 ± 34.16 |
| | roots | 105.71 ± 19.19 | 119.38 ± 10.62 | 196.41 ± 27.24 | 103.58 ± 13.42 | 121.96 ± 17.52 |
| ABA | intact leaves | 220.51 ± 60.61 | 167.57 ± 42.49 | 99.91 ± 16.83 | 192.19 ± 50.54 | 279.46 ± 86.94 |
| | inocul. leaves | 201.59 ± 27.38 | 229.00 ± 38.85 | 160.95 ± 23.73 | 187.39 ± 50.02 | 207.91 ± 40.81 |
| | roots | 5.14 ± 1.61 | 2.92 ± 1.69 | 1.35 ± 0.90 | 1.23 ± 0.76 | 1.79 ± 1.12 |

that could be clearly connected with the early resistant response of potato plants to infection $PVY^{NTN}$. In comparison to mock-inoculated leaves, 3 to 4-fold increase of JA was detected in virus-inoculated leaves of resistant cv. Santé at both time points, reaching the highest content at 1 hpi – 1070 pmol $g^{-1}$(f.m.). The same trend was also observed for OPDA. In the susceptible cv. Désirée the tendency of increase of JA and OPDA contents induced by infection was detected only at 1 hpi. There were no significant changes between treatments, in upper intact systemic leaves and in roots, at either time point.

Most reports have been concerned with the involvement of JA in response to wounding and to bacterial or fungal attack, and much less to viruses. In our previous study, we demonstrated that systemic $PVY^{NTN}$ infection of potato grown in tissue culture resulted in the accumulation of endogenous JA, especially obvious in

plant roots (Petrovič *et al.* 1997). Besides, JA treatment reduced endogenous JA content, most visibly in the roots of systemically infected potato plants (Petrovič *et al.* 1999). In *Phaseolus vulgaris* infected with clover mosaic potexvirus, quantitatively similar, transient increases of JA were found in both virus and water inoculated leaves within 12 hpi, which was attributed to wounding (Clarke *et al.* 2000). A second increase in JA occurred rather late, and only in virus inoculated leaves, which might, according to the authors, be too late to induce resistance. However, in the same plant-virus interaction, exogenous JA inhibited virus replication (Clarke *et al.* 1998, 2000). On the other hand, Seo *et al.* (2001) suggested that JA signal transduction is implicated during TMV infection of tobacco leaves, showing that JA accumulation preceded the appearance of hypersensitive cell death. Besides the investigations of endogenous JA, both the application of JA and the use of JA mutants have certainly implicated participation of JA in virus-induced upregulation of defence-related genes (reviewed in Jameson and Clarke 2002, Whitham *et al.* 2006).

SA has also been shown to mediate resistance in many plant-virus interactions (Murphy *et al.* 1999). However, the role of SA in pathogen defence in potato is controversial (reviewed in Halim *et al.* 2006). In contrast to JA, our data indicate that SA is not a limiting factor involved in the very early response of potato plants to $PVY^{NTN}$ infection, possibly because of the high basal SA level in potato. Accumulation of SA in other susceptible potato-$PVY^{NTN}$ interaction observed later in the plant response (1 and 11 d after infection) suggests that SA contributes to the general elevated levels of phenolic compounds as a response to stress caused by virus infection (Krečič-Stres *et al.* 2005). The present study also indicates that ABA and IAA are not implicated in early response of potato to $PVY^{NTN}$ infection although these plant hormones may play a role in defence against viruses (reviewed in Jameson and Clarke 2002, Whitham *et al. 2006*, Cluver and Padmanabhan 2007).

In conclusion this study indicates that jasmonate signalling pathway contributes to the resistance of potato to $PVY^{NTN}$. Drastic early increase of JA in inoculated leaves of resistant cutivar can therefore be considered as an endogenous signal, possibly leading to inhibition of virus replication or virus transport through the plant. In the susceptible cultivar the extent of JA and OPDA changes was probably insufficient.

## References


Clarke, S.F., Burritt, D.J, Jameson, P.E., Guy, P.L.: Influence of plant hormones on virus replication and pathogenesis-related proteins in *Phaseolus vulgaris* L. infected with white clover mosaic potexvirus. - Physiol. mol. Plant Pathol. **53**: 195-207, 1998.

Clarke, S.F., Guy, P.L., Jameson, P.E., Schmiere, D., Burritt, D.J.: Influence of white clover mosaic potexvirus infection on the endogenous levels of jasmonic acid and related compound in *Phaseolus vulgaris* L. seedlings. - J. Plant Physiol. **156**: 433-437, 2000.

Cluver, J.N., Padmanabhan, M.S.: Virus-induced disease: altering host physiology one interaction at a time. - Annu. Rev. Phytopathol. **45**: 221-243, 2007.

Dermastia, M., Ravnikar, M., Kovač, M.: Increased cytokinin-9-glucosylation in roots of susceptible *Solanum tuberosum* cultivar infected by potato virus $Y^{NTN}$. - Mol. Plant Microbe Interact. **8**: 327-330, 1995.

Fraser, R.S.S., Whenham, R.J.: Plant growth regulators and virus infection: a critical review. - Plant Growth Regul. **1**: 37-59, 1982.

Halim, V.A., Vess, A., Scheel, D., Roshal, S.: The role of salicylic acid and jasmonic acid in pathogen defence. - Plant Biol. **8**: 307-131, 2006.

Hinrichs, J., Berger, S., Shaw, J.G.: A hypersensitive response-like mechanism is involved in resistance of potato plants bearing the $Ry_{sto}$ gene to the potyviruses potato virus Y and tobacco ETCH virus. - J. gen. Virol. **79**: 167-176, 1998.

Howe, G.H.: Jasmonates as signals in the wound response. - J. Plant Growth Regul. **23**: 223-257, 2004.

Jameson, P., Clarke, S.F.: Hormone-virus interactions in plants. - Crit. Rev. Plant Sci. **21**: 205-228, 2002.

Krečič-Stres, H., Vučak, C., Ravnikar, M., Kovač, M.: Systemic potato virus $Y^{NTN}$ infection and levels of salicylic and gentisic acids in different potato genotypes. - Plant Pathol. **54**: 441-447, 2005.

Machinandiarena, M.F., Olivieri, F.P., Faleo, G.R., Oliva, C.R.: Isolation and characterization of a polygalacturonase-inhibiting protein from potato leaves. Accumulation in response to salicylic acid, wounding and infection. - Plant Physiol. Biochem. **39**: 129-136, 2001.

Mahdavian, K., Kalantari K.M., Ghorbanli M., Torkzade M.: The effects of salicylic acid on pigment contents in ultraviolet radiation stressed pepper plants. - Biol. Plant. **52**: 170-172, 2008.

Maksymiec, W., Krupa, Z.: Effects of methyl jasmonate and excess copper on root and leaf growth. - Biol. Plant. **51**: 322-326, 2007.

Mehle, N., Kovač, M., Petrovič, N., Pompe-Novak, M., Baebler, Š., Krečič Stres, H., Gruden, K., Ravnikar, M.: Spread of potato virus $Y^{NTN}$ in potato cultivars (*Solanum tuberosum* L.) with different levels of sensitivity. - Physiol. mol. Plant Pathol. **64**: 293-300, 2004.

Milavec, M., Ravnikar, M., Kovač, M.: Peroxidases and photosynthetic pigments in susceptible potato infected with potato virus $Y^{NTN}$. - Plant Physiol. Biochem. **3**: 891-898, 2001.

Müller, A., Düchting, P., Weiler, E.W.: A multiplex GC-MS/MS technique for the sensitive and quantitative single-run analysis of acidic phytohormones and related compounds, and its application to *Arabidopsis thaliana*. - Planta **216**: 44-56, 2002.

Murphy, A.M., Chivasa, S., Singh, D.P., Carr, J.P.: Salicylic acid-induced resistance to viruses and other pathogens: a parting of the ways? - Trends Plant Sci. **4**: 155-160, 1999.

Pan, X., Welti, R., Wang, X.: Simultaneous quantification of major phytohormones and related compounds in crude plant extracts by liquid chromatography-electrospray tandem mass spectrometry. - Phytochemistry **69**: 1773-1781, 2008.

Petrovič, N., Miersch, O., Ravnikar, M., Kovač, M.: Potato virus $Y^{NTN}$ alters the distribution and concentration of endogenous jasmonic acid in potato plants grown *in vitro*. - Physiol. mol. Plant Pathol. **50**: 237-244, 1997.

Petrovič, N., Miersch, O., Ravnikar, M., Kovač, M.: Relation between the endogenous jasmonic acid and decreased potato virus $Y^{NTN}$ concentration in potato treated with jasmonic acid. - Phyton **39**: 249-252, 1999.

Petrovič, N., Ravnikar, M: Interactions between jasmonic acid and potato virus $PVY^{NTN}$ in potato grown *in vitro*. - Aspects appl. Biol. **42**: 337-340, 1995.

Pompe-Novak, M., Gruden, K., Baebler, Š., Krečič-Stres, H., Kovač, M., Jongsma, M., Ravnikar, M.: Potato virus Y induced changes in the gene expression of potato (*Solanum tuberosum* L.). - Physiol. mol. Plant Pathol. **67**: 237-247, 2006.

Rojo, E., Solano, R., Sánchez-Serrano, J.J.: Interactions between signalling compounds involved in plant defense. - J. Plant Growth Regul. **22**: 82-98, 2003.

Seo, S., Seto, H., Yamakawa, H., Oaci, Y.: Transient accumulation of jasmonic acid during the synchronized hypersensitive cell death in tobacco mosaic virus-infected tobacco leaves. - Mol. Plant-Microbe Interact. **14**: 261-264, 2001.

Whitham, S.A., Yang, C., Goodin, M.M.: Global impact: elucidating plant responses to viral infection. - Mol. Plant-Microbe Interact. **19**: 1207-1215, 2006.

Yamada, K., Nishimura, M., Hara-Nishimura, I.: The slow wound-response of yVPE is regulated by endogenous salicylic acid in *Arabidopsis*. - Planta **218**: 599-605, 2004.

Yu, D., Liu, Y., Fan, B., Klessig, D.F., Chen, Z.: Is the high basal level of salicylic acid important for disease resistance in potato? - Plant Physiol. **115**: 343-349, 1997.