Plant growth promoter produced by *Trichoderma virens* and its effect on mungbean (*Vigna radiata* (L.) Wilczek) seedling

A Inayati 1, L Setyowati2, L Q Aini2 and E Yusnawan1
1 Researcher, Indonesian Legume and Tuber Crop Research Institute, Indonesia
2 Plant Protection Dept., Faculty of Agriculture, Brawijaya University, Indonesia
E-mail: alfiinayati2@gmail.com

**Abstract.** *Trichoderma virens* has great potency as promising biocontrol agents. As many as seven of *T. virens* strains which are effective to control soil borne pathogens are evaluated in this study for its capability to promote mungbean growth. *In vitro* evaluation showed that all strains were able to produce relatively high Indole-3-acetic acid (IAA) and performed effective phosphate solubilizing activity. IAA produced in Czapek dox agar varied from 5.2 μg mL⁻¹ to 71.5 μg mL⁻¹. Phosphate solubilizing activity showed after 2 days of incubation and the highest activity in plate assay was detected after 6 days after incubation. Phosphate solubilizing activity varied from 0.82 μg mL⁻¹ to 4.69 μg mL⁻¹. *In planta* study showed that *T. virens* Tv3 and Tv4 triggered the increase of IAA synthase in mungbean seedling as well as plant height and root length. A positive correlation was observed between IAA synthase of roots and several growth parameters (root fresh weight, plant height, and root length). Therefore, these two strains of *T. virens* could be suggested as plant growth promoters on mungbean.

1. **Introduction**

*Trichoderma* spp. have been known as the most widely used biological control agents due to its great capability to suppress various types of pathogens as well as to induce the resistance of host plants [1]. Recently, many studies have reported the potency of *Tricoderma* spp. as plant growth promoter besides its primary function as pathogen inhibitor. *Trichoderma* sp. can trigger plant growth and development directly by increasing the rate of plant germination, increasing plant dry weight, stimulating flowering, and increasing plant vigor which can indirectly increase the plant resistance to biotic and abiotic stresses [2, 3].

*Trichoderma* spp. promotes plant growth through various mechanisms, such as increasing the synthesis of phytohormones both from *Trichoderma* sp. and plants, producing vitamins, increasing absorption and translocation of nutrients, increasing root development, and increasing the rate of carbohydrate metabolisms, and photosynthesis [4]. Some selected *Trichoderma* spp. are able to produce phytohormones such as auxin and auxin-like secondary metabolites [5], gibberellic acid.
(GA3), ethylene [3], and to alter the balancing of auxin and cytokinins hormones [6]. A study conducted by Hoyos-Carvajal et al. [7] using 106 Trichoderma isolates showed that 60% of the isolates were able to produce IAA and auxin analogues.

*Trichoderma* spp. increase nutrient availability through its ability to solubilize inorganic phosphate (P) and convert the iron through the production of siderophores [7]. The use of phosphate-solubilizing microorganisms to help plant phosphorus absorption is promising sustainable strategy for managing P deficiencies in agricultural soils and increasing the efficiency of fertilizer absorption [2, 8]. The ability of fungi such as *Trichoderma* sp. to occupy wider space and range within the soil and plants as well as its ability to produce a variety of organic acids supported its capability as plant growth promoter [6, 9].

*T. virens* is one of the most common *Trichoderma* species found on rhizosphere of various crops in East Java, Indonesia, besides *T. asperellum* and *T. harzianum*. Our previous study showed that T. virens was effective to control soil borne pathogens such as *Rhizoctonia solani* (R.s1), *R. solani* (R.s2), and *Fusarium* sp. on dual culture assay [10]. However, the ability of indigenous *T. virens* to promote mungbean growth is still rarely reported. Mungbean is one of the important legume crops in Indonesia; unfortunately, this crop is relatively susceptible to soil-borne diseases such as *R. solani*, *Sclerotium rolfsii*, and *Fusarium* sp. [11] and the use of *T. virens* as biological control as well as plant growth promoter is quite promising. Considering the great potency of *T. virens*, this present study aims to evaluate plant growth promoter potential of *T. virens* *in vitro* and *in planta*. The production of IAA and P solubilizing ability of *T. virens* on specific media and its plant growth promoter potential on mungbean seedling were observed. The application of beneficial microorganism as bio-control agents as well as a bio-fertilizer offers promising opportunity to support sustainable agriculture.

2. Materials and method

2.1. Evaluation of plant growth promoting activities from *T. virens* *in vitro*

2.1.1. Fungal strains

Seven strains of *T. virens* isolates were provided by Mycology laboratory of Indonesian Legumes and Tuber Crops Research Institute (ILETRI), Malang, Indonesia. The isolates were maintained in potato dextrose agar (PDA) before used.

2.1.2. Determination of IAA produced by *T. virens*

The ability of *T. virens* to produce IAA in vitro was tested following the procedure from Yadav et al.,[12]. Seven strains of *T. virens* were grown on Czapek-dox broth media, supplemented with L-tryptophan (1 ml L\(^{-1}\)). The culture was then incubated at room temperature for 5 days. Five ml of filtrate was centrifuged at 3000 rpm for 5 minutes then 1 ml of the filtrate was added to 3 ml of Salkowski reagent. Positive reaction was indicated by the changes of culture color from clear yellow into red.

IAA concentrations produced by *T. virens* strains were measured following a method from Yadav et al. (2011) with slight modification. Seven strains of *T. virens* were grown on Czapek Broth media and incubated at room temperature for 7 days. Filtrate from fungal culture was used as a crude enzyme extract. The reaction was measured by mixing 1.5 ml of enzyme extract with 3 ml of Salkowski reagent and then incubated for 30 minutes before to be read at a wavelength of 530 nm.
2.1.3. Determination of Phosphate solubilization activity by T. virens

For qualitative estimation of phosphate solubilization ability, *T. virens* strains were cultured on Pikovskaya (PVK) media following the procedures from Zehra et al.,[13]) with slight modification. Three mycelial disks (d= 5 mm) were grown on PVK media without glucose and incubated at room temperature. A positive reaction represented by the formation of halo around the colony was monitored. The formation of clear zones after 2, 4, until 10 days were observed to determine the phosphate solubilization index. Solubilization index was calculated using following formula [14]:

\[
\text{PSI} = \frac{\text{colony diameter} + \text{halo diameter}}{\text{colony diameter}}
\]

Phosphate solubilization activity from *T. virens* strains on the media was quantitatively determined by ascorbic acids method Watanabe and Olsen [15]. Trichoderma was grown on liquid Pikovskaya media for 14 days with periodically shaking. Phosphatase from the filtrate was then extracted with ammonium bicarbonate-diethylene triamine pentaacetic acid (AB-DTPA). The enzyme reactions were measured by mixing 1 ml of extract with 9 ml of H\(_2\)O and 1.6 ml of coloring reagent consisting of 5N H\(_2\)SO\(_4\), 0.324 g K(SbO)C\(_6\)H\(_4\)O\(_6\).1/2 H\(_2\)O, 4 g (NH\(_4\))\(_2\) Mo\(_7\)O\(_24\) and 1.76 g ascorbic acid. The reaction mixture was then incubated for 5 minutes before measured with a spectrophotometer at 880 nm. Available phosphorus in growth media was calculated against KH\(_2\)PO\(_4\) standard curve [16].

2.2. Evaluation of plant growth promoting activities from *T. virens* in planta

2.2.1. Green house experiment

Sampeong cultivar, was grown in sterile soil. Before planted, seeds were sterilized with 0.5% NaOCl and rinsed with sterile distilled water twice. The seeds were then dipped into *T. virens* suspension at concentration of 106 CFU/g for 30 minutes. Two strains of *T. virens* (Tv3 and Tv4) were used as inoculants and for the control, mungbean seeds were dipped into sterile water before planted. All plants were harvested at 14 and 21 days after planting for observation.

2.2.2. Production of IAA-synthase and IAA-oxidase in planta

IAA-synthase and IAA-oxidase were determined using Phepl and Sequiera method [17] with modification. Enzyme was prepared by finely ground of 0.5 g of plant tissue (leaves and roots) then the samples were added with 5 ml of 0.05 M phosphate buffer saline, pH 5.8. For IAA-synthase, the reaction mixture containing 500 μl extract, 50 μl MnCl\(_2\), 10 μl MgSO\(_4\), 1500 μl PBS, and 500 μl L-tryptophan was mixed. The mixture was incubated at 37 °C for 30 min. The reaction was started by adding 2.5 ml of Salkowski reagent and incubated at room temperature for 15 minute to develop stable pink color and the absorbance was read at 530 nm. The activity was expressed as μg IAA produced per minutes per gram of tissue fresh weight.

IAA-oxidase reaction consisted of 500 μl extract, 50 μl MnCl\(_2\), 1500 μl PBS, and 500 μl IAA. The mixture was incubated at 37 °C for 60 min and the reaction was started by adding Salkowski reagent. The absorbance was read at 530 nm. The enzyme activity was expressed as μg IAA produced per minutes per gram of tissue fresh weight.

3. Results and Discussion

An *in vitro* assay showed that all strains were able to produce IAA in Czapek-Dox Broth media supplemented with L-tryptophan. Qualitative measurement showed variability in IAA production between strains as represented by different color intensity produced by each strain (Figure 1). The Tv1, Tv2, and Tv5 strains exposed darker color compared to other four strains which were suggested produce higher IAA.
Quantitative measurements using a spectrophotometer showed that \textit{T. virens} strains were able to produce relatively high IAA in media. The strains produced IAA varied from 5.2 to 71.5 \( \mu \text{g mL}^{-1} \) (Figure 2). Strain of Tv7 showed the highest IAA synthesis activity. This strain produced IAA 14-folds higher than strains of Tv5 which presented the lowest IAA synthase activity. The study conducted by Bader et al. [18] showed that \textit{Trichoderma} spp. produced IAA from 7.19 to 21.14 \( \mu \text{g ml}^{-1} \). However, other studies reported that \textit{Trichoderma} sp. was able to synthesize IAA up to 93.73 \( \mu \text{g / ml} \) [19].

This present study showed that the production of IAA was strain dependent, however, other external factors also associated with IAA synthesis. IAA biosynthesis in fungi mostly depends on L-tryptophan as a precursor; therefore the addition of tryptophan to the media is crucial [20]. Other external factors such as media composition; carbon sources, nitrogen sources, temperatures, and pH also affect IAA production by \textit{Trichoderma} sp. [21].

IAA is one of phytohormones that support plant growth especially in root growth and development. IAA and auxin-like compound could be produced by plants and by soil microbes including \textit{Trichoderma} species [22]. IAA produced by microbes was reported to be able to stimulate plant growth directly and indirectly by balancing other phytohormones such as gibberellic acid (GA3) in plants [3]. Therefore, it would be very meaningful to apply Trichoderma strains which are effective to suppress plant pathogens as well as to stimulate plant growth.
*T. virens* strains have the ability to solubilize inorganic phosphorus (Ca₃PO₄) supplemented in media *in vitro*. Phosphate solubilizing activity of *T. virens* varied among strains (Figure 3). All strains performed clearing zone around the culture after 48 h (2 days) due to the use of phosphate source in the media during *T. virens* growth. *Trichoderma* spp. and most microorganism could dissolve phosphorous compound in media through the production of phosphatase enzymes, including phytase which was able to hydrolyze an organic phosphate and to change it from into soluble inorganic forms such as orthophosphate that was easier to be absorbed by root plants [14, 23-25].

![Image of T. virens strains](image-url)
Figure 3. Phosphate solubilizing activity of *T. virens* in Pikovskaya medium, (a) 2 day, (b) 4 day, and (c), and 6 days of incubation

Most of the strains performed the highest solubilizing activity after 6 days of incubation. However, other strains need longer incubation period; for example Tv6 stains needs 10 days to perform the maximum solubilizing activity. The diameter of the clear zone formed by the *T. virens* strain at 2 days ranged from 5.12 mm to 6.94 mm and the highest activity was shown by Tv7 (15.76 mm) strain at 6 days of incubation. The potential isolate showed high phosphate solubilizing activity (halo diameter was greater than 10 mm) and relatively short incubation period [26]. In this study, three strains i.e. strain Tv2, Tv4, and Tv7, performed high solubilizing activity which were showed by halo diameter was wider than 10 mm at 4 days of incubation, which would be proposed as potential strains.

The highest PSI at sixth days of incubation was shown by Tv7 strain (2.25), while the lowest PSI showed by strain Tv1 (1.55) (Tabel 1). In general, phosphate solubility index increased along with incubation period, suggesting that several *T. virens* need certain time and inoculum density to perform the maximum activity.

### Table 1. Phosphate solubilization index (PSI) from *T. virens* strains

| Strain | PSI at 2,3,...10 days of incubation |
|--------|------------------------------------|
|        | 2        | 3        | 4        | 6        | 10       |
| Tv1    | 1.46 ±0.08<sup>ab</sup> | 1.53±0.06<sup>b</sup> | 1.55±0.10<sup>c</sup> | 1.77±0.30<sup>bc</sup> | 1.61±0.08<sup>b</sup> |
| Tv2    | 1.61 ±0.19<sup>ab</sup> | 1.63±0.12<sup>b</sup> | 1.62±0.22<sup>bc</sup> | 1.58±0.16<sup>c</sup> | 1.71±0.14<sup>b</sup> |
| Tv3    | 1.52 ±0.22<sup>ab</sup> | 1.76±0.34<sup>ab</sup> | 1.95±0.42<sup>ab</sup> | 2.00±0.26<sup>ab</sup> | 2.15±0.09<sup>a</sup> |
| Tv4    | 1.69 ±0.06<sup>a</sup> | 1.73±0.16<sup>b</sup> | 1.62±0.08<sup>bc</sup> | 1.53±0.02<sup>c</sup> | 1.68±0.13<sup>b</sup> |
| Tv5    | 1.64 ±0.04<sup>ab</sup> | 1.49±0.02<sup>b</sup> | 1.84±0.07<sup>bc</sup> | 1.93±0.19<sup>ab</sup> | 1.87±0.45<sup>ab</sup> |
| Tv6    | 1.41±0.09<sup>b</sup> | 1.49±0.09<sup>b</sup> | 1.67±0.09<sup>bc</sup> | 1.77±0.13<sup>bc</sup> | 1.94±0.34<sup>ab</sup> |
| Tv7    | 1.51±0.19<sup>ab</sup> | 2.04±0.15<sup>a</sup> | 2.25±0.15<sup>a</sup> | 2.13±0.09<sup>a</sup> | 2.13±0.20<sup>a</sup> |

PSI- Phosphate solubilization index (PSI).
Numbers followed by the same letters are not significantly different (LSD, α = 0.05).

Phosphate solubilizing activity of *T. virens* strains was measured using colorimetric Molybdate blue methods. The result showed that phosphate solubilization activity from *T. virens* at 14 days of incubation varied between 0.82 μgM<sup>-1</sup>L and 4.69 μgM<sup>-1</sup>L (Figure 4). The Tv5 and Tv7 strains were performed higher P solubilizing activity, which could solubilized 4.61 μgM<sup>-1</sup>L and 4.69 μgM<sup>-1</sup>L P in medium, while Tv3 showed the lowest activity which solubilized P less than 1 μgM<sup>-1</sup>L.
Figure 4. Concentrations of soluble phosphorous solubilized by *T. virens* strain in Phikovskaya media after 14 days of incubation

The *Tv7* strain showed the highest P solubilizing activity both in qualitative and quantitative measurements, however other strains showed inconsistent performance on different evaluation methods, which was suggesting a low correlation between qualitative and quantitative measurement (R=0.59). The ability of *Trichoderma* sp. to solubilize phosphate in the media varied depending on *Trichoderma* strains, the source of phosphorous compounds, and environmental factors [25].

Although there is no comprehensive explanation about the mechanism of phosphate solubilizing microorganism in suppressing pathogens simultaneously, many studies which show the ability of microbes to solubilize phosphate in soil have positive correlation with its ability as plant growth promoter as well as an effective pathogen suppressor [26, 27]. It can be suggested that *Trichoderma* species which have the ability to produce phytase have a great opportunity to be developed as promising bio-fertilizer or plant growth promoter agents.
An application of \textit{T. virens} on mungbean seeds was increased the total biomass and shoot as well as root fresh weight at 14 days after planting. However, there was no significant increase on mungbean biomass on inoculated seeds at 21 days old seedling compared to the control plant (Figure 5).

\textbf{Figure 5.} Mungbean seedling growth treated with \textit{T. virens} in sterile soil, (a) average of total fresh weight, root and shoot fresh weight at 14 days, (b) average total fresh weight, root and shoot fresh weight at 14 days, (c) plant height, and (d) root length

Plant height and root length were slightly increased on inoculated plants which suggested that \textit{T. virens} started to promote mungbean growth at early stage of the growth. Numerous studies reported that \textit{Trichoderma} spp. could improve plant growth and development through production of growth hormones such as IAA and GA3 [22], however, some studies mention that \textit{Trichoderma} application has no effect on root growth and development [5, 28]. In this present study, the growth promotion effect of \textit{T. virens} was not clearly identified.
*T. virens* treatment on mungbean seeds increased the synthesis of IAA both in roots and leaves compared to the un-inoculated seedling (Figure 6). However, IAA oxidase activity in mungbean seedling was not significantly affected by *T. virens* treatment.

![Figure 6. Concentrations of IAA-synthase (μg mL⁻¹) and IAA-oxidase (μg mL⁻¹) in root and leaves mungbean seedling treated with *T. virens* strains *in planta*](image)

Our study showed that IAA oxidase detected in leaves and root of mungbean seedling in treated plant was similar to that of untreated plants. The Tv3 strain induced IAA synthase on mungbean leaves of 2.5 folds higher than that of control while the Tv4 strain only increased 1.6 folds. In contrast, Tv4 strain could induce greater IAA synthase on mungbean roots compared to that of Tv3 strain. Positive correlations were observed between IAA synthase on roots and root fresh weight (R=0.76), plant height (R=0.98), and root length (R=0.92). However, the correlation between IAA productions in leaves with the growth parameters was mostly negative; indicating that the induction of IAA synthase by *T. virens* in mungbean leaves was not directly correlated with plant growth promotion.

4. Conclusion

Indigenous *T. virens* had great potency as a plant growth promoter due to their ability to synthesize IAA and to produce phosphate solubilizing enzymes *in vitro*. The Tv7 strain showed the highest IAA synthesis ability and had ability to solubilize phosphorous efficiently. An *in planta* study showed that *T. virens* strains of Tv3 and Tv4 increased IAA synthesis in mungbean seedling as well as promoted its growth. Therefore, those strains were promising to be further investigated as an effective bio-control agent which was able to stimulate mungbean growth.

Acknowledgment

The author would like to thank Indonesian Agency for Agricultural Research and Development (IAARD) for financial supporting of this research and Yulius Eko Laxmana Samba for his assistance in instrument preparation.
References

[1] Singh, B., et al., *Trichoderma harzianum* elicits induced resistance in sunflower challenged by *Rhizoctonia solani*. *Journal of Applied Microbiology*, 2014. 116(3): p. 654-666.

[2] Shoresh, M. and G.E. Harman, Differential expression of maize chitinases in the presence or absence of *Trichoderma harzianum* strain T22 and indications of a novel exo-endoheterodimeric chitinase activity. *BMC plant biology*, 2010. 10(1): p. 136.

[3] Stewart, A. and R. Hill, *Applications of Trichoderma in plant growth promotion*, in Biotechnology and biology of Trichoderma. 2014, Elsevier. p. 415-428.

[4] Harman, G.E., Multifunctional fungal plant symbionts: new tools to enhance plant growth and productivity. *New Phytophysiology*, 2011. 189(3): p. 647-649.

[5] Contreras-Cornejo, H.A., et al., *Trichoderma virens*, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in Arabidopsis. *Plant physiology*, 2009. 149(3): p. 1579-1592.

[6] Martinez-Medina, A., et al., Phytohormone Profiles Induced by Trichoderma Isolates Correspond with Their Biocontrol and Plant Growth-Promoting Activity on Melon Plants. Vol. 40. 2014.

[7] Hoyos-Carvajal, L., S. Orduz, and J. Bissett, Growth stimulation in bean (*Phaseolus vulgaris* L.) by Trichoderma. *Biological Control*, 2009. 51(3): p. 409-416.

[8] Khan, M.S., et al., Plant growth promotion by phosphate solubilizing fungi–current perspective. *Archives of Agronomy and Soil Science*, 2010. 56(1): p. 73-98.

[9] Shoresh, M., G.E. Harman, and F. Mastouri, Induced systemic resistance and plant responses to fungal biocontrol agents. *Annual Review of Phytopathology*, 2010. 48: p. 21-43.

[10] Yunsawan, E., A. Inayati, and Y. Baliadi, Isolation of antagonistic fungi from rhizospheres and its biocontrol activity against different isolates of soil borne fungal pathogens infected legumes. *Biodiversitas Journal of Biological Diversity*, 2019. 20(7): p. 2038-2054.

[11] Rahayu, M., Pathology and the seed health testing techniques of legumes. *Buletin Palawija*, 2016. 14(2): p. 78-88.

[12] Janardan, Y., J.P. Verma, and K.N. Tiwari, Plant growth promoting activities of fungi and their effect on chickpea plant growth. *Asian Journal of Biological Sciences*, 2011. 4(3): p. 291-299.

[13] Zehra, A., et al., Effect of different environmental conditions on growth and sporulation of some Trichoderma species. *Journal of Environmental Biology*, 2017. 38(2): p. 197.

[14] Alam, S., et al., In vitro solubilization of inorganic phosphate by phosphate solubilizing microorganisms (PSM) from maize rhizosphere. *J Int J Agric Biol*, 2002. 4(4): p. 454-458.

[15] Watanabe, F. and S. Olsen, Test of an ascorbic acid method for determining phosphorus in water and NaHCO₃ extracts from soil. *Soil Science Society of America Journal*, 1965. 29(6): p. 677-678.

[16] Desbois, A.P. and V.J. Smith, Antibacterial free fatty acids: activities, mechanisms of action and biotechnological potential. *Applied microbiology and biotechnology*, 2010. 85(6): p. 1629-1642.

[17] Phelps, R.H. and L. Sequeira, Synthesis of indoleacetic acid via tryptamine by a cell-free system from tobacco terminal buds. *Plant physiology*, 1967. 42(8): p. 1161.

[18] Bader, A.N., et al., Native *Trichoderma harzianum* strains from Argentina produce indole-3 acetic acid and phosphorus solubilization, promote growth and control wilt disease on tomato (*Solanum lycopersicum* L.). *Journal of King Saud University-Science*, 2020. 32(1): p. 867-873.

[19] Ng, L., et al., Potential of Trichoderma spp. as biological control agents against Bakanae Pathogen (*Fusarium fujikuroi*) in Rice. 2015. 9(2): p. 46-58.

[20] Hilbert, M., et al., Indole derivative production by the root endophyte *Piriformospora indica* is not required for growth promotion but for biotrophic colonization of barley roots. *J New Phytophysiology*, 2012. 196(2): p. 520-534.
[21] Nieto-Jacobo, M.F., et al., Environmental Growth Conditions of *Trichoderma* spp. Affects Indole Acetic Acid Derivatives, Volatile Organic Compounds, and Plant Growth Promotion. *Frontiers in Plant Science*, 2017. 8(102).

[22] Zhang, S., Y. Gan, and B. Xu, Mechanisms of the IAA and ACC-deaminase producing strain of *Trichoderma longibrachiatum* T6 in enhancing wheat seedling tolerance to NaCl stress. *J BMC plant biology*, 2019. 19(1): p. 22.

[23] Chagas, L.F.B., A.F.C. Junior, and H.G. de Castro, Phosphate Solubilization Capacity and Indole Acetic Acid Production By *Trichoderma* Strains for Biomass Increase on Basil and Mint *Plants Brazilian Journal of Agriculture-Revista de Agricultura*, 2017. 92(2): p. 176-185.

[24] Hidayat, B.J., N.T. Eriksen, and M.G. Wiebe, Acid phosphatase production by *Aspergillus niger* N402A in continuous flow culture. *FEMS microbiology letters*, 2006. 254(2): p. 324-331.

[25] Promwee, A., Role of *Trichoderma* spp. as phosphate solubilizing microorganism. *J Thai Journal of Soils Fertilizer*, 2011. 33(1): p. 17-30.

[26] Bononi, L., et al., Phosphorus-solubilizing *Trichoderma* spp. from Amazon soils improve soybean plant growth. *J Scientific Reports*, 2020. 10(1): p. 1-13.

[27] Shentu, X., et al., Antifungal activity of metabolites of the endophytic fungus *Trichoderma brevicompactum* from garlic. *Brazilian Journal of Microbiology*, 2014. 45(1): p. 248-254.

[28] Tucci, M., et al., The beneficial effect of *Trichoderma* spp. on tomato is modulated by the plant genotype. *Molecular Plant Pathology*, 2011. 12(4): p. 341-354.