Conditions That Increase Latent Infection of Grafted or Non-grafted Tomatoes with *Pseudomonas solanacearum*

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Abstract

Seedling roots of the susceptible tomato cultivar Ponderosa and the resistant rootstock cultivars LS-89 and BF-Okitsu 101, Ponderosa or LS-89 scions grafted on Ponderosa or LS-89 rootstocks were inoculated with *Pseudomonas solanacearum*. At 14 days after inoculation, seedlings were indexed for disease severity and harvested to recover the bacterial pathogen from stem tissues. Many of the resistant and susceptible seedlings did not show wilting symptoms but were latently infected with *P. solanacearum*. As plant age at the time of inoculation increased, and inoculum concentration or incubation temperature decreased, the frequency of latent infection and wilting decreased. In LS-89, plants grown at 25/20°C (day/night) showed almost no symptoms but had latent infection at 20-75%. Against five strains of *P. solanacearum*, the percentage of wilting and latent infection of seedlings was not different in Ponderosa or LS-89, but it was significantly different in BF-Okitsu 101. Both Ponderosa and LS-89 scions grafted on Ponderosa had nearly all wilted. However, Ponderosa scions grafted on LS-89 wilted at nearly 60%, whereas LS-89 scions grafted on LS-89 showed no wilting. Sixty-nine percent of these symptomless LS-89 scions and 35% of the symptomless Ponderosa scions did have latent infections. These results indicated that bacterial wilt of susceptible scions grafted on resistant rootstocks was due to a movement of the pathogen from latently infected rootstocks into the scions.

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Key words: *Pseudomonas solanacearum*, tomato, resistance, rootstock, latent infection, grafts.

INTRODUCTION

Bacterial wilt caused by *Pseudomonas solanacearum* is a major constraint on the production of solanaceous crops in tropical, subtropical, and some warm temperature regions worldwide⁹⁾. Control of the disease with chemicals³⁾ and crop rotation⁵⁾ is ineffective, because the pathogen is particularly well adapted for surviving in the soil and rhizosphere^{6,19,27)}. The use of cultivar resistance, therefore, is the most effective means of control¹²⁸⁾.

Resistance to *P. solanacearum* in tomato is controlled by many genes, most of which are recessive³¹⁾. However, no fresh market tomato cultivar possesses both high resistance as well as high fruit quality¹⁷⁾. To manage bacterial wilt, susceptible but high quality tomato cultivars have been grafted on resistant rootstocks. For this purpose, several highly resistant rootstock cultivars have been developed in Japan^{17,32)} and elsewhere²⁹⁾.

Bacterial wilt has been reported in susceptible tomato cultivars grafted on resistant rootstocks^{22,26,33)}. The disease in scions has been attributed to bacterial infection through wounds in scions produced during various farming practices^{13,14,18)}, increase in pathogen virulence to resistant rootstocks^{1,12,21,23,26)}, or local environmental

and climatic conditions such as high ambient temperature^{12,16,30)}.

Prior *et al.*²⁴⁾ reported latent infections of resistant tomato plants. However, the relationship between such latent infections in rootstocks and the development of wilting symptoms in scions remains obscure.

The present study reports the recovery of *P. solanacearum* from stems of non-symptomatic tomato seedlings or scions with various resistances after root-inoculation and examines the effects of inoculum concentration, temperature, plant age and rootstocks on the development of symptomless infections.

MATERIALS AND METHODS

Plants. Two resistant tomato cultivars, LS-89 (*Lycopersicum pimpinellifolium*), a selection from Hawaii 7998³²⁾, and BF-Okitsu 101 (*L. esculentum*), a selection from NC1953-64N²⁵⁾, and a susceptible cultivar Ponderosa (*L. esculentum*) were used. LS-89 and BF-Okitsu 101 have been used as rootstocks in Japan³²⁾. Tomato seedlings were grown individually in peat moss pellets (Jiffy-9, 50 mm single, Jiffy Products Ltd.) in a greenhouse under 25±5°C before use. Plant age at the time of inoculation was indicated by the number of leaves on the plant.

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Bacteria. Five bacterial strains of *P. solanacearum*, 8107 (biovar IV), 8225 (III), 8231 (I), 8257 (II) and 8266 (IV), were selected from the collection at Chugoku National Agricultural Experiment Station. They were originally isolated from diseased solanaceous plants in Japan and are highly pathogenic to a number of susceptible tomato cultivars²²). Cultures were stored in 100 g skimmed milk, 10 g Na-glutamate per liter of distilled water at -20°C to avoid possible development of avirulent mutants. Prior to inoculation, the stock culture was defrosted and streaked on the selective agar medium of Hara and Ono⁹) and incubated at 30°C for 48 hr. Bacteria in virulent colonies¹⁰) were collected using a plastic spatula and suspended in distilled water to a concentration of 10^5 to 10^8 cfu/ml by means of a colorimeter (Spectronic 20, Bausch & Lomb).

Inoculation and incubation. Tomato seedlings were inoculated by trimming lateral roots extending from the peat moss pellets, then immersing the pellets in the bacterial suspension in a plastic container ($34 \times 24 \times 15$ cm) for 24 hr in a growth chamber under 30,000 lux light intensity for 12 hr per day at either $30/25^{\circ}\text{C}$ or $25/20^{\circ}\text{C}$ (day/night). Inoculated plants were grown in a

plastic container in the growth chamber. To determine the effects of temperature, plant age and inoculum concentration on infection, nine to 12 plants each of Ponderosa, LS-89 or BF-Okitsu 101 seedlings at the 4-5, 6-7, or 8-9 leaf stage were inoculated with *P. solanacearum* 8107 at concentrations of 10^5 to 10^8 cfu/ml and grown under $30/25^{\circ}\text{C}$ or $25/20^{\circ}\text{C}$ for 14 days. The experiment was repeated four times. To compare percentage infection of *P. solanacearum* strains, Ponderosa, LS-89 and BF-Okitsu 101 seedlings at the ten-leaf stage were inoculated with five strains of *P. solanacearum* at 10^7 cfu/ml and kept at $30/25^{\circ}\text{C}$ for 14 days. The experiment was repeated three times. Seedlings of the three cultivars mock-inoculated with distilled water served as the control.

Recovery of bacterial pathogens from stems of non-symptomatic plants.

At 14 days after inoculation, seedlings were indexed for disease severity by giving weights of 4 to 1 for severe to mild wilting and a weight of 0 for no symptoms following the system of Winstead and Kelman³⁰). Non-symptomatic plants were each examined for possible latent infection as follows: 1 cm of the stem below the cotyledon was cut and macer-

Fig. 1. Percentage of wilted or latently infected seedlings and their disease severity index in Ponderosa, LS-89 and BF-Okitsu 101 14 days after root-inoculation with 10^5 to 10^8 cfu/ml *Pseudomonas solanacearum* 8107 at the 4-5, 6-7, or 8-9 leaf stages and grown at $30/25^{\circ}\text{C}$ or $25/20^{\circ}\text{C}$ (day/night). *: Leaf stage at the time of inoculation, ▨: Latently infected seedlings (%), □: Wilted seedlings (%), ●: Disease index.

ated in a test tube (1.5 cm in diameter and 10.5 cm long) using an aluminum stick with 3 ml sterile distilled water. After incubating the test tube at 5°C for 12 hr, 100 μ l of the tissue suspension was placed onto the selective agar medium and cultured at 30°C for 48 hr. Virulent colonies were distinguished by their white or pale red-fluidal appearances from other bacterial colonies on the agar medium⁸⁾. Plants that showed no wilting symptoms but gave positive recovery were considered latently infected.

Effect of rootstocks on latent infection of scions with *P. solanacearum*. Based on the results on the effects of temperature, plant age and inoculum concentration on seedling infection, twelve plants each of Ponderosa and LS-89 were selected and prepared for scion/rootstock combinations of LS-89 (LS)/Ponderosa (Pon), Pon/LS, LS/LS and Pon/Pon. Grafting was performed using two- or three-leaf stage rootstocks and scions. Rootstocks were topped below their cotyledon, and the cuttings were used as scions. With the graft supported by a ceramic pin (Tsugi-pin, Takii & Co., Ltd.), the plants were placed in a humid room (100% relative humidity, 28°C) for two days, then in a shaded house for five days. Grafted plants were root-inoculated at the 6-7 leaf stage as described above with *P. solanacearum* 8107 at 10^7 cfu/ml and kept in 25/20°C for 14 days. Seven and 14 days after inoculation, plants were scored for percentage wilting and disease severity. At 14 days, rootstock stems were excised and macerated for pathogen recovery. Plants of each scion/rootstock combination mock-inoculated with distilled water served as the control. The experiment was repeated four times.

Statistical analysis. The Fisher's exact probability test and the Kruskal-Wallis test were used in analysis on wilting and pathogen recovery, and disease severity index respectively.

RESULTS

Detection of pathogens in susceptible and resistant tomato seedlings without symptoms

In susceptible Ponderosa, most inoculated plants showed severe wilting regardless of leaf stage at the time of inoculation and subsequent growth temperature conditions, except when plants were inoculated at 10^5 or 10^6 cfu/ml (Fig. 1). When inoculated at 10^5 or 10^6 cfu/ml, 20-95% of plants did not show symptoms. Pathogen was recovered from 15-44% of those non-symptomatic plants, indicating their latent infection with the bacteria.

In resistant LS-89, percentage wilting of plants inoculated at 4-5 leaf stage with 10^5 to 10^8 cfu/ml was higher than 90% when inoculated plants were grown at 30/25°C, but zero when such plants were grown at 25/20°C (Fig. 1). Wilting of plants inoculated at 6-7 or 8-9 leaf stage and grown at 30/25°C decreased when inoculum concentration was lowered. Generally, infected LS-89 plants scored lower severity indices than those in Ponderosa ($p < 0.05$, Kruskal-Wallis test), even under

conditions where the percentage wilting reached to nearly 100%. The percentage of latently infected plants was 20-75% when inoculated plants were grown at 25/20°C. Plants grown at 30/25°C showed no latent infection when inoculated at the 4-5 leaf stage, but latent infection at 6-41% at the 6-7 leaf stage and at 26-45% at the 8-9 leaf stage.

In BF-Okitsu 101, percentage wilting and latent infection of inoculated plants grown at 30/25°C were similar to those in LS-89 (Fig. 1). At 25/20°C, the percentage of wilted plants was higher than 90%, when plants at the 4-

Fig. 2. Percentage of wilted or latently infected seedlings and their disease severity index in Ponderosa, LS-89 and BF-Okitsu 101 14 days after root-inoculation at ten leaf stage with five strains of *Pseudomonas solanacearum* (10^7 cfu/ml) and grown at 30/25°C (day/night). *: Values followed by different letters in the same column differed significantly in latent infection and wilting at the 0.5% level (Fisher's exact probability test), ▨: Latently infected seedlings (%), □: Wilted seedlings (%), ■: Disease index.

Table 1. Percentage wilting and disease severity index of scions 7 and 14 days after rootstocks at the 6-7 leaf stage were root-inoculated with *Pseudomonas solanacearum* 8107^{a)} and percentage of scions having the pathogen recovered from stems at 14 days

Cultivars ^{b)} (scion/ rootstock)	7 days		14 days			
	Wilted scions (%)	Disease index	Wilted scions (%) (A)	Disease index	Scions (%) with bacteria recovered (B)	Latent infection (%) (B-A)
LS/LS	0 a ^{c)}	0 a	0 a	0 a	68.8 a	68.8
Pon/LS	29.2 b	13.5 a	58.3 b	29.2 b	93.8 b	35.3
LS/Pon	91.6 c	68.8 b	91.7 c	83.9 c	100 b	8.3
Pon/Pon	81.8 c	62.5 b	100 c	78.6 c	100 b	0

a) Root-inoculation with 10⁷ cfu/ml and grown at 25/20°C (day/night).

b) LS=LS-89, Pon=Ponderosa.

c) Values followed by different letters in the same column differed significantly in wilted scions or scions (Fisher's exact probability test) at the 0.83% level, and disease index (Kruskal-Wallis test) at the 5% level.

5 or 5-6 leaf stage were inoculated at 10⁸ cfu/ml. The percentage of wilting and latent infection of plants inoculated at the 4-5, 6-7 or 8-9 leaf stage decreased when the inoculum concentration was lowered. Plants inoculated at the 8-9 leaf stage showed no symptoms but had latent infection at 10-40%.

Effect of *P. solanacearum* strains on latent infection of seedlings

Regardless of the bacterial strain used, 80-100% of inoculated Ponderosa plants severely wilted by 14 days after inoculation (Fig. 2). In LS-89 and BF-Okitsu 101, plants inoculated with the five strains showed wilting at 5-15%. Latent infection in non-symptomatic LS-89 and BF-Okitsu 101 plants was 20-80% with the five strains. The percentage of wilting and latent infection of seedlings was significantly different in BF-Okitsu 101 against the five strains ($p < 0.005$, Fisher's exact probability test), but it was not significant in Ponderosa and LS-89 against the same strains.

Effect of rootstocks on latent infection of scions

Table 1 shows percentage wilting and disease severity index of scions grafted on homologous or heterologous rootstocks at 7 and 14 days after inoculation. After 14 days, both LS-89 and Ponderosa scions grafted on Ponderosa had nearly all wilted and had high disease indices (Table 1) as did non-grafted Ponderosa plants treated similarly (Fig. 1). On the other hand, the Ponderosa and the LS-89 scions on LS-89 rootstock reacted differently to infection. In Ponderosa scions on LS-89, wilting reached nearly 60% by 14 days, but the disease index was relatively low. None of the LS-89 scions on LS-89 wilted but nearly 69% had latent infection.

DISCUSSION

Wilting and disease severity in *P. solanacearum*-infected tomato seedlings under the different conditions in these experiments were comparable to those reported earlier^{12,15,16,18,30)}. The younger the plants at the time of inoculation, the greater was wilting and disease index. Higher inoculum concentrations and temperature also

increased wilting and disease. Resistant rootstock cultivars had less disease when they were maintained at lower temperature after inoculation. Many of the asymptomatic resistant and susceptible plants were shown to be latently infected with *P. solanacearum* as previously reported^{24,30)}. Results of these experiments indicate that latent infections are not associated with specific lines or cultivars, but may occur commonly in tomatoes, regardless of susceptibility.

The frequency of latent infection and wilting decreased, when older plants were inoculated and inoculum concentration or incubation temperature was lower. In LS-89, plants grown at 25/20°C showed almost no symptoms but had latent infection. In potato, latent infection with *P. solanacearum* occurred at 20/8°C in plants inoculated by stem puncture and at 28/16°C with infection in the soil⁴⁾. Though field trials were not included in these experiments, latent infection of tomato may also increase in warmer temperature under natural conditions.

In grafted tomato plants, wilting with *P. solanacearum* infection varied depending on the rootstocks. About a half of Ponderosa scions on LS-89 rootstocks showed wilting, whereas LS-89 scions on LS-89 showed no wilting but had latent infection. Most of those LS-89 rootstocks were likely to have latent infection with *P. solanacearum*, as expected from the results obtained on LS-89 seedlings inoculated with the bacteria. Apparently, infection was due to the pathogen moved from the LS-89 rootstocks into both the Ponderosa and LS-89 scions but only caused wilting in the susceptible Ponderosa. On the other hand, infection with the bacteria did cause wilting of LS-89 scions grafted on Ponderosa at high frequency, which was unexpected from the results on LS-89 seedlings. This may indicate that LS-89 plants are latently infected with *P. solanacearum* but only show wilting when a high concentration of inoculum is supplied from susceptible rootstocks.

In these experiments, the wilting symptoms on Ponderosa grafted on LS-89 appeared later than did symptoms on LS-89 and Ponderosa grafted on Ponderosa.

The wilting of Ponderosa scions was lower than expected based on the results on non-grafted Ponderosa seedlings and their disease indices were generally lower. The resistance in LS-89 may be similar to that reported in tomato which was associated with the plant's ability to restrict bacterial invasiveness in the lower part of the stem⁷⁾. Earlier trials using grafted tomato plants had contradictory results. Some studies showed wilting of susceptible scions on resistant rootstocks^{11,22,26,33)} whereas others showed no wilting^{7,29,33)}. Wilting of susceptible eggplants grafted on resistant rootstocks has been recorded for both *P. solanacearum*-infested fields^{11,20)} and greenhouse tests²¹⁾. The extent that resistant rootstocks restrict bacterial infection in susceptible scions is likely to vary depending on bacterial strains, environmental conditions and host stage as shown in our study. The wilting of tomatoes and eggplants⁹⁾ by *P. solanacearum* grafted on resistant rootstocks, previously reported, therefore, may not necessarily be due to a breakdown of the resistance.

In these experiments, the percentage of wilting and latent infection produced by the five strains were significantly different in BF-Okitsu 101 but not in LS-89, indicating that the strains may differ in their ability to invade tomato plants. Similarly, Ciampi & Sequeira²⁾ reported that strains of *P. solanacearum* differed in their ability to cause latent potato tuber infection in different resistant clones.

In conclusion, the resistant rootstocks used in this study appeared to have insufficient resistance to protect the susceptible scion from bacterial wilt. However, appropriate cultivation practices to keep the environment unfavorable to *P. solanacearum* (i.e., cool ambient temperature, low soil humidity, low soil populations of the pathogen and appropriate planting time) would definitely increase the effectiveness in use of resistant rootstocks. Further study is needed to examine the relationship between latent infection of rootstocks and the wilting of grafted commercial cultivars in the field.

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和 文 摘 要

中保一浩・高屋茂雄・角田佳則：接ぎ木および自根トマトの青枯病菌による無病徴感染の条件

青枯病感受性トマト品種ボンデローザ，抵抗性台木品種 LS-89，BF 興津 101 の苗およびボンデローザと LS-89 を台木あるいは穂木として組み合わせた接木苗に青枯病菌 *Pseudomonas solanacearum* を断根接種した。抵抗性，感受性品種とも萎凋症状を示さなかった苗の多くが無病徴感染していたことを接種 14 日目に茎からの病原細菌の検出により確認した。発病と無病徴感染を合わせた苗の頻度は，接種時の苗齢が大きいほど，また，接種源濃度あるいは接種後の苗の栽培温度が低いほど減少する傾向が認められた。LS-89 は低温区 (昼 25/夜 20°C) においてほとんど発病せず 20~75% の苗が無病徴感染していた。青枯病菌 5 菌株に対しボンデローザ，LS-89 の苗では菌株間における発病と無病徴感染を合わせた苗の割合に差はなかったが，BF 興津 101 の苗では有意な差異が認められた。ボンデローザ台に接いだボンデローザと LS-89 はほとんどすべてが萎凋した。一方，LS-89 台に接いだボンデローザは 60% 萎凋したが，LS-89 は病徴を示さなかった。この場合，LS-89 の 69% および萎凋を示さなかったボンデローザの 35% は無病徴感染していた。以上の結果，抵抗性台木に接いだ感受性穂木の発病は，無病徴感染している台木からの病原細菌の移行により容易に生じることが示された。