

Inheritance and Selection Efficiency of Bacterial Wilt Resistance in Tomato

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Abstract

Bacterial wilt resistance of F₂, F₃, F₄ and F₅ generations was evaluated in tomato. Parents and each generation were transplanted into a field heavily infested with *Pseudomonas solanacearum* and inoculated with bacterial wilt. Bacterial wilt resistance was evaluated based on the date of plant death and a resistance index from 1 (susceptibility) to 13 (high resistance) was assigned to each plant. Mean resistance indices of the F₁ generations of the 2 crosses were 4.5 and 6.2, which were lower than the mid-parent values of 6.9 and 7.1, respectively. These findings suggest that bacterial wilt resistance is partially recessive as there was incomplete dominance toward susceptibility. There was no correlation between the resistance index and fruit weight in the F₂ generations of the 2 crosses ($r = -0.074$, $r = -0.019$), indicating that it is possible to select plants with both high resistance and large fruits in segregating populations. High parent-offspring correlation between the resistance indices of the parental F₂ plants and the resistance indices of the F₃ progenies was observed and the mean resistance indices of F₃, F₄ and F₅ progenies derived from highly resistant F₂, F₃ and F₄ plants were higher than the mean resistance indices of the progenies derived from susceptible or moderately resistant F₂, F₃ and F₄ plants. These findings indicate that selection of resistance in early generations is apparently effective.

Discipline: Plant breeding/Horticulture

Additional key words: breeding, *Lycopersicon esculentum*, fruit weight, correlation, *Pseudomonas solanacearum*

Introduction

Bacterial wilt of tomato caused by *Pseudomonas solanacearum* E. F. Smith is a serious disease in the tropics, subtropics and warm temperate regions⁶⁾. In Japan, the disease is one of the major constraint on the cultivation of tomatoes in warm areas from the Kanto region in the main island to Kyushu. The disease causes heavy losses in tomato production, as the application of chemicals, soil fumigation and crop rotation are practically ineffective. The use of resistant cultivars is the most effective method of control. Several bacterial wilt-resistant cultivars with high fruit quality, Zuiei, Momotaro 8 and others have been released by private seed companies, but the resistance of these cultivars is insufficient for

use in heavily infested fields, whereas highly resistant rootstock cultivars have already been developed and growers have been grafting fresh market cultivars onto resistant rootstocks to avoid infection in infested areas. Grafting, however, is a time- and labor-consuming practice and there is an urgent need to develop new highly resistant fresh market cultivars.

Resistant breeding materials and understanding of the mode of inheritance of resistance are important for resistance breeding. Varietal resistance has been studied^{3,8-10,12,13)}, but the resistance is reported to be controlled by a small number of genes¹⁾, or to be polygenic⁴⁾ or monogenic^{5,11)}. This paper reports the findings on the mode of inheritance of the resistance to bacterial wilt in F₁, F₂ and back-cross generations of tomato, and the selection efficiency of resistance in F₂, F₃ and F₄ generations.

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Materials and methods

1) F_1 , F_2 and backcross generations

Two resistant parents, D-9 introduced from Malaysia and Hawaii 7998 introduced from Hawaii, and 1 susceptible parent, Tomato Parental line 5 (TPL-5) were used. D-9 (P_1) and TPL-5 (P_2), and TPL-5 (P_3) and Hawaii 7998 (P_4) were crossed to obtain F_1 seed. The F_{1s} were backcrossed to each parent and self-pollinated to obtain F_2 seed. Resistance of the cross between D-9 and TPL-5 was evaluated in 1989, and in 1990 for the cross between TPL-5 and Hawaii 7998.

(1) Cross of D-9 \times TPL-5

Seeds of P_1 , P_2 , F_1 , BCP₁, BCP₂ and F_2 were sown on March 7, 1989 in a greenhouse. On April 1, seedlings were transplanted to 9-cm plastic pots containing sterilized field soil. On April 27, the seedlings were transplanted to a bacterial wilt-infested field at the National Research Institute of Vegetables, Ornamental Plants & Tea (NIVOT), Japan. A randomized complete block design was used with 3 blocks. Seven plants for the P_1 , P_2 and F_1 generations, 14 plants for the BCP₁ and BCP₂ generations, and 48 plants for the F_2 generation were planted per block. The plants were staked and pruned.

P. solanacearum was isolated from a diseased tomato plant. A pure culture was multiplied at 30°C for 48 h in Wakimoto medium¹⁵⁾. The bacterial concentration was adjusted to 2×10^8 viable cells/ml. On July 17, 81-day-old transplants were inoculated by pouring a 50 ml bacterial suspension into the soil at the base of each plant.

For the evaluation of resistance, the date of plant death was recorded from June 20 to August 26. Using this date, a resistance index from 1 to 13 was assigned to each plant (Fig. 1). The resistance categories described by the index were as follows: 1-2 = susceptibility; 3-5 = weak resistance; 6-8 = moderate resistance; 9-11 = resistance; 12-13 = high resistance. On July 7 and 12, fruits of each plant were harvested and weighed, and mean fruit weights were calculated for the evaluation of the fruit size.

(2) Cross of TPL-5 \times Hawaii 7998

The experiments for the cross of TPL-5 \times Hawaii 7998, F_3 , F_4 and F_5 generations were conducted using the same design as that for the cross of D-9 \times TPL-5.

Seeds of P_3 , P_4 , F_1 , BCP₃, BCP₄ and F_2 were sown on March 5, 1990 in a greenhouse. On March

30, the seedlings were transplanted to 9-cm plastic pots containing sterilized field soil. On May 1, the seedlings were transplanted to a bacterial wilt-infested field. Seven plants for the P_3 , P_4 and F_1 generations, 14 plants for the BCP₃ and BCP₄ generations, and 49 plants for the F_2 generation were planted per block. On June 28, the plants were inoculated and the dates of death were recorded from June 8 to August 10. On July 5, fruits of each plant were harvested and weighed.

2) F_3 generation

Six susceptible, 6 weakly resistant and 6 highly resistant plants were selected in the F_2 generation of the cross TPL-5 \times Hawaii 7998 and offsprings of the plants were used as F_3 progenies. Seeds of the parents and F_3 progenies were sown on March 8, 1991 and on April 2 and the seedlings were transplanted to 9-cm plastic pots containing sterilized field soil. On April 26, the seedlings were transplanted to a bacterial wilt-infested field. Five plants of each of the parents and the F_3 progenies were planted per block. On July 1, plants were inoculated and the dates of death were recorded from June 8 to August 10.

3) F_4 generation

Six susceptible, 6 moderately resistant and 6 highly resistant plants were selected in the F_3 generation of the cross TPL-5 \times Hawaii 7998 and offsprings of the plants were used as F_4 progenies. Seeds of the parents and F_4 progenies were sown on March 12, 1992 and on April 6 and the seedlings were transplanted to 9-cm plastic pots containing sterilized field soil. On May 6, the seedlings were transplanted to a bacterial wilt-infested field. Five plants of each of the parents and the F_4 progenies were planted per block. On July 7, plants were inoculated and the dates of death were recorded from June 15 to August 27.

4) F_5 generation

Six susceptible, 6 moderately resistant and 6 highly resistant plants were selected in the F_4 generation of the cross TPL-5 \times Hawaii 7998 and offsprings of the plants were used as F_5 progenies. Seeds of the parents and F_5 progenies were sown on February 23, 1993 and on March 17, seedlings were transplanted to 9-cm plastic pots containing sterilized field soil. On April 21, the seedlings were transplanted to a bacterial wilt-infested field. Five plants of each of the parents and the F_5 progenies were planted

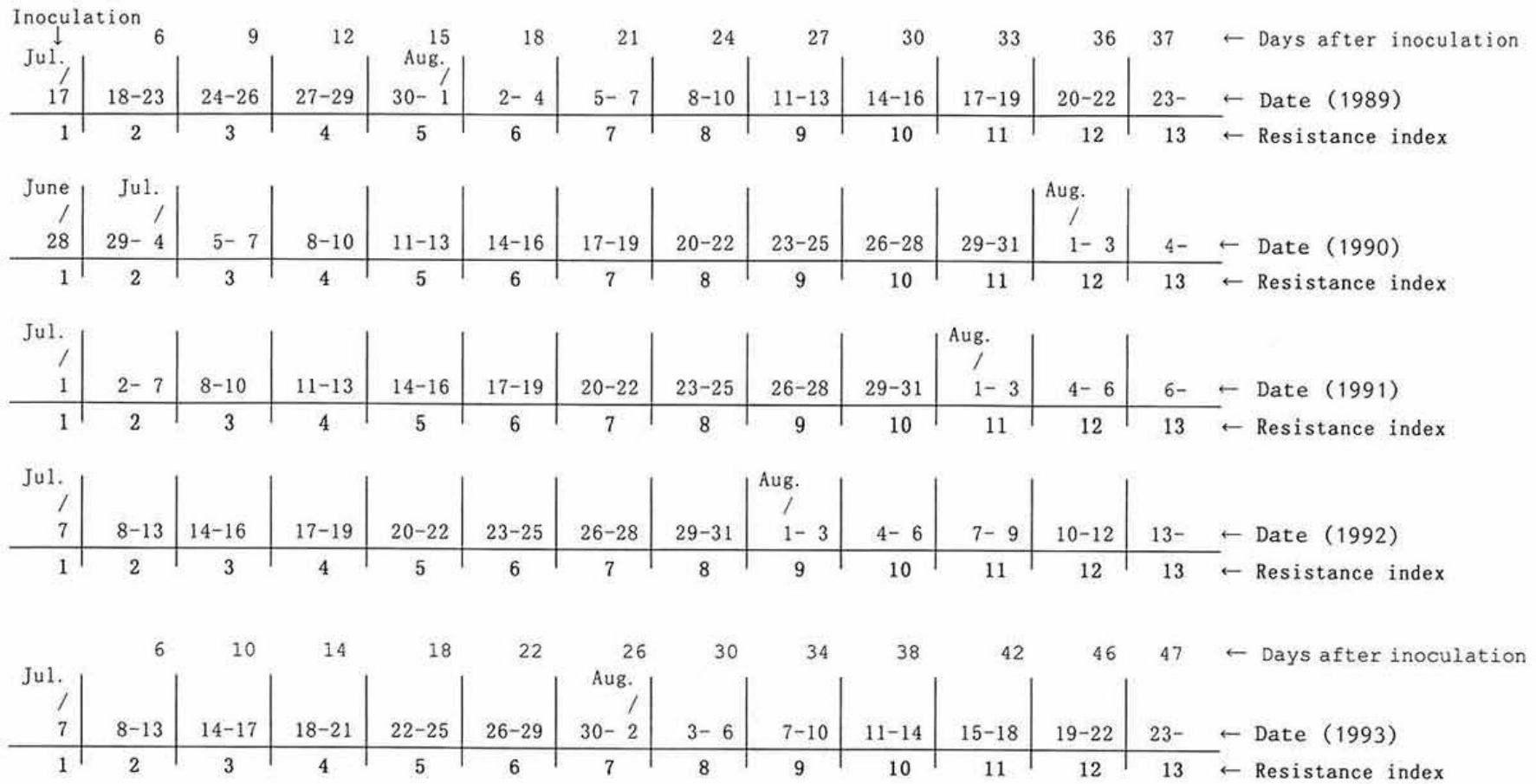


Fig. 1. Assignment of resistance index based on the date of plant death
Resistance index increased every 3 days in 1989 to 1992 and every 4 days in 1993.

per block. On July 7, plants were inoculated and the dates of death were recorded from June 8 to August 30.

Results

1) F_1 , F_2 and backcross generations

(1) Cross of D-9 \times TPL-5 in 1989

A difference in the frequency distribution of the resistance index between the resistant parent, D-9 (P_1) and the susceptible parent, TPL-5 (P_2) was evident and the frequency distribution of the resistance index for the F_1 was skewed toward the susceptible parent (Fig. 2). Almost all categories of resistant plants were observed in the BCP_1 . On the other hand, there were no resistant plants in the BCP_2 . The F_2 s segregated in a discontinuous pattern, which was skewed toward the susceptible parent. The plants with a high resistance accounted for 6% of the F_2 s.

The mean resistance indices of D-9 and TPL-5 were 12.8 and 1.0, respectively, and the mean

resistance index of F_1 was 4.5, which was significantly lower than the mid-parent value of 6.9 (Table 1). The mean resistance indices of BCP_1 and BCP_2 were close to those of the mid-parent and susceptible parent, respectively. The mean resistance index of the F_2 was close to that of the F_1 .

Fruits of 4 F_2 plants could not be harvested because the plants died of bacterial wilt before fruit maturity. These 4 plants were excluded from the correlation analysis between resistance and fruit weight. No correlation was observed between the

Table 1. Bacterial wilt resistance index and fruit weight of parents, F_1 , BCP_1 , BCP_2 and F_2 generations in the cross of D-9 \times TPL-5

| Parents & generation | Resistance index ^{a)} | Mean fruit weight (g) | Number of plants |
|----------------------|--------------------------------|-----------------------|------------------|
| P_1 : D-9 | 12.8 | 69.6 | 19 |
| P_2 : TPL-5 | 1.0 | 145.0 | 21 |
| F_1 | 4.5 | 145.0 | 21 |
| BCP_1 | 7.3 | 101.6 | 38 |
| BCP_2 | 1.9 | 127.0 | 32 |
| F_2 | 4.4 | 118.7 | 144 |
| <hr/> | | | |
| Mid-parent value | 6.9 | 107.3 | - |
| <hr/> | | | |
| LSD 5% | 1.0 | 22.1 | - |
| LSD 1% | 1.4 | 31.5 | - |

a): 1-2 = susceptibility, 3-5 = weak resistance, 6-8 = moderate resistance, 9-11 = resistance, 12-13 = high resistance.

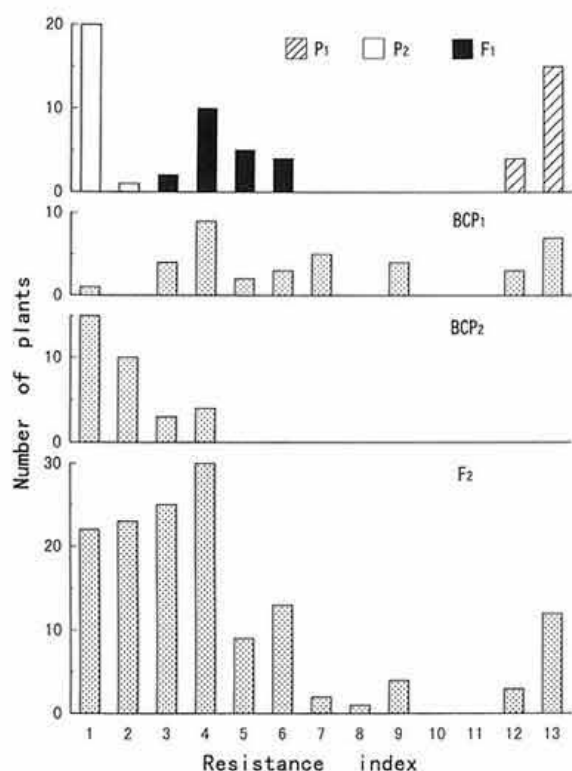


Fig. 2. Frequency distribution for bacterial wilt resistance index of resistant parent (P_1 : D-9), susceptible parent (P_2 : TPL-5), F_1 , BCP_1 , BCP_2 and F_2 generations

Higher values of resistance index indicate higher resistance, see Table 1.

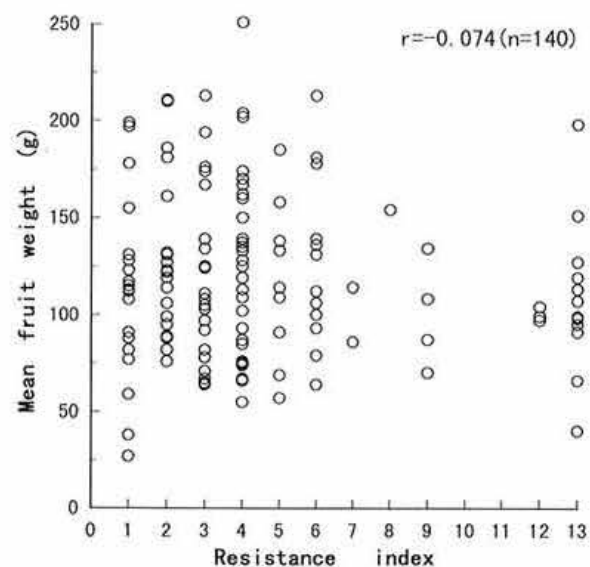


Fig. 3. Relationship between resistance index and mean fruit weight in F_2 generation of D-9 \times TPL-5
Higher values of resistance index indicate higher resistance, see Table 1.

resistance index and mean fruit weight among the F_{2s} ($r = -0.074$, Fig. 3).

(2) Cross of TPL-5 \times Hawaii 7998 in 1990

A difference in the frequency distribution of the resistance index between the susceptible parent, TPL-5 (P_3), and the resistant parent, Hawaii 7998 (P_4) was evident (Fig. 4). The frequency distribution of the resistance index for the F_1 was between, but slightly less than, parental means. The range for this F_1 was wider than that of the F_1 from D-9 \times TPL-5. All categories of resistant plants were observed in BCP_3 . Almost all categories of resistant plants were also observed in BCP_4 , in which plants with a resistance index of 13 showed the highest frequency. The F_{2s} segregated in a continuous pattern and the distribution was slightly skewed toward the susceptible parent. The plants with a high resistance accounted for 6% of the F_{2s} .

The mean resistance indices of TPL-5 and Hawaii 7998 were 1.1 and 13.0, respectively, and the mean resistance index of their F_1 was 6.2, which was

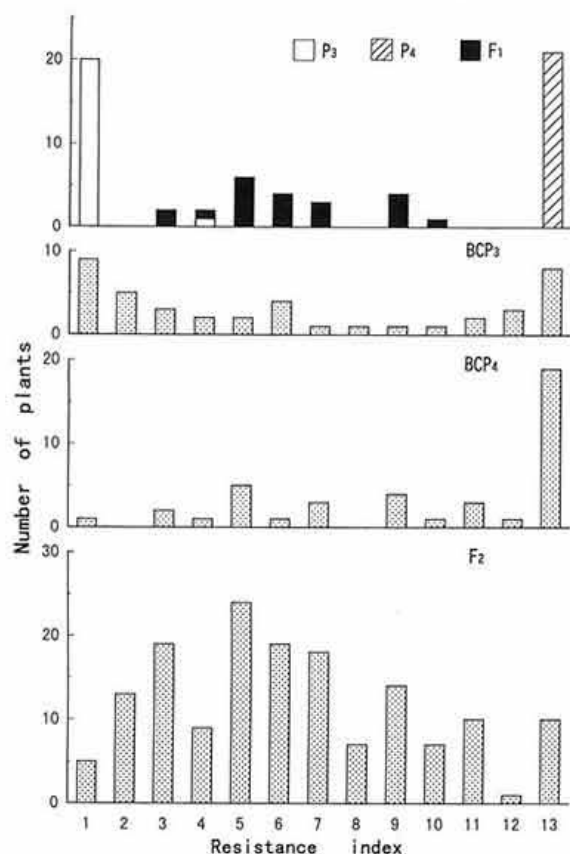


Fig. 4. Frequency distribution for bacterial wilt resistance index of susceptible parent (P_3 : TPL-5), resistant parent (P_4 : Hawaii 7998), F_1 , BCP_3 , BPC_4 and F_2 generations. Higher values of resistance index indicate higher resistance, see Table 1.

slightly lower than the mid-parent value of 7.1 (Table 2). The mean resistance indices of BCP_3 and the F_2 were the same as that of the F_1 . The mean resistance index of BCP_4 was higher than the mid-parent value.

Fruits of 1 F_2 plant could not be harvested because of bacterial wilt. This plant was excluded from the correlation analysis between resistance and fruit weight. No correlation was observed between the resistance index and mean fruit weight among the F_{2s} ($r = -0.019$, Fig. 5).

Table 2. Bacterial wilt resistance index and fruit weight of parents, F_1 , BCP_3 , BCP_4 and F_2 generations in the cross of TPL-5 \times Hawaii 7998

| Parents & generation | Resistance index ^{a)} | Mean fruit weight (g) | Number of plants |
|----------------------|--------------------------------|-----------------------|------------------|
| P_3 : TPL-5 | 1.1 | 147.0 | 21 |
| P_4 : Hawaii 7998 | 13.0 | 34.0 | 21 |
| F_1 | 6.2 | 61.3 | 21 |
| BCP_3 | 6.3 | 65.6 | 42 |
| BCP_4 | 9.8 | 58.2 | 41 |
| F_2 | 6.3 | 66.0 | 156 |
| <hr/> | | | |
| Mid-parent value | 7.1 | 90.5 | - |
| <hr/> | | | |
| LSD 5% | 2.1 | 18.7 | - |
| LSD 1% | 2.9 | 26.6 | - |

a): 1-2 = susceptibility, 3-5 = weak resistance, 6-8 = moderate resistance, 9-11 = resistance, 12-13 = high resistance.

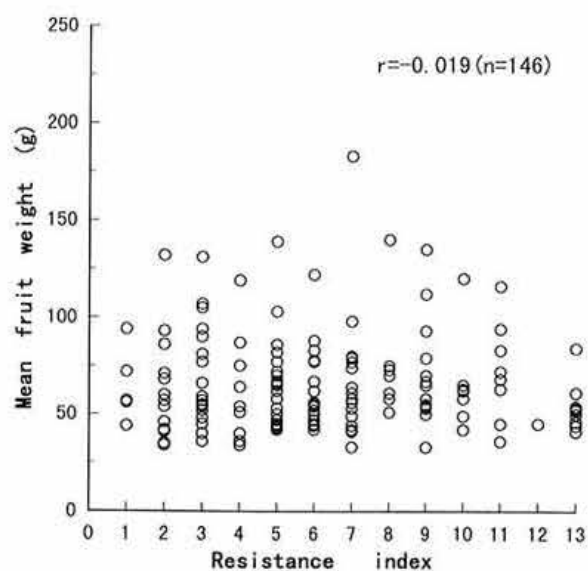


Fig. 5. Relationship between resistance index and mean fruit weight in F_2 generation of TPL-5 \times Hawaii 7998

Higher values of resistance index indicate higher resistance, see Table 1.

Table 3. Frequency distribution of the resistance index (RI) for the parents and F₃ progenies from the cross of TPL-5 × Hawaii 7998

| Parent and progeny | Number of plants in each RI | | | | | | | | | | | | | Number of plants | RI of F ₃ progeny ^{a)} | RI of parental F ₂ plant ^{b)} | |
|---|-----------------------------|---|---|---|---|---|---|---|---|----|----|----|----|------------------|--|---|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | | | | |
| P ₃ (TPL-5) | 14 | 1 | | | | | | | | | | | | | 15 | 1.1 | 1.1 |
| P ₄ (Hawaii 7998) | | | | | | | | | | | | 2 | 13 | | 15 | 12.9 | 13.0 |
| ----- | | | | | | | | | | | | | | | | | |
| F ₃ progeny derived from susceptible F ₂ plant | | | | | | | | | | | | | | | | | |
| T5L8-2 | 13 | 1 | | 1 | | | | | | | | | | | 15 | 1.3 | 1 |
| T5L8-16 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 2 |
| T5L8-59 | 14 | 1 | | | | | | | | | | | | | 15 | 1.1 | 2 |
| T5L8-70 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-118 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-146 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 2 |
| Mean | | | | | | | | | | | | | | | | 1.1 | 1.3 |
| ----- | | | | | | | | | | | | | | | | | |
| F ₃ progeny derived from weakly resistant F ₂ plant | | | | | | | | | | | | | | | | | |
| T5L8-15 | 4 | 3 | | | 1 | 2 | 1 | 1 | | | 2 | 1 | | | 15 | 5.1 | 5 |
| T5L8-36 | 1 | 7 | 1 | 1 | | | 1 | 2 | | 1 | 1 | | | | 15 | 4.4 | 5 |
| T5L8-68 | | 4 | 1 | 1 | 3 | | 1 | 2 | 3 | | | | | | 15 | 5.3 | 5 |
| T5L8-77 | 1 | 1 | | 1 | 1 | | | 2 | 1 | 1 | 5 | | 2 | | 15 | 8.5 | 6 |
| T5L8-102 | 2 | 1 | 2 | | 3 | | 1 | | 1 | 2 | 2 | | 1 | | 15 | 6.4 | 5 |
| T5L8-115 | 2 | 1 | | | 2 | | | 2 | 1 | 1 | 5 | | 1 | | 15 | 7.8 | 5 |
| Mean | | | | | | | | | | | | | | | | 6.3 | 5.2 |
| ----- | | | | | | | | | | | | | | | | | |
| F ₃ progeny derived from highly resistant F ₂ plant | | | | | | | | | | | | | | | | | |
| T5L8-18 | 5 | | | 1 | | | | 4 | | 1 | 3 | | 1 | | 15 | 6.5 | 13 |
| T5L8-31 | 4 | | 1 | | | | | 2 | | | 7 | 1 | | | 15 | 7.5 | 12 |
| T5L8-39 | | | | | 1 | | 1 | 1 | 2 | | 2 | 3 | 5 | | 15 | 10.7 | 13 |
| T5L8-62 | | | 1 | | | | | 1 | 1 | | 2 | 4 | 6 | | 15 | 11.2 | 13 |
| T5L8-99 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | | 2 | 2 | 2 | | 1 | | 15 | 6.8 | 13 |
| T5L8-141 | | | | 2 | | 1 | | 4 | 2 | | 3 | 1 | 2 | | 15 | 9.0 | 13 |
| Mean | | | | | | | | | | | | | | | | 8.6 | 12.8 |

a): RI of F₃ progeny = $\Sigma(\text{RI} \times \text{number of plants in each RI}) / \text{total number of plants}$.

b): Higher values indicate higher resistance, see Table 1.

2) F₃ generation

Almost all the plants of the 6 F₃ progenies derived from susceptible F₂ plants were susceptible (Table 3). The resistance indices of the F₃ progenies ranged from 1.0 to 1.3 and the mean resistance index of the F₃ progenies was 1.1.

F₃ progenies derived from weakly resistant F₂ plants segregated in the range from susceptible to highly resistant plants. The resistance indices of the F₃ progenies ranged from 4.4 to 8.5 and the mean resistance index of the F₃ progenies was 6.3.

The distribution of 6 F₃ progenies derived from highly resistant F₂ plants was skewed toward the resistant parent. Susceptible to highly resistant plants were observed in 3 F₃ progenies and there were no susceptible plants in the other 3 F₃ progenies. The resistance indices of the F₃ progenies ranged from 6.5 to 11.2 and the mean resistance index of the

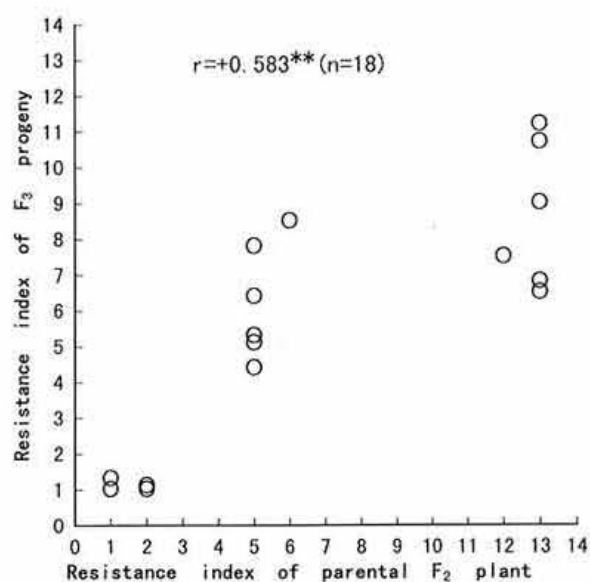


Fig. 6. Relationship between the resistance indices of 18 F₃ progenies and 18 parental F₂ plants. Higher values of resistance index indicate higher resistance, see Table 1.

Table 4. Frequency distribution of the resistance index (RI) for the parents and F₄ progenies from the cross of TPL-5 × Hawaii 7998

| Parent and progeny | Number of plants in each RI | | | | | | | | | | | | | Number of plants | RI of F ₄ progeny ^{a)} | RI of parental F ₃ plant ^{b)} | |
|---|-----------------------------|---|---|---|---|---|---|---|---|----|----|----|----|------------------|--|---|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | | | | |
| P ₃ (TPL-5) | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1.1 |
| P ₄ (Hawaii 7998) | | | | | | | | | | | | | 14 | | 14 | 13.0 | 13.0 |
| F ₄ progeny derived from susceptible F ₃ plant | | | | | | | | | | | | | | | | | |
| T5L8-2 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-16 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-59 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-70 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-118 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-146 | 11 | 4 | | | | | | | | | | | | | 15 | 1.3 | 1 |
| Mean | | | | | | | | | | | | | | | | 1.0 | 1.0 |
| F ₄ progeny derived from moderately resistant F ₃ plant | | | | | | | | | | | | | | | | | |
| T5L8-15 | | | | 1 | | | 1 | 2 | | 2 | 2 | 4 | 3 | | 15 | 10.4 | 8 |
| T5L8-36 | | | | | | 5 | 2 | 2 | | 2 | 1 | | 3 | | 15 | 8.7 | 8 |
| T5L8-68 | | 1 | | | | 1 | | 3 | | 2 | 2 | | 6 | | 15 | 10.1 | 8 |
| T5L8-77 | | | | | | | 1 | 1 | 3 | | 1 | 9 | | | 15 | 11.7 | 8 |
| T5L8-102 | | | | | | | | | 2 | 1 | | 12 | | | 15 | 12.5 | 7 |
| T5L8-115 | | 2 | | 3 | | | | | 1 | | | 9 | | | 15 | 9.5 | 8 |
| Mean | | | | | | | | | | | | | | | | 10.5 | 7.8 |
| F ₄ progeny derived from highly resistant F ₃ plant | | | | | | | | | | | | | | | | | |
| T5L8-18 | 2 | 1 | | | | 2 | | 1 | | 1 | 1 | | 7 | | 15 | 9.1 | 13 |
| T5L8-31 | | | | | | | 1 | 1 | | | 2 | | 11 | | 15 | 12.0 | 13 |
| T5L8-39 | | | | | | | 1 | | | | | | 13 | | 14 | 12.6 | 13 |
| T5L8-62 | | | 1 | | | | | | | | | 1 | 13 | | 15 | 12.3 | 13 |
| T5L8-99 | | | | 1 | | | 1 | | 1 | | 3 | 2 | 7 | | 15 | 11.2 | 13 |
| T5L8-141 | | 1 | | | | | 1 | 1 | 1 | 2 | 3 | 2 | 4 | | 15 | 10.3 | 13 |
| Mean | | | | | | | | | | | | | | | | 11.2 | 13.0 |

a): RI of F₄ progeny = $\Sigma(\text{RI} \times \text{number of plants in each RI}) / \text{total number of plants}$.

b): Higher values indicate higher resistance, see Table 1.

F₃ progenies was 8.6. This value was higher than the mean of the F₃ progenies derived from weakly resistant F₂ plants.

The relationship between the resistance indices of 18 F₃ progenies and the resistance indices of their parental 18 F₂ plants is shown in Fig. 6. There was a high correlation between the resistance indices of the F₃ progenies and the resistance indices of their parental F₂ plants ($r = +0.853^{**}$).

3) F₄ generation

All the plants of 6 F₄ progenies derived from susceptible F₃ plants were susceptible (Table 4).

The distribution of the 6 F₄ progenies derived from moderately resistant F₃ plants was skewed toward the resistant parent. Susceptible to weakly resistant plants were observed in 3 F₄ progenies and there were no susceptible to weakly resistant plants in the other 3 F₄ progenies. The resistance indices

of the F₄ progenies ranged from 8.7 to 12.5 and the mean resistance index of the F₄ progenies was 10.5.

The distribution of the 6 F₄ progenies derived from highly resistant F₃ plants was skewed toward the resistant parent. Susceptible to weakly resistant plants were observed in 4 F₄ progenies and most plants in the other 2 F₄ progenies were highly resistant. The resistance indices of the F₄ progenies ranged from 9.1 to 12.6 and the mean resistance index of the F₄ progenies was 11.2, higher than the mean of the F₄ progenies derived from moderately resistant F₃ plants.

4) F₅ generation

A few weakly resistant or resistant plants were observed, but most of the plants were susceptible among 6 F₅ progenies derived from susceptible F₄ plants (Table 5). The resistance indices of the 6 F₅

Table 5. Frequency distribution of the resistance index (RI) for the parents and F₅ progenies from the cross of TPL-5 × Hawaii 7998

| Parent and progeny | Number of plants in each RI | | | | | | | | | | | | | Number of plants | RI of F ₅ progeny ^{a)} | RI of parental F ₄ plant ^{b)} | |
|---|-----------------------------|---|---|---|---|---|---|---|---|----|----|----|----|------------------|--|---|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | | | | |
| P ₃ (TPL-5) | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1.0 |
| P ₄ (Hawaii 7998) | | | | | | | | | 1 | | | | 14 | | 15 | 12.8 | 13.0 |
| ----- | | | | | | | | | | | | | | | | | |
| F ₅ progeny derived from susceptible F ₄ plant | | | | | | | | | | | | | | | | | |
| T5L8-2-5-5 | 13 | 1 | | 1 | | | | | | | | | | | 15 | 1.3 | 1 |
| T5L8-16-1-1 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-59-2-1 | 12 | 1 | | | 1 | | | | 1 | | | | | | 15 | 1.9 | 1 |
| T5L8-70-1-6 | 15 | | | | | | | | | | | | | | 15 | 1.0 | 1 |
| T5L8-118-5-3 | 14 | | 1 | | | | | | | | | | | | 15 | 1.1 | 1 |
| T5L8-146-2-5 | 13 | 1 | 1 | | | | | | | | | | | | 15 | 1.2 | 1 |
| Mean | | | | | | | | | | | | | | | | 1.3 | 1.0 |
| ----- | | | | | | | | | | | | | | | | | |
| F ₅ progeny derived from moderately resistant F ₄ plant | | | | | | | | | | | | | | | | | |
| T5L8-15-9-8 | | | | | | 2 | | | 5 | 1 | 2 | 5 | | | 15 | 10.9 | 8 |
| T5L8-15-9-10 | | 1 | | | | | 1 | | 6 | | | 7 | | | 15 | 10.7 | 8 |
| T5L8-36-11-9 | | | | | | | 1 | 1 | 5 | | 2 | 6 | | | 15 | 11.1 | 8 |
| T5L8-36-11-14 | | | 1 | | 2 | 1 | | | 5 | | 4 | 2 | | | 15 | 9.5 | 8 |
| T5L8-68-4-15 | 1 | | | 1 | 2 | 3 | 1 | | 5 | | 1 | 1 | | | 15 | 7.7 | 8 |
| T5L8-77-4-8 | | | | | | | 1 | | 1 | | 2 | 11 | | | 15 | 12.3 | 8 |
| Mean | | | | | | | | | | | | | | | | 10.4 | 8.0 |
| ----- | | | | | | | | | | | | | | | | | |
| F ₅ progeny derived from highly resistant F ₄ plant | | | | | | | | | | | | | | | | | |
| T5L8-39-12-6 | | | | | | | | | 5 | | 6 | 4 | | | 15 | 11.6 | 13 |
| T5L8-62-13-6 | 1 | | | | | 1 | 1 | 1 | 6 | | | 5 | | | 15 | 9.8 | 13 |
| T5L8-62-13-10 | | | 1 | | | | | | 5 | | 1 | 8 | | | 15 | 11.3 | 13 |
| T5L8-99-12-1 | | | | | | | | | 4 | 1 | 4 | 6 | | | 15 | 11.8 | 13 |
| T5L8-99-12-2 | | | | | | | | | 2 | | 1 | 12 | | | 15 | 12.5 | 13 |
| T5L8-141-7-9 | | | | | | | | | 4 | | | 11 | | | 15 | 12.2 | 13 |
| Mean | | | | | | | | | | | | | | | | 11.5 | 13.0 |

a): RI of F₅ progeny = $\Sigma(\text{RI} \times \text{number of plants in each RI}) / \text{total number of plants}$.

b): Higher values indicate higher resistance, see Table 1.

progenies ranged from 1.0 to 1.9 and the mean resistance index of the F₅ progenies was 1.3.

The distribution of 6 F₅ progenies derived from moderately resistant F₄ plants was skewed toward the resistant parent. Susceptible to weakly resistant plants were observed in 3 F₅ progenies and there were no susceptible to weakly resistant plants in the other 3 F₅ progenies. The resistance indices of the F₅ progenies ranged from 7.7 to 12.3 and the mean resistance index of the F₅ progenies was 10.4.

The distribution of 6 F₅ progenies derived from highly resistant F₄ plants was skewed toward the resistant parent. Susceptible to weakly resistant plants were observed in 2 F₅ progenies and most plants in the other 4 progenies were resistant to highly resistant. The resistance indices of the F₅ progenies ranged from 9.8 to 12.5 and the mean resistance index of the F₅ progenies was 11.5, a higher value than the mean of the F₅ progenies derived from

moderately resistant F₄ plants.

Discussion

Differences in methodologies for evaluating host resistance may affect the final interpretation of the inheritance of bacterial wilt resistance. The evaluation of resistance should be quantitative, because resistance to bacterial wilt has been reported to be controlled by polygenes⁴⁾. Seedling inoculation methods such as clipping or root dipping have been applied for the selection of resistant seedlings, but the reaction of the inoculated seedlings is usually expressed by death or survival. The results from artificial inoculation are qualitative. Although the varieties that survived the natural infection were either resistant, moderately resistant, or susceptible when inoculated, it was pointed out that segregating populations were best screened under field conditions

at the flowering stage⁸⁾. In the method used in the present study natural infection from infested fields was combined with artificial inoculation to ensure the occurrence of the disease. The resistance of each plant was expressed by a resistance index based on the date of plant death. Differences in resistance classes among each parental line and generation evaluated by this method were clear, indicating that the method could be used for the evaluation or the selection of resistant plants in segregating populations and for the evaluation of varietal resistance.

Acosta et al.¹⁾ demonstrated that the resistance was partially dominant until 7 weeks after transplanting, but recessive in more mature plants, and that a small number of genes were associated with the resistance. Ferrer⁴⁾ reported that the F_1 population was intermediate between susceptible and resistant parents and that the resistance was polygenic, and Lum⁷⁾ described that several genes controlled the resistance, although it had been reported that the resistance of Hawaii 7998¹¹⁾ and Hawaii 7996⁵⁾ was controlled by a single dominant gene. The resistance index of the F_1 in the cross of D-9 \times TPL-5 was lower than the mid-parent value, and the resistance index of the F_1 from the cross of TPL-5 \times Hawaii 7998 was close to the mid-parent value. Consequently, it is considered that bacterial wilt resistance is partially recessive as there was incomplete dominance toward susceptibility depending on the degree of resistance of the resistant parent. The results obtained in this study were similar to those reported by Acosta et al.¹⁾ and Ferrer⁴⁾, but not to the results of Scott et al.¹¹⁾ and Grimault et al.⁵⁾. Differences in the conditions which affect the disease incidence, the bacterial wilt isolates used for inoculation and temperature during experiments, and difference in the resistant parents used are possible reasons for this discrepancy, because all or more than 70% of the F_1 plants were healthy in the results of Grimault et al.⁵⁾ or Scott et al.¹¹⁾, whereas all the F_1 plants died in the present study.

The frequency distribution of the resistance indices of the F_2 from TPL-5 \times Hawaii 7998 showed a continuous pattern. This finding indicates that the resistance was quantitative, as reported by Acosta et al.¹⁾ and Ferrer⁴⁾, although the number of genes controlling the resistance may be small, because the frequency distributions of the resistance indices of BCP₁ and F_2 from D-9 \times TPL-5 segregated in discontinuous patterns and the selection efficiency of resistance in early generations was high. The differences in frequency distributions of the 2 crosses were

evident, and the resistance of Hawaii 7998 was higher than that of D-9. To explain the difference in the resistance of the parents, it was assumed that the number of genes controlling the resistance in Hawaii 7998 was larger than in D-9, as an additive effect of the resistance gene was indicated⁴⁾.

It has been reported¹⁾ or described^{2,14)} that a small fruit size is associated with the resistance, leading to the problem of developing a resistant cultivar with good commercial quality. No correlation was observed between the resistance index and fruit weight in the 2 crosses of F_2 in our study, and Ferrer⁴⁾ reported that the fruit size was not correlated with the resistance. This fact indicates that selection for resistant materials with large fruit size can be achieved, and that it is possible to select plants with both high resistance and large fruit size in the segregating populations.

The selection efficiency of resistance to obtain a resistant progeny in the F_2 and successive generations is important for breeding. In our study a high parent-offspring correlation between the resistance indices of 18 F_2 plants and the resistance indices of 18 F_3 progeny was observed. Furthermore, the mean resistance indices of the F_3 , F_4 and F_5 progenies derived from highly resistant F_2 , F_3 and F_4 plants were higher than the mean resistance indices of susceptible or moderately resistant progenies derived from susceptible or moderately resistant plants. These results indicate that the selection of resistance in the early generations is apparently effective.

The F_3 , F_4 and F_5 progenies derived from the susceptible F_2 , F_3 and F_4 plants were susceptible and the selection of resistance in the early generations was effective in our study, although susceptible or weakly resistant plants were observed in 2 out of the 6 F_5 progenies derived from highly resistant F_4 plants. Consequently, it is considered that the susceptible character is fixed in the F_3 or F_4 generation and the resistant character is almost fixed in the F_5 generation, but successive selection of resistance after the F_5 generation is necessary to obtain a fixed line of resistance, since segregation of resistance was observed in some of the F_5 progenies.

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