SUSCEPTIBILITY OF SOME PEACH ROOTSTOCKS TO CROWN GALL

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SUMMARY

Crown gall susceptibility of six peach rootstocks ('Barrier 1', 'G.F.677', 'Mariana G.F. 8-1', 'Mr.S.2/5', 'Peach seedling' and 'P.S.') was assayed in field tests throughout four years and with many different strains of *Agrobacterium tumefaciens*. Plants were inoculated both in the roots and shoots; the plant responses of the two inoculation methods were highly correlated when bacterial suspensions of 10^7 cfu ml^{-1} were used. Thus shoot inoculation may become a very useful tool when a large number of genotypes have to be screened for crown gall resistance. With the exception of 'Mr.S.2/5' all the rootstocks displayed a very high level of sensitivity to crown gall. 'Mr.S.2/5' rootstock plants proved nearly insensitive when root inoculated and showed some susceptibility, but much lower than 'G.F.677', when shoots were infected with 35 different strains of agrobacteria under inoculum conditions very favourable to the pathogens.

RIASSUNTO

SUSCETTIBILITÀ DI ALCUNI PORTINNESTI DI PESCO AL TUMORE RADICALE. La suscettibilità al tumore radicale di sei portinnesti di pesco ("Barrier 1", "G.F.677", "Mariana G.F. 8-1", "Mr.S.2/5", "pesco franco" e "P.S.") è stata saggiata in tre anni di prove in campo e con diversi ceppi di agrobatteri. Le piante sono state inoculate sulle radici e sui germogli allo stato erbaceo ed è stata evidenziata un'elevata correlazione negli esiti dei due tipi di inoculazione quando sono state utilizzate sospensioni batteriche di 10^7 cfu ml^{-1}. Per questo motivo l'inoculazione sulle parti aeree può diventare una pratica molto utile se deve essere saggiato un gran numero di genotipi nell'ambito di programmi di miglioramento genetico. Con l'eccezione del "Mr.S.2/5" tutti i portinnesti si sono dimostrati molto suscettibili al tumore batterico. Le piante di "Mr.S.2/5", invece, sono risultate praticamente insensibili se inoculate all'apparato radicale e hanno mostrato una bassa sensibilità, rispetto a quella del "G.F.677", quando i germogli sono stati infettati con 35 ceppi di agrobatteri in condizioni molto favorevoli ai patogeni.

Key words: peach rootstock, crown gall, resistance, *Agrobacterium*.

INTRODUCTION

The soil bacterium *Agrobacterium tumefaciens* causes crown gall on many fruit tree and ornamental species throughout the world. The host range of crown gall is wide, including 643 plant species from 331 genera, mostly in dicot, some gymnosperm and a few monocot families (DeCleene and De Ley, 1976).

The ability of *A. tumefaciens* to induce galls is due to the presence in the bacterial cells of a large plasmid (200-400 Kb) named pTi (tumour inducing plasmid) (Ream, 1989). During infection the combined action of chromosomal genes and pTi virulence genes (*vir*), induce the transfer of the T-DNA region of the plasmid from the bacterium to the plant cell genome where it is integrated and expressed like native genes. As a consequence, the plant cell is stimulated to produce auxins and cytokinins that are responsible for an abnormal tissue proliferation and initiation of the galls on the crown, roots and in some cases the aerial parts of host plants.

Crown gall may cause serious econonomic losses to the growers because galled plants are unsalable and have to be discarded. At present, the sole effective method to control the disease consists of treating the plant roots before transplanting with a suspension of the antagonistic strain *A. radiobacter* K84 (New and Kerr, 1972), but some natural (Alconero, 1980; Bazzi and Burr, 1986) or transconjugant (Vicedo *et al.*, 1996) *Agrobacterium* populations resistant to K84 have been observed. Moreover the antagonist is not effective on infected asymptomatic plants and as yet sensitive methods to detect the bacteri-

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um on plant propagation material are not yet available. An alternative approach is to use resistant plants. Identification of rootstocks with low sensitivity to crown gall could benefit nurseries by reducing plant cullage and the cost of rootstock production. Genotypes resistant to *A. tumefaciens* have been described in different host plants such as aspen (Beneddra *et al.*, 1996), chrysanthemum (Miller *et al.*, 1975), grape (Sule *et al.*, 1994), peach (Pierronnet and Eyquard, 1993) and red raspberry (Zurowski *et al.*, 1985). In this study we have evaluated the relative susceptibility to *A. tumefaciens* of six *Prunus* spp. rootstocks commonly used in Italy. Four trials were performed through 1994 to 1997 using different methods of plant inoculation with many tumorigenic agrobacteria strains isolated from various hosts in different countries.

MATERIALS AND METHODS

Plant material. Six peach rootstocks of diverse genetic origin and with different physiological and agronomic characteristics were tested for sensitivity to crown gall (Table 1). The plant material used in the different trials was purchased each year from the same nursery. 'Peach seedlings' were from true seeds, while 'Barrier 1', 'G.F.677', 'Mariana G.F. 8-1', 'Mr.S.2/5' and 'P.S.' were *in vitro* micropropagated virus-free certified plants. 'Mariana G.F. 8-1' came from France, the other rootstocks were produced in Italy.

Table 1. Geographic and genetic origin of rootstocks.

Rootstock	Country	Genetic origin
Barrier 1	Italy	*P. persica* x *P. davidiana*
G.F.677	France	*P. persica* x *P. amygdalus*
Mariana G.F.8-1	France	*P. munsoniana* x *P. cerasifera*
Mr.S.2/5	Italy	*P. cerasifera* (free pollinated)
Peach seedling	Italy	*P. persica*
P.S.	France	*P. persica* x *P. domestica*

Bacterial strains and rootstock inoculations. Thirty five tumorigenic *Agrobacterium* strains of different origin and isolated from various host species were used. Strains were characterized to their biovar according to Kerr and Panagopoulos (1977) and for nopaline, mannopine and octopine utilization using the methods of Canfield and Moore (1991), (Table 2). Strains were stored in 20% glycerol at -80°C and were taken from the same frozen culture before each inoculation. Each year their virulence was checked by inoculating the bacterial suspension in 5 one month-old plants of tomato cv. 'Marmande'.

The first experiment was carried out in 1994 by inoculating the plant roots only with the strain 2P. In 1995, strains 2P, 152AM, B49c/83, F27/93 and T2a were used for root inoculations, and in 1996, the same strains as in 1995 were used for both root and shoot inoculation. All thirty five strains listed in the Table 2 were used in shoot inoculations in 1997.

Bacterial inocula for root inoculation were prepared by suspending the cultures grown on Yeast Dextrose Chalk Agar (Lelliott and Stead, 1987) for 36 hours at 27°C, in sterile distilled water (SDW) to a final concentration of 10^7 cfu ml^{-1}. In April, plantlets were root inoculated by 5 min immersion in the bacterial suspensions and then transplanted to field plots. Inoculated rootstocks were compared with control plants treated only with SDW. Eight months after inoculation surviving plants were uprooted and checked for the presence of galls. Disease incidence was evaluated as percentage of galled plants.

Shoot inoculations were performed in June 1996 and 1997 following two different methods: in 1996 bacterial suspensions (10^7 cfu ml^{-1}) grown as described above, were inoculated at the herbaceous internodes by introducing 10 µl suspension into 1 centimetre longitudinal wounds made with a sterile scalpel. Control inoculations were made with SDW. Tumour development was checked after two months and disease incidence was calculated as percentage of galled wounds. In 1997 one centimetre of bark was cut and raised and a sterile cotton wad, soaked with a bacterial suspension (10^8 cfu ml^{-1}), was placed under the small tongue of bark. In order to avoid rapid drying, wounds were wrapped with aluminium foil, removed three days later. After two months, tumour diameters were recorded and the sensitivity of rootstocks to crown gall was evaluated considering the percentage of galled inoculation points and the tumour dimensions.

Statistical analysis. Data were subjected to analysis of variance (ANOVA). Significance of mean differences of disease incidence was determined by Duncan's test and significance of mean differences of tumour size was determined by the T test. Correlation coefficients were calculated to determine the correspondence between root and shoot inoculation methods. Data were analyzed both as such and after transformation to arcsin. Because of the similarity of the results, only untransformed data are reported.

Experimental designs. Trials performed in 1994, 1995 and 1997 were carried out in Portici (Napoli) in the Phytopathological Garden of the Department of Horticulture, Botany and Plant Pathology. The 1996 experiment was carried out in Battipaglia (Salerno) at Torre Lama experimental farm of the University of Naples 'Federico II'.

Table 2. Characteristics of the strains used in the study.

Strain	Origin	Host	Biovar	Opine utilization
22AM	Italy	Peach	2	nopaline
65AM	Italy	M26	2	nopaline
116AM	Italy	Cherry	1	nopaline
142AM	Italy	Rose	2	nopaline
152AM	Italy	Rose	1	nopaline
188AM	Italy	Peach	2	nopaline
241AM	Italy	G.F. 677	2	nopaline
712AM	Italy	Rose	2	nopaline
713AM	Italy	Rose	2	nopaline
723AM	Italy	Rose	2	nopaline
760AM	Italy	Myrobalan	2	nopaline
780AM	Italy	Rose	2	nopaline
75G	Italy	G.F. 677	1	mannopine
95G	Italy	G.F. 677	2	nopaline
165G	Italy	Hansen2168	2	nopaline
210G	Italy	Plum	2	nopaline
340G	Italy	Peach	2	nopaline
2P	Italy	Peach	2	nopaline
At 20.5	Italy	Peach	2	nopaline
At114S3	Italy	Chrysanthemum	1	-
At139S10	Italy	Persimon	1	-
At140N6	Italy	Persimon	2	-
Fb99	Italy	Weeping fig	1	-
Fb120	Italy	Weeping fig	1	nopaline
Fb122	Italy	Weeping fig	intermediate	nopaline
AF3.10	Florida	Weeping fig	intermediate	octopine/nopaline
C58	NY State	Cherry	1	nopaline
B49c/83*	Oregon	Peach	2	nopaline/mannopine
F27/93	Oregon	CrabApple	2	nopaline/mannopine
238G	Tunisia	Pear	1	nopaline
T2a	Tunisia	G.F. 677	1	nopaline
T4A	Tunisia	Almond	1	nopaline
AtAs	Israel	Aster	1	mannopine
A. rubi ATCC 13335	USA	Rubus		-
A. vitis	Italy	Grape	3	nopaline

* Reisolated from apple

1994 experiment. Four rootstocks ('Peach seedling', 'P.S.', 'G.F.677', 'Mr.S.2/5') were root-inoculated with a suspension of strain 2P. Forty plants/rootstock were transplanted in the plots in a randomized block scheme with four replications.

1995 experiment. *Agrobacterium* strains T2a, 2P, B49c/83, F27/93 and 152AM were used to inoculate the roots of 'Peach seedling', 'P.S.', 'G.F. 677', 'Mr.S.2/5' and 'Barrier 1' rootstocks. Plants were transplanted to the plots in a split plot design with four replications. Twenty five plants/rootstock/block were inoculated.

1996 experiment. 'G.F. 677', 'Barrier 1' and 'Mr.S.2/5' rootstocks were root-inoculated with strains T2a, 2P, B49c/83, F27/93 and 152AM as in the previous experiment. Plants were transplanted to the field in a split plot design with four replications. Twenty five plants/rootstock/block were inoculated.

Shoot inoculations were performed on the same three rootstocks and also on 'Peach seedling' and 'Mariana G.F. 8-1'. Fifteen plants of each rootstock were randomly chosen in the experimental field and the five *Agrobacterium* strains were inoculated in twenty wounds on three different plants for a total of 60 inoculations for each combination strain/rootstock.

1997 experiment. Only shoot inoculations were done on 'G.F. 677' and 'Mr.S.2/5' rootstocks. Three 4 year-old plants for each rootstock were chosen and inoculated on young herbaceous shoots with thirty five *Agrobacterium* strains. Each strain was inoculated in ten different sites on each plant.

RESULTS

Data from root inoculations are reported in Tables 3, 4 and 5. 'Peach seedling', 'G.F. 677', 'Barrier 1' and 'P.S.' rootstocks were highly sensitive to crown gall throughout the experiments. Among these rootstocks, 'G.F. 677' was the most sensitive. Strains B49c/83, F27/93 and 2P appeared to be more virulent than T2a and 152AM even though disease incidences were not always significantly different. 'Mr.S.2/5' rootstock was almost insensitive to crown gall when root inoculated, and in fact, in each year, only one galled plant was detected among 'Mr.S.2/5' plants, while the other four rootstocks were always strongly affected. Results obtained with root inoculation were confirmed by shoot inoculation performed in 1996 (Table 6). 'Barrier 1', 'G.F. 677', 'P.S.' and 'Mariana G.F. 8-1' rootstocks were highly sensitive to shoot infection by *A. tumefaciens* and formed tumours at 50-90% of the inoculation sites.

Table 3. Incidence (%) of galled plants after root inoculation with strain 2P (1994).

Rootstock	Incidence (%)
G.F.677	96.0 a
Mr.S.2/5	0.6 c
P.S.	100.0 a
Peach seedling	72.0 b

Values followed by the same letter do not differ significantly at $P \leq 0{,}01$ according to Duncan's new multiple range test.

Table 5. Incidence (%) of galled plants after root inoculation (1996).

Strain	Incidence (%)		
	Barrier 1	G.F.677	Mr.S.2/5
2P	77 a	88 ab	0.0 b
152AM	64 a	68 b	0.1 a
B49c/83	73 a	93 a	0.0 b
F27/93	69 a	95 a	0.0 b
T2a	54 a	80 ab	0.0 b
All*	67 a	85 a	0.2 b

Values in the same column (* row) followed by the same letter do not differ significantly at $P \leq 0{,}01$ according to Duncan's new multiple range test.

Out of the sixty inoculations performed with each strain, only one tumour, induced by T2a, was detected on one 'Mr.S.2/5' plant.

No particular strain-rootstock specialization was observed: 2P, 152AM and T2a strains were able, in different trials, to induce a gall on 'Mr.S.2/5'. In the 1996 experiment, crown gall susceptibility of shoots was significantly correlated with corresponding data on roots at the 0.001 level ($r = 0.831$), pointing out the potential of shoot inoculation for screening for crown gall susceptibility among rootstocks.

In Table 7 the results are reported of shoot inoculations performed with 35 tumorigenic strains on two rootstocks. Twenty nine strains were able to induce disease on both 'G.F. 677' and 'Mr.S.2/5', but on the latter rootstock tumour diameters were very small and significantly different from the corresponding diameters measured on 'G.F. 677'. Differences were not significant for galls induced by strains 712AM, AT140N6 and ATas. Only strain 713AM induced galls of larger size on 'Mr.S.2/5' than on 'G.F. 677'. Almost all inoculation sites were galled on 'G.F. 677' (95.3%) while 'Mr.S.2/5' behaviour was related to the different bacterial strains and ranged from zero to 100%.

Table 4. Incidence (%) of galled plants after root inoculation (1995).

Strain	Incidence (%)				
	Barrier 1	G.F.677	Mr.S.2/5	Peach s.	P.S.
2P	61 a	66 ab	0.0 a	72 ab	61 ab
152AM	57 a	48 b	0.0 a	47 c	67 ab
B49c/83	74 a	90 a	0.1 a	85 a	82 a
F27/93	65 a	87 a	0.0 a	87 a	77 a
T2a	55 a	66 ab	0.0 a	55 bc	36 b
All*	62 a	71 a	0.2 b	69 a	65 a

Values in the same column (* row) followed by the same letter do not differ significantly at $P \leq 0{,}01$ according to Duncan's new multiple range test.

Table 6. Incidence (%) of galled wounds on shoots (1996).

Strain	Incidence (%)				
	Barrier 1	G.F.677	Mr.S.2/5	Mariana G.F 8-1	P.S.
2P	63 a	73 a	0.0 a	60 bc	70 a
152AM	80 a	77 a	0.0 a	50 c	60 a
B49c/83	60 a	70 a	0.0 a	90 a	73 a
F27/93	73 a	73 a	0.0 a	90 a	67 a
T2a	87 a	67 a	1.6 a	80 ab	77 a
All*	73 a	72 a	0.3 b	74 a	69 a

Values in the same column (*: row) followed by the same letter do not differ significantly at $P \leq 0{,}01$ according to Duncan's new multiple range test.

DISCUSSION

The search for rootstock genotypes resistant to *A. tumefaciens* is a way to reduce plant cullage and the related costs of plant production due to crown gall disease. Sources of resistance have been found in different plant species, but very little is known about the relative sensitivity of stone fruit rootstocks to *A. tumefaciens* infections.

In this study we have evaluated the susceptibility to crown gall of six stone fruit rootstocks most commonly used in Italy. The results of three year experiments showed that 'Peach', 'G.F. 677', 'P.S.', 'Barrier 1' and 'Mariana G.F.8-1' rootstocks were highly sensitive to crown gall disease. Among these rootstocks, 'G.F.677' appeared to be most sensitive as was previously shown (Zoina and Simeone, 1989; Loreti and Massai, 1999). Rootstock 'Mr.S.2/5' was almost immune to root infection by *A. tumefaciens*, in fact each year only one single plant was affected: in the first year one out of 160, and in the second and third years one out of 500. No strain-rootstock specialization was observed; 3 out of 5 strains were virulent and each year a different strain was able to induce root tumours on 'Mr.S.2/5'. In 1996, a shoot inoculation method was used to test the same plants that had been inoculated on the roots two months earlier. Disease incidence on shoots was highly comparable with root infections, showing again the low sensitivity of 'Mr.S.2/5' to crown gall.

In 1997, with the aim to compare the sensitivity of 'Mr.S.2/5' and 'G.F. 677' rootstocks with a wider group of strains, only shoot inoculations were performed with 35 tumorigenic strains by using inoculation conditions more favourable to the pathogens than in the experiment of 1996. Positive infections were established by 29 strains on both rootstocks, but overall tumour diameters were very small on 'Mr.S.2/5' and the percentage of galled wounds was much lower than on 'G.F. 677'. Although rootstock 'Mr.S.2/5' is more resistant to crown gall than 'G.F. 677', strain 713AM produced larger tumours on 'Mr.S.2/5' than on 'G.F. 677'. It will be interesting to verify this behaviour by shoot and root inoculations on 'Mr.S.2/5' and other plant species to see if this interaction is host-pathogen specific. The difference between shoot disease incidences in the data from 1996 and 1997 on 'Mr.S.2/5' can be explained by the different inoculation methods that were used. Probably, in 1997 the persistence of a higher level of inoculum, for a longer time on a larger wounded area were the factors that allowed the tumour initiation on many inoculation sites even on rootstock 'Mr.S.2/5', that, on the contrary, had proved highly resistant in the previous experiments both with root and shoot inoculations. Under the very favourable conditions provided in 1997 many strains were able to infect successfully, whereas less favourable inoculum conditions, much closer to the natural ones, seemed not conducive to crown gall development in 'Mr.S.2/5'. Results of shoot inoculations obtained in 1996 were highly correlated with root inoculation incidence, showing that shoot inoculation is as effective to show differences in sensitivity to crown gall among genotypes of different origin. This method could replace root inoculation for testing crown gall sensitivity of new rootstocks when a great number of genotypes have to be screened. Shoot inoculation is easy to perform and score and results are soon readable, while a lot of work has to be done and six-eight months are needed to determine disease incidence on roots (Stover and Walsh, 1998).

Different authors (Bush and Pueppke, 1991; Sule *et al.*, 1994; Nam and Gelvin, 1998) found that plant genotypes that are less susceptible to crown gall permit the transfer and nuclear transport of T-DNA, but are deficient in T-DNA integration. Integration of T-DNA in the nucleus is a critical step in tumorigenesis and the inhibition of this process seems strictly related to resistance to crown gall. Limited tumour induction in 'Mr.S.2/5' may also be caused by a low rate of T-DNA integration in the plant, but obviously this hypothesis has to be checked.

Table 7. Means of tumour diameters (± SD) and percentages of galled wounds two months after shoot inoculations (1997).

Mean of tumour diameters (mm)				Galled inoculation sites (%)	
Strain	G.F. 677	Mr.S.2/5	T test	G.F. 677	Mr.S.2/5
22AM	11.9±2.9	3.3±1.9	7.7***	100	100
65AM	12.8±7.1	4.7±4.6	3.0**	100	80
116AM	10.4±2.9	2.6±2.7	6.1***	100	60
142AM	9.2±2.3	2.6±3.5	4.9***	100	50
152AM	17.6±2.4	5.2±3.9	8.6***	100	80
188AM	9.4±5.7	1.0±2.8	4.1***	90	20
241AM	15.5±2.3	4.8±2.1	10.7***	100	90
712AM	10.7±2.0	10.1±2.2	0.6 ns	100	100
713AM	7.1±3.5	16.1±5.0	4.6***	100	100
723AM	12.2±3.1	5.9±3.5	4.2***	100	90
760AM	12.7±3.5	2.4±1.2	8.6***	100	90
780AM	9.9±5.1	3.0±1.2	4.1***	100	100
75G	15.9±2.0	0.0	24.8***	100	0
95G	11.7±4.1	0.8±1.0	8.1***	100	40
165G	9.6±2.5	1.9±1.6	7.9***	100	70
210G	16.2±5.0	4.4±1.9	6.9***	100	90
340G	14.3±2.9	1.7±2.6	10.1***	100	40
2P	14.5±2.9	0.7±1.0	13.9***	100	40
At 20.5	15.0±5.8	6.0±2.1	4.5***	100	60
At114S3	12.5±4.8	1.0±1.4	7.3***	100	50
At139S10	1.2±1.0	0.0	3.7**	60	0
At140N6	0.6±0.9	0.0	1.9 ns	30	0
Fb99	9.7±1.5	2.1±2.4	8.4***	100	60
Fb120	3.9±4.0	0.0	3.1**	80	0
Fb122	13.8±3.9	0.0	11.1***	100	50
AF3.10	14.4±2.7	0.2±0.4	16.6***	100	20
C58	13.3±3.9	0.9±0.8	9.8***	100	70
B49c/83	13.5±3.9	1.8±1.4	9.8***	100	40
F27/93	11.4±2.1	1.2±1.0	8.3***	100	70
238G	10.5±1.4	1.7±1.2	14.6***	100	90
T2a	10.2±2.4	2.4±2.2	10.1***	90	40
T4A	11.5±6.0	3.4±2.2	4.0***	90	90
AtAs	3.1±1.6	1.6±2.5	1.6 ns	100	40
A. rubi	16.1±3.1	0.0	16.6***	100	0
A. vitis	5.8±2.0	2.5±1.2	4.5***	100	100
All	11.3±4.6	2.7±3.5	8.1***	95.4a	57.7b

**: Significant at $P \leq 0.01$.
***: Significant at $P \leq 0.001$.

'Mr.S.2/5' was selected in Italy, at the University of Pisa, among a population of freely pollinated myrobalan seedlings on the basis of several physiological and agronomic traits other than crown gall resistance. At present in Italy, 'G.F. 677' and some peach seedling lines are the most versatile and widely used peach rootstocks, but all are very sensitive to crown gall, as are other stone fruit rootstocks. 'Mr.S.2/5' represents a good alternative in fertile soils where it reduces the size of vigorous trees, in poorly drained and limy soils, and in soils affected by peach replant disease. The rootstock seems to considerably improve fruit quality and, according to field observations, it is also less sensitive to *Armillaria mellea* and *Phytophthora* spp. (Loreti and Massai, 1999). It is difficult to bud, however, with some peach cultivars.

The genetic origin of 'Mr.S.2/5' is not well defined, but it is probably a natural hybrid of *P. cerasifera* x *P. spinosa* (Loreti *et al.*, 1989). Among *Prunus* rootstocks, Pierronnet and Eyquard (1993) found putative sources of resistance in *P. domestica* and *P. besseyi*, while *P. spinosa* hybrids varied in their sensitivity, depending on the characteristics of the other parental species. The very low susceptibility of 'Mr.S.2/5' was consistently demonstrated by our results over four years using both root and shoot inoculation. Because *P. cerasifera* is a susceptible genotype, the resistance of 'Mr.S.2/5' rootstock should be due to the *P. spinosa* parent or to a particular combination of the two genotypes. This hypothesis is under investigation.

AKNOWLEDGEMENTS

This work was supported by EU Contract: ERBIC18CT970198 'Integrated control of crown gall in Mediterranean countries'.

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Received 12 April 1999
Accepted 28 June 1999

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