A Greenhouse Method for Selecting Tomato Seedlings Resistant to Bacterial Canker

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ABSTRACT

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Infiltrations of suspensions of inocula (10^3–10^8 cfu/ml) into leaflets and stems were used to evaluate resistance to *Clavibacter michiganensis* subsp. *michiganensis* in 4- to 5-wk-old tomato seedlings. Disease increased at slower rates in infiltrated tissues of Heinz 2990 than in Floradade and Morden with all concentrations except 10^8 cfu/ml in leaflets and 10^3 and 10^4 cfu/ml in stems. Seedlings with low disease severity were selected from a segregating backcross population derived from Heinz 2990 following infiltrations of leaflets and stems with 10^5 and 10^8 cfu/ml, respectively. In field experiments, plants were inoculated by leaf excision with a scalpel dipped in inoculum of 10^8 cfu/ml. Heinz 2990 developed less disease ($P < 0.01$) than Floradade and Morden. Less disease ($P < 0.01$) also developed on selfed progeny of previously selected backcross plants than on the susceptible parent Grosse Lisse, and segregation for resistance occurred among nonselected backcross plants. Disease severity levels in field-grown plants were higher ($P < 0.01$) in Morden than in Floradade, and fruiting was earlier and more concentrated in time in Morden. The test of seedlings in the greenhouse has potential for rapid screening of lines for partial resistance and in tomato breeding programs.

Clavibacter michiganensis subsp. *michiganensis* (Smith) Davis et al causes bacterial canker disease of tomato (*Lycopersicon esculentum* Mill.). In southern Queensland, Australia, the pathogen is endemic in the Granite Belt and coastal districts, where annual yield losses of tomato fruit may approach 10% or A$1 million annually. Greatest loss occurs when seedlings are infected (5) and rainfall disperses the pathogen. A resistant cultivar is the objective of our breeding program, for which efficient selection methods are required.

Several *L. esculentum* accessions have resistance (1,2,4,10,15,16), characterized by less bacterial multiplication in stems (1,14,16). Concomitantly, disease incidence may be lower (2), and symptoms may be fewer and/or less severe (1,14,16). There is, however, no known qualitative resistance of outstanding value in the species.

Vascular tissue exposed to inoculum is the usual infection court in experimental work (1,2,15), because occlusion of vascular tissue results in wilting, chlorosis, and death of leaflets, leaves, and whole plants (3). Parenchyma cells of cotyledon, leaf, cortex, and pith also are susceptible (3,8,9,12,13). Lesion density in spray-inoculated cotyledons was correlated with resistance observed following root inoculation (9), but the correlation of foliar necrosis and vascular staining may not be strong in more closely related germ plasm (6).

We observed that inoculum infiltrated into areas of leaflets and stems of young seedlings caused disease of those tissues, and that disease severity increased at rates that differed among tomato cultigens. Our aim was to identify resistance in seedlings that was correlated with resistance in field-grown plants and to apply the methods to seedlings expected to be segregating for resistance.

MATERIALS AND METHODS

Seed stocks. Susceptible tomato cultigens Grosse Lisse, Floradade, and Morden; partially resistant Heinz 2990 (H2990); and the self-pollinated third backcross (BC_3-S_2) to Grosse Lisse of the cross between H2990 and Grosse Lisse were used in these tests. The BC_3-S_2 population was derived from field-grown plants in previous generations of (H2990 × Grosse Lisse) F_2, BC_1-S_2, and BC_2-S_2 (J. B. Heaton, *unpublished data*). Seeds (BC_3-S_3) were extracted by acid (3% HCl for 2 hr) from fruit of selected BC_3-S_2 plants.

Plant culture. Seedlings were raised in 60-cell polystyrene trays containing a fertilized peat-vermiculite mix. In the greenhouse, plants were grown in every other row (four plants per row), and each tray contained 32 seedlings. Trays were kept in galvanized tin trays containing sufficient water to satisfy daily transpiration demands. Temperatures in the greenhouse ranged between 18 and 30 C. Seedlings for field experiments were transplanted at 6 wk of age to a site at the Granite Belt Horticultural Research Station near Stanthorpe in southern Queensland. Row spacing was 2 m and plant spacing was 0.4 m. Plants were trellised and grown according to district recommendations.

Inoculum preparation. Strain Q 1986 of *C. m. michiganensis* was used in all experiments and maintained by periodic subculturing and storage at 4 C. This strain, a recent isolate from tomato, was aggressive, virulent, and seedborne and had typical cultural characteristics including development of all symptoms in inoculated tomato plants. Inocula were prepared from late-log-phase nutrient broth cultures derived from single colonies on nutrient agar plates. Cultures were centrifuged at 1,000 × *g*; the bacterial pellets were suspended in sterile tap water, and the suspension was standardized photometrically to an absorbance of 0.3 at 600 μm wavelength, which approximated a density of 10^8 cfu/ml. The suspension was either used directly or serially diluted. Concentrations were confirmed by replicated colony counts from 0.05-ml subsamples of serial dilutions spread on nutrient agar plates.

Inoculations. In all experiments in the greenhouse, a leaflet of each of the lowest two leaves and the stem of each 4- to 5-wk-old seedling were infiltrated with inoculum. Hypodermic syringes fitted with 27-gauge needles were used to infiltrate stems. A portion of stem approximately 2 cm in length was infiltrated. In one experiment, syringes fitted with needles were also used to infiltrate leaflets, but in all other experiments syringes without needles were used because that was faster. Approximately 2.5–3 cm^2 per leaflet was infiltrated in all experiments. Field-grown plants were inoculated 2 wk after transplanting by excision of the lowest healthy leaf with a scalpel blade dipped in inoculum (10^8 cfu/ml) (5).

Inoculum concentrations in seedlings. Six inoculum concentrations (approximately 10^3, 10^4, 10^5, 10^6, 10^7, and 10^8 cfu/ml) were tested in leaflets and stems of Morden and H2990 in the greenhouse. A tray of seedlings was used for each inoculum concentration. Each tray contained four rows each of four plants of both cultigens. Rows were randomized in each tray, and the position of trays was rerandomized each day. In each tray, 14 plants of each cultigen were inoculated with bacteria and two with sterile tap water. Leaflets and stems were infiltrated using a syringe and needle.

The second experiment used three

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concentrations of bacteria (approximately 10^4, 10^6, and 10^8 cells/ml) in leaflets and stems of Floradade and H2990. Plants were treated as described above except that leaflets were infiltrated with only the syringe.

Resistance in a segregating population of seedlings. One hundred and forty-four seedlings of BC_3-S_2 were grown in trays as described previously. Each tray contained a row (four plants) each of Floradade and H2990 and 24 plants of the BC_3-S_2 cross. Leaflets were infiltrated with a suspension of 10^5 cfu/ml and stems with 10^8 cfu/ml. Leaflets were inoculated 1 day earlier than stems.

Correlation of resistance in greenhouse and field. Three experiments were run simultaneously in the field during the summer of 1990–1991. In the first, disease progress was compared in Floradade, H2990, and Morden. There were three replicates in randomized block design. In each replicate there were two plots, each of eight plants, of each cultigen.

In the second experiment, BC_3-S_3 plants that were progeny of 10 BC_3-S_2 plants selected from the earlier experiment in the greenhouse were evaluated for bacterial canker. There were three replicates of six-plant plots of the BC_3-S_3 lines and the control Grosse Lisse.

In the third experiment, field resistance in 186 plants of BC_3-S_2 was compared with that in 30 plants of control Grosse Lisse. Grosse Lisse plants were in six plots, of five plants each, placed at random in the rows of BC_3-S_2 plants. All plants were inoculated in all three experiments.

Disease assessment. Severity of visible disease on each plant was subjectively rated on a scale of zero to seven at timed intervals after inoculations in greenhouse and field trials (Table 1). In the greenhouse, we ceased rating plants when inoculated tissue was completely necrotic. Field ratings continued until 3 wk after first harvest of fruit. Leaflet ratings from the greenhouse experiments were averaged for each plant, and leaflet and stem ratings were averaged for each tomato cultigen at each time of rating. From field experiments, plot means of single plant ratings were obtained where appropriate.

Evaluation of disease progress data. Linear regression of mean disease severity ratings against time was used to compare cultigens. Where the fit to linear regression was poor, the area under disease progress curve (AUDPC) (11) for each plant was computed and used as the basis for comparison.

Table 1. Rating scale of disease severity in seedlings and field-grown tomato plants inoculated with strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis*

Rating scale	Symptoms		
	Inoculated tissues of seedlings		
	Leaflets	Stems	Field-grown plants
0	Nil	Nil	Nil
1	Very small, white discrete lesions	Slight chlorosis	Trace, 1 leaf symptomatic
2	White, discrete lesions	Chlorosis with limited necrosis	Slight, 2 leaves symptomatic
3	Coalescing lesions and chlorosis	Slight necrosis	Moderate, >2 leaves symptomatic
4	Light necrosis	Light brown necrosis	Severe, half plant affected
5	Increasing brown necrosis	Increasing brown necrosis	Very severe, half to whole plant affected
6	Severe necrosis	Severe necrosis	Stunted, with extensive collapse
7	Complete necrosis	Complete necrosis	Dead

Table 2. Disease severity in leaflets of tomatoes Heinz 2990, Morden, and Floradade inoculated with strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis*

Cultigen Inoculum concn (log_{10})	Disease severity[a]			
	Rate of increase[b]	r^2[c]	Final rating	Day of final rating
Heinz 2990				
2.8	<0.01	0.21	0.1	14
3.9	0.05	0.64	0.6	16
4.0	0.05	0.85	0.4	14
4.9	0.26	0.95	2.8	14
5.8	0.67	0.98	5.7	12
6.0	0.57	0.98	6.5	15
6.6	0.81	0.97	5.4	9
7.6	0.83	0.94	6.1	8
8.2	1.03	0.88	6.8	8
Morden				
2.8	0.04	0.69	0.6	14
4.0	0.22	0.93	2.4	14
4.9	0.55	0.99	5.7	14
5.8	0.76	0.95	6.9	12
6.6	1.04	0.94	6.9	8
7.6	0.82	0.85	6.8	7
Floradade				
3.9	0.17	0.92	1.9	17
6.0	0.83	0.96	6.9	12
8.2	0.99	0.86	6.9	8

[a] Severity rated on a scale of 0 (no visible necrosis) to 7 (complete necrosis of inoculated tissues).
[b] Linear rate (slope) of increase over time.
[c] Coefficient of determination of linear regression.

RESULTS

Optimum inoculum concentration for leaflets. Disease severity ratings of leaflets increased with days after inoculation in both H2990 and Morden (Table 2, Fig. 1). Visible disease occurred earlier when inoculum concentration was high. Except for the lowest inoculum concentration, disease ratings increased

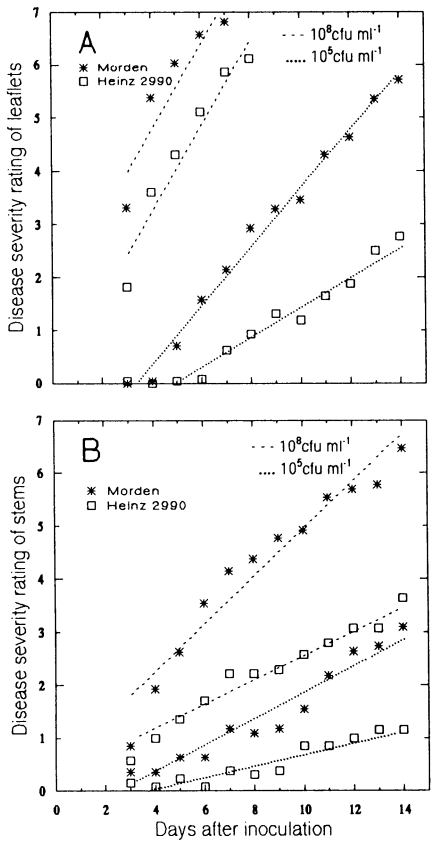

Fig. 1. Rates of increase in disease severity ratings of (**A**) leaflets and (**B**) stems of tomatoes Heinz 2990 and Morden following inoculation with approximately 10^5 and 10^8 cfu of strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis* per milliliter of suspension. Each rating point represents the mean of 14 plants.

approximately linearly over time, and coefficients of determination (r^2) ranged between 0.85 and 0.99. Rates of linear increase were lower for H2990 than for Morden except at the highest inoculum concentration (Table 2), and the difference between them was greatest at an inoculum concentration of 10^5 cfu/ml. Similar results occurred when Floradade and H2990 were compared at three concentrations of inoculum (Table 2). The rates of linear increase were lower for H2990 than Floradade inoculated with 10^4 and 10^6 but not 10^8 cfu/ml, and the greater difference between them occurred at 10^6 cfu/ml.

Optimum inoculum concentration for stems. Disease severity ratings of stems of both H2990 and Morden also increased with days after inoculation. Highest ratings occurred with the highest inoculum concentration, 10^8 cfu/ml (Table 3, Fig. 1). With the exception of the two lowest inoculum concentrations (10^3 and 10^4 cfu/ml), r^2 values ranged between 0.89 and 0.99. Rates of linear disease increase were lower for H2990 than for Morden at all inoculum concentrations, and the difference between them was greatest at 10^8 cfu/ml. With inoculum at 10^8 cfu/ml, ratings at day 14 were 6.5 and 3.6 for Morden and H2990 (Table 3, Fig. 1).

Similar results occurred when Floradade and H2990 were inoculated with three concentrations of bacteria. Rates of linear increase were lower for H2990 than for Floradade, and the greatest difference in ratings occurred with 10^8 cfu/ml at day 17 (Table 3).

Visible necrosis on both stems and leaflets occurred sooner in Morden and Floradade than in H2990 (Fig. 1) at all inoculum concentrations except the highest. On any one day after inoculation, ratings of disease severity in H2990 and Morden were about equal when tissues of H2990 received inocula with 10 times more bacteria than tissues of Morden.

Resistance in a segregating population. Mean disease severity ratings for both leaflets and stems of BC_3-S_2 progeny and Floradade and H2990 controls increased with days after inoculation, but at a lower rate in H2990 than in Floradade, and means for the BC_3-S_2 population were intermediate (Table 4). However, the r^2 values of disease ratings regressed against time differed widely between individual BC_3-S_2 plants (data not shown), and AUDPC values were used to compare plants. The frequency distributions of AUDPC values for leaflets and stems of the BC_3-S_2 plants were continuous and wide-ranging (Table 5). The AUDPC means were intermediate to those of H2990 and Floradade. More overlap of AUDPC values occurred for stems of H2990 and Floradade than for leaflets. The AUDPC values for leaflets and stems of plants of the BC_3-S_2 were weakly correlated ($r = 0.25$), but the correlation was slightly greater ($r = 0.35$) when data from all plants of H2990, Floradade, and BC_3-S_2 were included.

We selected 10 BC_3-S_2 plants for seed increase. Their AUDPC values for leaflets and stems averaged (± standard error) 26.1 ± 2.1 and 21.9 ± 3.0.

Resistance in field-grown plants. Disease severity ratings increased over time for plants of H2990, Floradade, and Morden (Fig. 2) after inoculation of field-grown plants. Ratings were higher for Floradade and Morden than for H2990 throughout the experiment, especially during the first 75 days, and from the time of flowering and fruit set reached high levels sooner for Morden than for Floradade. The AUDPC values differed significantly ($P < 0.01$) between the three cultigens, and averaged 131, 276, and 335 day-rating units for H2990, Floradade, and Morden.

The mean AUDPC values for plants of the 10 BC_3-S_3 families from selected BS_3-S_2 parent plants were significantly lower than for Grosse Lisse, and one (cultigen 283) was significantly lower than two others (cultigens 671 and 643, Table 6). The AUDPC values of six of the 10 cultigens (283, 562, 542, 661, 241, and 381; Table 6) were similar to those of H2990 in the adjacent experiment, described above (Fig. 2), whereas the AUDPC value of Grosse Lisse was similar to that of Floradade.

The mean AUDPC value (132 ± 3.6) of 186 plants of an unselected BC_3-S_2 population was significantly lower ($P < 0.01$) than the mean value of 27 plants of Grosse Lisse (185 ± 8.8), and wide variation occurred among them.

Table 3. Disease severity in stems of tomatoes Heinz 2990, Morden, and Floradade inoculated with strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis*

Cultigen / Inoculum concn (log_{10})	Disease severity[a] Rate of increase[b]	r^2[c]	Final rating
Heinz 2990			
2.8	0	0	0.1[d]
3.9	0.04	0.92	0.3[e]
4.0	0.03	0.71	0.3[d]
4.9	0.11	0.89	1.2[d]
5.8	0.25	0.96	2.6[d]
6.0	0.16	0.94	1.6[e]
6.6	0.30	0.99	3.6[d]
7.6	0.25	0.96	3.6[d]
8.2	0.29	0.97	3.9[e]
Morden			
2.8	0.08	0.58	1.3[d]
4.0	0.13	0.75	2.2[d]
4.9	0.26	0.94	3.1[d]
5.8	0.47	0.98	4.9[d]
6.6	0.42	0.98	5.4[d]
7.6	0.46	0.94	6.5[d]
Floradade			
3.9	0.13	0.96	1.4[e]
6.0	0.25	0.94	3.2[e]
8.2	0.44	0.96	6.0[e]

[a] Severity rated on a scale of 0 (no visible necrosis) to 7 (complete necrosis of inoculated tissues).
[b] Linear rate (slope) of increase over time.
[c] Coefficient of determination of linear regression.
[d] Final ratings were 14 days after inoculation for comparisons between Heinz 2990 and Morden.
[e] Final ratings were 17 days after inoculation for comparisons between Heinz 2990 and Floradade.

Table 4. Rates of increase in severity of disease in leaflet and stem tissues of tomatoes Floradade, Heinz 2990, and BC_3-S_2 inoculated with strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis*

Tomato cultigen[a]	Leaflets[b] Rate[c]	r^2[d]	Stems[b] Rate	r^2
Floradade	0.44	0.88	0.36	0.95
BC_3-S_2[e]	0.39	0.93	0.32	0.93
Heinz 2990	0.36	0.90	0.26	0.82

[a] Twenty-two plants each of Floradade and Heinz 2990 and 144 plants of BC_3-S_2 were inoculated.
[b] Leaflets and stems were infiltrated with inoculum of 10^5 and 10^8 cfu/ml, respectively.
[c] Linear rate (slope) of increase.
[d] Coefficient of determination of linear regression.
[e] Selfed progeny (S_2) of third backcross (BC_3) to cv. Grosse Lisse of the cross (Heinz 2990 × Grosse Lisse).

DISCUSSION

The three main symptoms of bacterial canker of tomato in Queensland are firing of leaves, bird's-eye spot of fruit, and wilting (12). Wilting may follow disease of leaf and fruit parenchyma. Aerial dispersal of bacteria and natural invasion of leaves may be equally as important in disease spread as direct invasion of vascular tissues exposed by wounds or pruning (8). The main thrust of our work was to evaluate the importance of resistance to disease in leaf and stem tissues using an infiltration method of inoculation because of its practicality in providing a rapid and discrete method for evaluating progeny.

Our evaluation of seedling resistance to bacterial canker by this method was sufficiently reliable to reflect field resistance in southern Queensland. We recommend the method for inclusion in the range of methods used by other workers (1,2,5,7,9,15). The main use would be to eliminate plants that are susceptible. In our experiments, progeny of selected seedling plants from a segregated backcross population were not all equally resistant in the field in comparison with their susceptible backcross parent.

Our technique selected among seedlings before flowering. However, flowering and fruiting phenology may subsequently modify disease severity in

Table 5. Percentages of plants in categories of areas under disease progress curves (AUDPC) following inoculations of leaflets and stems of seedlings of three tomato cultigens with strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis*

Tomato cultigen	Percentage of plants: Upper limit of AUDPC (in day-rating units)												Population mean ± SE of AUDPC
	<14	18	22	26	30	34	38	42	46	50	54	58	>58	
Leaflets[a]														
Heinz 2990	39	43	9	...	9	...	...	...	...	...	...	...	...	16.2 ± 0.9
Floradade	...	...	...	4	...	5	5	27	9	32	9	5	4	44.9 ± 1.8
BC_3-S_2[b]	...	2	9	12	10	15	20	13	8	7	2	1	...	33.7 ± 0.8
Stems[a]														
Heinz 2990	...	...	17	21	33	8	13	8	...	...	...	...	...	28.9 ± 1.4
Floradade	...	...	4	4	4	4	8	4	17	21	13	8	13	45.0 ± 2.5
BC_3-S_2	2	1	3	11	13	9	21	15	15	5	2	3	...	35.8 ± 0.8

[a] Leaflets and stems of each plant inoculated with approximately 10^5 and 10^8 cfu/ml, respectively.
[b] Selfed progeny (S_2) of third backcross (BC_3) to Grosse Lisse of the cross (Heinz 2990 × Grosse Lisse).

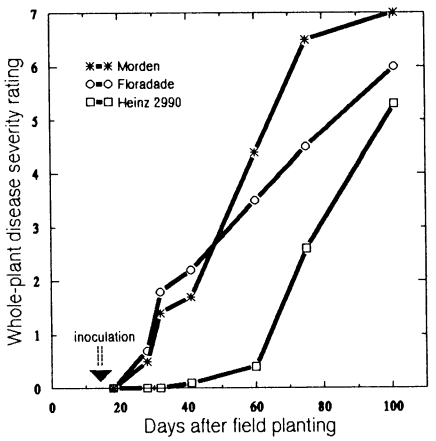

Fig. 2. Increase in disease severity ratings of tomatoes Heinz 2990, Floradade, and Morden in a field planting inoculated with strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis*. Each rating represents the mean of 48 plants.

Table 6. Mean area under disease progress curve (AUDPC) of field-grown plants of tomato cv. Grosse Lisse and 10 inbred backcross breeding lines (BC_3-S_3) inoculated with strain Q 1986 of *Clavibacter michiganensis* subsp. *michiganensis*

Tomato cultigen[a]	AUDPC means[b] (in day-rating units)
283	123 w
562	127 wx
542	135 wx
661	136 wx
241	138 wx
381	138 wx
171	159 wxy
163	160 wxy
671	167 xy
643	184 y
Grosse Lisse	242 z

[a] Numbered lines are selected selfed (S_3) third backcross progeny (BC_3) of Heinz 2990 and recurrent parent Grosse Lisse.
[b] Means not followed by same letter differ significantly at $P = 0.01$.

the field. The cultigens Morden, Floradade, and H2990 are all of determinate plant habit. Morden has the least vigorous bush, and it flowers and fruits earlier. Morden was more severely diseased than Floradade from the time that concentrated fruit set occurred. Tolerance, rather than resistance, may depend on phenology. This may be an important consideration in selection of genotypes with partial resistance, especially when comparing determinate and indeterminate cultigens.

The stem tissues of seedlings in our greenhouse experiments required a higher inoculum concentration (10^8 cfu/ml) than leaflets (10^5 cfu/ml) to most clearly show differences between cultigens. Confluent necrosis of inoculated areas of leaflets and stems occurred with inoculum of 10^5 cfu/ml (or greater), but the severity of necrosis increased faster in leaflets than in stems at that concentration. These results indicate that leaves are more sensitive to *C. m. michiganensis* than stem tissues and that both tissue types should be inoculated to evaluate resistance. The different sensitivities of leaf and stem tissues are reflected in the low correlation of AUDPC values computed from 144 BC_3-S_2 plants. Other research (6) also has noted a low correlation between symptoms on leaves and discoloration of stems of field-grown plants. Low incidence and severity of bacterial canker in leaves may be a reflection of plant genotype and be an important selection criterion.

The longer time required for disease symptoms to appear and to increase in H2990 seedlings showed their resistance compared with seedlings of Morden and Floradade. In the field, plants of H2990 also had lower disease ratings for a longer time. Under most circumstances, this type of resistance should result in more harvests and make production economical in areas prone to canker losses in susceptible cultigens. This yield advantage will be optimized where sanitation is used to eliminate sources of inocula and to delay the onset of an epidemic.

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