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Breeding transgressive lines of pepper for resistance to *Phytophthora capsici* in a recurrent selection system

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Summary

In order to increase the resistance level of pepper (*Capsicum annuum*) to *Phytophthora capsici* the main sources of genetic resistance were intercrossed. The parents included 7 varieties from different origins of partial resistance to *P. capsici* and to other soilborne pathogens. Two cycles of recurrent selection were performed by 7 plant breeders who screened the plants at two developmental stages with various isolates and at two temperatures. Analysis of data revealed a strong influence of the testing conditions on the evaluation of the plants. The level of resistance of the progenies further depended on the pathogen isolate used to screen the plants. Improvement of the whole population was more significant during the first cycle and lines with enhanced level of resistance as compared to the parents i.e. transgressive lines were fixed from the two cycles. These lines were resistant to much higher inoculum concentrations than the original parents and the expression of resistance was stable at high temperature (32° C). These new sources of polygenic resistance were included into a new breeding program to improve the agronomic characters.

Introduction

In plant disease control, the use of partial polygenic resistance is a relevant strategy when monogenic resistance is lacking or when the monogenic resistance is easily broken down by the pathogens. The recombination of genes controlling partial resistance components can lead to resistant (transgressive) genotypes and resistance can be progressively constructed thanks to the pertinent use of natural variability and 'conventionnal' breeding methods (Lecoq et al., 1982; Parlevliet, 1985; Pochard & Daubèze, 1989). It has been previously demonstrated that spectacular transgressions for resistance to *Verticillium* can be obtained from pepper (*Capsicum annuum*) varieties displaying only low susceptibility levels (Palloix et al., 1990).

In the case of *Phytophthora capsici* the causal agent of pepper root rot, several sources of resistance were found in local populations of *Capsicum annuum* from diverse origins (Smith et al., 1967; Saini & Sharma, 1978; Guerrero & Laborde, 1980; Barksdale et al., 1984; Peter et al., 1984; Matsuoka, 1985). Although these authors first reported that one or two genes controlled the resistance, further breeding practice demonstrated it to be more complex. Indeed, it remains very difficult to introduce *Phytophthora* resistance into susceptible cultivars. A resistant variety backcrossed to a susceptible bell pepper cultivar leads to a decrease of resistance with threshold effects. The resulting varieties show a lower resistance level than the resistant parent probably due to the loss of secondary resistance genes. Further studies (Pochard & Dau-

bèze, 1980, Pochard et al., 1983) showed that the resistance is under polygenic control and can be divided into several genetic components that are unequally distributed among the varieties. Resistance sources are partial and can be overcome by aggressive strains of the fungus (Clerjeau et al., 1976; Pochard & Daubèze, 1980), or at high temperatures (Pochard et al., 1983) or by high inoculum concentrations (Palloix et al., 1988b).

As the classical backcross method was unsuccessful another breeding strategy was considered and performed in collaboration with six private breeders: the recombination of resistance genes of the varieties was promoted in a source population in order to increase their general resistance level. In this population, varieties were included that showed resistance to two other soilborne pathogens that may be simultaneously present in the soil: *Verticillium dahliae* and *Meloidogyne* nematodes. In a second step, genes for agronomic quality will be progressively introduced in this population.

This paper reports the results of the first step of the program: progress of the source population for resistance to *P. capsici* during two recurrent cycles, and evaluation of the new resistant lines originating from this population.

Materials and methods

Breeding program

Seven pepper lines (P0 to P6) from different origins were included in the program. Resistance levels, identification and origin of these lines are indicated in Table 1. A schematic representation of the breeding program has been published previously (Palloix et al., 1990). Six parental lines (P1 to P6) were crossed to the seventh (P0) and the resulting F1 hybrids were selfed to form the PVN 0 population. This population was divided into two equal subpopulations: one was screened for resistance to *P. capsici,* the other for resistance to *V. dahliae.* The recurrent selection cycle included one intercrossing between these two subpopulations followed by one selfing. Plants were screened either for resistance to *P. capsisi* or for resistance to *V. dahliae* after each crossing and selfing. The intercrossing was performed by hand pollination of the plants using a pollen mixture collected on the plants from the two subpopulations, promoting genetic exchanges between the *Phytophthora* resistant and the *Verticillium* resistant plants.

Two cycles of recurrent selection were achieved by seven breeders in various seed companies and INRA. After each crossing or selfing, seeds obtained by each breeder were collected, mixed together and randomly distributed to every one. At each generation, each breeder screened 1200 plants for resistance to *P. capsici* and selected 12 elite genitors for the next generation.

Inoculation procedure and symptom evaluation

Resistance was tested with three different isolates

Table 1. Original parents of the population, resistance factors and origin

Parent	Code	Resistance factors		Origin
		V. dahliae	*P. capsici*	
PM 217	P0	r	R	PI 201234 (P.G. Smith, USA)
PM 701	P1	S	R	L 29.6 (A. Guerrero INIA Mexico)
PM 702	P2	r	R	Criollo de Morelos 334 (‘ ’)
PM 687	P3	S	r	PI 322 719 (G. Sowell, USA)
PYC 22.2	P4	S	S	Conic (Malasia)
PM 659	P5	S	r	Perennial (J. Singh, Lhudiana, India)
PM 700	P6	r	S	Podarok Moldavii (M. Lobb, USSR)

(R = resistant, r = low resistant level, S = susceptible).

of *P. capsici* (S 73, S 107, S 197) showing different pathogenicity levels (Clerjeau et al., 1976; Pochard & Daubèze, 1980). Plants were first tested at the plantlet stage by root inoculation and later the surviving plants were tested again by stem inoculation at high (32° C) or at low temperature (22° C). Each breeder performed the two successive tests with one single isolate and at one temperature.

Root inoculation of the plantlets

Inoculation and disease evaluation procedures were published elsewhere (Palloix et al., 1988a). Two weeks old plantlets grown in a growth chamber (12 h light, 22° C) were uprooted. Roots were washed in tap water and the plants were transfered into glass containers for culture on a nutritive solution. Seven days later, mycelium plugs (4 mm diameter) of *P. capsici* isolates grown on V8 agar medium in petri dishes, were taken off at the margin of the colonies and were put into the nutritive solution of the plants. Disease severity was assessed seven days later. Plants were individually sorted into six symptom classes (0 to 5) according to the extend of root necrosis. Analysis of results was performed by calculating the mean disease index (DI) for each set of plants and comparing the distributions in symptom classes, or by comparing the proportions of healthy plants (classes 0 and 1).

For zoospore inoculations, the procedures were similar, except that dipping the mycelium plugs was replaced by soaking the roots of plants during one hour in zoospore suspensions obtained as indicated by Molot et al. (1976).

Stem inoculation of plants

When plants surviving the root inoculation test reached the first-branched flowering stage, they were inoculated as indicated by Pochard & Daubèze (1980): plants were detopped below the first flower, a mycelium plug of *P. capsici* was put on the cutting of the stem and wrapped in an aluminium sheet. The progression of necrosis due to fungal infection of the stem was measured every three to four days and the speed of fungal invasion (mm/day) was calculated. The changes with time of this speed allowed to evaluate the resistance of the plant. Stem inoculation was performed in a growth chamber, 12 h light, either at 22° C or 32° C depending on the breeder.

Results

Evaluation of the population during two cycles of selection

Distributions of the population in symptom classes after root inoculation by the isolate S 197 are shown in Fig. 1. Comparisons of these distributions with the Kolmogorov-Smirnov test showed that they all differ from each other at the 1% level of significance. In the PVN 0 population, resistant and susceptible genotypes segregated with a low proportion of resistant plants: only 28% of plants are included in the 0 and 1 classes. However after the first intercrossing cycle, the PVN 1 population contained an increased number of resistant plants (58%) and the selfing of these plants eliminated most of the susceptible genotypes: 77% of the plants from the PVN1 I1 population are resistant (classes 0 and 1). The second intercrossing lead to the PVN 2 population with an important proportion of susceptible plants (47%). However after selfing, 81% of plants from the PVN2 I1 population were highly resistant.

The distributions of the control variety P2 in the populations were not significantly different except in PVN1 I1 were P2 was slightly more affected.

Evaluation of the screening tests

During the two intercrossing cycles progenies from plants screened by the three *P. capsici* strains were harvested and tested separately. In the second cycle the temperature of the test was also recorded whereas in the first cycle progenies were recorded according to their female parental origin (original cross and F2 family in PVN 0). Data collected from every breeder were analysed, allowing the evaluation of a third source of variation: the experimenter.

Tables 2 and 3 show the analyses of variances of

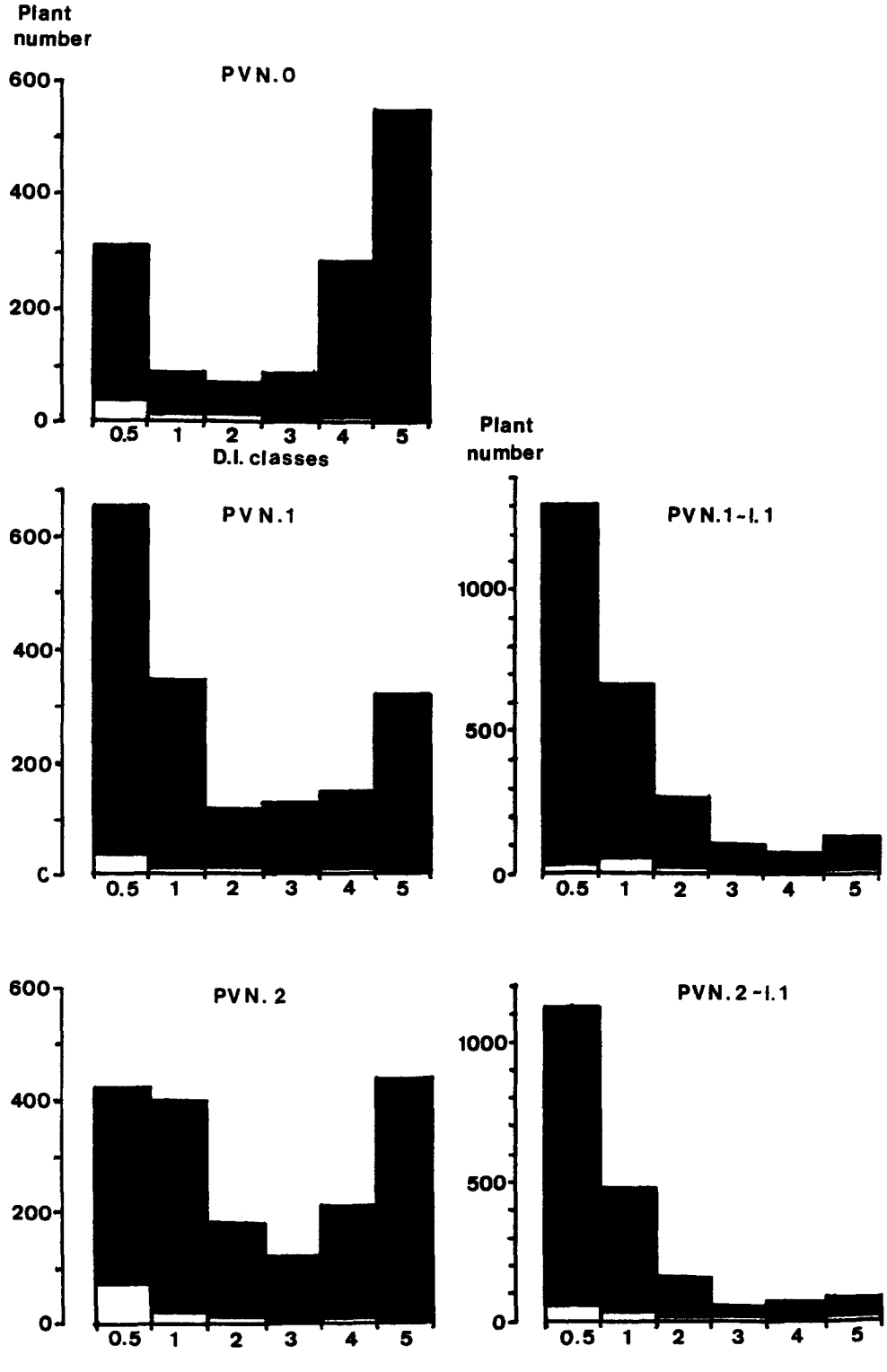

Fig. 1. Distribution of the population in disease index (DI) classes during the cycles of selection. DI was evaluated after root inoculation of the plantlets by the isolate S 197. White bars: distribution of the control (resistant parent P2).

Table 2. Analysis of variance of the percentage of resistant plants (classes 0 and 1) in the PVN 1 population

Source of variation	D.F.	Mean square	F-value	Probability
Total	89	9167.4		
P. capsici isolate	2	804.5	3.3	0.048
Experimenter*	4	11768.8	48.4	0.000
Parental origin	5	1497.9	6.2	0.000
isolate × Experim.	8	127.8	0.5	0.831
isolate × Parent.	10	557.9	2.3	0.031
Experim × Parent.	20	454.2	1.9	0.046
Residual	40	243.2		

Percentages were transformed into arcsin before analysis.
* Only 5 experimenters delivered analysable data.

the percentages (after arcsin transformation) of plants noted 0 and 1 after root inoculation of the PVN 1 and PVN 2 populations. In both populations, effect of the experimenter on the evaluation is highly significant. Influence for the *P. capsici* strain used to screen the parental plants on the level of resistance of the progenies is also significant in both cycles of selection but the effect of the temperature was not detected in the second cycle. In the PVN1 population we also observed a significant influence of the parental origin of the progenies. Interactions between the *P. capsici* strain and the parental origin and between the experimenter and the parental origin were also significant in the PVN1 population, showing that the families were not screened similarly by the different strains and were not evaluated similarly by the different experimenters.

Comparison of the treatment means (Newman-Keuls test) showed that the screening of parental plants by the strains S 917 and S 107 lead to the highest proportions of resistant plants in the progenies (Table 4).

The Table 5 shows that the hybrids (P0 × P2) and (P1 × P0) produced the most resistant progenies whereas (P4 × P0) and (P0 × P3) were intermediary and progenies from (P6 × P0) and (P0 × P5) were the less resistant.

Evaluation of the transgressive lines

The mean disease indices (DI) of the selfed-progenies from plants of the PVN 1 and PVN 2 populations are shown in Fig. 2. Most lines display a similar or lower DI than the resistant parents P0, P1 and P2. Comparisons of the distributions of the lines in DI classes (Kolmogorov-Smirnov test, p =

Table 3. Analysis of variance of the percentage of resistant plants (classes 0 and 1) in the PVN 2 population

Source of variation	D.F.	Mean square	F-value	Probability
Total	35	508.7		
P. capsici isolate	2	780.1	5.3	0.027
Temperature	1	23.5	0.2	0.698
Experimenter*	5	2206.9	15.0	0.000
isolate × Temperat.	2	190.3	1.3	0.316
isolate × Experim.	10	218.1	1.5	0.271
Temper. × Experim.	5	231.5	1.6	0.252
Residual	10	146.8		

Percentages were transformed into arcsin before analysis. The effect of parental origin was not analysed at that generation.
* Only 6 experimenters delivered analysable data.

0.05) showed that 7 lines from PVN 1 and 15 lines from PVN 2 population had significantly lower average DI than P2.

In the PVN 1 population we attempted to determine the origin of these transgressive lines. Inbred lines from the six families (6 to 9 lines per family) were ranged according to their mean DI and the six families were compared two by two using the rank comparison test (Mann-Whitney U test) (Table 6). Results show that crosses with P2 produced the most resistant inbred lines, crosses with P1 and P4 produced lines with intermediary resistance and crosses with P3 and particularly P5 and P6 the least resistant lines. These two last families never produced lines with higher resistance than P2.

After four selfed-generations in PVN 1 and three selfed-generations in PVN2, four of the most resistant lines from every cycle of selection were inoculated on the roots with increasing inoculum concentrations (isolate S 197). From the relationships between inoculum concentration and mortality in log-probit scale, regression curves were calculated and the inoculum concentrations necessary to kill 50% of the plants were intrapolated (Table 7). Correlation coefficients were highly significant for all the lines and parents ($p < 0.001$). Slopes of the regression lines varied from 0.73 to 1.27 for the lines from the population and from 0.77 to 1.22 for the parents. However the LD 50% were highly variable: LD 50% of the resistant parents run from 173 to 1100 zoospores/ml, whereas LD 50% of the PVN1 I4 lines run from 3020 to 15380 zoospores/ml and those of the PVN2 I3 lines run from 8500 to 38440 zoospores/ml, suggesting a quantitative transgression.

Table 4. Mean percentage of resistant plants (classes 0 and 1) in the progenies of plants that were screened by the different isolates (S 197, S 107, S 73) at the two selection cycles

Screening isolate	PVN 1	PVN 2
S 197	37.8 a*	61.9 a
S 107	38.3 a	53.0 ab
S 73	31.9 b	48.2 b

* Different letters in the same column indicate significantly different means (Newman-Keuls test of arcsin transformed data, $p = 0.05$).

These lines where also inoculated on the stem with the same isolate (S 197) and at 32° C. Lines from the first cycle (Fig. 3) always showed a high initial speed of fungal invasion similar to that of the parents P0 P1 and P3 (9.5 to 12 mm/day). However the decrease was very steep and the fungus was stopped between the 10th and the 14th day after inoculation, whereas the fungal progression fluctuated between 0 and 0.5 for P2 and decreased very slowly in P0 and P1. Partially resistant varieties like P3 or P5 displayed a susceptible behaviour under these conditions of inoculation. Some lines from the second cycle (Fig. 3) displayed a low initial speed of fungal invasion (4.5 to 6 mm/day). The decrease was also steep, stopping the fungal growth between the 7th and the 14th day. This induced fungistatic activity was stable during the following days, except for the lines that displayed a low initial speed.

Discussion

The objective of this work was to combine the various resistances to *P. capsici* identified in several varieties in order to increase the general level of resistance and to stabilize its expression against very aggressive strains, high inoculum levels and at high temperatures. We assume that it was possible thanks to the use of different conditions of selection. However, it involved some problems concerning the collation of the observations and the

Table 5. Mean percentage of resistant plants (classes 0 and 1) of the different families of the PVN 1 population

Parental origin	% classes 0 & 1
P1 × P0	42.7 a*
P0 × P2	46.1 a
P0 × P3	37.7 ab
P4 × P0	37.2 ab
P0 × P5	24.0 c
P6 × P0	29.5 bc

Parental origin is the maternal origin of PVN 1 plants in the PVN 0 population.

* Different letters indicate significantly different means (Newmann-Keuls test of arcsin transformed data, $p = 0.05$).

analysis of results. Indeed the evaluation of the population was significantly affected by the experimenters at every selection cycle. This should not be surprising since they all used different screening conditions i.e. pathogen strain and temperature. However, the successive generations of selection did not allow to repeat the ranking of the experimenters suggesting that the major part of this source of variation was uncontrolled. Moreover everyone did not deliver analysable results from every test so that it was not possible to evaluate the progress from cycle to cycle for resistance to the three isolates.

Nevertheless the results showed that screening simultaneously for different *P. capsici* isolates was useful. In both selection cycles the resistance level of the progeny depended on the strain used to screen the parental generation. Selection by either strain S 197 or S 107 lead to more resistant progenies. The differences between these isolates for virulence cannot be evaluated because of the experimenter effect. However previous studies (Pochard & Daubèze, 1980; Pochard et al., 1983) reported that S 197 and S 107 were more agressive than S 73 on susceptible and partially resistant plant. We also detected a significant interaction between the isolate and the families of the PVN1 I1 population showing that progenies from different crosses did not respond similarly to selection by different isolates. Specific interaction between host and isolate genotypes ocurred showing that general resistance in the population involves not only additive but also interactive gene actions. Such host-pathogen relationships involving polygenic resistance was reported and interpreted by Parlevliet & Zadoks (1977) who showed that horizontal resistance can result from several genes with vertical effects. These observations emphasized the usefulness of performing various tests and exchanging the seeds in order to avoid the selection of a resistance directed toward one single isolate.

The progress of the population for resistance to the isolate S 197 did not seem continuous. The increase of resistance was strong between PVN 0 and PVN 1 but the proportion of resistant plants decreased in PVN 2. Irregularities in recurrent selection have been described in other systems (Leng, 1961; Vear & Tourvieille de Labrouhe, 1984). It may result from phenotypic variability: improvement seems continuous over a large number of cycles of selection but individual generations may display reversed tendencies. The lack of improvement can also be attributed to genetic causes: a strong selection pressure reducing the variation of the population may have resulted in too little

Table 6. Mean ranges of the families of PVN 1 I1 lines

Parental Origin	Number of lines	Mean range	U-Test
P1 × P0	5	12.4	ab*
P0 × P2	9	11.2	a
P0 × P3	6	20.0	bc
P4 × P0	5	16.0	ab
P0 × P5	6	25.5	c
P6 × P0	5	27.0	c

PVN1 I1 lines were ranged according to their mean DI and the mean ranges presented are the averages of the ranges of the lines from each family.

* Different letters indicate significantly different mean ranges when families are compared two by two using the Mann-Whitney U-test ($p = 0.05$).

Table 7. Relationship of percentage mortality to inoculum concentration and DL 50% for the resistant parents and the most resistant PVN1 I4 and PVN2 I3 lines inoculated by the strain S 197

Genotype	Correlation coefficient	Regression coefficient	DL 50%
P0	0.99	0.77	173
P1	0.99	1.22	308
P2	0.98	0.73	1100
PVN1 I4 Lines:			
L1-1	0.96	0.90	3020
L1-2	0.98	1.13	7320
L1-3	0.96	1.27	9180
L1-4	0.99	0.93	15381
PVN2 I4 Lines:			
L2-1	0.98	0.76	8500
L2-2	0.99	0.74	15800
L2-3	0.99	1.06	20530
L2-4	0.98	0.90	38440

Regression parameters were calculated after log-probit transformation and values of DL 50% (in zoospores/ml) were intrapolated on the regression lines.

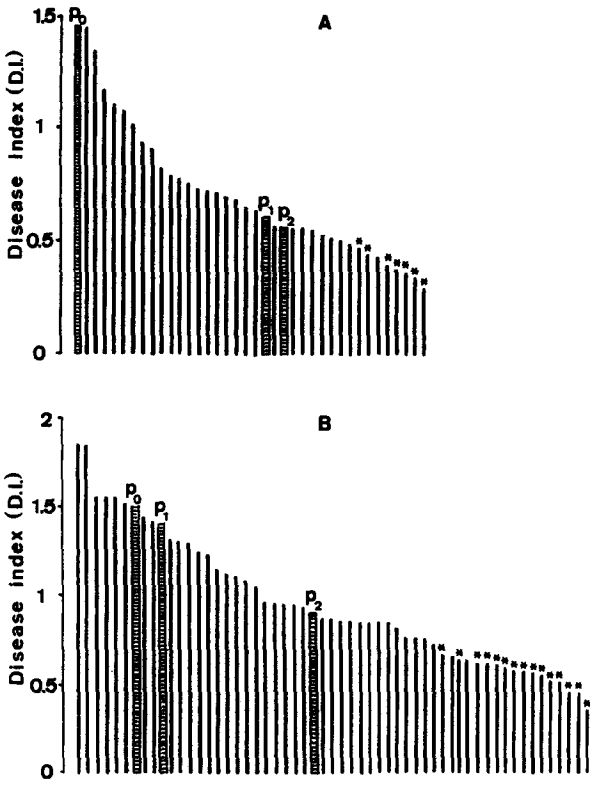

Fig. 2. Mean disease index of PVN1 I1 (A) and PVN2 I1 (B) lines after root inoculation of the plantlets by the isolate S 197. Each black bar represents the self progeny of one PVN plant. Hatched bars are the original resistant parents P0, P1 and P2. * lines showing a significantly different distribution and a lower DI than the most resistant parent P2.

recombination. However, in our case the genetic diversity might have been restored at each intercrossing since only half the number of plants of the population was screened for resistance to *P. capsici* while the other half was screened for resistance to *V. dahliae*. Thus, the apparent lack of improvement can result from crosses with *Verticillium* resistant but *Phytophthora* susceptible plants. Moreover after two intercrossing cycles, at most five of the seven parents may have been involved in the ancestry of PVN 2 plants indicating that new gene combinations can be expected from further intercrossing cycles.

Although the progress of the populations was irregular, many lines are being fixed from the two cycles that show a higher resistance level than the parents of the population (transgressive lines). A quantitative evaluation of these transgressions is possible by comparing the mortality due to a range of increasing inoculum concentrations. Lethal doses (LD) 50% of the resistant parents of the population run from 173 to 1100 zoospores/ml for the isolate S 197. These values are very close to those obtained in previous work (Palloix et al., 1988b) suggesting that infection levels were similar. For the most resistant lines of the population the LD 50% values run from 3500 to 38000 zoospores/ml. The slopes of the regression lines of mortality/inoculum concentration after log-probit transformation are very similar or slightly higher for the lines (0.74–1.27) than for the parents (0.73–1.22). According to Baker (1971) and Van der Plank (1975) slopes lower than 2 after log-probit transformation indicate that the ratio mortality/inoculum decreases when inoculum increases i.e. the spores are in competition for infection. The regression coefficient in Table 8 are closer to 1 than to 2 and confirm previous observations (Palloix et al., 1988b), that a strong competition between spores occurs for infection of resistant varieties. When inoculated on the stem at high temperature, the initial speed of fungal progression (receptivity) was similar to or higher than that of the most resistant parents except for some lines from the second cycle, showing that progress for this component of resistance was slight. The selected lines were remarkable for the steep and rapid decrease of the speed of fungal growth (induction of resistance). The low speed of fungal growth was then maintained at similar or lower rates than for P2 suggesting that the induced resistance mechanisms were stable despite of the high temperature.

In the *Verticillium* resistant population, the origin of the transgressions was not foreseeable: most of the transgressive lines were obtained from crosses involving susceptible plants (Palloix et al., 1990). Concerning resistance to *P. capsici,* most of the transgressive lines from the first selection cycle came from crosses between the resistant parents: P0 × P2 and P1 × P0, suggesting that the genes of major effects brought by these varieties are necessary and complementary for resistance expression. However the progenies of hybrids including P4 also produced transgressive lines, suggesting that sec-

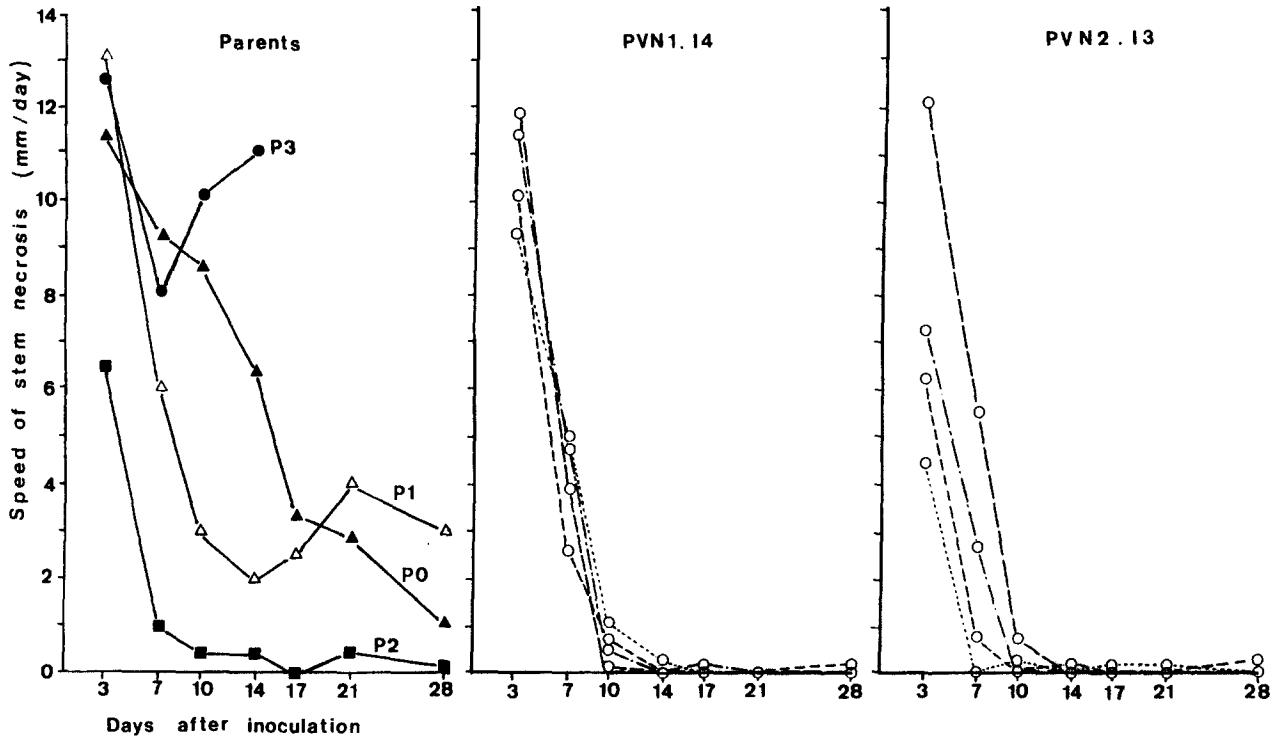

Fig. 3. Changes of the speed of stem necrosis with time after stem inoculation at 32° C by S 197 for the original parents P0, P1, P2 and P3, for four lines from the PVN1 and four lines from the PVN2 populations (4th. and 3rd. selfed-generations respectively).

ondary genes for resistance were also present in this apparently susceptible variety.

The new lines obtained are characterized by an enhanced level of resistance against several isolates, but they produce small pungent fruits with various shapes and colors. They will be included into a further breeding program in which genes for agronomic value will be introduced.

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