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Variability in virulence and the race concept in Phytophthora infestans (Mont.) de Bary

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Variability in virulence and aggressiveness was studied in 102 single zoospore isolates originating from 4 field isolates of *Phytophthora infestans*. Field isolates appeared to be mixtures of a wide spectrum of phenotypes differing in both characters as mentioned above. Race concept in *P. infestans* has been discussed.

INTRODUCTION

Late blight of potato caused by *Phytophthora infestans*, which in 1845-1846 was responsible for starvation in Ireland of more than two million people, since then became economically one of the most important diseases of potato in the world. Thereafter, many scientists devoted their lives to study the problems of resistance against late blight and biology of the fungus.

Two types of resistance have been distinguished in potato: vertical, determined mono- or oligogenically and horizontal resistance, determind polygenically (Van der Plank 1963). This classification system had a great impact on terminology used in biological and genetic studies of *P. infestans*. Respectively, the term virulence corresponds with vertical and aggressiveness with horizontal resistance.

The most researchers studying various aspects of *P. infestans* assume that the interaction between potato and *P. infestans* is based on the "gene for gene" theory proposed by Flor for flax and flax rust system (Sidhu 1975). So far, 11 major genes (called R genes) controlling vertical resistance in potato have been detected and 11 complentary genes controlling virulence in *P. infestans*. Thus, theoretically, 2^n races may appear in the fungus. In breeding potatoes resistant against late blight since early twenties to the late

fifties different wild *Solanum* spp. (mostly *S. demissum*) were used as a source of resistance controlled by R-genes. This has finally resulted in an almost complete disappearance of multigenic resistance from potato varieties of that time, which caused an immediate breaking down of vertical resistance by newly emerging races of the fungus. In early sixties potato breeders started to indroduce horizontal (multigenic) resistance to newly created cultivars. This type of resistance as controlled polygenically is considered durable or at least difficult to overcome by the fungus. However, the breeders have been continuing the use of *Solanum* species such as *S. demissum*, *S. microdontum*, *S. verrucosum*, *S. phureja*, *S. stenotomum*, *S. chacoense*, *S. yungasense*, *S. tariense*, *S. gourlayi*, *S. vernei* and many others to raise the level of resistance against late blight, to viruses as well as to enrich their materials in oter characters. According to Umaerus (1973) and Graham (1963), at least *S. vernei* and *S. verrucosum* are carrying R-genes. The breeders have also been using in their programmes old potato varieties carrying R-genes. Thus, it appears that there still exist possibility to introduce these genes into the breeding material. Therefore, it seems necessary to use in the selection procedures isolates of the fungus carrying combination of all known virulence genes to compensate the effect of R-genes if present in the material, and reveal the level of horizontal resistance. Unfortunately, *P. infestans* as the other representatives of *Peronosporales* is highly variable, which makes selection of isolates with stable virulence at least very difficult.

Variation in virulence of *P. infestans* was reported by many authors (Waggoner, Wallin 1952; Thurston 1961; Wilde 1961; Upshall 1968; Leach, Rich 1969; Caten, Jinks 1968; Denward 1970; Malcolmson 1970; Swiszczewska et al. 1971; Shaw et al 1973; Shattock 1976; Shattock, Shaw 1976; Shattock et al. 1977; Pietkiewicz et al. 1975; Pietkiewicz, Piotrowski 1976; Pietkiewicz 1978ab; Tooley et al. 1986). Results of their studies are difficult to synthesize, probably because of major differences in methods of isolation and maintaining the fungus in culture both before and during the experiments. More information on variation potential both within a population of *P. infestans* as well as within a pathotype may be delivered via analysis of single zoospore cultures. This has been followed by rather a small number of reseachers. For *P. infestans* it was reported by Graham (1955), Wallin (1957), Gallegly, Eichenmuller (1959) and Caten 1970, 1971). All the authors as cited above except of Graham observed marked variation in virulence among single zoospore isolates. Graham found suprising stability in virulence among 100 single zoospore cultures. However, the authors as mentioned above used the differentials carrying single R genes, usually R1-R4, which made a complex analysis of virulence impossible and this because of two reasons:

1. single R gene differentials do not alow to find out, whether we have to

do with a simple or complex race or with a mixture of simple or complex races.

2. the use of R1 and R4 made the whole analysis at least ambigous, since race 1 and 4 and their combinations dominated those days *P. infestans* population in the world.

Keeping in mind that we still do not know how many R genes are available in *Solanum* spp. used in various breeding programmes, we are rather unable to say with how complex host genotypes and with how complex races in the fungus we have to do.

There were more reports on variability in virulence in other members of the genus *Phytophthora* (Ruthefored et al. 1985, Hilty, Schmithenner 1962 in *P. megasperma* var. sojae; Budenhagen 1958, Kennedy et al. – 1986 in *P. cactorum*). Similarly as in *P. infestans* a great variation in virulence among single zoospore cultures was observed.

The purpose of this study was to have a closer look at variability in virulence among single zoospore isolates originating from a field isolate as well as to look at the variation in this respect of single zoospore isolates coming from the same colony. It was also attempted to estimate stability of *P. infestans* phenotypes in subsequent generations as well as depending on the medium which the isolates were passed through.

MATERIAL AND METHODS

The experiments were carried out at Mlochow in 1986-1987. Four field isolates were used in the study (Tab. 1) Before the experiments were started, the isolates were maintained for 3-6 months in culture on rye agar. Single zoospore isolates were obtained according to Caten and Jinks (1968). In total, 102 single zoospore isolates (further called clones) were studied, including 11 of them in two subsequent generations and 12 after a single passage through leaves of the potato susceptible variety "Tarpan". Virulence (understood as a specific pathogenicity) was tested against 20 Black's differential genotypes obtained from SVP Wageningen, The Netherlands, which are listed below:

r	R5	R11	R2R4
R1	R7	R1R3	R1R2R3
R2	R8	R1R4	R1R2R4
R3	R10	R2R3	R2R3R4
R4	R1R2	R3R4	R1R2R3R4

Virulence of a clone was assessed on 3 detached leaves of each of 20 differential genotypes which made in total 60 leaflets per clone. The differentials were grown in the glasshouse in the spring and early summer.

Table 1

Characteristic of *P. infestans* isolates used in the study

Isolate no in collection	Origin of the isolate	Initial virulence (1986)	Virulence verified in 1987
MP 201	Netherlands*	0	1.2.3.4.10.11
MP 202	Netherlands*	4	1.2.3.4.10.11
MP 118	Poland S.E.	1.2.3.4.5.7.8.10.11	1.2.3.4.5.10.11
MP 121	Poland S.E.	1.2.3.4.5.7.8.10.11	1.2.3.11

* IPO Wageningen

The leaflets were detached from the middle part of a plant 5-6 weeks in age and their lower surfaces were inoculated by placing agar discs 5 mm in diameter covered with sporangiophores. After 6-8 days of incubation at 15°C and 100% R.H. appearance of regular sporulating lesions was noted, which was considered as an expression of virulence of the clones. In 1986, aggressiveness of 48 clones deriving from two field isolates was tested against susceptible potato variety using the same inoculation technique as described above. Lesion area in mm^2 was accepted as a measure of this character. Results are presented in tables according to the international nomenclature of virulence genes as proposed by Black et al. (1953).

RESULTS

Virulence and aggressiveness of clones studied in this experiment was found to vary in majority of cases. Most clones differed in virulence from their parent. Expression of single or complex or single and complex virulence genes was shown in the clones. Big differences were also noted in virulence of clones coming from the same race and colony. These differences ranged from avirulence (inability to infect any genotype, r (recessive) included) to a high virulence complexity (Tables 2-4). Clones of the same field isolate tested in subsequent years showed quite different virulence spectrum in comparison to the first year testing (Tables 3, 4).

Most frequently, virulence genes 4, 1.4 and 1.2 were expressed, reaching about 20%, 14% and 12%, respectively. The genes as mentioned above and their combinations dominated the population of the fungus under study, and constituted ca 46% of all combinations observed in the experiment. The frequency of remaining gene combinations ranged from about 0.6% to 0.9% (Table 5). Suprisingly high frequency of so called higher virulence genes was

Table 2

The pattern virulence in the clones of *P. infestans* originating from the Polish field isolate MP 121

Clone No	Expression of virulence in the clones grown on	
	rye agar	potato leaves*
1	1+4+1.2+1.4+2.4	1+4
5	1+4+1.4	1+4+10+1.4
6	1+4+1.2+1.4+2.4	1+4+1.4
9	1+4+1.2+2.4	1+4+1.4
12	1+4+11+1.4+2.4+2.3.4	4+11+1.4
13	1+4+1.4+2.4	1+4+1.4
16	1+4+7+1.2+1.4+2.4+2.3.4	1+4+1.4
17	1+3+4+1.4+2.4+1.3.4	nt
18	1+4+5+1.4	1+4+1.2+1.4
20	1+4+1.4+2.4	1+4+1.4
23	1+4+1.4+2.4	1+4+1.4
26	1+4+1.4	1+4+1.4
28	1+4+1.4	1+4+1.4
Control**	1+4+1.4+2.3+2.4	

* the clones were passed once through leaves of potato susceptible cv "Tarpan"

** parent isolate maintained on potato tuber slices

noted in the study, i.e. genes numbered 5-11, especially when taking into account that complementary R-genes are rather lacking in the Polish potato varieties. For instance, the frequency of virulence gene 7 was 2.6% and that of virulence gene 11 was ca 6% (Table 5). Analysis of virulence in two subsequent generations of clones revealed that this character varied dramatically in the second generation. For instance a clone showing avirulence in the first generation behaved as the race 1.2.3.4.7 in the second one (Table 6).

There were also large differences in aggressiveness among clones of the same field isolate ranging from a complete lack of disease symptoms to a large sporulating lesions reaching in a few cases over 900 mm^2 which means the surface of a middle size leaflet (Tables 3 and 4). Preliminary experiments on the influence of the medium, through which the fungus was passed before testing for virulence, revealed marked reduction of virulence spectrum and an increase of virulence homogeneity after a single passage through leaves of susceptible potato variety. Eight clones of 12 studied behaved as a mixture of races 1.4 and 1 and 4. The remaining ones but one have also expressed additional virulence characters (Table 2).

Table 3

The pattern of virulence in clones of the Dutch *P. infestans* isolate MP 202 (in 1986)

Clone No	Expression ofvirulence		Abgressiveness mm^2 (1986)
	in 1986	in 1987	
1	0	avirulent	900
2	4+1.4	4+2.4	700
3	4	4+2.4	830
4	4+1.4+7	4+1.4+2.4+1.2.3.4	nt
5	0	1.4+2.4	800
6	1.2	4+7+1.2+1.3.4+2.3.4	690
7	4	avirulent	830
8	1.2	1+4+11+1.3+1.4+2.4	640
9	4	1.4+2.3	940
10	avirulent	nt	np
11	avirulent	3+4+1.4+2.3+2.4	np
12	1.2	4	820
13	4+11	3+4+11+1.2+1.3+1.4+2.3+2.4	740
14	4+1.2	3+4+1.2+1.3+1.4+2.3+2.4	570
15	11+1.2	3+4+11	780
16	avirulent	4+1.3+1.4+2.3+2.4	np
17	4+1.2	1.4	800
	nt	4+7+1.4	nt
	nt	4+1.4	nt
	nt	3+5+1.4	nt
	nt	4+11+1.4+2.3	nt

nt – not tested

Table 4

The pattern of virulence in the clones of the Polish *P. infestans* field isolate MP 118 in the two consecutive years

Clone No	Expression of virulence		Aggressiveness in mm^2 (1986)
	in 1986	in 1987	
1	5+1.4	4+11+1.2	600
2	1+4	1+3+4+1.2+1.4	420
3	4	4+2.3	250
4	4	1+3+4+1.4	320
5	1+4+1.2	3+1.4	160
6	4+1.4	3+5+1.2+1.4+1.2.3	760
7	0	7+1.4	520
8	0	3+1.4	150
9	1+4+7	nt	370
10	1.2.3	4+1.2+2.3+1.2.3.4	360

Table 5

The frequency of the virulence genes in the single zoospore progeny of four *P. infestans* isolates

Virulence genes	Per cent (approximate)	Total percentage in groups (approximate)	
0	4.24		
1	4.74		
2	0.00		
3	6.03		
4	19.83		
1.2	11.64		
1.3	4.31		
1.4	13.79	single genes	48.90
2.3	6.90	double genes	40.95
2.4	4.31	triple genes	7.76
1.2.3	2.16	quadruple genes	0.86
1.2.4	0.00	avirulence genes	2.59
1.3.4	1.72		
2.3.4	3.88		
1.2.3.4	0.86		
5	3.88		
7	2.59		
10	1.29		
11	6.03		
avirulence	2.59		

Table 6

The pattern of virulence in the two subsequent generations of clones originating from the Dutch isolate MP 201

Clone No	First generation	Second generation
3	1.3+2.4	1+4+1.2+1.4+2.3+2.4
5	0	3+2.3
6	3+10+1.2	1.4+2.3
7	0	11+1.4+2.3+2.3.4
10	avirulent	3+7+1.4+2.3+2.3.4
11	avirulent	0
13	nt	1.4+2.3
14	10+1.4	1+41.4
16	1+4+11	4+1.4+2.3
17	1.4	1+3+1.4
24	3	1.4+2.3

nt = not tested

DISCUSSION

Studies on variation in virulence of *P. infestans* and other members of the genus *Phytophthora* at the vegetative level, especially those via single zoospore cultures are considered difficult. These difficulties are mainly logistic ones (Rutheford et al. 1985). To get a holistic picture of virulence of an isolate, it seems necessary to make several clones of it and then to test them against a large amount of plant material in several replications (best, in an experiment statistically designed). However, such an approach seems to be unrealistic for an average in size laboratory. It means that the choice of a proper option including the number of clones (representative for the fungus population) and replications as well as the number of parent (field) isolates in an experiment will depend upon the purpose of the study. For instance, to make a detailed analysis of virulence of a single field isolate, a representative sample of clones should probably be tested on leaflets of a differential series in several replications, while to analyze virulence of a population of field isolates, it will be first essential to test a representative sample of these isolates and their clones against a series of differentials and possibly resign from replications. More difficulties yet arise when one is aiming to study variation of virulence in subsequent generations. In this experiment the most important difficulty apart of logistic ones was lack of growth of the parent isolates during the winter and weak, in general, sporulation of single zoospore cultures, despite of the short period, the parental isolates were maintained in culture.

Nevertheless, variation in virulence and aggressiveness of *P. infestans* is of the key importance for breeding potatoes durably resistant to late blight, and therefore, in spite of the difficulties as mentioned above, the methodological problem of studying variation of both characters should be resolved.

Researchers cited in the introduction did not observed such a big variation in virulence and aggressiveness as it was presented in this report. According to Denward (1970), Caten (1971) and Graham (1955) the medium on which the fungus is cultivated or passed through, exerts selective influence on the population of nuclei or particular genotypes supporting their growth and multiplication while retraining that of others. It might be the reason of ambigouities when attempting to synthesize results of the studies on variation in virulence of *P. infestans* obtained with incomparable methods. One cannot exclude that certain role played also the isolation techniques both of field the isolates as well as those of individual clones. It seems quite obvious, that we have to do with a highly heterogenous population in which particular genotypes may appear and disappear with a certain frequency. Thus, the method of isolation both of the field isolates and that of clones,

especially when working together with a selective influence of the medium on particular genotypes or nuclei may be crucial for the range of variation in virulence and aggressiveness. What has been said above seems to be particularly important when compared with the statement of Denward (1970):

"It must be kept in mind, however, that these experiments (those of him) as well as Black's (1952) were carried out with a set of races which have been propagated on Black's R-gene hosts for a considerable time. The adaptation whether physiological or genetical, must have rendered a high degree of constancy to different races, let it be temporary if the differentiation is based upon physiologic adaptation."

or with that of Caten (1971):

"Studies on variability of single zoospoore, single sporangium or single hyphal tip derivatives of colonies of *P. infestans* suggest that individual mycelia consist of mosaic of different cytoplasmic "genotypes" which are continually available for selection."

In this paper the method of Caten et Jinks (1968) was used to obtain single zoospore isolated but reversely to them and the most reserchers who used single R-gene differentials (mostly R1, R4, and R1R4) to assess virulence of clones, in this experiment almost all known differentials were used, carrying single R-genes and their combinations. The results of Caten (1970) have shown that 50% of clones gave expected reaction against host genotypes R4 and R1R4. However, Caten was unable to check, whether there were other virulence genes in the fungus since he did not test his clones against other host genotypes. Taking into account that most authors of that time (Graham 1955; Kedar et al. 1959; Gallegly, Eichenmuller 1959; Thurston 1961; Pietkiewicz, Piotrowski 1976) observed increased frequency of virulence 4 in *P. infestans* population, the results of Caten cannot be considered representative for *P. infestans* population. The domination of virulence 4 and 1.4 has also been confirmed in this paper (ca. 34% of all gene combinations observed), although, reversely to Caten apart of race 4, complex races were used to obtain the clones. Caten limitted his speculations to the statement that variability in virulence among single zoospore isolates cannot be considered a source of new physiologic races in *P. infestans*.

Graham (1955) studied virulence of 100 clones originating from race 1[t].4 (t = tomato race) against the differentials carrying R1, R2, R3, R1(t), r(t) and r (t = tomato differentials). He noted that 96 of them reacted identically as the parent isolate while the remaining four he recognized avirulent, although, it was not justified without testing the whole set of differentials. Graham concluded that *P. infestans* is a heterokaryon, and that the medium the fungus is maintained on may exert selective influence on the pathogen population. He suggested, that there may exist inhibitors in the potato tissues, that make multiplication of nuclei of some races impossible. He also stated that:

"if the fungus is transferred to a purely saprophytic medium this selective factor of the host cannot operate and the nuclei of any race that may be present are probably permitted to multiply."

Because of genetic uniformity of isolates used both by Graham and Caten, results of their studies do not contribute to much to the variation potential of *P. infestans* population. However, their hypotheses could explain the variability in virulence among single zoospore isolates presented in this paper.

More information on variation potential is given for other *Phytophthora* species. For instance Hilty et Schmithenner (1962) tested 94 single zoospore derivatives of *P. megasperma* f. sp. glycinea and found considerable variation in virulence. Similarly, Rutheford et al. (1985) found marked variation in virulence of several clones of *P. megasperma* var. *soyae* including that in subsequent generations. They concluded, that this kind of variation may be a source of new races in the fungus and suggested that a random distribution of cytoplasmic genes during zoosporogenesis might have been the reason of this variation. Results obtained in this study suggest that the parent isolates were the mixtures of simple and complex phenotypes, which means that a whole range of races may be obtained by cloning them. It is in accordance with what has been suggested by Rutheford et al. (1985). It seems that expression of particular virulence genes may depend upon their frequency in the fungal population. This hypothesis seems to be supported by the data obtained in the experiments on the effect of zoospore and sporangia concentration in the inoculum on expression of virulence. It was shown, that in parallel with an increased zoospore or sporangia concentration, there was an increase noted in virulence complexity of an isolate (Sujkowski unpublished data). It seems to point out that for a virulence gene to be expressed certain infection threshold should be reached, which may be different for particular virulence genes. It may also indicate, that in the pathogen population a wide range of virulence genes is available and whether they will be expressed or not may depend upon their frequency as well on the selection pressure exerted by the host. Depending on the strenght of this pressure, one or another phenotype of the pathogen would dominate in the population. This is in accordance with the statement of Denward (1970) who suggested that:

"in *P. infestans* as a nonseptate, multinuclear organism, the possibility of the presence of different mutant nuclei in the same hyphae and the same cytoplasm is obvious. Consequently the genetically based variation can be presumed unlimitted. Depending upon the selective properties of the substrate (host genotype) all proportions of mutant structures in the cytoplasm of a hyphae or a derived colony are conceivable."

This point of view has also been shared by Caten (1971) and Graham (1955).

It is conceivable that all considerations as presented above will also be valid for variation in aggressiveness of single zoospore isolates.

Keeping in mind variation in virulence among clones deriving from the same race or colony of *P. infestans*, there arises the question, whether the use of the race concept is justified to describe an isolate which is able to infect a variable range of the host genotypes.

According to Parlevliet (1985) race is a population of individuals possessing the same combination of virulence genes. Browder et al. (1980) when critically discussing the race concept distinguished 3 different terms: 1. race as a taxon below species which possess common features and a formal name: 2. race as an abstract group of individuals possessing the same features but no formal name; 3. race as a biological material under experiment; the last term considered by the authors nonacceptable. Caten (1987) distinguished 4 race concepts: 1. simple races (necrotrophic fungi) specificity of which is determined by 1 or 2 genes (in this case the number of races is limitted to two); 2. physiologic races (biotrophic fungi), the term introduced by Stakman and used to assess reaction against a series of differential varieties possessing different genes for resistance. Such races have been distinguished in rusts (*Puccinia*), *Peronosporales* and *Erysiphales* potential number of races is determined by the number of resistance sources and since it is 2^n. 3. aggressive races (an equivalent of physiologic races), the term introduced by Van der Plank and considered as an artefact. 4. biological races, intraspecies group, distinguished by morphological and other criteria.

As it may be seen from presented above considerations none of the proposed race concepts seems to be adequate to what has been observed in this study. Because of dramatic variation in virulence of clones the statement that we have to do with a group of individuals carrying the same genes or their combinations is not justified despite of distinguishing several virulence characters in the clones. Therefore, it seems that it would be more convenient or practical to talk about the frequency of virulence genes and races and consequently to study variation potential of the population and not individual races or isolates. However, results presented in this paper do not allow to draw final conclusions. The experiments are continued to fully explain the problem.

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Zmienność wirulencji i koncepcja rasy u Phytophthora infestens (Mont.) de Bary

Streszczenie

W latach 1986-87 przeprowadzono metodą kultur jednopływkowych analizę wirulencji u 4 izolatów *Phytophthora infestans*. Oceniono wirulencję 102 kultur, w tym 11 w dwóch kolejnych generacjach i 12 po jednokrotnym pasażu przez listki podatnej odmiany ziemniaka. Przebadano również 48 kultur pod względem agresywności. Stwierdzono, że większość badanych kultur jednopływkowych różniła się od izolatów macierzystych zarówno liczbą jak i rodzajem czynników wirulencji. Na ogół wśród badanych kultur, tam gdzie odpowiednie kombinacje genów R w roślinach testowych na to pozwalały, stwierdzono niezależną ekspresję większości zarówno pojedynczych jak i złożonych czynników wirulencji. Wśród kultur jednopływkowych zanotowano duże różnice w poziomie agresywności. Wystąpiły również znaczne różnice wirulencji w dwóch kolejnych generacjach u 11 kultur jednopływkowych. Jednokrotny pasaż 12 kultur przez listki podatnej odmiany ziemniaka spowodował zmniejszenie zarówno zakresu zmienności jak i spektrum wirulencji.