Relationship of General Resistance: Late Blight of Potato

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In order to discuss general resistance to *Phytophthora infestans* (Mont.) d By., terms that have been used or suggested for it should be listed. It is not my purpose in this paper to introduce any new terms into the already overcrowded terminology. However, the present list is rather long, and includes field resistance; tolerance [this term should not be used as it is used in a different and specific sense by Caldwell et al. (13) for rust resistance]; partial resistance; horizontal resistance; nonspecificity; nonhypersensitive resistance; relative *Phytophthora* resistance; nonspecific resistance; nonrace-specific resistance; generalized resistance; multigenic resistance; polygenic resistance; minor gene resistance; multiple gene resistance; multiple allele resistance; and quantitatively inherited resistance. Most of these terms describe either the nature of the resistance or the manner of inheritance of the resistance. Space does not permit a discussion of the relative merits or inadequacies of these terms, but probably all of them describe the same type of resistance. Conforming with the titles of this symposium, I will use the terms "general" and "specific" resistance, using other terms only when necessary in describing the results of other workers. Specific and general resistance are used with the meanings that Hooker (36) gave in discussing the genetics and expression of rust resistance, "specific resistance (race specific) which functions against certain races or biotypes but not against others; and generalized resistance (race non-specific) which functions against all biotypes."

General resistance to P. infestans in Solanum tuberosum subsp. tuberosum.—Jones et al. (39) in 1912 were probably the first to publish on the nature of general resistance to *P. infestans.* They studied three susceptible cultivars of *S. tuberosum* subsp. *tuberosum* and found differences in the number of infections in the field when plants had equal opportunities for infection. They also inoculated leaf tips, and found differences in the invasion rate of the fungus by marking lesions and measuring their development. General resistance was the only type available for many years, and fairly high levels were observed. Many investigators, including Stuart (78), Ito (37), Reddick (66), Bonde (10), and Stevenson et al. (77) noted its occurrence in potatoes during the period before the utilization of simply inherited (specific) resistance derived from *Solanum demissum.*

An important question about general resistance to *P. infestans* is whether it is stable, or whether such resistance will be lost in time with the appearance of more aggressive (43) races of the fungus. The history of cultivars with general resistance in the field indicates that such resistance is stable. Large (47) mentions the general resistance of Champion, which was grown in Ireland for over 50 years. Toxopeus (80), De Bruyn (12), and Davidson (16) noted a loss in the level of resistance of Champion. According to Davidson, Champion was introduced into Ireland in 1877, and had begun to lose its resistance by 1885. However, in 1898, 70% of the acreage still was planted to Champion, and in 1926, 22%. In 1928, its resistance was about equal to that of the cultivar President. President still has a high level of general resistance. Davidson claimed that when virus-free seed of Champion was obtained, it recovered its original level of resistance. Decline in acreage was probably due to virus infection, not to a loss in blight resistance. Paxman (64) discussed the "apparent" loss of resistance of Champion and concluded that the evidence was not really sufficient to show that it indeed had a "loss of resistance". Muller & Haigh (55) and Muller (54) in 1953 found that Champion had a very high level of general resistance both in the field and in the laboratory.

Bonde et al. (11) stated in 1940, "President, Sebago, and several seedling varieties have been grown for a period of 10 years in Aroostook County with no evidence that they have lost their resistance to late-blight infection". President and Sebago have general resistance to *P. infestans.* Niederhauser & Cervantes (61), Niederhauser (59), and Cervantes (15) found that Mexican potato cultivars have maintained the same level of general resistance under severe late blight conditions for many years. More recent information (J. S. Niederhauser, *personal communication*) indicates that a slight decline was noted in certain clones over a period of 15 years of field-testing in Mexico, but no sudden breakdowns or losses in the level of blight resistance occurred. Although it is difficult to obtain reliable information on the relative general resistance levels of potato cultivars over a long period of time, the best evidence in the literature indicates that such resistance has not been suddenly lost in nature or in the laboratory. Both in Europe and in North America, potatoes with known levels of general resistance still retain this resistance when compared to other cultivars with known levels of general resistance. After 8 years of observations, Thurston et al. (79) stated that the relative general resistance levels of *S. tuberosum* subsp. *tuberosum, S. tuberosum* subsp. *andigena,* and *S. phureja* clones did not change from year to year when compared with standard cultivars. Seventeen years after these observations were begun, there still is no evidence to change this statement (J. Guzman, *personal communication*). Several hundred clones of these species were planted once or twice a year during 8 of 17 years of observations.

Specific resistance to P. infestans.—The discovery of simply inherited (specific) resistance to *P. infestans* in *Solanum demissum* by Salaman (70), Muller (53), and others, the subsequent discovery of additional *R*-genes and races of *P. infestans* which would attack them, as well as the elucidation of their inheritance by Black et al. (9), Black (6), and others are well reviewed by Gallegly & Niederhauser (23) and Gallegly (22). Nine *R*-genes have been found to date (7). For several decades, almost all potato breeders dropped their work on general resistance and concentrated on obtaining commercial potato varieties with *R*-genes. In the absence of specific races of *P. infestans* capable of attacking them, these gave complete freedom from disease in the field. Unfortunately, the fungus produced new races faster than breeders could produce cultivars, although occasionally a 2-3 year period of freedom from blight was obtained following the introduction of a potato cultivar with specific (*R*-gene) resistance. Currently, only those "*R*-gene" cultivars also possessing high levels of general resistance are of practical value where late blight is severe. In the Toluca Valley of Mexico, no clone of *S. demissum* tested was immune to blight (62). Niederhauser (60) further stated in 1968 that no tuber-bearing *Solanum* species has been found immune to *P. infestans* in Mexico. The subsequent discovery of the sexual stage of *P. infestans* in Mexico helped explain the extraordinary variability of the fungus there.

A reawakening of awareness of the value and importance of general resistance has been aroused in plant breeders and plant pathologists as specific resistance has failed to give lasting resistance in nature.

Nature of general resistance.—Many studies have been made, primarily with *S. tuberosum* subsp. *tuberosum,* to elucidate the nature of general resistance following the early study of Jones et al. (39). Vowinckel (88) found that *P. infestans* had a longer incubation period and produced smaller lesions on cultivars with general resistance. In 1951, Schaper (71) found marked differences between different German cultivars (*S. tuberosum* subsp. *tuberosum*) and even greater differences between clones of *S. tuberosum* subsp. *andigena* in the time necessary after inoculation to produce sporangia in a moist chamber. Muller (54) and Muller & Haigh (55), by inoculation of leaf discs of English cultivars with a dilute zoospore suspension, estimated the "probability of becoming infected per unit area of foliage". They correlated this with the reaction of the same cultivars to *P. infestans* in the field. It is noteworthy that Champion had the highest degree of general resistance in both the field and laboratory tests. Deshmukh & Howard (17) obtained results similar to Muller's, but also found that the fungus had a longer incubation period and produced less sporangia on cultivars with general resistance.

Van der Zaag (87) considered that general resistance consisted of these components: (i) the chance of infection; i.e., the chance that a spore can penetrate a leaf; (ii) the extension rate of mycelium in leaf tissue; (iii) rate (or speed) of sporangial production; and (iv) the quantity of sporangia produced per leaf area. Subsequent workers had similar results. Umaerus (84, 85, 86), Lapwood (44, 45), Lapwood & McKee (46), Guzman (29), Guzman et al. (30), Knutson (42), Jeffrey et al. (38), and Hodgson (35) made detailed studies of these phenomena as they affected general resistance. Thus, general resistance consists of several host plant-*P. infestans* interactions which can be measured independently.

Grechushnikov (28), Kammermann (40), Kedar (41), and Umaerus (84, 85) found a positive correlation between peroxidase activity in the foliage and general resistance to *P. infestans*. According to Umaerus (84), this correlation exists only in clones of *S. tuberosum* subsp. *tuberosum*, and not in hybrids derived from *S. demissum*. Henniger & Bartel (33) did not find the peroxidase test suitable for testing for general resistance. Fehrmann & Dimond (20) stated, "a positive and striking correlation was found between peroxidase activity in different organs of the potato plants and resistance to *P. infestans*". Sakai & Tomiyama (69) found no correlation between peroxidase activity and blight resistance in the early stages of growth.

Numerous factors influence testing for general resistance to *P. infestans*.

Factors that influence the expression of general resistance to P. infestans.—Plant age.—There is some disagreement among investigators on the effect of age on susceptibility to blight. Most workers cited by Beaumont (3) found older plants most susceptible. Grainger (27) and Lowings & Acha (48) found plants to be susceptible when very young, and again after flowering during tuber production; plants were most resistant during the intermediate stage of vigorous foliage development. However, Beaumont (3) attributed changes in susceptibility at different ages to differences in the microclimate caused by differential foliage density found at different stages in plant growth. Toxopeus (81) reported a close correlation of general resistance to late maturity, to the point that it was difficult to combine earliness with a high degree of resistance. Umaerus (86) has reviewed the work on plant age in relation to general resistance.

Nutrition.—Awan & Struchtemeyer (2) indicated that lesion size can be influenced by N, P, and K, although in the field only excessive N affected (increased) lesion size. Grainger (27) found newly emerged and tuber-producing plants most susceptible to blight. This high susceptibility was correlated with a high ratio of total carbohydrate in the whole plant to the residual dry wt of the shoot. Lowings & Acha (48) reported that high N was correlated with increased blight resistance under some conditions. Main & Gallegly (49) found that when plants grown under conditions of normal nutrition were inoculated with *P. infestans*, those with general resistance survived, whereas when the same clones were grown under conditions of high nutrition, all plants, both those with and without general resistance, were killed.

Day-length.—Kammermann (40) and Umaerus (84) reported day-length as a factor which influences general resistance. Umaerus gave as one example the observation that the cultivar Alpha in Mexico (short days) is considered susceptible, whereas in Minnesota (long days) it has a high level of general resistance. This difference may be due to environmental factors other than day-length. He further stated that light conditions influence peroxidase levels; i.e., under short day conditions there is less peroxidase activity. Pohjakallio et al. (65) also reported that lesions appeared earlier on the foliage of potato varieties grown under short daily light exposures.

Leaf position.—Leaf position is an important consideration in testing for general resistance to *P. infestans*. Lowings & Acha (48) and Hodgson (34) found the top leaves most resistant, the middle leaves intermediate in resistance, and the bottom leaves most susceptible. In the field, Bjorling & Sellgren (4) found that 7-8 times as many lesions occurred on upper leaves. Mooi (52) found the lower, and sometimes apical, leaves more diseased than upper leaves.

Plant source.—Knutson (42) found that greenhouse-grown plants were more resistant than plants grown in the field. He found less sporulation and fewer lesions on greenhouse grown plants. Muller (54) reported greenhouse grown plants usually more susceptible.

Muller & Munro (56) reported plants infected with virus X or virus Y more resistant to infection. Richardson & Doling (67) found plants with leaf roll virus also more resistant than nonvirus infected plants.

All of these factors should be considered in programs of testing for general resistance to *P. infestans*.

General resistance to P. infestans in S. tuberosum subsp. andigena and other South American species.—Most of the above work was done with *S. tuberosum* subsp. *tuberosum* and hybrids of *tuberosum* with *S. demissum*. The potato subspecies most widely grown in the center of origin of the cultivated potato is the tetraploid *S. tuberosum* subsp. *andigena*. Goodrich (24) in 1863 wrote an article (Trans. N. Y. State Agr. Soc.) giving evidence that resistance to late blight was heritable. It is reasonably certain that he was working with *Solanum tuberosum* subsp. *andigena*, and possibly also *S. tuberosum* subsp. *tuberosum*. It is also reasonably certain that this resistance to *P. infestans* was general resistance as opposed to specific resistance. In 1937, Sidorov (73) stated, "of the endemic varieties of cultivated potatoes of South and Central America, highly resistant forms and varieties were observed in the polymorphic species *Solanum andigenium*". Mundkur et al. (57) reported in 1937 that the majority of the cultivars of *andigena* which they observed in an epidemic of late blight in India were resistant. Navarrete (58), however, reported that of the varieties of *andigena* which he tested, all were susceptible except Quincha. Castronovo (14) found all 132 clones of *S. tuberosum* subsp. *tuberosum* from Chile tested to be susceptible, whereas among 231 clones of *S. tuberosum* subsp. *andigena* from Peru, Bolivia, and Northern Argentina, a few had a degree of resistance. Estrada (18) reported that Algodona and other cultivars of *andigena* had a good degree of general resistance. Hawkes (32) stated, "field resistance has been shown to occur in certain commercial varieties of *S. tuberosum*, including subsp. *andigena* but by far the greatest amount is found in Mexican wild species". Melard (51) found certain clones of *andigena* which he received from Schaper had general resistance. In spite of these observations, very few potato workers have used *andigena* as a source of blight resistance in breeding programs. No major genes (specific resistance) have been reported to date in *andigena*.

Ochoa (63) reported that the species *Solanum chiquidenum* and *S. puirae* from Peru were immune to 5 races of *P. infestans*. Ross & Rowe (68), in their inventory of tuber-bearing species, list clones of ten species from South America as resistant: *S. andreanum* (Colombia); *S. chiquidenum* (Peru); *S. marinasense* (Peru); *S. microdontum* (Argentina); *S. multidissectum* (Peru); *S. phureja* (Colombia); *S. sparsipilum* (Bolivia); *S. toralapanum* (Bolivia); and *S. tuberosum* subsp. *andigena* (Peru, Colombia, Ecuador). These reports of resistance were compiled from published or unpublished reports of cooperators sending collections to the IRI Potato Collection. There is no indication whether the resistance reported is specific or general.

Guzman et al. (30) studied clones of *S. tuberosum* subsp. *tuberosum*, *S. tuberosum* subsp. *andigena*, and *S. phureja* which had low, intermediate, and high general resistance to *P. infestans* in the field. They found less sporulation, slower sporulation, smaller lesions, and fewer lesions produced per given quantity of inoculum on resistant clones. Subsequently, Guzman (29) expanded this work with similar results with the same species and subspecies. Both greenhouse grown foliage and field-grown foliage gave essentially the same results.

Thurston et al. (79) reported in 1962 the results of 8 years of field observations on general resistance to *P. infestans* in the Colombian potato collection. In 1961 the collection consisted of 750 clones of cultivated and wild species including 263 clones of *S. tuberosum* subsp. *andigena* and 200 clones of *S. phureja*. *Solanum tuberosum* subsp. *tuberosum* clones were also included in the field observations. Very high levels of general resistance were found in *andigena* and *S. phureja;* these levels gave almost complete control of *P. infestans* in the field under severe blight conditions. The commercial cultivar Monserrate (a *tuberosum* × *andigena* cross with a very high level of general resistance), has been grown in Colombia since 1954 (19), and has maintained its resistance to the present. Monserrate also had a high level of partial resistance when grown in the Toluca Valley of Mexico. Guzman (29) and Guzman et al. (31) developed greenhouse tests for screening large numbers of *andigena* seedlings for general resistance to *P. infestans*. Greenhouse methods were shown to be as effective as selecting for general resistance in the field under epidemic conditions.

Genetics of resistance.—It is often difficult to determine from the literature whether investigators were working with general or specific resistance. The mode of inheritance of such resistance appears to be the primary consideration; a second is whether the reaction to blight was a hypersensitive reaction. This generally was considered as evidence of specific or simply inherited resistance. This may not necessarily be the case.

Stevenson et al. (77) studied the progeny of a cross between two cultivars (No Blight and Erkishiazu) with general resistance and found they were all more resistant than Green Mountain (susceptible check), with 16.7% showing no infection and only 7.3% more heavily infected than either parent. They concluded, "blight resistance in the cultivated varieties is inherited as a recessive character probably controlled by multiple genes", that is, quantitatively inherited. Black (5) stated, "Genetically speaking, field resistance is presumed to be controlled by a series of minor genes which determine the degree of susceptibility in susceptible varieties and the extent of necrosis in field-immune forms. In contrast with field immunity, field resistance gives partial protection against all the specialized races of the parasite that have arisen in the search for hypersensitive varieties." Black & Gallegly (8) defined field (general) resistance as "all forms of inherent resistance that plants possess with the exception of hypersensitivity as controlled by *R*-genes". They attributed its inheritance to the operation of a polygenic system. They also stated, "in extreme cases, polygenic resistance alone may be high enough to produce only resistant offspring under standard test conditions". Subsequently, Black (6) defined field (general) resistance as "the degree of resistance exhibited by a plant towards all races of the parasite capable of causing more than a hypersensitive reaction on it". Malcolmson & Black (50) found their standard greenhouse test slightly less severe than the field test in the Toluca Valley of Mexico; their detached leaf test was more severe. Their progeny test showed that field resistance was inherited in a polygenic fashion. They also stated, "in certain breeding lines, however, virtual immunity was obtained in two generations from a susceptible × resistant parent. Results suggest complementary factors in the parents." It is not clear what reaction is meant by "virtual immunity". Gallegly (21) also found that general resistance to *P. infestans* in tomato was quantitatively inherited.

Graham (25) studied the inheritance of general resistance in *Solanum verrucosum*, and concluded that resistance was inherited on a quantitative basis. Graham (26) later studied the partial (general) resistance to *P. infestans* of *Solanum bulbocastanum* Dun. and *S. verrucosum*, diploid Mexican species. After analyzing the reaction to race 1,2,3,4 of F_1, F_2, and F_3 progeny of crosses between resistant and susceptible clones within each species, he concluded that inheritance of resistance was quantitative. Some of the resistant progeny gave hypersensitive reactions to the fungus and there seemed to be no clear distinction between this reaction and one indicating partial resistance.

Toxopeus (81) reported that field (general) resistance was combined with late maturity, but other investigators have not always found this true (72, 76). Toxopeus (82, 83) also found that the degree of field (general) resistance of the material he studied seemed to be governed by a series of minor genes.

Solanum tuberosum subsp. *andigena* has not been widely used in breeding programs in the USA, Canada, and Europe. Probably the main reason for this is that it generally requires short days for tuberization. *Andigena* potatoes are generally of high quality, have a long rest period, and are highly variable in respect to size, shape, form, etc. Simmonds (74, 75) was able to recreate *S. tuberosum* subsp. *tuberosum* from South American *S. tuberosum* subsp. *andigena* materials. In his mass selection program, seedlings that produced tubers were selected, regrown in a bulk tuber plot, true seeds from these plants were planted, and again tubers of the better plants were kept. These successive generations of seedlings were also exposed to epiphytotics of *P. infestans* in the field. Selection was for survival and yielding ability, and not for blight resistance per se. Simmonds & Malcolmson (76) stated that there are no *R*-genes (specific resistance) in *andigena*. They tested about 100 *andigena* clones which had undergone two or three generations of natural selection for general resistance to blight using race 1,2,3,4,5,7 (because the *tuberosum* control materials, though not the *andigena*, had several *R*-genes). Their results showed that these clones had higher levels of general resistance than *tuberosum*, and that many individuals (8%) were highly resistant. No clones with a hypersensitive reaction were specifically reported in their results.

Probably the most difficult problem in evaluating the literature on general resistance to *P. infestans* is interpreting and correlating the disease reactions given by different investigators. Many phrases such as "highly resistant", "virtually immune", "high levels of resistance", etc., are used, or disease reaction is given as percentage defoliation. Many schemes have been proposed (1, 6, 26, 76, 79) for evaluating resistance, but few precisely describe lesion size under standard test conditions, and hypersensitive reactions are usually not included. However, Graham's system (26) does this. When no infection occurs it is often not known whether this is due to escape from infection or to a hypersensitive reaction. Need exists for a precise definition of terms used by late blight workers and a standard scheme for evaluation of resistance.

R. L. Plaisted and L. C. Peterson at Cornell have been selecting clones of *andigena* which tuberize in the field at Ithaca, allowing them to self and also crossing them, and reselecting in the field for yield and tuber production. Several hundreds of these clones have been inoculated with either race 2,4, or 1,2,3,4, of *P. infestans* in growth chambers and the greenhouse and grown in the field by V. Garcia and me with good blight infection of susceptible *tuberosum* checks. Material from N. W. Simmonds was also tested. About 40% of Simmond's clones and 19% of Plaisted's and Peterson's material gave a hypersensitive reaction. None of this *andigena* material is known to have any specific resistance (*R*-genes), and no specific resistance to *P. infestans* is reported in the literature. The question is, therefore, whether sufficient genes have been accumulated to give a hypersensitive reaction. If such a level of general resistance could be obtained, and if such resistance were not broken down by new races, then freedom from disease ("field immunity") without loss of resistance might finally be achieved. This material was recently tested in the Toluca Valley of Mexico; all clones had sporulating lesions. However, many clones had lesions of a type associated with general resistance. Thus, it is still unknown whether the hypersensitive lesions produced by the fungus on *andigena* clones in New York are due to specific resistance or general resistance. Inheritance studies and tests with the most broadly virulent races of the fungus will be necessary to clarify this question.

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