

REVIEW — RESEÑA

IDENTIFICATION OF RESISTANCE AND TOLERANCE TO POTATO CYST NEMATODES AND THEIR PRACTICAL IMPLICATIONS [IDENTIFICACION DE RESISTENCIA Y TOLERANCIA A LOS NEMATODOS ENQUIS-TADORES DE LA PAPA Y SUS IMPLICACIONES PRACTICAS]. Rodrigo Tarté, Unión de Países Exportadores de Banano, Apartado 4273, Panamá 5, Panamá.

SUMMARY

The efficient utilization of resistant and tolerant cultivars as a means of control of potato cyst-nematodes requires that proper consideration be given to those factors which affect the reaction of the plants in their relationship with nematode populations and environment.

The external and internal factors that affect a plant's reaction in the presence of a nematode infestation are discussed. The influence of the physiological condition of the plant, environmental factors, and other organisms are emphasized.

The necessity of a proper identification of the nematode pathotypes and variants to which material tested is either resistant or tolerant is emphasized. Some comments are made on the pathotype classification schemes now utilized.

Because of the danger of selecting other pathotypes or more aggressive variants, it is advisable to consider, in most cases, the use of resistance and tolerance only as part of integrated control programs.

Because of variability in nematode populations and ecological conditions in different regions of the world where potatoes and cyst-nematodes co-exist integrated control methods should be developed accordingly for each particular location or area.

INTRODUCTION

The use of cultivars resistant and tolerant to potato cyst-nematodes is one of the most effective and least expensive control measures of these pests. Their efficient use, however, is dictated by our understanding of biological, genetical, and ecological considerations involved in their relationships with the nematode populations under consideration in the locations where they are to be used.

In this paper, I discuss what I believe are the important aspects to consider when searching for and using resistant and tolerant genetic material for the control of potato cyst-nematodes. No attempt was made to make an extensive literature review on the subject. However, to emphasize important concepts and findings, some literature is cited and some examples are used in which nematode species other than potato cyst-nematodes are considered.

In the following discussion I present some information concerning aspects that are often overlooked or are not necessarily of special interest to research workers in this field, but which I believe are valuable.

SEARCH FOR RESISTANCE AND TOLERANCE

The extensive variability in potato cyst-nematodes and their distribution among different ecological habitats that affect the relationship between potato plants and nematodes, immediately suggest three important considerations when searching for

resistant or tolerant varieties. First, proper identification of resistance and tolerance in genetic material evaluated is needed; second, correct identification of the nematode races or variants to which such material is either resistant or tolerant must be done, and, third, the factors (external or internal) that affect the reaction of the material to the nematode should be adequately identified.

To identify resistance and tolerance, we must measure the sensitivity of the host as well as the changes in population densities of the nematode parasitizing it. Because these aspects may be affected by many different factors, as a consequence of the interactions between nematodes, plants and environment, they must be properly characterized.

IDENTIFICATION OF RESISTANT AND TOLERANT GENETIC MATERIAL

Although it may be modified by the environment, the efficiency of resistance of a plant is determined by its genotype. The main feature of resistance is its effect on the reproduction of the nematode. Based on this criterion, a large variation among potato cultivars and wild relatives, has been found, ranging from very high resistance, governed by major genes, to intermediate degrees of resistance, governed by polygenic systems (22). With potato cyst-nematodes, however, even the highly resistant clones have a certain degree of susceptibility. Apparently, they all respond to some extent to the stimulus to form a syncytium in which a nematode can feed and develop (19) even if the nematode is unable to complete its life cycle.

Testing for resistance is, therefore, based on the reproduction of the nematode. Such testing is relatively simple when resistance is governed by one dominant gene, as generally occurs in *Solanum andigena* hybrids, or by a small number of dominant genes, but is not so simple when minor genes are involved as in *Solanum vernei* hybrids. When *S. vernei* was introduced into the breeding program in the Netherlands, a testing method entirely different from the test for pathotype A resistance (*S. andigena*) had to be developed (26), because root ball counts as a percentage of the number of cysts produced on a susceptible clone were not as reliable as when total number of cysts produced were counted (20). Even in *S. andigena* clones, some evidence of minor genes has been found (5). Also in the United Kingdom, Parrott and Trudgill (34) observed some variability in the resistance of *andigena* hybrids suggesting that this resistance probably depends on additional genes, rather than on differences in the H1 gene. On the other hand, experience in the Netherlands with a polygenic inheritance mechanism, as found in the tuberosum - *vernei* hybrids, suggests that major genes are present since potato cyst nematodes were found readily multiplying on the roots of clones (22). Such resistance mechanism makes it difficult to conclude that the tuberosum - *vernei* hybrids are a simple solution to the problem of pathotypes, as has been argued. Unfortunately, the resistance reaction of clones with major genes is easily overcome by small changes in the nematode population.

The existence of different degrees of resistance suggests that great care must be exerted in the identification of resistant material. External factors affecting resistance as well as nematode behavior may modify plant reaction in such a way that resistance or susceptibility could be masked. If resistance is measured by reproduction of the nematode, any factor that affects reproduction needs to be considered also.

Similar considerations govern the search for tolerant material. Tolerance of the plant is measured in terms of damage caused by nematodes readily reproducing on it. This reaction can probably be more affected by external factors than can the multiplication aspect of a nematode in a plant evaluated for resistance. Yields of nematode-

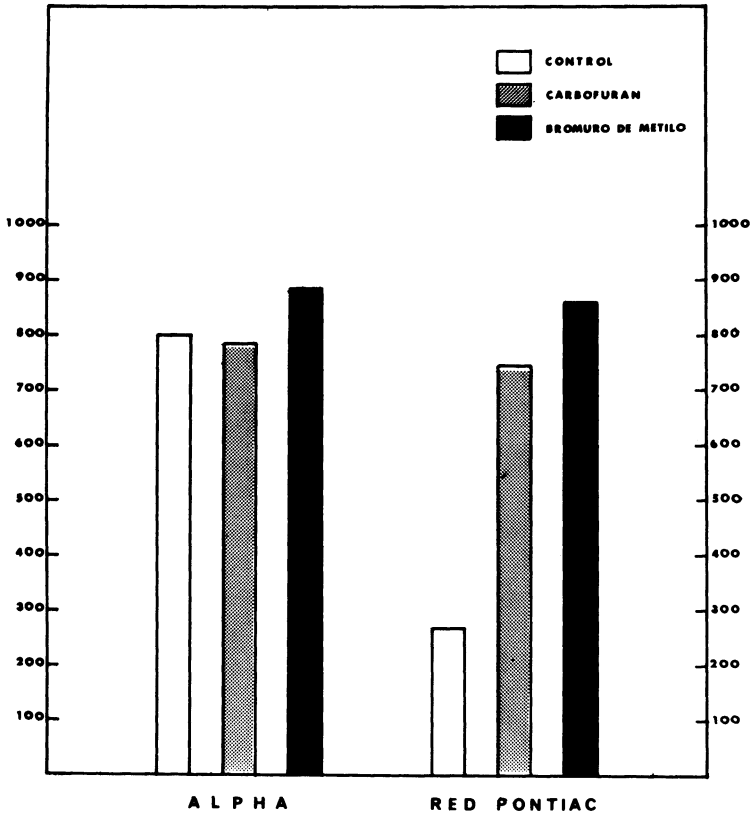


Fig. 1. Effect of two chemical soil treatments (methyl bromide and carbofuran) on yield (grams of tubers) of two potato varieties grown on a soil infested with 500 eggs and larvae of *H. rostochiensis* per cm^3 of soil.

infected plants as compared to non-infected controls indicate their tolerance to nematode attack and can be related in terms of nematode population density. The tolerant level was determined in The Netherlands by Seinhorst and den Ouden (37) as 6 eggs per gram of soil for the tolerant variety "Multa" as compared to 1.5 eggs per gram of soil for the non-tolerant variety "Libertas", when grown at a low Nitrogen fertilizer level. The potato variety "Alpha" has been found to be tolerant to high infestations of a *Globodera rostochiensis* population from Panama (40) (Fig. 1). The belief that tolerance is pathotype independent has led to this kind of research at the International Potato Center (6), where tolerance has been found in several clones from Perú and in several native cultivars from Colombia.

Identification of resistance and tolerance can be improperly recognized unless we understand the factors that affect the interactions between nematodes and the plants they parasitize.

EFFECT OF INTERNAL AND EXTERNAL FACTORS

The physiological condition of the plant is a factor quite often overlooked. It may have a direct influence on the reaction of the plant to the nematode as well as on the rate of reproduction of the nematode parasitizing it. This was demonstrated by Dolliver (9) with *Pratylenchus penetrans*, who found that treatments that moderately reduced dry weight of "Wando" pea plants, such as less favorable light and temperature, excision of plant parts, or limitation of the nutrient supply, increased populations of *P. penetrans*. On the other hand, treatments that considerably reduced dry weight as well as removing flowers and pods, reduced nematode numbers. With the same nematode species, Tarté and Mai (39) found that a crenate-tailed variant of *P. penetrans* was more pathogenic to peas than a smooth-tailed variant of the same population when pea plants were grown at a light intensity of 3,900 lux, but not when grown at a higher light intensity.

Environment plays a major role in the physiological condition of the potato plant. Changes in the chemical composition of the tubers and the subsequent growth and development of the potato crop are affected by climate. Moreno (31) found biochemical variations in potato tubers as affected by photoperiod; the content of free amino acids was higher in tubers formed in short days (10 hrs.) than in those formed in long days (14 hrs.). Tubers formed in long days were small and lost dormancy rather quickly. He also found biochemical differences in potato tubers harvested in different local climates in Perú. When these tubers were planted in one locality, differences in the sprouting behavior and growth occurred giving rise to plants with different growth habits. He stated that the chemical composition of the seed-tuber seemed to give a definite potential for the development of its sprouts and the plant derived from it. This confirmed Went's (49) suggestion that potato tubers have different potentialities to produce tubers in plants of the following generation according to the previous environmental conditions in which mother plants were developed.

Tarté and Rodríguez (40) stressed that the physiological condition of the plant is a factor to consider when evaluating the reaction of a potato plant to potato cyst-nematodes. They found in a pot experiment that the potato variety "Alpha" did not express tolerance, 82 days after planting, when all the sprouts, except one, were removed soon after emergence, as compared to plants where all the sprouts were allowed to grow (Fig. 2). According to Dutch workers (46), physiological age of the potato seed tuber as well as climate determine the number of sprouts on seed-tubers and the duration of the rest period. The number of sprouts of course has an influence on growth and development of the potato crop. Removal of sprouts in some of the tubers of this experiment merely attempted to simulate partially two different physiological conditions. This was done because "Alpha", the main potato variety grown in Panamá, is planted twice a year; a large December planting, with seed-tubers imported from the Netherlands, and a smaller June planting, with seed-tubers harvested in Panamá the previous season. Obviously, the physiological condition of seed-tubers originating from different localities is different, and this may explain why sometimes a low yield is obtained in the presence of heavy infestations of the nematode while most times yield does not seem to be affected.

It is possible that when several sprouts are present, plants may compensate for the destruction of roots by the formation of adventitious roots produced through a hormonal regulatory effect. When only one sprout is present the destructive effect is greater than the compensatory effect. In the relationship between plant damage and nematode populations it has been suggested (48) that both effects act simultaneously; if the inhibitory processes predominate, growth or yield is reduced; if the compensa-

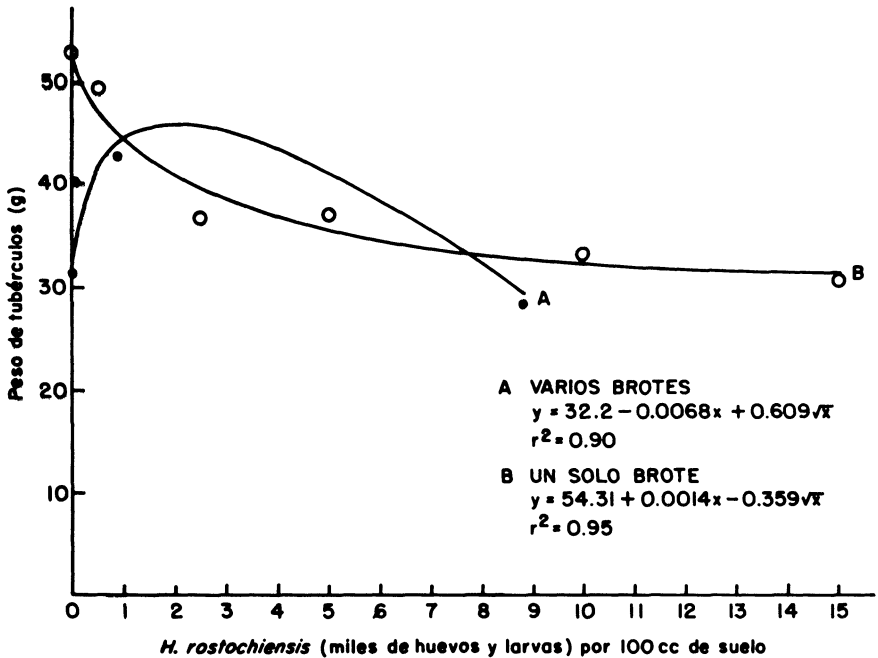


Fig. 2. The relationship between initial population density of *H. rostochiensis* (thousands of eggs and larvae per 100 cm³ of soil) and yield (grams of tubers) of the potato variety Alpha, 82 days after planting, when all the sprouts were allowed to grow (A) and when all the sprouts, except one, were removed soon after emergence (B).

tory effects predominate there is no growth reduction and an increase in growth may occur if an excess of growth regulatory substances is produced. These kinds of influences need to be studied more. In Tarté and Rodríguez's experiment (40), it is possible that if data were taken at harvest, or later than 82 days after planting, a compensatory effect in the one-sprout plants may have appeared, similar to the findings of Seinhorst and den Ouden (37). These workers found that an inhibitory effect of nematodes disappeared in two potato varieties when growth data were taken at a later date. This kind of evidence may be difficult to observe when trying to develop a technique to determine tolerance by a pot method as has been recommended (6).

There is evidence that growth regulators are probably involved in resistant reactions. Giebel and Wilski (18) found an increase of IAA in potato plants susceptible to *G. rostochiensis* and a decrease in resistant plants. Dropkin et al (11) showed that the application of kinetin to tomato plants decreased their resistance to *Meloidogyne incognita* and concluded that the extent of reversal from resistance to susceptibility is dependent on cytokinin concentration. It would be interesting to observe the effects of gibberellic acid applications on the reaction of potato plants to cyst-nematode attack. Gibberellic acid is applied in some cases to promote sprouting of seed-tubers.

In addition to the effect on the physiological condition of the plant, the environment may affect some aspects of nematode behavior such as dormancy, hatching, reproductive capacity, longevity, and survival. Potato cyst-nematodes have a pronounced

dormant period (38) in which hatching does not commence until favorable conditions are attained. Hatching may cease also in response to other stimuli. Temperature is most often mentioned as influencing dormancy or cessation of hatching. Magi (in Clarke and Perry) (7) observed a diapause commencing in July in cysts of *G. rostochiensis* from the previous year. This is somewhat similar to what occurs with *Heterodera avenae* (25), in which hatching commences as the temperature rises after winter and ceases in May before soil temperatures reach 20°C. This type of dormancy appears to be synchronized with the host's life cycle and is often a feature of the parasitic mode of life. According to Parrot and Berry (33) *Globodera pallida* hatches less freely than does *G. rostochiensis* at higher temperatures and is possibly adapted to lower temperatures. They suggested *G. pallida* would be more persistent in soils which may be important in relation to competition between these two species when long crop rotations are employed. Ellenby and Smith (12) found a difference in response to low temperature between different populations of *G. rostochiensis* and suggested that adaptation of one population to lower temperatures than others is possibly related to the early planting and harvesting of potatoes in the area. Studies at the International Potato Center (5) revealed that the Peruvian population of *G. pallida* is less sensitive to temperature extremes than the "white" British *G. pallida*.

Although temperature seems to play a major role, Dropkin (10) has suggested that the cessation of hatching stimuli may derive from some metabolites of soil biota rather than from the physical factors of the environment. There are substances that inhibit hatching of *G. rostochiensis* such as diffusates of mustard roots and certain solanaceous plants (38). Magi (in Clarke and Perry) (7) reported that root diffusates from *Archangelica litoralis*, *Heracleus sibiricum*, *Anthriscus silvestris*, *Pimpinella saxifraga*, and *P. major* inhibited the hatching of *G. rostochiensis* by 36-56%. McParland (in Clarke and Perry) (7) found that exudates of *Rhizoctonia solani* also inhibited hatching of *G. rostochiensis*. Freshly heat-sterilized soil sometimes inhibits hatch of *G. rostochiensis* (38). Interestingly, hatching of *H. avenae* was found to be inhibited by solutions of calcium nitrate (7), which indicates that soil infestations of this nematode may be limited by the application of suitable amounts of calcium nitrate. We must be more aware of how fertilizers or other substances influence hatching of *G. pallida* and *G. rostochiensis*.

A curious example of inhibition of hatching in *G. rostochiensis* has been found in Costa Rica*. Viable cysts were found in a soil from the Cartago area, but they are unable to reproduce in all susceptible varieties tested. However, when cysts were sent to the Netherlands for identification, they reproduced well and a host differential test revealed them to belong to pathotype A of *G. rostochiensis* (35).

Soil types have a marked influence on reproduction of *G. rostochiensis* and *G. pallida*. Studies at the International Potato Center (5) revealed that reproduction of both species on soil from Arequipa was ten times that on soils from Tarma and Cajamarca. Detailed soil analysis did not reveal which factors contributed to such variation in reproduction in these soils.

Quite often it is difficult to distinguish whether environment affects the plant, the nematode, or both. A plant's response resulting from a direct effect of the environment on the nematode seems rather unusual. If we understand all those factors that influence an organism's chance to survive or reproduce (48), we can see how any given reaction involving two or more organisms in any particular environment is the product of their interactions with that environment. Photoperiod for instance, plays a role in plant growth and consequently on nematode reproduction. Ellenby (in Wallace) (48) stated that increasing day length appears to be associated with increased number of cysts of *G. rostochiensis* on potato plants. It is likely, however, that such

*A. Ramírez, personal communication.

photoperiod favors increased plant growth and this in turn favors higher nematode reproduction (47). The rate of invasion and development of both species of potato cyst-nematodes is affected also through the host by day-length (5).

The degree of resistance or tolerance in potato plants may be influenced by soil fertility and humidity. For example, better soils gave higher percentages of tolerant plants in Perú than did poorer soils (2). A similar situation was indicated by Trudgill et al (44), who suggested that small densities of the nematode may cause economic yield losses when soils are deficient in plant nutrients. Evans et al (15) found that infected plants in soils with high Nitrogen and Phosphorus grew almost as well as did those treated with aldicarb. A much larger growth response was obtained with aldicarb over nontreated plants when lower initial nutrient levels were used.

Evans et al's (14) finding that irrigation had little effect on the water relations of nematode infected plants, except for the decreased water stress in young plants infected with high numbers of nematodes indicates that the effect of soil moisture level probably needs to be more extensively studied. Water relations of nematode-infected plants are very important with other species of plant parasitic nematodes. O'Bannon and Reynolds (32) found that when the soil was kept at field capacity, cotton plants infected with *Meloidogyne* spp. grew as well as non-infected plants, but when the soil was allowed to dry to 50% of field capacity between waterings, infected plants grew more slowly than non-infected ones.

Other organisms may also play a role in the relationship between potato plants and cyst nematodes. The existence of organisms that parasitize or prey upon *Heterodera* spp., was noted by Van der Laan (in Sheperd) (38). Fungi found in *G. rostochiensis* cysts from the Netherlands and Perú include *Phialophora heteroderae*, *Phoma tuberosa*, *Montospora daleae*, *Penicillium vermiculatum*, *Pseudeurotium ovalis*, *Anixiopsis sterioraria*, *Margarinomyces heteromorpha* and *Sclerophulariopsis* sp. On the other hand, associations between fungi and nematodes may be of more importance than parasites and predators. Several experiments have shown that these associations are not just a question of competition for some resource but that they interact at the biochemical level and as a result physiological changes occur in the host which may affect nematode populations. In a study of the association between *G. rostochiensis* and the causal fungus of brown root rot of tomatoes James (23) found that the nematode did not increase the susceptibility of the roots to invasion by the fungus, but that the fungus decreased the rate of hatch and invasion by the nematode and the subsequent number of new cysts produced. On the contrary, there is ample evidence that numbers of the nematodes in a plant increase when another parasite is present, e.g. *H. glycines* in the presence of *Fusarium* (36), *Pratylenchus penetrans* in the presence of *Verticillium albo-atrum* (30) and *P. minyus* in the presence of *V. dahliae* (16). We must be aware of the fact that, quite probably in soil, the relationship between just a single organism and the plant does not exist. The remark by Wallace (48) that the incursion of a fungus into the plant system may produce a plant that is more resistant or more susceptible to the nematode, may refer to a rather common phenomenon in nature.

IDENTIFICATION OF NEMATODE SPECIES, PATHOTYPES AND VARIANTS

Proper identification of the nematode pathotypes and variants to which the material tested may be either resistant or tolerant is a necessity. The correct identification of the potato cyst-nematodes involves not only the identity of species and pathotypes but the detection of variants, within and among populations, differing in aggressivity

towards potato plants.

Several pathotypes of *G. rostochiensis* and *G. pallida* have been identified in Europe on the basis of the reaction of differential hosts. However, it is highly probable that many more pathotypes do exist. This is particularly true for the Andean region where variability among potato cyst-nematodes larger than that found in Europe has been observed. When 34 populations of the nematode from the Andean zone were studied for female color, none of them presented a pattern identical to those registered for the British pathotypes (3). When clones with resistant genes H1, H2, and H3 were tested against 44 Andean and nine European populations of potato cyst-nematodes results showed that the Andean populations were able to overcome H genes (5). De Scurrah (8) indicated that genes for resistance to populations from Perú are very rare among the tetraploid clones of *Solanum tuberosum* sp. *andigena*.

Because only a small portion of the total nematode gene pool was apparently introduced to Europe from South America, we can assume that there is less variation there than in the Andean region of South America. Observations and experimentation led to the conclusion that populations found in the Andes do not fit into the European systems of classification of pathotypes. This has also been observed by European workers e.g., a Bolivian population that morphologically resembled British pathotype A but behaved like British pathotypes B and E (2).

A new scheme of classification was erected by Canto and de Scurrah (4), under which British and Dutch pathotypes as well as Andean populations of the potato cyst-nematode could be identified. An attempt to understand better the genetic variation of these nematodes and to provide a basis for selecting representative populations of the nematode to use in breeding and screening for resistance was the main purpose of this new scheme. This scheme was criticized by European workers (28), who at the same time proposed an international scheme to bring together the formerly separate schemes of the United Kingdom and the Netherlands. However the classification system proposed by Canto and de Scurrah (4) seems more justifiable in the light of its usefulness, than the international scheme in which only Dutch, German, and British pathotypes were considered.

Populations that are mixtures of pathotypes exist. In such cases, competition may change the balance of pathotypes. Trudgill and Parrott (43) indicated that when pathotypes A and E occur together, A becomes dominant. It is very important to identify populations of mixed pathotypes, but more important to identify variants differing in aggressivity among populations. Evans and Franco (13) indicated that aggressivity of different populations towards a resistant clone is as important as determining the species to which they belong. Because differences in aggressivity are often associated with differences in morphology, the possibility of relating a morphological feature with a certain pathogenic behavior should be given some concern. Evans and Franco (13) found considerable morphological variation among 100 populations from South America, with some characters showing considerable variation within populations as well.

The extensive variability in potato cyst-nematodes and the little knowledge of the extent of such variability makes proper identity of many populations difficult. Hopefully, new pathotype classification schemes will improve this situation. However, emphasis should be on identification of aggressive variants as they affect resistant and tolerant reaction.

UTILIZATION OF RESISTANCE AND TOLERANCE

Variability in nematode populations and ecological conditions undoubtedly affect

Table 1. Yield and effect on nematode population density of some Dutch cultivars grown on a soil infested with 220 eggs and larvae of *H. rostochiensis* per cm³ of soil, as compared to "Alpha" (tolerant) and "Red Pontiac" (susceptible).

Cultivars	Yield (ton/ha)	<i>H. rostochiensis</i> (eggs and larvae)	
		% Reduction	% Increase
Aminca	27.5 a	1.4	-
Ukama	26.3 abc	35.0	-
Veenster	24.8 abcd	27.0	-
Alpha	23.7 cd	-	138.0
Marijke	23.6 cd	-	48.3
Cardinal	22.7 d	35.8	-
Diamant	22.0 d	-	53.6
Amigo	19.6 efg	-	44.5
Alcmaria	18.3 fg	-	39.7
Red Pontiac	18.0 g	-	168.8
Satelliet	16.7 gh	29.8	-

the reaction of potato cultivars in different ways. Perhaps a great extent of nematode variability is related to aggressivity. Some reports indicate that the reaction of several European cultivars to potato cyst-nematodes in Latin America differs from their reaction to similar pathotypes in Europe. The Dutch variety "Alpha" is normally tolerant in Panamá (40-41), but is susceptible to potato cyst-nematodes in México (17). In Venezuela 24 European resistant varieties were only tolerant (17). In Panamá, of 22 Dutch cultivars resistant to *G. rostochiensis*, thirteen reduced the nematode population between 1.4 and 35.8% while nine increased the population between 4.4 and 53.6% (41) (Table 1).

Differences in aggressivity increase the danger of selecting more aggressive variants. The aggressive variant replaces the one for which the variety was bred (2). Selection in the United Kingdom and the Netherlands has usually resulted in the replacement of *G. rostochiensis* Rol (1) by *G. pallida* Pa3(1) after growing up to five successive crops of a resistant cultivar bearing gene H1 (24).

The rapidity of appearance of new pathotypes depends on the frequency of resistance breaking genes in the nematode (21). In some cases this frequency seems to be very low or zero, such as in populations from New York State that have remained pure pathotype A and have not been able to multiply on ex andigena after several generations. In such cases, the use of resistant varieties will afford better control than the use

(1) Race classification according to the new European scheme.

of nematocides (43). When the frequency of resistance breaking-genes is high matings could result in gene combinations of new biotypes. In some cases, the frequency of such genes is high enough that even after the first crop of resistant potatoes new biotypes appear, which makes further use of the resistant varieties unprofitable (21).

The danger of selecting another race is a real one. It is generally agreed that cropping of tolerant cultivars does not select another pathotype because tolerance is pathotype independent. However, cropping of susceptible potato cultivars, did not prevent pathotype shift in the Netherlands. Kort and Jaspers (27) grew 3 potato cultivars for 3 years in soil with an equal mixture of Dutch pathotypes A (*G. rostochiensis*) and D (*G. pallida*). A shift in pathotype ratio as determined by single cyst tests on ex andigena potatoes was found at the end of each year. Both pathotypes and hybrids between them occurred within a single cyst, which confirms hybridization and competition between species of the potato cyst-nematode. They concluded that alternate growing of susceptible and resistant cultivars will not prevent pathotype shifts. Will tolerant

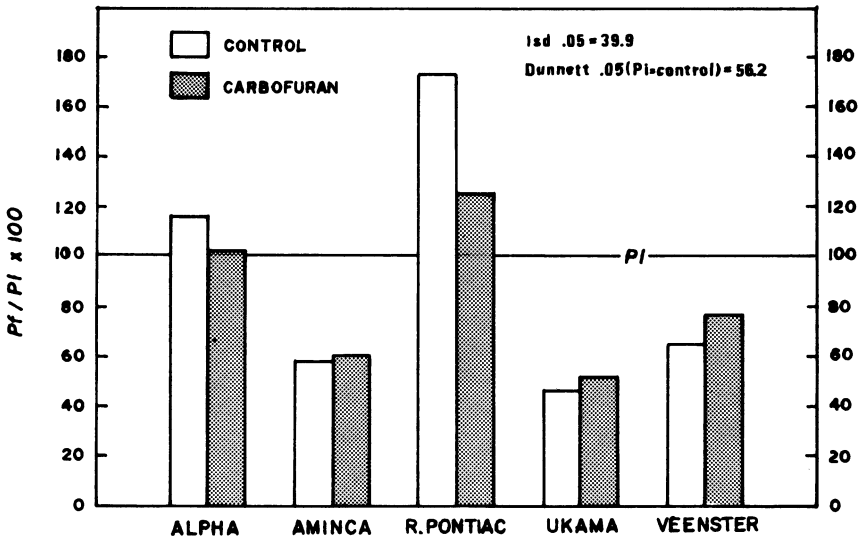


Fig. 3. Effects on nematode population density of three resistant cultivars (Aminca, Ukama and Veenster), one tolerant (Alpha) and one susceptible (Red Pontiac) grown on a soil infested with 309 eggs and larvae of *H. rostochiensis* per cm³ of soil (Pi), with and without application of a nematocide (carbofuran).

varieties react in the same way? Chances are greater that they will if competition between species of variants occur, and one of them is favored by the host, or if selection pressures other than host plants are present. Since the relation of tolerance to pathotypes is not known, the continuous use of a tolerant variety should perhaps be avoided.

The existence of some degree of interbreeding between *G. rostochiensis* and *G. pallida* indicates that there are no clear-cut differences between them. It is apparent that *G. rostochiensis* and *G. pallida* are in the process of speciation since one or more of the three characteristic properties of species (reproductive isolation, morphological distinguishability and ecological difference) (29) are only incompletely developed.

Thus, the existence of some degree of interbreeding could maintain in mixed populations a genetic variability capable of altering in a short period and depending on the kind of selection pressure involved, the resistant or tolerant reaction of a given potato variety.

Due to the danger of shifting pathotype densities it is advisable to consider the use of resistance and tolerance only as part of integrated control programs. In some cases, it might be possible to use resistant varieties for a long time without pathotype shifts. When properly used, either alone or as a part of an integrated control program, their efficiency in suppressing nematode population is not equaled by other control measures such as use of nematicides. Tarté and Rodríguez (41) and Brodie (1) found that the use of a nematicide maintained the original population density of *G. rostochiensis* whereas monoculture of a resistant cultivar reduced the population density considerably. When managing nematode populations, control methods have to be tested under local conditions and no generalizations should be attempted. Tarté and Rodríguez (42), found that the use of some resistant varieties alone gave a better control of *G. rostochiensis* than a pre-plant nematicide application (Fig. 3). In the United Kingdom, on the other hand, fumigation increased yield of the resistant variety "Maris Piper" in the presence of a high nematode infestation (45). Integrated control methods, therefore, should be developed accordingly for each particular location or area. The aim in all cases, however, is to regulate nematode populations and keep them below damaging levels.

RESUMEN

La utilización eficiente de cultivares resistentes y tolerantes como medio de combatir los nematodos formadores de quistes en la papa requiere prestar cuidadosa atención a aquellos factores que afectan la reacción de las plantas y su relación con las poblaciones del nematodo y el ambiente.

Se discuten los factores externos e internos que afectan la reacción de la planta ante la presencia de una infestación de nematodos y se hace énfasis en la influencia de la condición fisiológica de la planta, factores ambientales y otros organismos.

Se destaca la necesidad de identificar apropiadamente los patotipos y variantes del nematodo a los que el material probado es resistente o tolerante. Se hacen algunos comentarios sobre los esquemas de clasificación de patotipos utilizados actualmente.

Debido al peligro de seleccionar otros patotipos o variantes de mayor agresividad, es aconsejable en la mayoría de los casos, considerar el uso de resistencia y tolerancia solamente como parte de programas de control integrado.

Debido a la variabilidad en las poblaciones del nematodo y en las condiciones ecológicas existentes en las diferentes regiones del mundo donde co-habitan los nematodos formadores de quistes y el cultivo de la papa, los métodos de control integrado deben ser desarrollados específicamente para cada localidad o área productora.

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