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An early generation screen for combined cyst nematode (*Globodera* spp.) and blight (*Phytophthora infestans*) resistance in potato

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Summary

A technique is described which enables potato clones to be screened for resistance to both species of potato cyst nematode (*Globodera rostochiensis* and *G. pallida*) and to blight (*Phytophthora infestans*) in the foliage during the winter and first spring following harvest of seedlings grown from true seed.

A container test, used to assess resistance to both species of *Globodera* in a mixed inoculum, is followed by an assessment of resistance to foliage blight, using the same plants in the glasshouse. This screen can be completed in time for duplicate tubers of the resistant clones to be planted for multiplication in the second growing season.

The close correlation between results obtained using this system and those predicted from the known inheritance of the characters selected and the gain in efficiency achieved in breeding, are illustrated by examples.

Introduction

The cyst nematodes *Globodera rostochiensis* and *G. pallida* are among the most important pests of potato in the United Kingdom (Trudgill, 1986a). One pathotype of each species is important in Britain; pathotype Rol of *G. rostochiensis,* which can be completely controlled by the dominant gene *H1* from *Solanum tuberosum* spp. *andigena* (Andigena) (Cole & Howard, 1957), and pathotypes Pa2 and Pa3 of *G. pallida* (Stone, 1972), which are now considered to be one heterogeneous pathotype, Pa2/3 (Trudgill, 1986b). Pathotype Pa1 has also been found in the UK but is rare (Kort et al., 1977) and can be controlled by the dominant gene *H2* from *S. multidissectum* (Dunnett, 1962). Resistance to pathotype Pa2/3 has been introduced from some accessions of Andigena (Howard et al., 1970), *S. vernei* (Howard & Fuller, 1975), and from other *Solanum* species (Van Soest, 1983). All these sources of resistance operate by inhibiting the development of mature females in the root system (Rice et al., 1985). Andigena and *S. vernei* have been most commonly used in breeding for resistance.

Resistance to *G. pallida,* pathotype Pa2/3, is controlled by a number of genes (Phillips & Trudgill, 1983), making the production of resistant cultivars difficult,

though new cultivars with moderate resistance are now becoming available. A major aim of the potato breeding programme at the Plant Breeding Institute (PBI), Cambridge, is the production of cultivars with resistance to both species of cyst nematode. The Andigena clones used as nematode-resistant parents generally have low resistance to blight (*Phytophthora infestans*) and material bred from these parents has to be selected for moderate resistance to this disease.

Each potato seedling is potentially a new cultivar; it is multiplied vegetatively and is assessed with successively greater precision as tuber stocks increase (Howard et al., 1978). The natural multiplication rate of potato is about eight-fold per year but not all tubers can be used for tests because some must be kept as stocks in virus-free conditions, both to fulfil the mandatory British plant health requirements for commercial multiplication and to provide uniform virus-free planting stock for each subsequent year's trials. Tissue culture is now partly removing this constraint (Thomson et al., 1985) but, with finite resources, there has to be a balance between the number of clones tested and the scale of the tests. Hence it is important that selection procedures are applied in the correct order and at the correct intensity for the most rapid identification of required genotypes without a waste of resources or time. It is efficient to select at an early stage for characters that are chosen as essential requirements in a particular breeding programme and that can be reliably assessed. Thus all further tests, including the more detailed quality assessments and replicated trials, are carried out on a reduced number of clones of established value.

A procedure has been developed for screening breeding clones for combined resistance to *G. rostochiensis* and *G. pallida,* and for moderate resistance to foliage blight, during the winter and spring following the sowing of the true seed, i.e. on the first clonal material. This is before any multiplication, either in vitro or in the British high-grade seed area, has commenced and rejection of clones at this stage thus leads to a great saving of resources. This procedure is described below and representative results are given.

Materials and methods

All clones from progenies derived from nematode-resistant parents are tested for resistance to both cyst nematode and blight. At the PBI the majority of such crosses have utilised derivatives from the Andigena clone CPC 2802 as the source of resistance to pathotype Pa2/3 of *G. pallida,* because they are of better agronomic quality than other sources of nematode resistance (Howard, 1978). Although clones of *S. vernei,* which confer polygenically inherited resistance to both *G. rostochiensis* pathotype Ro1 and *G. pallida* pathotype Pa2/3 (Phillips & Trudgill, 1983), have also been used, they may have poorer tuber quality and can transmit unacceptably high glycoalkaloid levels.

The main disadvantage of the clones with resistance to *G. pallida* derived from Andigena is that they do not have any useful resistance to *G. rostochiensis,* so that the gene *H1* has to be introduced from other sources. Non race-specific blight resistance also has to be introduced, but often an adapted European cultivar such as Cara, which has moderate resistance to blight as well as possessing gene *H1*, can be used as the source of both characters. Crosses between such cultivars and clones with resistance to *G. pallida,* derived from Andigena or *S. vernei,* will produce progenies with at least 50 % of clones resistant to *G. rostochiensis,* many of which will also

have high resistance to *G. pallida.* It is possible to select within these resisters for clones with acceptable yield, quality and other desirable characters. Four representative progenies, selected to show the range of resistances, are used as examples in this paper and are described in Table 1.

Botanical seed was sown in March and seedlings transferred to 10 cm diameter pots in an aphid-proof, heated glasshouse. At harvest in late June selection was made for tuber colour and stolon habit only, as these can be reliably assessed at this stage (Howard, 1963; Anderson & Howard, 1981). Two tubers from each uniquely identified clone that had been retained were stored at 5 °C until autumn; one tuber was kept in store as the nucleus of the virus-free stock, while the other was used in the cyst nematode and foliage blight screens. Tubers for testing were taken out of store at weekly intervals in batches of about 1000 and kept at room temperature for 4–5 weeks to induce sprouting; tubers with approximately 5 mm sprouts were used for the tests. Appropriate control cultivars were also harvested from glasshouse-grown plants and treated similarly. These cultivars were: Cara, with *G. rostochiensis* resistance (*H1*) and moderate blight resistance (National Institute of Agricultural Botany (NIAB) rating 6); Caxton, a clone with *G. pallida* resistance; King Edward, a blight-susceptible cultivar (NIAB rating 4); Stormont Enterprise, a blight-resistant cultivar

Table 1. Parents of typical progenies.

Family	Parents	Nematode resistance	Blight* resistance	Predicted Ro1 resistance ratio
4	Cara D42 – 8	Ro1 Pa1,2/3	6 3 – 4	1:1
7	Cromwell ZA64 – 2	Ro1, Pa1,2/3 Pa2/3	3 4	1:1
9	Cara ZD77 – 11	Ro1 Ro1, Pa2/3	6 NT	3:1
11	Corsair** D42 – 8	Ro1, Pa1,2/3 Pa2/3	4 – 5 3 – 4	1:1

* Blight resistance scored on a 1 to 9 scale where 1 = very susceptible. Data from the Recommended List of the National Institute of Agricultural Botany (NIAB) (Anon., 1985) or equivalent ratings from PBI tests. NT = not tested – *Krautfäulenresistenz, bewertet in einer Skala von 1 bis 9 (1 = sehr anfällig). Daten stammen von der 'Recommended List' des National Institute of Agricultural Botany (NIAB) (Anon., 1985) oder von entsprechenden Bewertungen von PBI-Tests. NT = nicht getestet – La résistance au mildiou est notée de 1 à 9 (1 = très sensible). Les données proviennent de la Liste Officielle du National Institute of Agricultural Botany (NIAB) (Anon., 1985) ou du PBI test. NT = non testé.*

** Corsair has *G. pallida* resistance derived from *S. vernei* – *Corsair besitzt G. pallida-Resistenz aus S. vernei – Corsair, issu de S. vernei, possède des gènes de résistance à G. pallida.*

Tabelle 1. Eltern typischer Nachkommen.
Tableau 1. Caractéristiques des croisements étudiés.

(NIAB rating 7) (NIAB ratings from Anon., 1976, 1985).

Resistance to cyst nematodes was assessed in a modified closed-container test (Phillips et al., 1980) in which tubers to be tested were grown in the presence of the nematode in transparent plastic containers holding 100 ml of soil. The inoculum was a suspension of eggs and larvae of both *G. rostochiensis* pathotype Ro1 and a *G. pallida* population identified as Little Ouse, changed, and classified as Pa2 on the basis of its response to differential hosts (Kort et al., 1977). The cysts had been extracted from beds where they had been maintained as pure cultures by growing the appropriate differential host. The concentration of the inoculum was adjusted to give a population of 1500 larvae of each nematode species per 100 ml of potting soil (John Innes Number 2 formula brought to approximately 30 % water content by the inoculum). The containers were stored in a dark room at 15 to 20 °C for approximately 6–7 weeks while the cysts formed and developed their distinctive colours, pale yellow for *G. rostochiensis* and white for *G. pallida*. Cyst development was checked by regular examination, particularly of the susceptible control clones, and recording commenced when the majority of the *G. rostochiensis* cysts were yellow and *G. pallida* were white. The timing was critical for the identification of species, as very immature cysts of both species are white and mature cysts are brown. Yellow, white and brown cysts visible through the walls of the plastic containers were counted. Counts above 15 were all recorded as 16 and indicated extremely susceptible clones.

Clones were regarded as being resistant to *G. rostochiensis* only if there were no yellow cysts, while a clone with a white cyst count of two or less was classified as resistant to *G. pallida*.

Those plants assessed as resistant to cyst nematodes and still growing strongly were transferred from their containers to 15 cm diameter pots and grown in batches in a heated glasshouse for blight tests. The technique for screening for blight resistance was similar to that described by Malcolmson (1976) and Stewart et al. (1983). When the plants were about 45 cm tall and growing strongly, they were transferred to a polythene tunnel within an unheated glasshouse. After one day the plants and surrounding soil were wetted using an overhead mist irrigation system and the plants were inoculated with *P. infestans* during late afternoon. The inoculum was a zoospore suspension of a complex isolate (possessing virulence genes 1,2,3,4,8), obtained by washing sporangia from sporulating lesions on detached leaves using distilled water, adjusting the concentration to ca. 10 000 spores/ml, and incubating for 2 h at 10 °C to release zoospores. The inoculum was applied with a gas-pressurised sprayer to give a uniform cover.

The tunnel house was closed for the night (ca. 16 h) to maintain a high humidity and then the plants were incubated under intermittent mist until over 95 % of plants had developed lesions and the most susceptible ones had over 80 % necrotic tissue. This took about 11 days. In one test, a set of differential varieties was included (excluding R6 and R9) and this confirmed the virulence gene composition of the isolate. The overall amount of necrotic tissue per plant was scored on a scale of 1 (>90 % necrotic) to 9 (<10 % necrotic) as described by Malcolmson (1976) and Cruickshank et al. (1982).

The four families described in this paper were tested in two separate batches; batch 1 contained families 4 and 7 and was inoculated on 11 April and batch 2 contained families 9 and 11 and was inoculated on 25 April.

Results

Cyst nematode

At the time of recording there were very few brown, mature cysts, particularly on plants otherwise classified as resistant. For example, in family 4 only 23 of the 385 clones recorded as resistant to both nematode species (dual resisters) (Table 2) had up to three brown cysts visible. Mature cysts were relatively more common on the susceptible plants, though few had more than two. Due to the low numbers, and to simplify presentation of the data, the incidence of mature cysts is omitted from Table 2 and Fig. 1.

The distribution of counts for yellow and white cysts for each family is shown in Figs. 1A and 1B. The clear distinction between clones with no yellow cysts and those with some (Fig. 1A) demonstrated the effectiveness of the resistance gene *H1* and made selection of resistant clones straightforward. The distribution of white cyst counts (Fig. 1B) was also as expected, and similar to that found by Dale & Phillips (1982), with no clear separation into resistant and susceptible clones. An arbitrary division was therefore chosen, clones with two or less white cysts being classed as resistant. This resulted in approximately 50 % of the progeny from a cross between resistant and susceptible parents being thus classified.

One advantage of this early generation screening technique is that it enables genetic ratios to be examined. The only selection that had been practised on these progenies previously was in the glasshouse for characters unlikely to be linked with pest or disease resistance. The selected populations were still relatively large. Table 2 shows the population sizes, numbers of resistant plants using the assumptions given above, and calculated resistance ratios.

The similarity of the ratios of resistant to susceptible clones to that predicted (Table 1) was tested for *G. rostochiensis* using the χ^2 test, and the results are shown in Table 2. If *G. pallida* resistance and *G. rostochiensis* resistance are inherited

Table 2. Resistance ratios calculated for four families.

Family	Total	Number of clones resistant to			Percentage of clones resistant to			
					Ro1 (χ^2)	Pa2	both	
		Ro1	Pa2	both			actual	predicted
4	1216	536	612	385	44.1 (17.7*)	50.4	31.7	(22.2)
7	317	183	204	121	57.7 (7.6)	64.4	38.2	(37.2)
9	170	111	118	87	65.3 (8.6)	69.4	51.2	(45.3)
11	488	257	308	174	52.7 (1.4)	63.1	35.7	(33.3)

* Significantly different from expected ratio at $P=0.05$ – *Vom erwarteten Verhältnis signifikant unterschieden ($P=0,05$) – Différence significative au seuil 5 % d'avec les résultats théoriques.*

Tabelle 2. Errechnete Resistenzverhältnisse bei vier Familien.
Tableau 2. Ségrégation de la résistance chez quatre familles.

Fig. 1. Distribution of resistance to cyst nematodes (*Globodera rostochiensis* and *G. pallida*) and foliage blight (*Phytophthora infestans*) in four potato progenies, expressed as a percentage of clones tested.
A, *G. rostochiensis* (cyst number); B, *G. pallida* (cyst number); C, *P. infestans* score (1–9, 9 indicating no visible blight lesions).

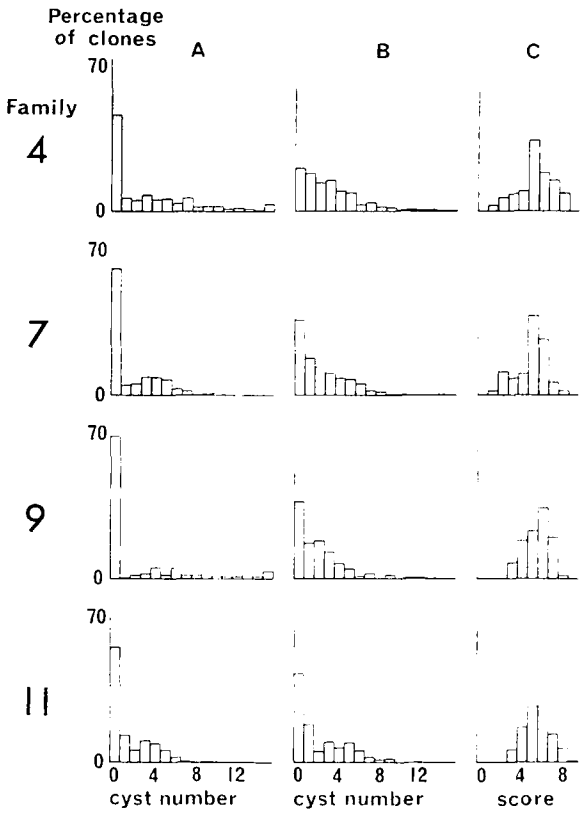

Abb. 1. Verteilung der Resistenz gegenüber den Zystennematoden (Globodera rostochiensis und G. pallida) und Krautfäule (Phytophthora infestans) in vier Kartoffelnachkommenschaften, ausgedrückt in Prozenten der getesteten Klone.
A: G. rostochiensis (Anzahl der Zysten); B: G. pallida (Anzahl der Zysten); C: P. infestans Bewertung (1–9, 9 bedeutet keine sichtbaren Krautfäule-Läsionen).
Fig. 1. Distributions exprimées en valeur relative de la résistance à Globodera rostochiensis, G. pallida et à Phytophthora infestans.
A: G. rostochiensis (nombre de kystes neoformés); B: G. pallida (nombre de kystes neoformés); C: P. infestans échelle de 1 à 9, 9 correspondant à une absence totale de symptômes visibles.

independently, then the percentage of the progeny found to be dual resisters should be the product of the two separate resistances. This calculated figure is shown in Table 2 as 'predicted', alongside the percentage found.

Table 3. Blight resistance of four families.

Family	Number of clones tested	Mean score	Percentage of clones	
			rejected (score <6)	moderately resistant or resistant (score >6)
4	308	5.7	59	23
7	102	4.8	67	8
9	68	5.4	47	21
11	156	5.5	47	20

Tabelle 3. Krautfäuleresistenz bei vier Familien.
Tableau 3. Résistance au mildiou chez quatre familles.

Blight

Some plants were so weakened by the container test that they could not be transferred to pots and others rotted in the containers. However, 82 % of the clones identified as nematode-resistant grew well when they were transferred to the glasshouse. The distribution of blight scores for each family are shown in Fig. 1C. For each family the modal class was 5 or 6. Only clones having a score higher than 5 (more resistant than King Edward) were selected. The percentage of rejected clones, and also of those rated as resistant or moderately so (scores >6), is shown in Table 3. Families 4, 9 and 11, which each had one parent moderately blight-resistant (Table 1), had a similar percentage of moderately resistant or resistant clones but family 4 had the highest percentage of rejects. Family 7, a cross between two *G. pallida*-resistant but blight-susceptible clones, had a low percentage of moderately resistant or resistant clones and the highest rejection rate.

Discussion

The distribution of cyst counts for *G. rostochiensis* (Fig. 1A) was typical for single dominant gene inheritance. Families 4, 7 and 11, which comprised progenies of simplex *H1* crossed with nulliplex parents, were expected to produce resistant and susceptible plants in the ratio 1:1, while for family 9, simplex crossed with simplex, the ratio was expected to be 3:1 (Table 1). The only ratio to deviate significantly ($P<0.05$) from that expected was for family 4 (Table 2). Here the slightly low figure (43 %) for yellow cysts could be explained by random chromatid segregation (expected ratio 1 resistant:1.3 susceptible, χ^2 1.2, n.s.) or by misclassification of immature *G. rostochiensis* cysts, which are white.

The distribution of *G. pallida* cyst counts within families was also as expected. Although no clear divisions were seen, families with two resistant parents gave the largest number of resistant progeny. The distribution for family 11 (Fig. 1B), where there was a distinct group of plants with about four cysts, was unexpected. This was a cross between *S. vernei*-derived and Andigena-derived clones, so there could be some interaction between the resistance genes.

For all families, except family 4, there was a good agreement between the percentage of clones classified as dual resisters and the percentage predicted if both

resistances acted independently. In family 4 more dual resisters than expected were found. In comparison with the families which had both parents resistant to *G. pallida* (Table 1), the percentage of *G. pallida*-resistant clones in this family was also high. This could be the result of the misclassification of *G. rostochiensis* cysts postulated above.

An unreplicated early-generation screening test of the type described here enables the identification of highly susceptible clones despite the possibility of some erroneous results. It is unlikely that any clone with a high cyst count has adequate resistance to nematode infection. Resistant clones not identified in the test are likely to be partial resisters at best and therefore not within the selection parameters chosen for these families. It is more likely that errors are made by keeping susceptible clones on which cysts failed to develop. These will be identified, and rejected if necessary, in later confirmatory tests. Similarly a proportion of the clones assessed as having adequate blight resistance may be escapes from infection. Stewart et al. (1983), using two plants per clone in a glasshouse test, found correlations with field results ranging from $r=0.504$ ($P<0.05$) to $r=0.834$ ($P<0.001$). Field scores gave a better separation of resistant and susceptible clones than the glasshouse scores. However, as concluded by Stewart et al. (1983), rejection of apparently susceptible clones in the glasshouse test should remove highly field-susceptible clones.

The four families described in this paper were typical of the material screened and 35 % of the tested clones were selected as resistant to both *G. rostochiensis* and *G. pallida* and of these 42 % were retained after selection for blight resistance. This gives a selection rate of 15 %, broadly similar to rates previously obtained based on field observations of tuber characters at the seed site.

An important advantage of this screening system was that all recording was completed by the spring following the sowing of true seed. Thus stored tubers of clones with multiple resistance were planted for further multiplication without any loss of time and those of susceptible clones discarded with no further inputs. The number of clones to be screened for quality characters was thus greatly reduced enabling this key assessment to be based on detailed observation of plots rather than visual assessments of single plants.

Zusammenfassung

Eine auf früher Stufe stattfindende Prüfung auf kombinierte Resistenz gegenüber Zystennematoden (Globodera spp.) und Krautfäule (Phytophthora infestans) bei Kartoffeln

In Kartoffelzuchtprogrammen müssen viele Eigenschaften berücksichtigt werden. Die Reihenfolge ihrer Selektion kann grossen Einfluss auf die gesamte Arbeitsleistung haben. Dort wo die Aufspaltung der Nachkommenschaft bedeutsam ist, kann eine frühe Selektion leicht erkennbarer Eigenschaften, wie Resistenz gegenüber Schädlingen und Krankheiten, die Populationsgrösse wirkungsvoll verringern. Dies könnte den starken Selektionsdruck auf Knolleneigenschaften als erste Hauptprüfung in Kartoffelzuchtprogrammen ersetzen.

In dieser Arbeit wird eine Technik zur Prüfung auf kombinierte Resistenz gegenüber Kartoffelnematoden und Krautfäule beschrieben, und es werden die Ergebnisse für Nachkommen aus typischen Kreuzungen mitgeteilt (Tabelle 1). Die Nematodenresistenz wurde mit Hilfe eines Gefässtestes ermittelt, bei dem ein Inokulumgemisch aus Larven von *Globodera rostochiensis* und *G.*

pallida verwendet wurde. Dies ergab die in Tabelle 2 dargestellten Befunde und eine Verteilung der Zystenproduktion, wie sie in den Abbildungen 1A und 1B gezeigt wird. Diese Ergebnisse bestätigten, dass die nicht wiederholten Tests Reaktionen ergaben, wie sie von der bekannten Vererbung der Eigenschaften erwartet wurden, und ein Chi-Quadrat-Test (Tabelle 2) ergab bei drei von vier Familien, dass keine Abweichung von den erwarteten Verhältnissen für H1, von dem sich die *G. rostochiensis*-Resistenz herleitet, vorlag. Eine vorkommende Abweichung (Tabelle 2, Familie 4) liess sich mit der ungenügenden Unterscheidung der unreifen Zysten von beiden *Globodera*-Arten erklären. Bei der Selektion auf Resistenz gegenüber den beiden Arten ist diese Fehlerquelle unbedeutend.

Die als nematodenresistent ermittelten Pflanzen wurden in Töpfen bei hoher Luftfeuchtigkeit in einem Polythen-Tunnel in Gewächshaus angezogen und mit einer Zoosporensuspension aus einem Isolatkomplex von *Phythophthora infestans* besprüht. Die Anfälligkeit wurde ermittelt, indem die ungefähre Blattfläche der entstehenden nekrotischen Läsionen bewertet wurde. Die Ergebnisse in Tabelle 3 und die Verteilung der resistenten Klone (Abb. 1C) weisen – wie erwartet – auf die polygene Vererbung hin. Bei den angewandten Selektionsstufen erhielt man ungefähr 15 % der Nachkommen mit hinreichender Resistenz gegenüber den drei vorgegebenen Eigenschaften. Die Teste wurden in der Lagerzeit der Knollen, die ursprünglich von Sämlingspflanzen stammten, abgeschlossen, so dass sie in der der Aussaat nachfolgenden Saison ausgepflanzt werden konnten.

Résumé

Tests précoces de résistance à Globodera sp. et à Phytophthora infestans chez la pomme de terre

Dans les programmes de sélection de la pomme de terre, de nombreux caractères sont pris en compte et le choix de la succession de leurs mesures a une forte importance sur l'efficacité globale du travail. Quand il y a ségrégation pour des caractères importants et facilement mesurables comme la résistance aux ravageurs et aux maladies, on peut réduire le travail de maintenance du matériel en réalisant des cribles précoces pour ces caractères. Ces tests peuvent être d'abord réalisés à la place des tests de qualité, classiquement effectués en début de programme.

Les auteurs décrivent ici une technique de tests de résistance à la fois vis-à-vis des nématodes à kyste et du mildiou. Les résultats de tests de descendance de quatre croisements sont détaillés. La résistance aux nématodes est mesurée par des tests en conteneurs dans lesquels le substrat est infesté par un mélange de larves infestantes de *Globodera rostochiensis* et de *G. pallida*. On trouve les résultats globaux en Tableau 2 et les distributions exprimées en valeur relative du nombre de kystes neoformés sont représentées en figures 1A et 1B. Malgré l'absence de répétitions, ces résultats sont en accord avec ceux espérés: le χ^2 (Tableau 2) ne montre pas de différence significative pour 3 familles sur 4 avec les résultats théoriques quand c'est la résistance due au gène H1 qui est mesurée. Le cas de non concordance (Tableau 2, famille 4) est explicable par une possible confusion des espèces à la lecture. Cependant, cette source d'erreurs est peu importante quand la sélection est dirigée en même temps contre ces deux espèces.

Les clones jugés résistants sont alors testés vis-à-vis de *Phytophthora infestans*. Ils sont placés en pots et cultivés en serre sous tunnel de polyethylène pour entretenir une forte humidité relative. Une suspension de zoospores d'un isolat complexe est pulvérisée et la sensibilité est appréciée par la surface approximative des lésions nécrotiques du feuillage. Les résultats du Tableau 3 et la distribution relative de la fréquence des clones résistants confirment l'hérédité polygénique de la résistance au mildiou.

Environ 15 % des familles sont ainsi rete-

nues comme ayant un bon niveau de résistance aux deux espèces de *Globodera* et à *P. infestans*. Les tests, réalisés en hiver, sont achevés à temps pour que les duplicatats, conservés à basse température, identifiés comme résistants puissent être plantés au champ en temps utile, l'année qui suit les semis de graines.

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