

LABORATORY ASSESSMENTS OF THE SUSCEPTIBILITY OF POTATO-TUBER TISSUE TO BLIGHT (*PHYTOPHTHORA INFESTANS*)

D. H. LAPWOOD

Rothamsted Experimental Station, Harpenden, Herts., England

Zusammenfassung, Résumé, p. 228

SUMMARY

Fifty five potato varieties were compared with *Majestic* for the resistance of their tuber tissues to infection by *Phytophthora infestans* (MONT.) DE BARY in three kinds of test using 1. halved tubers; 2. tuber slices and 3. whole tubers.

Tissue resistance was better indicated by the extent surface mycelium developed after the fungus had grown through a slice of standard thickness (Test 2) than by the density of surface mycelium on the inoculated surface (Test 1) or by the area of necrotic tissue (Test 1 and 3).

Most varieties that suffer few tuber infections when grown as field crops were rated as resistant by these tests. Tissue resistance as assessed by these simple laboratory tests, which require only few replicates, could be used to select tuber-resistant varieties.

1. INTRODUCTION

A simple, quick but reliable method of selecting for tuber resistance to blight, needing few replicates, is required, as breeders have many seedlings to test but only a few tubers of each. In an attempt to devise such a test, tubers of 55 potato varieties were compared with *Majestic* by three methods during the winters of 1959 and 1960. Fewer blighted tubers are generally found in field crops of the maincrop variety *Majestic* than in many other varieties, and tests of tubers in the laboratory show it to be consistently resistant. Comparisons were made to see whether the results of laboratory tests correlated with the field performance of the varieties.

2. MATERIALS

The varieties were grown in small plots at Rothamsted and the crop kept in a cool store after harvest; all tests were done before the tubers sprouted. For convenience, varieties were tested in groups, generally of twelve, with the variety *Majestic* as a standard; early, maincrop and late varieties were included in each group. Cultures of *Phytophthora infestans* were maintained on potato slices or on leaves, and dense suspensions of sporangia and zoospores were used as inoculum.

Accepted for publication 11th July, 1965

Eur. Potato J., Vol. 8 (1965) No. 4 (Dec.)

3. METHODS

The susceptibility of tuber tissues was assessed in three ways which, for convenience, are referred to as the 'half-tuber', 'tuber-slice' and 'whole-tuber' tests.

3.1. Half-tuber test

This was based on a technique described by MULLER, CULLEN and KOSTROWICKA (1955). Three tubers of each variety were cut lengthwise and each half inoculated in two positions, at opposite ends of the exposed face, with a filter-paper disc (7 mm diameter) previously dipped in the spore suspension. Six "Polythene"-lined boxes were used for each test group and in each were placed half tubers of each of the 12 varieties plus *Majestic* in varying order. Damped "Airovorena" (a foamed polyurethane sheet supplied by Progress Mercantile Co. Ltd., London E.C. 1) was placed over each box and covered by a flap of "Polythene". After inoculation, the boxes were put in an unheated store at 13–14°C. The filter-paper discs were removed two days later and, after one week, the extent and density of surface mycelium was graded subjectively in four categories, from 1 (no response) to 4 (maximal response). At the end of the experiment (10 days) the tubers were cut and the internal spread of the fungus was assessed from the depth of necrotic tissue; again four categories were used: 1 = no penetration; 2 = penetration less than 2 mm; 3 = penetration less than 5 mm; and 4 = penetration more than 5 mm. In 1960 the surface assessments were made after 6 days and penetration 7 days after inoculation.

3.2. Tuber-slice test

A disadvantage of the half-tuber test is that the internal spread of the fungus is not directly related to the amount of necrotic tissue, because varieties differ in the rate at which cells die after infection. To overcome this, the rate at which the fungus advanced through the tuber tissues was estimated by inoculating an 11-mm thick slice of tuber tissue on one surface, and then recording the amount of aerial mycelium appearing on the opposite surface after a specified interval (LAPWOOD and MCKEE, 1961).

Two slices were cut from each of six tubers of each variety and the twelve replicates then placed in separate boxes as in the half-tuber test. A filter-paper disc dipped in the inoculum was placed at each end of the slice, a. on the outer cortical tissues at the edge of the slice for six of the replicates, and b. on the central medullary region for the remainder (in 1959 only one medullary inoculation in the centre of the slice was used). The discs were removed after 2 days and the slices turned over, so that the uninoculated surface was uppermost. In 1959, the extent and density of aerial mycelium on this surface was determined after 4, 5, 6 and 8 days, using the subjective key as in the half-tuber test, but in 1960 the time for penetration of each slice was estimated by observing the first signs of aerial mycelium.

3.3. Whole-tuber test

This method was devised to test the resistance of the cortical tissues of the tuber and to use smaller wounds than the previous tests, in which the tuber was damaged extensive-

ly by cutting. Tubers were thoroughly washed but not surface-sterilised and two, widely-spaced, shallow cuts, just sufficient to pierce the periderm, were made with a No. 3 cork borer (6 mm diameter). The small disc of periderm was removed with forceps and the exposed tissue inoculated with filter-paper discs. Five or six (1960) tubers were arranged in different positions within and between boxes as already described. After 24 hours at 13–14°C, tubers were transferred from the "Polythene"-lined to normal seed-boxes, and kept at 20°C for 14 days. Tubers were then cut and penetration of the fungus assessed from necrosis, as previously described. Varieties differed in their reactions; some showed extensive necrosis in the outer cortex with little or no penetration through the vascular ring into the inner cortical and medullary tissues, whereas with others the reverse was true. Thus an assessment based on depth of penetration was of little value. The various necrotic patterns shown in the FIGURE, were used to describe the rot on each tuber. For convenience of presentation, the various patterns are grouped in three basic types.

3.4. Field estimates of tuber resistance

These estimates proved more difficult to obtain than expected for, in 1959, there was little information on the field susceptibility of tubers of some new varieties. In 1960, Dutch varieties were included in the tests so that laboratory results could be compared with the Dutch List (HOGEN ESCH and ZINGSTRA, 1957) which gives the tuber resistance of varieties widely grown in the Netherlands. However, the Dutch assessments for some British varieties are at variance with our experience, for example *Arran Pilot* (early) and *King Edward* (maincrop), both tuber-susceptible varieties in Britain, are rated more resistant than *Majestic*. The assessments in TABLE 5 are based on information from various sources including the Dutch List, National Institute of Agricultural Botany (N.I.A.B.) field trials, the survey work of KEHOE (1961–1963) in Eire, and from discussion with many field workers.

4. RESULTS

TABLES 1 and 2 give results in the different tests for 1959 and 1960 respectively. The varietal order within the groups was determined by maturity class and by the mean of individual test scores for the three tests; varieties with tuber resistance in field crops considered to equal or exceed that of *Majestic* are shown in bold type.

To assess the value of a particular test to a breeder two criteria were used: – 1. the number of field-resistant varieties not detected by the test and 2. the number of field-susceptible varieties indicated as resistant by the test score. The largest *Majestic* scores were used in these comparisons; for example, in the 1959 half-tuber tests (TABLE 1), the largest score for sporulation in five independent tests was 2.4 and for penetration 2.8 (see TABLE 3a).

4.1. Efficiency of the half-tuber test

Assessments were based on the density of surface mycelium and on the amount of

TABLE 1. Detailed results of the performance of 46 varieties of different maturity (E – early; M – maincrop; L – late), when compared with *Majestic* in 1959 (Details of tests in text)

Variety	Maturity	Half tubers		Tuber slices		Whole tubers ¹		
		sporulation scores ²	penetration scores ²	sporulation medulla ³	scores ² cortex ³	1	II	III
Group I								
Duke of York	E	3,2	3,6	2,3	3,3	–	4	6
Craigs Alliance	E	3,1	2,8	2,7	2,5	–	10	–
Arran Pilot	E	3,1	3,5	2,5	1,2	–	4	4
Arran Banner	M	2,9	3,8	2,5	3,8	–	3	7
Russet Burbank	M	3,0	3,0	3,0	3,3	–	1	7
Sebago	M	3,2	3,5	2,5	2,5	1	5	3
Katahdin	M	2,9	2,8	3,0	2,8	–	9	1
Arran Viking¹	M	2,7	3,6	2,8	1,5	1	3	6
Ontario	M	2,2	2,0	2,2	1,6	5	1	3
Arran Victory	L	2,5	3,7	2,7	2,0	1	6	1
Golden Wonder	L	1,9	3,0	1,3	1,7	7	1	–
E 57 ²		3,5	3,8	3,5	2,2	–	8	2
Majestic	M	2,2	2,5	2,0	1,5	–	–	–
Group II								
Epicure	E	3,7	3,9	2,5	3,2	–	–	10
Home Guard	E	3,2	3,2	3,2	3,8	–	4	6
Eclipse	E	3,2	3,9	3,2	3,8	6	3	1
Viola	E	2,3	3,2	3,2	2,3	–	–	8
Ulster Grove	M	3,1	3,1	3,2	3,5	–	–	8
King Edward	M	3,4	2,7	2,7	3,2	–	6	2
Doon Star	M	3,2	3,1	2,7	2,9	1	8	1
Pentland Crown	M	2,1	2,4	1,7	1,8	–	6	4
Record	M	1,6	2,2	2,0	2,0	6	1	3
Kerr's Pink	L	2,1	3,1	3,2	3,7	–	5	3
Shamrock	L	2,2	2,3	1,3	1,3	8	–	–
E 62 ²		4,0	3,8	3,5	3,6	–	–	10
Majestic	M	2,4	2,8	1,3	1,8	–	–	–
Group III								
Ulster Premier	E	4,0	3,6	3,7	3,5	–	–	10
Sharpe's Express	E	3,5	3,8	3,3	3,0	–	9	1
Ulster Chieftain	E	3,0	3,8	3,0	1,1	–	9	1
Ally	M	3,2	2,2	3,5	3,0	–	7	3
Majestic	M	2,2	2,6	2,0	2,0	2	4	–
Stormont Dawn	M	1,9	3,2	1,0	2,1	1	7	–
Ulster Supreme	L	3,5	3,8	3,3	3,8	–	1	5
Ackersegen	L	2,6	2,6	1,8	2,3	1	7	–
Skerry Blue	L	2,9	2,2	2,7	1,2	2	4	4
Champion	L	2,8	3,1	1,3	1,6	6	1	1
Spry's Abundance	L	1,8	2,3	1,0	1,9	1	3	4
As	L	1,5	2,1	1,0	1,0	–	8	2
Majestic	M	1,9	2,2	1,8	1,8	–	–	–

LABORATORY ASSESSMENTS OF THE SUSCEPTIBILITY OF POTATO-TUBER TISSUE TO BLIGHT...

TABLE 1. (continued)

Variety	Maturity	Half tubers		Tuber slices		Whole tubers ¹		
		sporulation scores ²	penetration scores ²	sporulation medulla ³	scores ² cortex ³	rot pattern I II III		
Group IV								
Ulster Prince	E	3.0	4.0	2.8	3.2	-	3	7
Craigs Royal	E	3.2	3.1	2.3	1.4	6	3	1
Ulster Tarn	M	2.8	3.7	3.8	2.6	-	2	6
King Edward	M	3.7	3.0	2.7	2.7	-	-	-
Frühperle	M	3.7	2.2	3.2	2.7	4	-	4
Ulster Cromlech	M	3.0	3.1	2.7	3.0	5	4	-
Ulster Beacon	M	1.5	2.2	1.7	1.6	3	2	-
Leinster Wonder	L	2.8	3.7	2.8	3.3	2	7	1
Up-to-Date	L	2.7	2.8	2.7	2.8	4	1	5
Irish Chieftain	L	3.2	2.0	2.0	1.0	8	2	-
Pimpernel	L	3.0	2.4	1.0	1.1	1	9	-
Robijn	L	2.2	2.0	1.0	1.0	9	1	-
Majestic	M	2.1	2.7	1.5	1.1	-	-	-

Sorte	Reifezeit	Halbe Knollen		Knollenscheiben		Ganze Knollen ¹		
		Sporulationswerte ²	Eindringungswerte ²	Sporulationswerte ² Mark ³	Rinde ³	Befallsflächenansicht I II III		
<i>Variété</i>	<i>Maturité</i>	<i>Demi-tubercules</i>		<i>Tranches de tubercule</i>		<i>Tubercules entiers³</i>		
		<i>sporulation cote²</i>	<i>pénétration cote²</i>	<i>cote de sporulation² moelle³ écorce³</i>		<i>aspect de pourriture I II III</i>		

¹ See FIGURE (I - resistant to III - susceptible) - siehe ABBILDUNG (I - resistent bis III - anfällig) - voir FIGURE (I - résistant à III - susceptible).

² Score based on 4 categories (1 - no response to 4 - maximum response) - die Bewertungsskala basierte auf 4 Kategorien (1 - keine Reaktion bis 4 - stärkste Reaktion) - cotation en 4 catégories (1 - réaction nulle à 4 réaction maximale).

³ Medulla inoculation scored 5 days and cortex 6 days after inoculation - Inokulation des Marks nach 5 Tagen bonitiert und die der Rinde nach 6 Tagen - cotations faites sur la moelle 5 jours après l'inoculation et celles sur la couche corticale 6 jours après l'inoculation.

⁴ Varieties in bold type show tuber resistance in the field (see TABLE 5) - die in Fettdruck angezeigten Sorten besitzen Knollenresistenz im Feld (siehe TABELLE 5) - les variétés en gros caractères montrent de la résistance du tubercule dans le champ (voir TABLEAU 5).

⁵ Seedlings from N. Ireland found to be highly susceptible to tuber blight at Rothamsted - Sämlinge von Nord-Irland, die in Rothamsted als sehr anfällig gegen Knollenfäule befunden wurden - plantules de l'Irlande du Nord trouvées hautement susceptibles au mildiou du tubercule à Rothamsted.

TABELLE 1. Ausführliche Ergebnisse betreffend Verhalten von 46 Sorten mit verschiedenen Reifezeiten (E - früh; M - Haupternte; L - spät) im Vergleich mit Majestic im Jahre 1959. Die Testmethoden sind im Text beschrieben.

TABLEAU 1. Résultats détaillés des performances de 46 variétés de diverses maturités (E - hâtive; M - principale récolte; L - tardive) en comparaison avec Majestic en 1959, dans les tests décrits dans le texte.

TABLE 2. Detailed results of the performance of 24 varieties of different maturity when compared with *Majestic* in 1960 (Details of tests in text)

Variety	Maturity	Half tubers		Tuber slices		Whole tubers ¹			
		sporulation scores ²	penetration scores ²	medulla No. ⁶	cortex No. ⁶	rot pattern			
						I	II	III	(IV) ⁷
Group I									
Duke of York	E	3,8	2,8	—	—	0	4	7	1
Arran Pilot	E	3,2	2,4	12	2	0	0	10	2
King Edward	M	3,2	2,3	10	9	0	4	8	0
Cayuga	M	3,4	3,1	8	7	5	2	1	4
Koopman's Blauwe¹	M	3,7	3,7	4	6	1	8	2	1
Great Scot	M	3,4	2,2	6	10	4	6	2	0
Furore	M	3,6	3,0	6	3	1	11	0	0
Noordeling	M	2,2	2,9	6	4	7	5	0	0
Record	M	1,8	2,6	2	0	6	0	1	5
Voran	L	1,8	2,8	4	3	1	8	1	2
Populair	L	3,5	2,4	2	0	11	0	0	1
Regina	L	1,4	2,5	2	1	2	9	0	1
Majestic	M	2,2	2,4	4	5	4	5	3	0
Group II									
Bintje	M	3,7	3,2	12	12	0	2	10	0
Redskin	M	3,1	2,3	10	12	0	0	12	0
Dr. McIntosh	M	3,2	3,2	10	10	4	5	3	0
Eigenheimer	M	3,7	2,3	12	9	0	4	8	0
Gineke	M	1,3	2,7	2	10	5	7	0	0
Sientje	M	1,2	2,2	4	6	5	0	5	2
Prof. Broekema	M	0,2	2,1	0	1	6	5	0	1
Loman 43-35	L	2,1	2,5	4	9	2	1	7	2
Zeeburger	L	0,8	1,8	6	7	5	7	0	0
Robijn	L	2,7	2,2	0	2	7	5	0	0
Pimpernel	L	2,6	2,0	2	0	10	1	0	1
Libertas	L	0,8	2,0	2	1	1	6	5	0
Majestic	M	2,0	2,3	2	7	2	4	6	0
<i>Sorte</i>	<i>Reifezeit</i>	<i>Halbe Knollen</i>		<i>Knollenscheiben</i>		<i>Ganze Knollen¹</i>			
		<i>Sporulationsswerte²</i>	<i>Eindringungswerte²</i>	<i>Mark Zahl⁶</i>	<i>Rinde Zahl⁶</i>	<i>Befallsflächenansicht</i>			
						I	II	III	(IV) ⁷
<i>Variété</i>	<i>Maturité</i>	<i>Demi-tubercules</i>		<i>Tranches de tubercules</i>		<i>Tubercules entiers¹</i>			
		<i>sporulation cote²</i>	<i>pénétration cote²</i>	<i>moelle nombre⁶</i>	<i>écorce nombre⁶</i>	<i>aspects de pourriture</i>			
						I	II	III	(IV) ⁷

¹, ² and ⁴ See corresponding notes in legend TABLE 1 - siehe die entsprechenden Anmerkungszeichen in der Legende auf TABELLE 1 - voir les notes correspondantes dans la légende du TABLEAU 1.

⁶ Number out of 12 slices penetrated by fungus 5 days from inoculation - Anzahl Knollenscheiben (von 12), in die der Pilz 5 Tage nach der Inokulation eingedrungen war - nombre de tranches sur 12 pénétrées par le champignon 5 jours après inoculation.

⁷ See FIGURE - siehe ABILDUNG - voir FIGURE.

TABELLE 2. Ausführliche Ergebnisse des Verhaltens von 24 Sorten verschiedener Reifezeit im Vergleich mit *Majestic* im Jahre 1960. Die Untersuchungsmethoden sind im Text beschrieben.

TABLEAU 2. Résultats détaillés des performances de 24 variétés de diverses maturités en comparaison avec *Majestic* en 1960 dans les tests décrits dans le texte

TABLE 3. Evaluation of the half-tuber and tuber-slice tests in 1959 from a. the number of varieties resistant in the field which are not detected and b. susceptible varieties misclassified as resistant, when varietal scores (TABLE 1) are compared with *Majestic*

a. Half-tuber test ¹		2. Penetration scores ³ (1) (<i>Majestic</i> 2.8)	
1. Sporulation scores ² (1) (<i>Majestic</i> 2.4)		Resistant varieties (2) excluded ¹ (3)	Susceptible varieties (2) included ² (3)
Resistant varieties (2) excluded ¹ (3)	Susceptible varieties (2) included ² (3)	Arran Viking Champion Golden Wonder Stormont Dawn	Ally Craig's Alliance Frühperle Katahdin King Edward Pentland Crown Skerry Blue Up-to-Date
Ackersegen Arran Viking Champion Irish Chieftain Pimpernel	Pentland Crown Kerr's Pink		
b. Tuber-slice test ⁶		2. Cortex scores ⁸ (1) (<i>Majestic</i> 2.0)	
1. Medulla scores ⁷ (1) (<i>Majestic</i> 2.0)		Resistant varieties (2) excluded ¹ (3)	Susceptible varieties (2) included ² (3)
Resistant varieties (2) excluded ¹ (3)	Susceptible varieties (2) included ² (3)	Ackersegen Stormont Dawn	Arran Pilot Arran Victory Craig's Royal Skerry Blue Ulster Chieftain
Arran Viking Ontario	Pentland Crown		

(1) From TABLE 1 (highest *Majestic* score used as a basis for comparison) — siehe TABELLE 1 (Vergleichsbasis: höchste Note von *Majestic*) — voir TABLEAU 1 (la note la plus haute de *Majestic* utilisée comme base de comparaison).
 (2) Field susceptibility: see TABLE 5 — Felde Anfälligkeit: siehe TABELLE 5 — susceptibilité au champ. Voir TABLEAU 5.
 (3) Indicates field-resistant varieties with scores greater than *Majestic* and therefore excluded from the selection, and field-susceptible varieties with scores equal to or less than *Majestic* and therefore included in the selection — bezeichnet feldresistente Sorten mit höheren Herten als *Majestic*, die deshalb bei der Selektion verworfen wurden, sowie auf dem Feld anfällige Sorten mit gleichen oder niedrigeren Herten als *Majestic*, die deshalb bei der Selektion berücksichtigt wurden — indique: les variétés résistantes au champ avec des cotes plus élevées que *Majestic* et pour cette raison exclues de la sélection, et aussi les variétés susceptibles au champ avec des cotes égales ou inférieures à *Majestic* et pour cette raison incluses dans la sélection.

¹ Test mit halben Knollen — test sur demi-tubercules.
² Sporulationswerte — cotes de sporulation.
³ Eindringungswerte — cotes de pénétration.
⁴ Resistente Sorten verworfen — variétés résistantes exclues.
⁵ Anfällige Sorten berücksichtigt — variétés susceptibles incluses.
⁶ Test mit Knollenscheiben — test sur tranches de tubercule.
⁷ Werte für Mark — cotations de la moelle.
⁸ Werte für Rinde — cotations de l'écorce.

TABELLE 3. Bewertung der Testmethoden (1959) mit halben Knollen und mit Knollenscheiben nach a. der Anzahl resistenter Sorten im Feld, die nicht entdeckt wurden, und b. anfälligen Sorten, die beim Vergleich der sortentypischen Werte (TABELLE 1) mit jenen von *Majestic* fälschlicherweise als resistent bezeichnet wurden

TABLAU 3. Appréciation des tests de 1959 sur demi-tubercules et tranches de tubercules à partir du nombre a. de variétés dont la résistance au champ n'a pas été décelée et b. des variétés susceptibles classées erronément comme résistantes, les cotations variétales (TABLEAU 1) étant comparées à *Majestic*

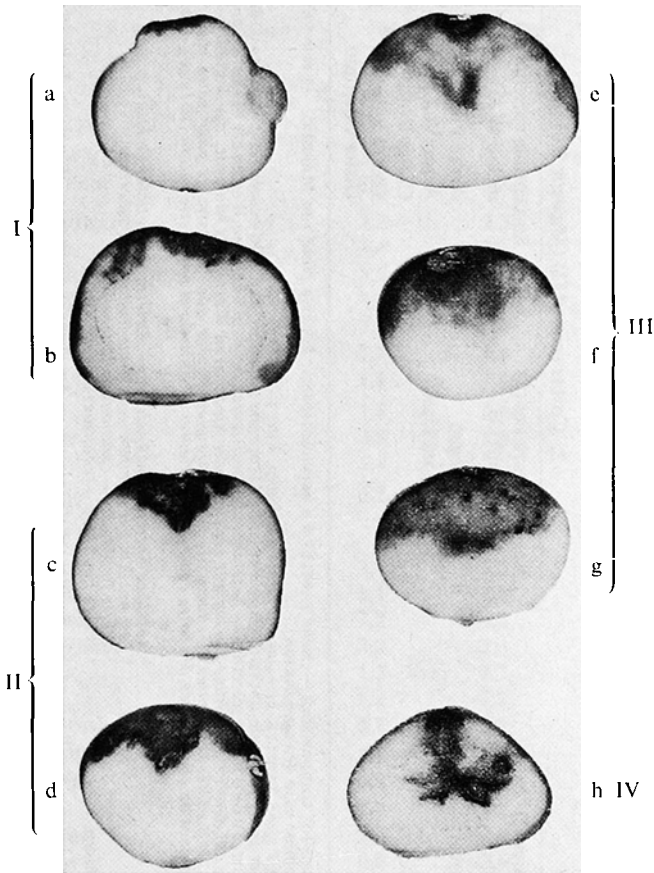


Photo: Rothamsted Experimental Station

FIGURE
Rot pattern 14 days after in-
oculation of a surface wound

ABBILDUNG
Ansicht der Befallsflächen 14
Tage nach Impfung einer ober-
flächlichen Verletzung

FIGURE
Aspect de pourriture 14 jours
apres l'inoculation d'une bles-
sure superficielle

The FIGURE shows the range of reactions: - a. *Populair*, b. *Robijn*, c. *Koopman's Blauwe*, d. *Eigenheimer*, e. *Redskin*, f. *Bintje*, g. *Duke of York* and h. *Record*, and how they were condensed for TABLES 1 and 2: - Type I (a - b) resistant; II (c - d) intermediate; III (e - f - g) susceptible and Type IV (h); see text and TABLE 2.

Darstellung des Reaktionsbereiches: a. Populair... h. Record, und wie sie zusammengefasst wurden für die TABELLEN 1 und 2: Typ I (a - b) resistent; II (c - d) mittel; III (e - f - g) anfällig und Typ IV (h); siehe Text und TABELLE 2.

Illustration d'une série de réactions: a. Populair... h. Record, et cotées dans les TABLEUX 1 et 2: Type I (a - b) résistent; II (c - d) intermédiaire; III (e - f - g) susceptible et Type IV (h); voir texte et TABLEAU 2.

necrotic tissue. When the efficiency of the method was based on the 1959 sporulation scores (TABLE 3 a.1), 5 varieties with resistant tubers in the field gave scores greater than *Majestic* (2,4), and, therefore, would not have been selected, whereas the field-susceptible *Kerr's Pink* and *Pentland Crown*, with scores smaller than *Majestic*, would

have been selected as resistant. Comparing the 1959 penetration scores with *Majestic* (TABLE 3 a.2) indicate even more field-susceptible varieties as resistant. Penetration was estimated from the depth of necrotic tissue but, as noted above, the host reaction differs greatly in different varieties, and depends on the degree of resistance. Most resistant varieties show a dark brown 'pitted' rot, whereas susceptible ones show a very light brown reaction, which makes the exact area of necrosis difficult to define. Some varieties, *Pimpernel* for example, support a dense surface mycelium with little penetration into the tissues; however, surface reaction probably indicates the suitability of the cut surface as a food base for the fungus, rather than reflecting the extent to which the fungus has penetrated. Thus a selection based on this test would be inefficient because it would class too many field-susceptible varieties as resistant.

4.2. Efficiency of the tuber-slice test

In this test, the fungus has first to grow through a slice of tissue of standard thickness and then to appear as a mycelium on the opposite surface. The extent and density of this mycelium should estimate resistance of the tissues better than the half-tuber test, which is based on the rate at which cells die. The slices were inoculated either on the central medulla or on the outer cortical tissues.

Comparing medulla scores for 1959 (TABLE 3 b.1) with *Majestic*, *Ontario* and *Arran Viking* are the only field-resistant varieties undetected and *Pentland Crown* is the only field-susceptible graded as resistant. With cortical inoculation (TABLE 3 b.2), *Ackersegen* and *Stormont Dawn* are not shown as resistant and several field-susceptible varieties are, which suggests that the outer cortex of some varieties is more resistant than the inner cortex and medulla; this is also suggested by results of the whole-tuber test.

4.3. Whole-tuber test

This was the least satisfactory and yet perhaps the most interesting of the three methods. The shape of the rotted area often differed between replicates, although both highly resistant and susceptible varieties showed consistent patterns. In many varieties, the rot was extensive in the outer cortex with little or no penetration of the fungus into the inner cortex or medulla. *Record* was of particular interest because some replicates showed a restricted rot of the *Populair* type (Type I, FIGURE) whereas, in others, the medulla was completely rotted (Type IV, FIGURE). The rot pattern seemed to depend on the distance of the inoculation site from an eye and to involve the medulla when this was small. This suggested that the inner medulla was susceptible and was, perhaps, being protected in some way by the outer cortex; alternatively, the vascular ring (dividing the outer cortex from the inner cortex and medulla) may have been a barrier to the fungus. The effect of breaking through the vascular ring was, therefore, tested, using 6 tubers each of 12 varieties, including *Record*. Each tuber had two wounds, one shallow as used in this test previously and the other deep. The deep one was made by removing, with a No. 3 cork borer, a plug of tissue 6 mm in diameter and 7 mm deep which was replaced after inoculating the cavity; the surface was then sealed with wax. The results (TABLE 4) showed that the depth of the wound had some effect on the exten-

TABLE 4. Effect of inoculating tubers with blight, either at a surface wound or one 7 mm deep, on the amount of rot of the outer cortex and inner cortex and medulla

Variety	Surface wound		Deep wound	
	cortex ² (cm)	medulla ¹ (sq. cm)	cortex (cm)	medulla (sq. cm)
Bintje	2.5 ³	1.2	3.7	5.7
King Edward	2.8	1.0	3.4	2.9
Ulster Supreme	3.6	3.5	4.2	9.8
Furore	2.6	0.4	3.1	2.0
Majestic	2.5	0.5	2.8	1.6
Record	1.3	0.2	2.6	3.4
Prof. Broekema	1.4	0.2	2.2	1.1
Zeeburger	2.5	0.1	2.8	1.3
Populair	1.7	0.1	2.0	1.0
Regina	1.6	0.2	2.7	1.2
Pimpernel	2.3	0.1	1.8	0.1
Robijn	1.4	0.0	2.1	1.3

Sorte	Oberflächliche Verletzung		Tiefe Verletzung	
	Rinde ² (cm)	Mark ¹ (cm ²)	Rinde ² (cm)	Mark ¹ (cm ²)
Variété	Blessure superficielle		Blessure profonde	
	écorce (cm)	moelle (cm ²)	écorce (cm)	moelle (cm ²)

¹ Area of invasion beyond vascular ring. Product of mean depth and lateral extension in tissues – *Befallsfläche über den Gefäßbündelring hinaus. Produkt aus mittlerer Tiefe und seitlicher Ausdehnung in den Geweben* – *aire d'envahissement au-delà de la zone vasculaire. Produit de la profondeur moyenne par l'extension latérale dans les tissus.*

² Invasion of cortex when tuber cut through inoculation point – *Befall der Rinde, wenn die Knolle beim Inokulationspunkt durchgeschnitten wird* – *envahissement de la couche corticale au travers du point d'inoculation révélé en sectionnant le tubercule.*

³ Mean figures from 6 tubers, each tuber having one shallow and one deep inoculation – *Mittelzahlen von 6 Knollen, jede mit einer oberflächlichen und einer tiefen Inokulation* – *chiffres moyens de 6 tubercules ayant reçu chacun une inoculation superficielle et une profonde.*

TABELLE 4. Die Wirkung der Impfung von Knollen mit *P. infestans*, entweder durch eine oberflächliche oder eine 7 mm tiefe Verletzung, auf den Umfang der Fäule in der äusseren und der inneren Rinde sowie des Markes

TABEAU 4. Effet de l'inoculation de tubercules avec le mildiou, soit sur une blessure superficielle, soit sur une de profondeur de 7 mm, sur l'importance de la pourriture dans la couche corticale externe et interne, et dans la moelle

sion of the rot in the outer cortex but a larger effect on infection of the medulla, which rotted more with the deeper wound. Of the resistant varieties, *Pimpernel* was least and *Record* most susceptible to medullary infection. If the vascular tissues can be considered as a barrier protecting the susceptible medulla of *Record*, the barrier may be breached at an eye where the vascular elements and medulla approach the tuber surface. Thus infection through a lenticel in *Record* may produce a restricted rot, whereas infection through the eye may allow the fungus direct access to the central susceptible

tissues. Tuber infection of many varieties in the field often occur through eyes (LAPWOOD, 1961), so the resistance score of the medulla in tissue tests may be of more value than that of the outer cortex. This requires further investigation.

5. DISCUSSION

The tuber-slice test gives results that correlated with field resistance to tuber infection. Medulla scores (TABLE 5) indicate the most field-resistant varieties, but do not distinguish varieties of intermediate or low resistance.

However, had a breeder based his selection on the above tests, using the reactions of *Majestic* as a guide, most of the resistant varieties in the 55 tested would have been detected. There are inconsistencies; examples are *Arran Viking* which had susceptible tissue but is as resistant as *Majestic* in the field, and *Spry's Abundance*, which, although reputed resistant in the field and having resistant tissues, had 16% and 8% blighted tubers in Irish trials in 1961 and 1962 when *Majestic* (not tested in 1961) had only 1% (KEHOE, 1962 and 1963).

A test for resistance during the growing period, or based on the inoculation of intact tubers, might be expected to assess tuber resistance better than one based on the reactions of tuber tissue during the early storage period, but such a method will waste breeders' materials. BONDE, STEVENSON and CLARK (1940), WEIHING and O'KEEFE (1962), DAVILA (1964) and many others have dipped or sprayed tubers and determined the proportion infected and the amount of tissue rotted but, in my experience, although such tests give a more complete picture of varietal susceptibility or resistance, they require 40–50 tubers for reliable results. MOOI (1963) found good correlations between such laboratory and field assessments but only after several tests, each involving 12–24 tubers.

Tests based on tissue resistance cannot be expected to give all the information required by the plant pathologist but, as tissue resistance seems to be a feature common to many field-resistant varieties, it is a useful characteristic for the breeder to use in making preliminary selections. JONES, GIDDINGS and LUTMAN (1912) assessed sporulation on tuber plugs and found some correlation with field estimates of resistance, but MÉLARD (1961), who compared sporulation on tuber sections, failed to distinguish resistant from susceptible varieties. The tuber-slice test described here, is based on the development of surface mycelium on the face distant from the site of inoculation at a given time after inoculation and depends on the rate the fungus grows and its capacity to sporulate on the host tissues; it may thus measure tissue resistance more accurately than methods based on recording the density of mycelium on the inoculated surface, or on estimating fungal invasion from the depth of necrotic tissue.

A test of this type, using 4 slices cut from 2 tubers, has been used in the breeding programme at the Max Planck Institute, Cologne, Germany, but has not been published (FRANSEN – personal communication). Each tuber is first halved and a 1½ cm slice is cut from each half with a plane. The surface exposed by the second cut is inoculated with zoospores and is then replaced on the remainder of the half tuber. A further 5 mm is later cut from the slice, so that the fungus mycelium after penetrating the 1-cm slice

TABLE 5. Comparison between tuber-tissue resistance (as estimated from the tuber-slice test by inoculating the medullary tissues) and field susceptibility

	Susceptible ¹ (3-4) (I)	Intermediate ² (2-3)	Resistant ³ (0-2)
1. 1959			
Early ¹	Ulster Premier-3 (3) Sharpe's Express Eclipse	Ulster Prince-3 Craigs Alliance-5 Arran Pilot-3	Epicure Duke of York-3 Craigs Royal-5
Main-crop ²	Ulster Tarn-6 Ally Frühperle Ulster Grove	Arran Viking Doon Star King Edward-3 Ulster Cromlech	Majestic-7 Record-7, 8, III Ulster Beacon-7 Pentland Crown-6
Late ³	Ulster Supreme-I-II Kerr's Pink-II	Katahdin Russet Burbank Leinster Wonder Up-to-Date-I-II Arran Victory Skerry Blue	Stormont Dawn-III Irish Chieftain Ås Pimpernel-9 Robijn-9 Golden Wonder-III Spry's Abundance-III Shamrock-III
2. 1960	(9-12) (2)	(5-8)	(0-4)
Early ¹	Arran Pilot-3		
Main-crop ²	Binje-3 Eigenheimer-3 Dr. McIntosh-II-III	Furore-6 Great Scot Noordeling-8	Koopman's Blauwe-8 Sientje-6 Gineke-8 Record-7, 8, III
Late ³		Zeeburger-9	Majestic-7 Prof. Broekema-9 Populair-9 Regina-9 Robijn-9 Pimpernel-9

D. H. LAPWOOD

- (1) Scores from TABLE 1 — *Dutch score system*.
- (2) Numbers of slices penetrated 5 days after inoculation (TABLE 2) — *Anzahl der 5 Tage nach der Impfung vom Pilz durchdrungenen Scheiben (TABLEAU 2) nombre de tranches pénétrées 5 jours après inoculation (TABLEAU 2)*.
- (3) Estimates of field susceptibility: Dutch List (HOGEN ESCH & ZINGSTRA, 1957) — *bold type, and N.I.A.B. List, 1964* — *normal type; low numbers susceptible, high numbers resistant*.
Irish Trials: 11-0-5⁰; 11-3-15⁰; 1-15⁰ plus, blighted tubers by weight, Arran Viking as resistant as Majestic (N.I.A.B. and Rothamsted); As, Champion, Irish Chieftain and Loman 43-35 resistant from reports of field workers.
Bewertung der Anfälligkeit auf dem Feld: Holländische Sortenliste (HOGEN ESCH & ZINGSTRA, 1957) — Fettdruck, und N.I.A.B.-Liste, 1964 — Normaldruck; niedrige Zahlen — anfällig, hohe Zahlen — resistent.
Irische Versuche: 11-0-5⁰; 11-5-15⁰; 1-15⁰ und mehr, mit P. infestans befallene Knollen in ⁰ des Gewichtes, Arran Viking ebenso resistent wie Majestic (N.I.A.B. und Rothamsted); As, Champion, Irish Chieftain und Loman 43-35 resistent gemäß Berichten der Beobachter auf dem Feld.
Estimations de la susceptibilité au champ: Liste hollandaise (HOGEN ESCH & ZINGSTRA, 1957) — gros caractères, et Liste N.I.A.B., 1964 — caractères normaux; chiffres inférieurs — susceptibles, chiffres élevés — résistants.
Essais irlandais: 11-0-5⁰; 11-5-15⁰; 1-15⁰ et plus, tubercules atteints de mildiou en ⁰ du poids, Arran Viking aussi résistent que Majestic (N.I.A.B. et Rothamsted); As, Champion, Irish Chieftain et Loman 43-35 résistants selon les rapports des observateurs au champ.
- ¹ Anfällig — susceptible.
² Intermediär — intermédiaire.
³ Resistent — résistent.
⁴ Frühreifend — précoce.
⁵ Spätreifend — tardive.
⁶ Haupternte — culture principale.

TABELLE 5. Vergleich zwischen Resistenz des Knollengewebes (wie im Knollenscheiben-Test mittels Impfung der Markgewebe beurteilt) und der Anfälligkeit auf dem Feld

TABLEAU 5. Comparaison entre la résistance des tissus du tubercule (détermination par inoculation des tissus médullaires dans le test sur tranches de tubercule) et la susceptibilité au champ

emerges through a non-suberising surface. The material is then scored on 2 or 3 consecutive days and the results compared with standard varieties.

A further advantage of the test is that the apical section of tubers can be saved and planted.

ACKNOWLEDGEMENTS

I thank Messrs. R. BAIN, J. CLARKE, J. C. CULLEN, J. A. HOGEN ESCH, J. J. MAJOR, Mrs. N. McDERMOTT and the late Dr. H. J. TOXOPEUS, for supplying tubers of the varieties used in these experiments and Mr. N. O. FRANDSEN for permission to refer to an unpublished technique. I also thank Mrs. A. PHILIPS for technical assistance.

ZUSAMMENFASSUNG

LABOR-BEURTEILUNGSMETHODEN BETREFFEND ANFÄLLIGKEIT DES KARTOFFELKNOLLENGEWEBES GEGEN KNOLLENFÄULE (*Phytophthora infestans*)

In dieser Arbeit werden Untersuchungen beschrieben, die 1959 und 1960 mit Knollen von 55 Sorten angestellt wurden. Es handelte sich darum, die Fähigkeit der *P. infestans* die Knollengewebe zu befallen im Vergleich zu dieser Fähigkeit bei der Sorte *Majestic*, deren Knollen sehr resistent sind, zu ermitteln.

Es wurden drei Untersuchungsmethoden angewendet: 1. halbierte Knollen, 2. Knollenscheiben und 3. ganze Knollen sowie rasche Bewertungsmethoden nach Punktzahlen, in der Regel von 1 (keine Reaktion) bis 4 (maximale Reaktion). Die Ergebnisse sind in den TABELLEN 1 und 2 dargestellt, Sorten mit gleicher oder grösserer Knollenresistenz im Feld als *Majestic* sind in Fettdruck angegeben.

Um den Nutzen einer einzelnen Untersuchungsmethode (TABELLE 3) zu bewerten, wurden zwei Kriterien betrachtet: 1. die Anzahl der feldresistenten Sorten, die durch den Test nicht entdeckt wurden (die Bewertungszahlen für *Majestic* fan-

den beim Vergleich als Standard Verwendung), 2. die Anzahl der im Feld anfälligen Sorten, die anhand des Labortests als resistent beurteilt wurden.

Der Knollenscheibentest vermittelte die eindeutigsten Angaben bezüglich Resistenz gegenüber Knolleninfektionen unter Feldbedingungen (TABELLE 5) und wird für den Züchter als nützlich betrachtet.

Vergleiche zwischen Sorten (nach Impfung der ganzen Knollen) basierten auf der Form des befallenen Gewebes (ABBILDUNG). Obwohl der Test selbst von beschränktem Wert war, wurden die Unterschiede in der Resistenz der verschiedenen Knollenteile deutlich aufgezeigt.

Bei einigen Sorten z.B. *Record*, schien der Gefässbündelring als eine Sperre gegenüber dem Pilz zu wirken. Wurde die Sperre durchbrochen, so wurde das innere Markgewebe umfassend befallen (TABELLE 4).

RÉSUMÉ

COTATION DE LABORATOIRE DE LA SUSCEPTIBILITÉ DU TUBERCULE DE POMME DE TERRE AU MILDIOU (*Phytophthora infestans*)

Le travail décrit les tests exécutés en 1959 et en 1960 sur des tubercules de 55 variétés; la capacité du *P. infestans* d'envahir les tissus du tubercule se détermine par comparaison avec *Majestic*, dont les tubercules sont résistants.

Les tests sont de trois sortes et portent sur 1. des

demi-tubercules, 2. des tranches de tubercules et 3. des tubercules entiers. Les évaluations sont rapidement cotées suivant l'échelle 1 (aucune réaction) à 4 (réaction maximale). Les résultats sont détaillés dans les TABLEAUX 1 et 2 dans lesquels les variétés de résistance du tubercule au

champ égale ou plus grande que *Majestic* sont imprimées en gros caractères.

La valeur d'un test quelconque (TABLEAU 3) est basée sur les deux critères suivants: 1. le nombre de variétés qui sont résistantes au champ et dont la résistance n'est pas décelée par le test, les cotes de *Majestic* servant de comparaison, et 2. le nombre de variétés susceptibles au champ que le test de laboratoire considère comme résistantes. Le test sur tranche de tubercule donne l'indication la plus claire de la résistance du tubercule dans les conditions au champ (TABLEAU 5) et est

considéré utile à l'améliorateur.

Les comparaisons variétales à partir d'inoculation de tubercules entiers sont basées sur la forme des tissus pourris (FIG. 1) et bien que le test lui-même soit de valeur limitée, des différences de résistance de diverses régions du tissu du tubercule se révèlent clairement.

Dans quelques variétés, par ex. *Record*, la zone vasculaire se révèle agir comme une barrière et quand la barrière est rompue les tissus médullaires internes pourrissent fortement (TABLEAU 4).

REFERENCES

- BONDE, R., F. J. STEVENSON and C. F. CLARK (1940): Resistance of certain potato varieties and seedling progenies to late blight in the tubers. *Phytopathology*, **30**, 733-748.
- DAVILA, E. (1964): Late blight infection of potato tubers. *Amer. Potato J.* **41**, 103-112.
- HOGEN ESCH, J. A., and H. ZINGSTRA (1957): Geniteurslijst voor Aardappelrassen. Commissie ter bevordering van het onderzoek van nieuwe aardappelrassen, Wageningen. 147 pp.
- JONES, L. R., N. J. GIDDINGS and B. F. LUTMAN (1912): Investigations of the potato fungus *Phytophthora infestans*. *Bull. Vermont Agric. Exp. Sta.* No. 168, 100 pp.
- KEHOE, H. W. (1962-1964): Potato Variety Trials. In: *Res. Rep.* (for 1961-1963), Pl. Sci. Crop Husb. Div., The Agric. Inst. Dublin.
- LAPWOOD, D. H. (1961): Haulm and tuber resistance to *Phytophthora infestans*. In: *Rep. Rothamst. Exp. Sta.* 1960. 123-124.
- and R. K. MCKEE (1961): Reaction of tubers of R-gene potato clones to inoculation with specialized races of *Phytophthora infestans*. *Eur. Potato J.* **4**, 3-13.
- MÉLARD, V. (1961): L'amélioration de la résistance au *Phytophthora* de la pomme de terre en Belgique. *Eur. Potato J.* **4**, 40-51.
- MOOI, J. C. (1963): A laboratory method for testing tubers of potato varieties for 'field resistance' to late blight. In: *Proc. 2nd trienn. Conf. Eur. Ass. Potato Res. Pisa, 1963*. 195.
- MULLER, K. O., J. C. CULLEN and M. KOSTROWICKA (1955): Testing 'true resistance' of the potato to blight *Phytophthora infestans*. *J. nat. Inst. agric. Bot.* **7**, 341-364.
- National Institute of Agricultural Botany, Cambridge (1964): Varieties of Potatoes. *Fmrs. Leaflet, natn. Inst. agric. Bot.* No. 3, 8 pp.
- WEIHING, J. L., and R. B. O'KEEFE (1962): Epidemiological potentials of potato varieties in relation to late blight. *Phytopathology*, **52**, 1268-1273.