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Transmission of *Helminthosporium solani* from potato seed tubers and effects of soil conditions, seed inoculum and seed physiology on silver scurf disease

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SUMMARY

The transmission of silver scurf (*Helminthosporium solani*) disease of potatoes was examined in field experiments at Cambridge University Farm in 1988–90. Treatment factors examined were seed size, seed age, seed incubation, soil moisture regime and planting date. A laboratory experiment investigated the viability of conidia of *Helminthosporium* in soil stored under different conditions.

Incubation of seed at high humidity before planting increased sporulation of *Helminthosporium* on seed tubers after planting and fewer conidia were produced from small seed than from larger seed. Delay in planting caused more rapid growth of *Helminthosporium* on seed tubers after planting.

Early planting and late harvesting increased the severity of silver scurf on progeny tubers. Severity of silver scurf was also increased by ageing seed and by incubating seed. Weight loss of potato tubers during storage tended to be greater from treatments with most severe silver scurf in all years but a significant linear regression of weight loss on silver scurf severity was found in only one year out of three from a late harvest. The viability of conidia added to soil was found to decrease rapidly so that by 10 weeks after addition, < 1% of conidia were apparently viable.

INTRODUCTION

Silver scurf, caused by the fungus *Helminthosporium solani*, is a blemishing disease of potatoes which can become severe on stored tubers. The severity of the disease can be reduced by the use of fungicides on seed tubers (Hide *et al.* 1980; Hide & Read 1985) but isolates of *Helminthosporium* resistant to thiabendazole have been found (Hide *et al.* 1988; Hall & Hide 1992) and whilst imazalil is still effective (Hall & Hide 1992) other methods of reducing the disease are sought. A better understanding of the transmission and development of the disease may allow increased control by the use of appropriate agronomic practices.

Inoculum of *Helminthosporium* is mainly seed tuber-borne (Jellis & Taylor 1977) but increased infection of seed is not necessarily associated with increased silver scurf on progeny tubers (Lennard 1970; Jellis & Taylor 1977; Adams & Hide 1980; Read & Hide 1984) because older lesions of severely infected seed lose the capacity to sporulate and a negative correlation between seed infection and progeny infection can result.

Jellis & Taylor (1977) reported that the whole of the seed tuber surface is colonized by *Helminthosporium* within a few weeks of planting. The colonization results in copious production of conidia, so that a delay in the onset of tuber formation could result in less inoculum being transmitted. The experiments reported in this paper investigated the spread of *Helminthosporium* over the seed tuber surface in relation to crop development, the transmission of silver scurf to progeny tubers and the development of the disease at harvest and after storage.

MATERIALS AND METHODS

Field experiments using the potato cultivar Estima were grown on a sandy clay loam at Cambridge University Farm in 1988–90. Elite grade Scottish seed was graded over a riddle or hand weighed to obtain the seed sizes used. The treatments for the experiments are listed in Table 1. In Expts 1 and 2, seed was graded then placed in wooden trays at 10 °C for 6 (Expt 1) or 4 (Expt 2) weeks. Half of the trays (chosen at random) were covered with plastic and the relative humidity within these covered trays was maintained > 90%. High humidity was maintained by periodically blowing steam into the chambers in Expt 1 and by placing trays above reservoirs of water in Expt 2. After treatment at 10 °C, tubers were transferred either to 2 °C (young seed) or 13 °C (old seed) until

Table 1. *Details of the field experiments investigating silver scurf disease of potatoes*

	Expt 1	Expt 2	Expt 3
Year	1988	1989	1990
Harvest date	22 Aug, 26 Sep	7 Sep, 5 Oct	5 Sep, 2 Oct
Treatment factors			
Planting date	18 Apr, 17 May	8 May, 5 Jun	14 Mar, 11 Apr, 9 May, 6 Jun
Seed size* (g) (range of seed size)	15 (20–30 mm) 67 (60–70 g)	18 (20–30 mm) 67 (40–45 mm)	29 (30–35 mm) 61 (30–55 mm) 84 (45–50 mm)
Seed age (day degrees > 4 °C)	210, 580	130,620	0, 300
Incubation at high humidity (weeks)	0, 6	0, 4	—
Covered from rain (weeks from planting)	0, 4	0, 4	—

* Sizes planted at different spacings – see text.

Table 2. *Rainfall and irrigation (mm) applied to the experiments*

	Expt 1		Expt 2		Expt 3	
	Rain	Irrigation	Rain	Irrigation	Rain	Irrigation
Apr	37	0	76	0	28	0
May	41	0	7	0	8	50
Jun	39	25	41	0	26	43
Jul	99	0	39	30	26	58
Aug	44	40	27	45	23	105
Sep	45	0	13	0	41	0

the first planting, after which all seed was held at 2 °C until the second planting. In Expt 3, young seed was held at 2 °C after grading whilst old seed was stored at 13 °C to accumulate 300 day degrees > 4 °C, and then at 2 °C until planting.

Fertilizer was applied by machine to the entire experimental area before the first planting date at the rate (kg/ha) of 136 N, 60 P, 170 K and 36 Mg in Expts 1 and 3 and 126 N, 55 P, 158 K and 34 Mg in Expt 2. In all years, seed was planted by hand into ridges 71 cm apart using a dibber. The herbicide Opogard (terbutryne and terbuthylazine) was applied before emergence for each planting date. Paraquat was also applied as necessary to control weeds which had already germinated. Irrigation was applied by overhead sprinkler as indicated in Table 2.

Experiments 1 and 2 each consisted of two complete replicates of all combinations of two levels of five factors (Table 1). The plots were arranged in eight blocks with partial confounding of 3-factor and 4-factor interactions. Treatment combinations were allocated at random to plots within each of the blocks. Plots were six rows wide × 6 m long; the outer rows were guard rows. Small seed was planted 15 cm apart along the row and larger seed was planted 30 cm apart. Planting densities for larger seed were close to those recommended by MAFF (1982) whilst those for small seed (for which no comparable recommendations were available) were chosen in an attempt to achieve similar stem densities. Plots were separated by 1 m along the row with unplanted guard rows (two in Expt 1 and one in Expt 2) between plots. Dry treatments were covered by polythene shelters which were removed 4 weeks after planting. Plots left open to the rain for the first and second plantings received 46 and 55 mm of rain in Expts 1 and 9 and 39 mm in Expt 2.

In Expt 3, there were three randomized complete blocks. Plots were four rows wide × 10 m long; the outer rows were guard rows. Seed with a diameter of 30–35, 30–55 and 45–50 mm was planted 15, 24 and 30 cm apart within rows, respectively. Planting densities for larger seed were chosen to be close to recommended rates (MAFF 1982) but also so that the surface area of seed tuber planted, calculated using the relationship of Banks (1985), would be similar for all seed sizes.

Assessment of silver scurf on seed tubers before and after planting was made by washing tubers, recording the percentage of surface area affected and then cutting plugs of tissue with a 9 mm diameter borer. Five plugs from each seed tuber were incubated in humid chambers at 20 °C for 10 days (8 days in Expt 3) then examined under a binocular microscope. The number of plugs with sporulating conidiophores was recorded. So as to exclude moribund conidiophores,

plugs with conidiophores not producing conidia were not counted. The infection of seed tubers at planting was determined by examining a total of 160 tubers in Expts 1 and 2 and 180 in Expt 3. A random selection of equal numbers of tubers from each seed treatment was examined at both plantings in Expt 1, once between planting dates (22 May) in Expt 2 and at the first, second and final plantings in Expt 3.

In Expt 1, two seed tubers/plot were dug 1, 3, 5, 7, 9, 11, 13 and 15 weeks after the first planting with the first two samples dug only from the first planting. For these samples in Expt 1, two randomly selected progeny tubers/plot (where present) were also examined for infection by *Helminthosporium* as for seed tubers or by incubating whole tubers in the case of tubers < *c.* 20 mm in diameter. In Expt 2, three samples of eight seed tubers were dug 3, 6 and 9 weeks after planting for both planting dates and in Expt 3, eight seed tubers were dug 2, 4, 6, 8 and 10 weeks after each planting.

For samples dug after planting, the number of conidia produced by seed tubers was determined. Washed tubers were incubated for 2 weeks at 20 °C above water in plastic bags. Tubers were then shaken with water to remove conidia and the conidia were counted on a Haemocytometer slide examined under a microscope. In Expts 1 and 2, the tubers were washed with 80 ml water which was then centrifuged at 2000 rpm for 15 min. The sediment was resuspended in 5 ml water before counting. In Expt 3 tubers were washed in *c.* 60 ml of water and counts were made directly on the suspension. In Expt 3 only the samples dug at 8 and 10 weeks after planting were used for determination of conidia production. No data were obtained for conidia production of tubers from the sample 3 weeks after the first planting in Expt 1.

The date of 50% plant emergence was recorded for each plot and the percentage foliar ground cover was assessed regularly throughout growth using a grid (Burstall & Harris 1983). In all experiments, two harvests (dates listed in Table 1) were dug by hand and tubers were graded in 10 mm increments using a riddle before disease assessment and storage. The area for each harvest was 2·6 m^2/plot in Expts 1 and 2 and 1·7 m^2 in Expt 3. Throughout growth, soil temperature at a depth of 10 cm was recorded on a datalogger at hourly intervals.

A sample of at least 25 tubers (> 40 mm) was weighed and put into net bags (paper sacks in Expt 3) and stored at 7 °C and 95% relative humidity from *c.* 1 week after harvest. Sprout growth was controlled by application of Chlorpropham (CIPC) sprout inhibitor as required. In Expt 1, a duplicate sample was placed in a commercial store where temperatures were reduced during September and October to a holding temperature of 3 °C thereafter. Tubers were stored until mid-May the following year so that the storage period ranged from 31 to 38 weeks depending on harvest date.

Assessment of disease on ware tubers was made by inspection of a randomly selected sample of *c.* 25 tubers (> 40 mm) at harvest and after storage (only two tubers per plot at harvest in Expt 1). Tubers for assessment were washed and the percentage of the surface covered by silver scurf was noted. Silver scurf was recorded either as nil or in class intervals of 5% surface area and the mean percentage area affected was calculated by multiplying the number of tubers in each class by the mid value of each class. In Expt 1, samples of two tubers were removed from the bags on 7 December, 8 February and 5 April, assessed for disease and the weight of the sample recorded. In Expt 2, a sample of 25 tubers was removed on 24 January, assessed for disease and the weight recorded. At the end of storage, samples were reweighed to determine weight loss.

In 1989, a laboratory experiment was set up to examine the viability of conidia of *Helminthosporium* in soil. The experiment compared the viability of conidia in wet or dry soil stored at 10 or 20 °C. Potatoes (*c.* 10 kg) affected with silver scurf were washed, incubated at 20 °C for 2 weeks then shaken in batches with 500 ml of water to obtain a concentrated suspension of conidia. The concentration of conidia was assessed by counting 10 aliquots of this suspension on a Haemocytometer slide under a microscope. Bottles (50 × 25 mm) were filled with 20 g of sieved, air-dried field soil (sandy clay loam) and to 50 of these bottles 3 ml of tap water was added followed by 3·5 ml of conidial suspension containing *c.* 1·5 million conidia. To a further 50 bottles, 3·5 ml of conidial suspension was added to the dry soil. Caps were fitted to the bottles and 25 of the wet and dry treatments were placed in incubators at both 10 °C and 20 °C. Four bottles of each treatment were taken 1, 3, 5 and 10 weeks after adding the suspension and conidia were extracted in mineral oil using the method of Chinn *et al.* (1960) used by Jellis & Taylor (1977). After extraction, 8 ml of potato dextrose agar was added to the emulsion containing the conidia which was then weighed. A drop of emulsion (*c.* 10 µl) was put onto a weighed glass slide, reweighed and covered with a cover slip. Two slides from each bottle were prepared and placed at 20 °C to incubate for *c.* 24 h then examined under a microscope to record the total number of conidia extracted and the number which had germinated.

RESULTS

Silver scurf on seed tubers

The percentage of seed tubers found to have plugs with *Helminthosporium* was higher in Expt 1 (67%) and Expt 2 (88%) than in Expt 3 (31%) and the mean surface area affected corresponded to these differences

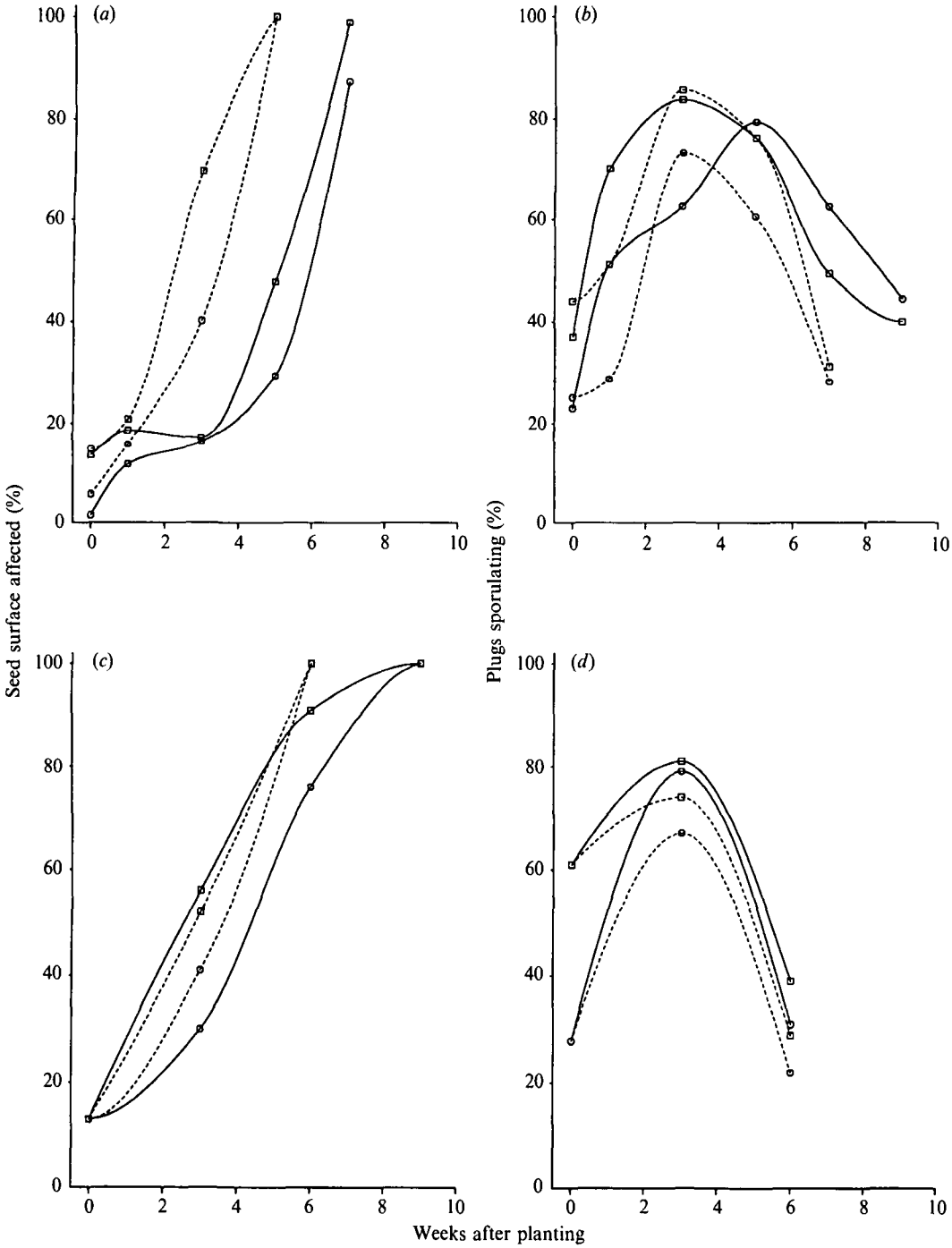

Fig. 1. Effect of seed incubation and planting date on growth and sporulation of *Helminthosporium solani* in Expts 1 and 2. (*a*) and (*b*) Expt 1, (*c*) and (*d*) Expt 2. Seed not incubated (○), seed incubated (□), early planting (——), late planting (– – –).

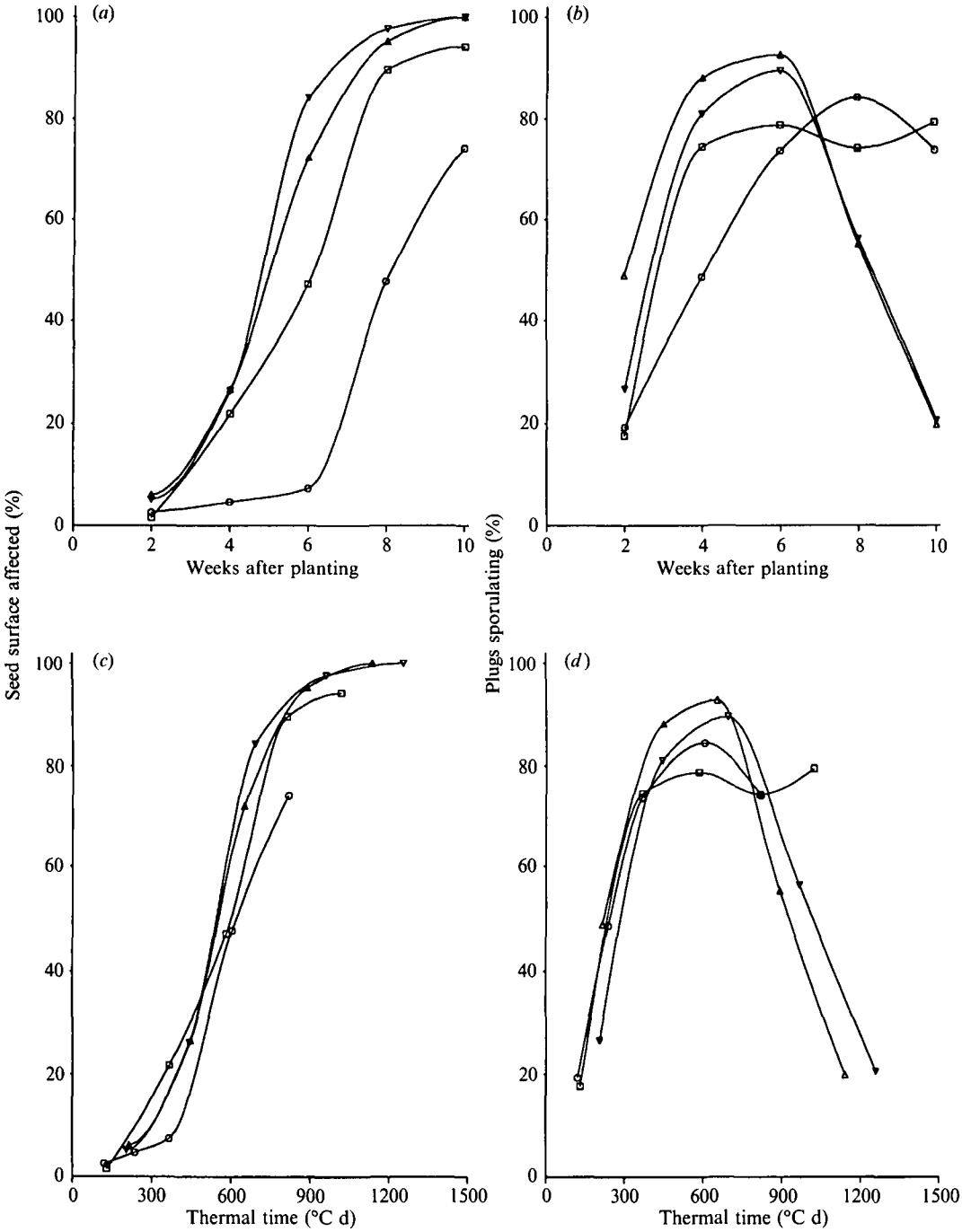

Fig. 2. Effect of planting date on growth and sporulation of *Helminthosporium solani* in relation to time and thermal time in Expt 3. 1st planting (○), 2nd planting (□), 3rd planting (△), 4th planting (▽).

(8·6, 12·1 and 2·9% surface area for Expts 1–3 respectively). The number of plugs with *Helminthosporium* sporulating was greater ($P\ \chi^2 < 0{\cdot}001$) for seed incubated at high humidity in Expts 1 and 2 (41 and 61% respectively) than for seed kept at ambient humidity (24 and 28%). The sporulation of plugs was also greater ($P\ \chi^2 < 0{\cdot}001$) for large seed (42%) than for small seed (23%) in Expt 1 but not in other years.

Table 3. *Effects of planting date, seed treatment and covering of plots on the production of* Helminthosporium *conidia (10^4/seed tuber)*

	Weeks after planting			
Expt 1	1	3*	5	7
Early planting	31·0	—	16·2	10·4
Late planting	19·2	33·6	20·5	3·1
Small seed	17·0	14·9	7·7	4·1
Large seed	33·2	52·4	29·0	9·5
Young seed	25·6	32·6	25·9	8·2
Old seed	24·5	34·7	10·8	5·4
Untreated seed	20·3	24·9	12·4	4·1
Incubated seed	29·8	42·4	24·4	9·5
Uncovered plots	26·8	33·3	17·9	8·5
Covered plots	23·3	34·0	18·9	5·0
S.E. (D.F.)	3·47 (32)	7·37 (16)	3·56 (31)	2·16 (31)

	Weeks after planting		
Expt 2	3	6	9
Early planting	16·8	53·2	18·8
Late planting	57·8	42·6	5·8
Small seed	22·9	26·0	9·5
Large seed	51·7	69·7	15·2
Young seed	38·0	55·9	13·9
Old seed	36·7	39·8	10·7
Untreated seed	26·7	46·5	13·2
Incubated seed	47·9	49·2	11·4
Uncovered plots	35·2	47·3	11·4
Covered plots	39·4	48·4	13·2
S.E. (31 D.F.)	5·04	5·33	2·19

	Weeks after planting	
Expt 3	8	10
1st planting	72·7	51·5
2nd planting	51·1	33·2
3rd planting	28·2	9·3
4th planting	28·3	10·2
S.E. (46 D.F.)	4·33	3·62
30–35 mm seed	39·7	21·2
30–55 mm seed	52·9	29·0
45–50 mm seed	42·6	27·9
S.E. (46 D.F.)	3·75	3·13
Young seed	61·1	33·8
Old seed	29·0	18·3
S.E. (46 D.F.)	3·06	2·56

* Late planting only.

The surface area affected by silver scurf increased slightly with delay in planting but there was no significant increase in the percentage of plugs with *Helminthosporium*. There was no significant effect of seed age on the percentage of plugs with *Helminthosporium* sporulating at planting in any year.

Table 4. *Effects of planting date and seed age on the number of days from planting to 50% emergence*

	1st planting		2nd planting		3rd planting		4th planting		
Seed age...	Young	Old	Young	Old	Young	Old	Young	Old	S.E. (D.F.)
Expt 1	27	25	17	17	—	—	—	—	0·45 (31)
Expt 2	19	16	20	16	—	—	—	—	0·48 (31)
Expt 3	51	38	35	23	29	18	23	16	0·25 (46)

Silver scurf on seed tubers after planting

The surface area initially affected by *Helminthosporium* after planting was greater on seed incubated at high humidity than on untreated seed at both planting dates in Expts 1 and 2 (Fig. 1) but eventually every tuber became completely affected. In Expt 3, spread of *Helminthosporium* was more rapid with delay in planting (Fig. 2*a*) but the rate of spread in thermal time (soil temperature in day degrees > 0 °C) was similar for all plantings (Fig. 2*c*). There was little difference in the spread of *Helminthosporium* on the seed between seed ages or seed size in any year. The sporulation of *Helminthosporium* on plugs after planting increased to a peak after which the proportion of plugs with moribund conidiophores increased. Incubation of seed in Expts 1 and 2 increased the initial proportion of plugs sporulating (Fig. 1). In Expt 3, the increase in sporulation on seed was more rapid with delay in planting (Fig. 2*b*) but, as with the spread of *Helminthosporium* over the seed surface, the increase in relation to day degrees was similar for all plantings (Fig. 2*d*). In Expt 3, the percentage of plugs sporulating on old seed reached a slightly lower peak than young seed did and remained lower at subsequent samples for all plantings.

Production of conidia from seed tubers

The number of conidia produced per seed tuber after incubation was greater for large seed than for small seed at all samplings in Expts 1 and 2 (Table 3) but in Expt 3, the ungraded seed produced more conidia than did either small or large seed sampled at 8 weeks after planting and there was no significant difference between seed sizes at 10 weeks after planting.

The humid incubation of seed before planting in Expts 1 and 2 tended to increase the number of conidia at early sampling times but differences were not statistically significant until 5 weeks after planting in Expt 1 and 3 weeks after planting in Expt 2 (Table 3). More conidia were produced by seed tubers sampled 1 and 3 weeks after planting in Expt 1, and 3 weeks after planting in Expt 2, than at later samplings. At later sampling times, numbers of conidia were highest from early plantings (Table 3). The production of conidia from the sample taken 10 weeks after planting in Expt 3 was low for all treatment combinations of the third and final planting and treatment effects for this sample were significant only for the earlier plantings.

In the sample taken 5 weeks after planting in Expt 1, the number of conidia (10^4/tuber) produced from large seed was greater for young seed ($44{\cdot}8 \pm 5{\cdot}04$) than for old seed (13·3) but there was no effect of age for small seed. Ageing also reduced the number of conidia produced from all seed sizes 6 weeks after planting in Expt 2 and at both 8 and 10 weeks after planting in Expt 3 (Table 3).

In samples taken 6 or more weeks after planting in Expt 1, some seed tubers had rotted. In Expt 1, 13 weeks after the first planting, 72% of seed tubers from the first planting and 34% from the second planting had rotted. In Expt 2, 9 weeks after planting, there were slightly more rotten tubers of small seed (45%) than of larger seed (29%). In Expt 3 there were few rotten tubers 10 weeks after planting for the first two plantings but there were 35 and 25% rotten tubers at the third and fourth plantings respectively.

Growth, yield and numbers of tubers

Emergence was more rapid with delay in planting and more rapid with old seed than young seed except at the late planting in Expt 1 (Table 4). Effects of seed age in Expts 1 and 2 were smaller than in Expt 3 (Table 4). In Expt 2, emergence was *c.* 2 days earlier with large seed than with small seed and at the later planting, emergence was delayed *c.* 2 days by covering from the rain.

There was little effect of seed age on foliar ground cover at either planting in Expt 1 but in Expt 2 ground cover was initially greater for old seed than young seed at the early planting, and old seed senesced before young seed without reaching full cover (Fig. 3). There was no effect of seed age on ground cover at the late planting in Expt 2. However, in Expt 3, earlier emergence of old seed at all plantings resulted in earlier initial ground cover than for young seed, but old seed also senesced earlier at all plantings (Fig. 3). There was little effect of seed size on ground cover in any year and covering plots from rain had no effect on ground cover except at the early planting in Expt 1 when uncovered plots had earlier initial ground cover and senesced slightly earlier than covered plots.

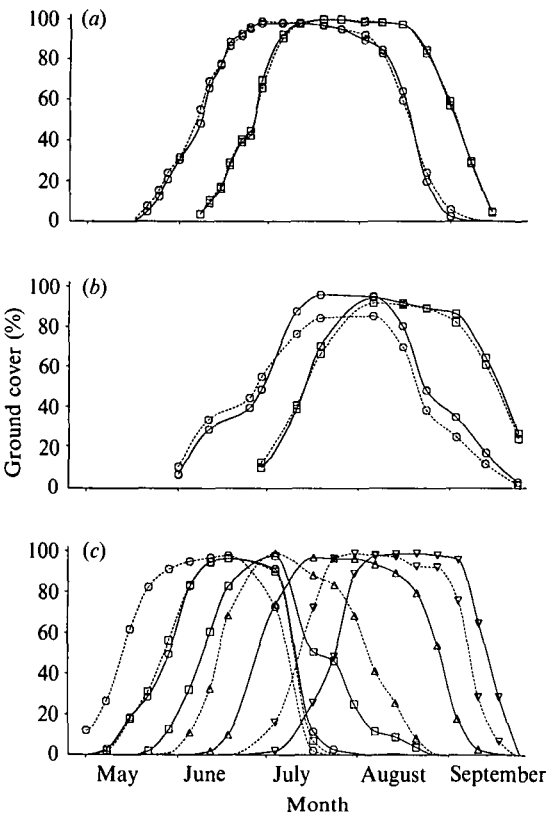

Fig. 3. Effect of seed age and planting date on foliar ground cover in Expts 1–3. (*a*) Expt 1, (*b*) Expt 2, (*c*) Expt 3. 1st planting (○), 2nd planting (□), 3rd planting (△), 4th planting (▽), young seed (——), old seed (– – –).

There were more above-ground stems/seed tuber for larger seed than for small seed in all years but the planting densities compensated for this so that there was no effect of seed size on the number of above-ground stems in Expts 1 and 2 (Table 5) whilst in Expt 3, number of stems was reduced with increase in seed size as a result of the differences in planting density (Table 5). There were more above-ground stems from young seed than from old seed in Expts 1 and 2 but in Expt 3, old seed had more stems than young seed (Table 5).

In Expts 1 and 2, there were few secondary stems for any treatment whereas in Expt 3 young seed had few secondary stems (*c.* 2000/ha) but old seed had *c.* 77000 secondary stems/ha, which accounted for much of the difference in the number of above-ground stems. The number of above-ground stems/ha was similar for young seed in all years but old seed had more stems in Expt 3 than in other years.

Yield

Early planting increased yield at early harvests in all years (Table 6) and increased yield at the late harvest in Expts 2 and 3 but not in Expt 1. There was little effect of seed age on total tuber yield in Expt 1 (Table 6). At the early harvest in Expt 2, yield from young seed planted early (51·4 ± 1·23 t/ha) was greater than yield from old seed (44·9 t/ha) but there was no effect of age at the later planting and little effect of seed age at the later harvest. In Expt 3, yield from old seed was greater than from young seed for all planting dates at the early harvest but at the later harvest yield from old seed planted at the first (54·9 ± 1·84 t/ha) and second dates (48·3 t/ha) was greater than from young seed (46·6 and 42·4 t/ha) but there was no effect of age at later plantings.

Yield was greater from large seed than from small seed in Expt 1 (Table 6) but there was no effect of seed size on yield in other years. Covering plots from rain had no effect on yield in Expt 1 but it decreased yield slightly at the early harvest in Expt 2 (Table 6).

Number of tubers

In Expt 1, covering plots from rain reduced the total number of tubers at both harvests (Table 6). In Expt 2, the number of tubers at the late planting was less from covered plots (493000 ± 17000/ha for both early and late harvests) than from uncovered plots (early harvest 597000, late harvest 578000/ha) but at the early planting, at which only 9 mm of rain fell while plots were covered, there was little effect of covering plots. Late planting produced fewer tubers

Table 5. *Effect of seed age and seed size on the total number of stems (000/ha)*

	Expt 1	Expt 2	Expt 3
Young seed	151	152	156
Old seed	123	124	261
S.E. (D.F.)			5·7 (46)
Seed size 1	146	140	236
Seed size 2	127	137	206
Seed size 3	—	—	184
S.E. (D.F.)	7·7 (31)	3·6 (31)	7·0 (46)

Table 6. *Effect of planting date, seed treatments and covering of plots on total tuber yield (t/ha) and total number of tubers (000/ha)*

	Early harvest			Late harvest		
	Expt 1	Expt 2	Expt 3	Expt 1	Expt 2	Expt 3
			Total tuber yield (t/ha)			
1st planting	63·4	48·2	53·0	63·8	47·3	50·8
2nd planting	55·1	41·1	47·2	60·7	44·4	45·4
3rd planting	—	—	44·3	—	—	44·6
4th planting	—	—	38·0	—	—	41·1
S.E. (46 D.F.)			1·07			1·30
Seed size 1	56·8	45·0	44·1	59·0	45·5	44·8
Seed size 2	61·6	44·3	46·2	65·6	46·3	44·4
Seed size 3	—	—	46·6	—	—	47·2
S.E. (46 D.F.)			0·92			1·13
Young seed	58·0	46·4	44·0	62·6	46·1	43·9
Old seed	60·5	42·9	47·2	62·0	45·6	47·0
S.E. (46 D.F.)			0·76			0·92
Untreated seed	58·5	45·4	—	60·9	47·2	—
Incubated seed	60·0	43·9	—	63·6	44·6	—
Uncovered plots	59·5	45·9	—	59·6	46·5	—
Covered plots	58·9	43·4	—	58·5	45·3	—
S.E. (31 D.F.)	1·16	0·87		1·23	0·88	
			Total number of tubers (000/ha)			
1st planting	511	730	671	468	726	649
2nd planting	538	545	641	462	536	640
3rd planting	—	—	670	—	—	644
4th planting	—	—	891	—	—	747
S.E. (46 D.F.)			21·7			13·2
Seed size 1	515	651	742	451	637	735
Seed size 2	534	624	712	478	625	633
Seed size 3	—	—	701	—	—	641
S.E. (46 D.F.)			18·8			11·5
Young seed	537	654	597	485	649	557
Old seed	511	621	839	444	613	783
S.E. (46 D.F.)			15·3			9·4
Untreated seed	550	644	—	484	638	—
Incubated seed	498	631	—	446	624	—
Uncovered plots	553	670	—	488	660	—
Covered plots	495	606	—	442	602	—
S.E. (31 D.F.)	8·7	12·0		8·2	11·9	

than early planting did in Expt 2 (Table 6) but effects of other treatments in Expts 1 and 2 were small.

In Expt 3, there were more tubers from old seed than from young seed and more tubers from the smallest seed than from larger seed (Table 6). The number of tubers from the final planting in Expt 3 was higher than from earlier plantings, particularly at the early harvest when many small tubers were still present (Table 6). The increase in the number of tubers with seed age in Expt 3 was smaller at the first planting than at subsequent plantings (Table 7). The effect of seed age on number of tubers in Expt 3 decreased with increase in seed size at the early harvest but not at the later harvest.

Silver scurf infection on progeny tubers

In Expt 1, sporulation of *Helminthosporium* on progeny tubers was first detected on incubated samples dug 11 weeks after the first planting date. At this sampling, 3% of tubers from the early planting were found to be affected but infection was not

Table 7. *Effect of seed age and planting date on number of tubers (0000/ha) and weight loss (%) after storage (Expt 3)*

	Early harvest		Late harvest	
Seed age...	Young	Old	Young	Old
	Number of tubers (000/ha)			
1st planting	627	715	603	695
2nd planting	510	771	494	786
3rd planting	544	796	519	768
4th planting	707	1075	610	883
S.E. (46 D.F.)		30·7		18·7
	Weight loss after storage (%)			
1st planting	13·6	16·1	15·6	16·9
2nd planting	12·8	14·0	14·1	15·3
3rd planting	13·7	12·6	12·4	14·4
4th planting	15·2	14·0	8·2	9·8
S.E. (46 D.F.)		0·48		0·43

Table 8. *Effects of planting date, seed treatments and covering of plots on severity of silver scurf (% surface area affected) at harvest*

	Early harvest		Late harvest		
	Expt 2	Expt 3	Expt 1	Expt 2	Expt 3
1st planting	5·1	22·5	9·4	10·4	23·9
2nd planting	0·6	20·8	4·5	2·2	24·6
3rd planting	—	13·3	—	—	16·0
4th planting	—	0·2	—	—	1·2
S.E. (46 D.F.)		1·39			1·74
Seed size 1	2·2	14·6	4·2	4·9	19·0
Seed size 2	3·4	13·1	9·7	7·7	14·2
Seed size 3	—	14·9	—	—	16·0
S.E. (46 D.F.)		1·21			1·51
Young seed	2·5	12·0	5·7	4·5	14·2
Old seed	3·2	16·4	8·2	8·1	18·6
S.E. (46 D.F.)		0·99			1·23
Untreated seed	2·5	—	6·8	5·2	—
Incubated seed	3·1	—	7·2	7·5	—
Uncovered plots	2·7	—	8·4	5·4	—
Covered plots	3·0	—	5·5	7·2	—
S.E. (31 D.F.)	0·33		1·58	0·54	

detected on progeny from the later planting. At the next sampling, 2 weeks later, 23% of tubers from the early planting and 5% of tubers from the later planting were found to be infected so that for both planting dates, infections were first recorded 8–9 weeks after emergence.

At harvest

In all years, silver scurf at harvest was more severe at the later harvest date than at the early harvest (Table 8). Silver scurf at harvest was less severe from late planting than from early planting in Expts 1 and 2 and less severe with delay in planting in Expt 3 (Table 8). Silver scurf at harvest was more severe from large seed than from small seed in Expts 1 and 2 but there was no effect of seed size in Expt 3 (Table 8). Silver scurf infection was more severe from seed incubated at high humidity than from untreated seed at the late harvest in Expt 2 and whilst there was no statistically significant difference between incubated and untreated seed in Expt 1 or at the early harvest in Expt 2, silver scurf was more severe from incubated seed (Table 8).

At the late harvest in Expt 2, silver scurf was more severe from old seed planted early ($13{\cdot}8 \pm 0{\cdot}77$%) than from young seed planted early (7·1%) but progeny from the late planting had little infection from either seed age. In Expt 3, silver scurf was significantly more severe for old seed than for young seed at both harvests. In Expt 1, and at the early harvest of Expt 2, whilst silver scurf was more severe from old seed than from young seed, the differences were not statistically significant.

After storage

Silver scurf increased during storage in all years, with a greater increase at 7 °C than at 3 °C in Expt 1 (Table 9). Silver scurf on tubers in Expt 2 had increased by January but many tubers remained slightly affected whereas, by the end of storage, tubers of all treatments were almost completely covered with silver scurf. Effects of treatments found at harvest were maintained during storage (up to January in Expt 2) and the differences between treatments in percentage surface area affected were usually larger after storage. Incubation of seed resulted in significantly greater severity of silver scurf after storage at 7 °C for the late harvest in Expt 1 and for both harvests of Expt 2 (up to January), whereas at harvest the difference was significant only for the late harvest in Expt 2. Similarly, silver scurf after storage to January was more severe for old seed than for young seed for both harvests in Expt 2 whereas at harvest there was a significant effect for the late harvest only.

In samples from the early harvest of Expt 1 stored at 7 °C there was little effect of seed size on severity of silver scurf from old seed but silver scurf on progeny of young seed was more severe from large seed ($27{\cdot}0 \pm 2{\cdot}27$%) than from small seed (17·1%). In samples from the late harvest of Expt 1 stored at 7 °C there was little effect of seed age on severity of silver scurf for the late planting but, for the early planting, silver scurf was more severe from old seed ($35{\cdot}1 \pm 2{\cdot}2$%) than from young seed (26·7%).

In samples from the early harvest of Expt 2 stored to January there was little effect of seed size or seed incubation from the late planting, for which silver

Table 9. *Effect of planting date, seed treatments and covering of plots on silver scurf severity (% surface area affected) and weight loss (%) after storage*

	Early harvest					Late harvest				
Experiment...	1	1	2*	2	3	1	1	2*	2	3
Storage temperature (°C)...	3	7	7	7	7	3	7	7	7	7
					Silver scurf severity (% surface area)					
1st planting	27·1	33·9	12·3	96·7	53·4	21·2	30·9	20·3	96·2	77·1
2nd planting	7·3	13·9	2·5	93·5	47·6	10·7	21·4	7·5	92·4	67·7
3rd planting	—	—	—	—	35·5	—	—	—	—	63·6
4th planting	—	—	—	—	13·2	—	—	—	—	25·3
S.E. (46 D.F.)					2·36					2·36
Seed size 1	15·4	22·1	5·1	95·1	39·0	13·3	23·9	11·9	92·0	58·9
Seed size 2	19·0	25·7	9·7	95·2	34·9	18·6	28·4	15·9	96·6	55·6
Seed size 3	—	—	—	—	38·4	—	—	—	—	60·7
S.E. (46 D.F.)					2·04					2·05
Young seed	16·6	22·0	6·1	94·6	33·2	14·9	24·4	11·8	92·7	55·1
Old seed	17·8	25·7	8·7	95·6	41·7	16·9	28·0	15·9	95·9	61·8
S.E. (46 C.F.)					1·67					1·67
Untreated seed	15·8	21·7	5·0	94·6	—	14·6	23·7	10·7	93·7	—
Incubated seed	18·6	26·1	9·9	95·6	—	17·3	28·7	17·1	94·9	—
Uncovered plots	15·9	26·4	7·7	94·5	—	14·5	25·7	13·1	94·3	—
Covered plots	18·5	21·4	7·1	95·8	—	17·4	26·7	14·7	94·3	—
S.E. (31 D.F.)	1·77	1·60	0·68	0·87		0·97	1·57	1·02	1·43	
					Weight loss after storage (%)					
1st planting	7·6	13·7	4·1	8·4	14·9	7·0	12·8	2·5	5·5	16·3
2nd planting	8·4	14·6	5·4	9·4	13·4	6·6	10·6	2·2	4·5	14·7
3rd planting	—	—	—	—	13·2	—	—	—	—	13·4
4th planting	—	—	—	—	14·6	—	—	—	—	9·0
S.E. (46 D.F.)					0·34					0·30
Seed size 1	8·0	14·1	4·7	8·5	14·1	6·6	11·5	2·6	5·1	13·9
Seed size 2	8·0	14·2	4·8	9·2	13·7	7·0	11·8	2·2	4·9	13·1
Seed size 3	—	—	—	—	14·2	—	—	—	—	13·0
S.E. (46 D.F.)					0·30					0·26
Young seed	7·9	14·0	4·9	8·9	13·8	6·5	11·4	2·0	4·5	12·6
Old seed	8·0	14·3	4·6	8·9	14·2	7·1	12·0	2·8	5·6	14·1
s.e. (46 d.f.)					0·24					0·21
Untreated seed	8·0	14·1	4·7	8·8	—	7·1	11·6	1·8	4·4	—
Incubated seed	7·9	14·2	4·8	9·0	—	6·6	11·8	2·9	5·6	—
Uncovered plots	7·9	13·9	4·6	8·8	—	6·8	11·6	2·4	5·1	—
Covered plots	8·1	14·4	4·9	8·9	—	6·9	11·7	2·3	5·0	—
S.E. (31 D.F.)	0·16	0·25	0·15	0·19		0·23	0·27	0·48	0·48	

* Stored to January (all others to May).

scurf was not severe, but tubers from the early planting had more severe silver scurf from incubated seed than untreated seed and from large seed than small seed (Table 10). In samples from both harvest dates of Expt 2 stored to January, the increase in silver scurf from incubating seed was greater for large seed than small seed (Table 10).

Linear regression of severity of silver scurf after storage on severity at harvest

Linear regression of severity of silver scurf after storage on severity at harvest indicated a positive dependence in all years ($P < 0{\cdot}001$) but the regression coefficients differed between harvest dates and years

Table 10. *Effect of planting date, seed size and seed incubation on silver scurf severity (% surface area affected) after storage to January, early harvest and late harvest (Expt 2)*

	Early planting		Late planting		
Seed size...	Small	Large	Small	Large	S.E. (31 D.F.)
			Early harvest		
Untreated seed	6·3	9·7	1·2	2·6	
Incubated seed	11·4	21·8	1·4	4·8	1·36
			Late harvest		
Untreated seed	16·6	15·0	4·0	7·2	
Incubated seed	21·7	27·8	5·4	13·5	2·04

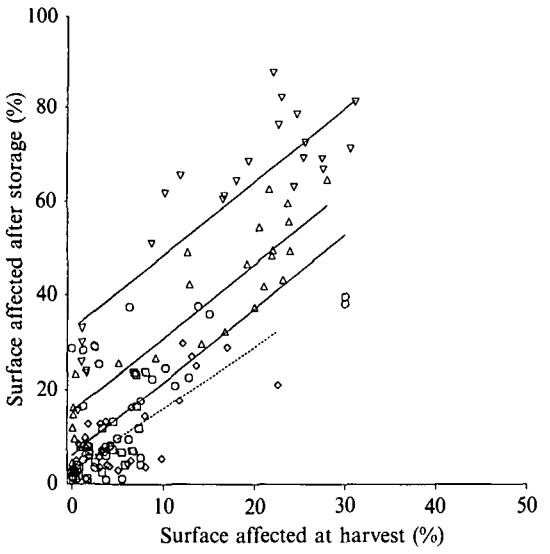

Fig. 4. Relationship between severity of silver scurf after storage and silver scurf at harvest in Expts 1–3. Fitted lines, $y = bx + c$. For solid lines, $b = 156 \pm 0{\cdot}124$; Expt 1 late harvest (○, $c = 5{\cdot}9 \pm 1{\cdot}95$); Expt 3 early harvest (△, $c = 15{\cdot}3 \pm 2{\cdot}68$); Expt 3 late harvest (▽, $c = 32{\cdot}8 \pm 2{\cdot}86$). For the broken line, $b = 1{\cdot}32 \pm 0{\cdot}145$; Expt 2 both harvests stored to January (early harvest □, late harvest ◇, $c = 2{\cdot}7 \pm 0{\cdot}90$).

(Fig. 4). Silver scurf at the early harvest in Expt 1 was negligible and no relationship was established for this harvest. The data for Expt 2 were not compared directly with those for other years as by the end of storage all treatments were almost completely affected, but a linear regression of silver scurf after storage to January on silver scurf at harvest was calculated. The data from the late harvest in Expt 1 and both harvests in Expt 3 were combined and the relationship between silver scurf after storage and at harvest could be represented by three parallel lines with different intercepts (Fig. 4). The data for Expt 2 gave a less close fitting relationship than was obtained for the other years and a single relationship for both harvest dates was as close as separate lines for each harvest date (Fig. 4).

Weight loss during storage

Weight loss for the early harvest was greater from the late planting than from the early planting in Expts 1 and 2 (Table 9) whilst in Expt 3, weight loss at the early harvest was greater for the first and last planting than for intermediate plantings. For the later harvest in Expt 1, weight loss was less for the late planting than for the early planting stored at 7 °C, but there was no significant difference at 3 °C (Table 9). There was no effect of planting date on weight loss from the late harvest in Expt 2 (Table 9). In Expt 1, initial weight loss at 7 °C (to 7 January) from the early harvest was much greater for the late planting ($9{\cdot}2 \pm 0{\cdot}19$%) than for the early planting (6·6%) but subsequently the rate of weight loss was greater for the early planting so that the difference between plantings was reduced. At the later harvest initial weight loss (to 7 January) was similar for both the early planting ($4{\cdot}8 \pm 0{\cdot}13$%) and the later planting (4·5%). Weight loss for the later harvest in Expt 3 decreased with delay in planting (Table 9).

In Expt 2, weight loss was greater for large seed than for small seed but there was no significant effect of seed size in other years. For the early harvest in Expt 3, weight loss was greater for old seed than for young seed at the first planting but there was little difference between seed ages at later plantings (Table 7). For the late harvest in Expt 3, weight loss was greater for old seed than for young seed at all plantings (Table 7).

Linear regression of weight loss on silver scurf after storage

Linear regression of weight loss on severity of silver scurf after storage indicated that there was no significant dependence of weight loss on silver scurf in Expts 1 and 2. In Expt 3, where silver scurf after

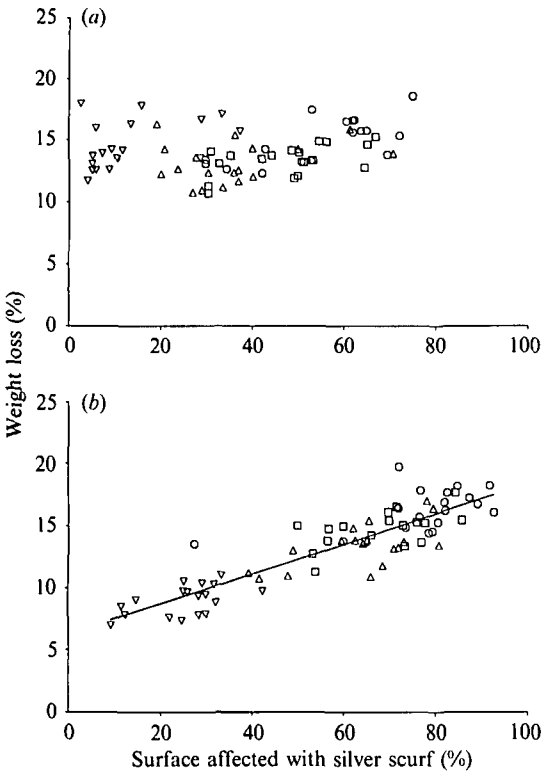

Fig. 5. Relationship between weight loss and severity of silver scurf after storage in Expt 3. (*a*) Early harvest, (*b*) late harvest. Fitted line, $y = bx + c$ where $b = 0{\cdot}120 \pm 0{\cdot}0075$ and $c = 6{\cdot}3 \pm 0{\cdot}47$. 1st planting (○), 2nd planting (□), 3rd planting (△), 4th planting (▽).

Table 11. *Effect of storage temperature on the viability of conidia in soil (number of conidia 000/g) recovered and germinated (72800 conidia were added/g soil)*

	Weeks after adding conidia			
	1	3	5	10
	Number of conidia recovered (000/g)			
10 °C	20·5	14·3	7·9	11·7
20 °C	16·4	8·9	5·8	5·6
S.E. (12 D.F.)	2·50	2·45	1·24	1·93
	Number of conidia germinated (000/g)			
10 °C	10·5	3·3	1·15	0·35
20 °C	3·7	1·8	0·36	0·12
S.E. (12 D.F.)	1·10	0·59	0·164	0·114

storage was very severe for some treatments, weight loss increased linearly with increase in severity of silver scurf for the late harvest but not for the early harvest (Fig. 5). For the late planting, weight loss was greater from the early harvest than from the late harvest despite low silver scurf infection. For the late harvest of Expt 3, much of the variation in weight loss was accounted for by differences in severity of silver scurf (Fig. 5).

Viability of conidia in soil

The number of conidia recovered from soil 1 week after adding a suspension of conidia was less than one-third of the number added. The number recovered decreased more rapidly with time at 20 °C than at 10 °C so that by 10 weeks after adding the conidia, the number recovered after storage at 20 °C was about half that recovered at 10 °C (Table 11). There was no difference in the survival of conidia between wet and dry soil. Of the conidia recovered 1 week after addition of the suspension, the proportion which germinated after incubation in agar was greater at 10 °C (53 %) than at 20 °C (23 %) and the proportion decreased rapidly with time at both temperatures (Table 11) so that by 10 weeks after addition, the number of apparently viable conidia was < 1 % of the number originally added.

DISCUSSION

Although potato seed tubers are the main source of inoculum of *Helminthosporium solani* for ware production (Jellis & Taylor 1977) the means by which inoculum moves from seed to progeny tubers is unknown. Some infection may occur at harvest when mixing of soil and tubers occurs but much of the infection by *Helminthosporium* occurs before harvest. The results of Jellis & Taylor (1977) and of the experiments reported here show that infections can first be detected by incubation of progeny tubers at *c.* 6 weeks after tuber initiation. The importance of transmission during the early stages of growth is supported by the rapid reduction in the viability of conidia with time found in the laboratory experiment. Conidia may be carried by water in the soil and their flow along the stolon would facilitate transfer to the progeny tuber. Infections are often first noted at the stolon end of progeny tubers, nearest to the seed tuber, which indicates that the spatial separation is a limiting factor in transmission. The large numbers of conidia produced on the seed tuber increase the probability of successful transmission and factors which reduce the production of conidia would be expected to reduce the incidence of silver scurf.

The transmission of *Helminthosporium* from potato seed tubers to progeny tubers is particularly difficult to control because even low levels of *Helminthosporium* on the seed can result in the production of copious conidia as the fungus spreads over the seed tuber surface. All seed tubers became completely covered with *Helminthosporium* after planting in these experiments but complete cover was earlier with increase in soil temperature at later plantings. The

effect of soil temperature on the growth of *Helminthosporium* did not significantly alter the relative timing of production of conidia and tuber initiation as increasing soil temperature also advanced plant emergence and thus tuber initiation (Firman *et al.* 1991).

Incubation of seed to increase the severity of seed infection did not affect plant emergence but did advance the growth of *Helminthosporium* over the seed surface and increase the production of conidia during the first few weeks after planting. The production of more conidia during early growth was associated with more severe infection of progeny tubers. Seed which was not incubated did not produce more conidia at later sampling dates probably because seed tubers began to decay around 6 weeks after planting (depending on planting date).

Although the small increase in seed infection generated by incubating the seed resulted in only a small increase in the severity of silver scurf on the progeny tubers, the results suggest that despite previous reports of a negative relationship between seed and progeny tuber infection (Lennard 1970; Jellis & Taylor 1977; Adams & Hide 1980), production of seed with very little silver scurf may be worthwhile for reducing transmission. Use of seed with low levels of *Helminthosporium* could reduce transmission of silver scurf as the growth of *Helminthosporium* over the seed surface is delayed and fewer conidia may be produced if seed tubers decay before *Helminthosporium* has fully exploited the seed surface. Nevertheless, where conditions favour disease development, severe infection of progeny tubers can result from seed with a low percentage of surface affected ($< 5\%$), as in Expt 3. The interval from planting to decay of seed tubers may vary considerably according to soil conditions, pests and diseases, so that these factors may indirectly affect the transmission of silver scurf.

The higher incidence of silver scurf on progeny tubers from more severely affected seed is the reverse of the findings of Jellis & Taylor (1977), where greater initial levels of infection on seed were compared and severely affected seed probably produced fewer conidia. In the experiments reported here, most of the seed tuber surface was uninfected at planting for both incubated and untreated seed, so that although the time course of conidial production was affected by initial seed infection, copious conidia were produced for both seed treatments. Even with severely affected seed (80–100% surface affected), Read & Hide (1984) found greater infection of progeny tubers from severely affected seed than from slightly affected seed in one year out of three.

Although some conidia are viable for at least 50 days as found by Jellis (1972), results of the laboratory experiment suggest that the viability of conidia decreases rapidly and only a small proportion of conidia remain viable for > 3 weeks, particularly in warm soil. Delay in tuber initiation might therefore be expected to reduce infection of silver scurf, as many conidia are produced before tuber initiation. The effects of seed age on emergence were small in Expts 1 and 2 but old seed emerged up to 4 days earlier and severity of silver scurf was slightly increased by seed age except at the late planting in Expt 1, when there was no effect of seed age on emergence. The later emergence and therefore tuber initiation of young seed than of older seed may have contributed to the reduction in severity of silver scurf, which supports the contention that small changes in the timing of tuber initiation and production of conidia can affect disease transmission. In Expt 3, differences in seed age were even greater, as the young seed was completely unsprouted, and there were larger differences in emergence and in severity of silver scurf between seed ages. The difference in emergence between seed ages were such that the time from tuber initiation to harvest was significantly longer for old seed than young seed and this may account for the increase in the severity of silver scurf. In Expt 3 the reduction in silver scurf with young seed was at the expense of a lower tuber yield due to the change in the growth pattern of the crop.

The soil in covered plots was drier than in open plots during the first few weeks after planting, particularly in Expt 1, but there was no consistent effect on the production of conidia or severity of silver scurf on progeny tubers. There was also no effect of soil moisture on viability of conidia in the laboratory experiment. Irrigation has been found to reduce silver scurf (Adams *et al.* 1987; Firman & Allen 1993) but soil moisture content during the early stages of growth may be less important than later. The relatively small reduction in numbers of tubers in plots kept completely dry for 4 weeks after planting indicates that the influence of soil moisture on number of tubers in commercial crops may seldom be important.

Jellis & Taylor (1977) showed that silver scurf increased on progeny tubers as sampling was delayed, and early harvesting has been found to reduce severity of silver scurf after storage (Wilcockson *et al.* 1985). Although this was also shown in these experiments, effects of planting date were larger than those for harvest dates despite a similar interval between planting dates and harvest dates (*c.* 4 weeks). In Expt 3, there was little difference in severity of silver scurf between the first two planting dates; this may partly be explained by slow emergence after the first planting date so that the relative difference in time from tuber initiation to harvest was smaller for these plantings than subsequent ones.

The results of these experiments suggest that the interval from tuber initiation to harvest is a major determinant of severity of silver scurf at harvest and after storage. The largest effects were, however, found when the interval was so short that yields were

reduced and the skin of the tubers was not fully set. For ware production, the reduction in disease from a very short growing season needs to be evaluated against any loss of yield and skin set requirements. For seed production, however, a very short growth period is practical (O'Brien & Allen 1992) and should provide small seed with less disease than longer periods.

The greater severity of silver scurf from crops planted with large seed than with small seed in Expts 1 and 2 was associated with the production of more conidia from large tubers. The greater surface area of larger seed might be expected to allow for the production of more conidia. Differences between seed sizes in the production of conidia in Expt 3 were less clear than in Expts 1 and 2 possibly as a result of the decay of some seed tubers during incubation from the relatively late harvests assessed. The surface area of larger seed, calculated according to the formula of Banks (1985) was *c.* 82 cm^2 in both Expts 1 and 2, which was more than twice that of small seed in either year (*c.* 30 and 34 cm^2 in Expts 1 and 2 respectively), so that the effective area for production of conidia was lower for small seed even when planted at double the density. In Expt 3, the effective surface area of seed of all sizes was similar and there was no effect of seed size on severity of silver scurf. The surface area of seed planted may be a determinant of severity of silver scurf on progeny tubers and, as there is often little effect of seed size on total yield (Allen *et al.* 1992), there may be the potential to reduce silver scurf by using smaller seed without prejudicing yield.

In a study which examined a number of commercial stocks over 5 years, Hide & Adams (1980) reported that linear regressions of silver scurf after storage (tubers affected) on incidence of tuber infection at harvest (eye or skin plugs) were significant in only one year when silver scurf was not prevalent. When silver scurf is prevalent most tubers are affected with silver scurf to some extent after storage and the statistic of the number of tubers affected may not have allowed discrimination between samples with different disease severity. In the experiments reported here, estimates of the surface area affected with silver scurf were made and, although positive linear regressions of severity of silver scurf after storage on severity at harvest were found in all years, large differences in the coefficients of regression were found between harvest dates and years. Thus, even with controlled storage conditions, severity of silver scurf after storage cannot be predicted easily from assessments of infection at harvest. In Expt 3, the severity of silver scurf at harvest increased little between harvest dates, but after storage silver scurf was much more severe from the later harvest than from the early harvest so that late harvesting may result in the establishment of infections which are not apparent at harvest but which develop during storage. In Expt 2, silver scurf almost completely covered tubers by the end of storage, although infection in January was only moderate. Removal of half of the tubers for assessment in January may have dispersed conidia, resulting in severe infection.

A significant dependence of weight loss on severity of silver scurf after storage was found only at the late harvest in Expt 3, where there were large differences in weight loss between treatments. In Expts 1 and 2, the range in weight loss was small and, although a significant linear regression of weight loss on severity of silver scurf was not found, both weight loss and silver scurf were greater following early planting than late planting at the later harvest. In all years, tuber skin set following late planting was incomplete at the early harvest and the high initial weight loss from the tubers as found in Expt 1 countered effects of silver scurf on weight loss.

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REFERENCES

Adams, M. J. & Hide, G. A. (1980). Relationships between disease levels on seed tubers, on crops during growth and in stored potatoes. 5. Seed stocks grown at Rothamsted. *Potato Research* **23**, 291–302.

Adams, M. J., Read, P. J., Lapwood, D. H., Cayley, G. R. & Hide, G. A. (1987). The effect of irrigation on powdery scab and other tuber diseases of potatoes. *Annals of Applied Biology* **110**, 287–294.

Allen, E. J., O'Brien, P. J. & Firman, D. (1992). An evaluation of small seed for ware-potato production. *Journal of Agricultural Science, Cambridge* **118**, 185–193.

Banks, N. H. (1985). Surface area estimation of potato tubers. *Potato Research* **28**, 487–496.

Burstall, L. & Harris, P. M. (1983). The estimation of percentage light interception from leaf area index and percentage ground cover in potatoes. *Journal of Agricultural Science, Cambridge* **100**, 241–244.

Chinn, S. H. F., Ledingham, R. J. & Sallans, B. J. (1960). Population and viability studies of *Helminthosporium sativum* in field soils. *Canadian Journal of Botany* **38**, 533–539.

Firman, D. M. & Allen, E. J. (1993). Effects of windrowing, irrigation and defoliation of potatoes on silver scurf (*Helminthosporium solani*) disease. *Journal of Agricultural Science, Cambridge* **121**, 47–53.

Firman, D. M., O'Brien, P. J. & Allen, E. J. (1991). Leaf

and flower initiation in potato (*Solanum tuberosum*) sprouts and stems in relation to number of nodes and tuber initiation. *Journal of Agricultural Science, Cambridge* **117**, 61–74.

HALL, S. M. & HIDE, G. A. (1992). Fungicide treatment of seed tubers infected with thiabendazole-resistant *Helminthosporium solani* and *Polyscytalum pustulans* for controlling silver scurf and skin spot on stored progeny tubers. *Potato Research* **35**, 143–147.

HIDE, G. A. & ADAMS, M. J. (1980). Relationships between disease levels on seed tubers, on crops during growth and in stored potatoes. 3. Silver scurf. *Potato Research* **23**, 229–240.

HIDE, G. A. & READ, P. J. (1985). Assessing fungicides as potato seed tuber treatments for controlling silver scurf in stored tubers. *Tests of Agrochemicals and Cultivars* **6** (*Annals of Applied Biology* **106**, *Supplement*), 60–61.

HIDE, G. A., CAYLEY, G. R., READ, P. J. & FRASER, J. H. (1980). Treatment of seed and ware potato tubers with thiabendazole for control of storage diseases. *Annals of Applied Biology* **96**, 119–131.

HIDE, G. A., HALL, S. M. & BOORER, K. J. (1988). Resistance to thiabendazole in isolates of *Helminthosporium solani*, the cause of silver scurf disease of potatoes. *Plant Pathology* **37**, 377–380.

JELLIS, G. J. (1972). *Silver scurf disease of potatoes*. PhD thesis, University of Manchester.

JELLIS, G. J. & TAYLOR, G. S. (1977). The development of silver scurf (*Helminthosporium solani*) disease of potato. *Annals of Applied Biology* **86**, 19–28.

LENNARD, J. H. (1970). Silver scurf (*Helminthosporium solani*) development in relation to level of seed tuber infection, soil type and storage temperature. *Experimental Work. The Edinburgh School of Agriculture, 1969*, pp. 24–25.

MINISTRY OF AGRICULTURE, FISHERIES AND FOOD (1982). *Seed Rate for Potatoes Grown as a Maincrop: Short Term Leaflet 653*. Alnwick: MAFF.

O'BRIEN, P. J. & ALLEN, E. J. (1992). Effects of date of planting, date of harvesting and seed rate on yield of seed potato crops. *Journal of Agricultural Science, Cambridge* **118**, 289–300.

READ, P. J. & HIDE, G. A. (1984). Effects of silver scurf (*Helminthosporium solani*) on seed potatoes. *Potato Research* **27**, 145–154.

WILCOCKSON, S. J., ALLEN, E. J., SCOTT, R. K. & WURR, D. C. E. (1985). Effects of crop husbandry and growing conditions on storage losses of Pentland Crown potatoes. *Journal of Agricultural Science, Cambridge* **105**, 413–435.