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Effects of shading and seed tuber spacing on initiation and number of tubers in potato crops (*Solanum tuberosum*)

P. J. O'BRIEN, D. M. FIRMAN* AND E. J. ALLEN

Cambridge University Farm, Huntingdon Road, Girton, Cambridge CB3 0LH, UK

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SUMMARY

Twelve field experiments, carried out over 7 years, examined effects of shading and seed tuber spacing on plant growth, initiation and retention of tubers in four cultivars: Estima, Maris Piper, Maris Peer and Record. Ten of the experiments were carried out at Cambridge and two near Valencia, Spain. Other treatments included in some experiments were floating polythene mulch and planting date.

Shading by up to 75% did not affect the timing of onset or cessation of tuber initiation in Estima but shading by 50% or more delayed the completion of tuber initiation in Maris Piper compared with less severe shading. Except for intensely shaded treatments (50% or more), the majority of tubers were initiated in a very short period (4–7 days). Shading by 37% or more during the period of tuber initiation and increasing planting density, decreased number of tubers per stem initiated in all experiments, but number of tubers was not affected by shading at other stages of growth. At Cambridge, effects of shading on number of tubers > 10 mm retained later in growth from normal planting dates (March to early May) were similar to effects on number of tubers initiated, but effects were much reduced or absent following later plantings at Cambridge and in both experiments in Valencia. The decreased effects of shading on number of tubers > 10 mm at late plantings at Cambridge were associated with the initiation of fewer tubers at these plantings. Effects of shading, planting density and planting date on number of tubers were a consequence of changes in the frequency of occurrence and tuberization of different stolon types. Increasing shading and planting density and delaying planting reduced the number of lateral and branch stolons and the frequency of their tuberization but there were no effects on number of primary stolons or their tuberization. Consequently, at Cambridge a similar number of tubers was borne on primary stolons in shaded and unshaded crops. In Valencia a greater proportion of initiated tubers was retained at final harvest from shaded treatments than at Cambridge, which accounts for the absence of effects of shading on number of tubers > 10 mm. The greater retention of tubers late in growth in Spain may have been associated with the higher peak growth rates achieved in higher radiation fluxes than at Cambridge.

Linear regressions of the data for normal planting dates at Cambridge and from Valencia indicated that the number of tubers > 10 mm late in growth was dependent on the radiation environment during the period of tuber initiation. Radiation flux during the brightest period of the first few days of initiation appeared to be the most crucial aspect of radiation affecting number of tubers. As incident radiation can vary greatly over the short period of tuber initiation, it is potentially an important factor affecting number of tubers in field crops.

INTRODUCTION

Number of tubers is an important characteristic of potato crops, affecting multiplication rate of seed crops and tuber-size distribution in all crops. It has been reported to be affected by a wide range of husbandry and environmental factors (e.g. Ewing & Struik 1992) but there have been few critical studies of the effects of any factor on the initiation, retention and number of tubers under field conditions (O'Brien *et al*. 1998).

Effects of incident radiation on the timing of tuber initiation have not been established, largely because timing of initiation has not been defined and long sampling intervals in many reports have precluded its

* To whom all correspondence should be addressed. Email: d.firman@farm.cam.ac.uk

accurate assessment. It is, nevertheless, widely believed that initiation of tubers is delayed by decrease in irradiance (Bodlaender 1963; Menzel 1985; Struik 1986; Ewing & Struik 1992). In field experiments, Demagante & Vander Zaag (1988) found that even moderate shading (26%) delayed tuber initiation in several cultivars in the Philippines, but Sale (1973, 1976) found no effects of 34% shading on the timing of initiation in the cultivar Sebago in Australia.

The number of tubers initiated and retained is also believed to be affected by the light environment during initiation. At low light intensities in growth-room experiments, number of tubers has generally been found to decrease with decreasing irradiance (Gregory 1965; Menzel 1985) but Menzel (1985) found that the effects of irradiance greatly decreased as temperatures were reduced from *c*. 26 to 20 °C. At much higher irradiance under field conditions, Gray & Holmes (1970) in the UK found that reducing incident radiation by 85% during the period of initiation decreased number of tubers initiated but increased number of tubers retained later in growth compared with full radiation. In contrast, Sale (1973, 1976) found no effect of 21 and 34% shading during initiation on total number of tubers initiated, but 34% shading produced fewer tubers > 10 mm late in growth than no shading. Struik (1986) reported variable effects of shading on number and size distribution of tubers in two cultivars at different sites and Demagante & Vander Zaag (1988) found fewer tubers, especially in long days, from a 48% reduction in incident radiation. Thus, although there is evidence in the literature that incident radiation affects the initiation, retention and size distribution of tubers, there is little consistency in the direction of effects and the causal relationship between crop development and light environment has not been established.

This paper reports field experiments which examined the effects of shading and planting density on the initiation and retention of tubers in three potato cultivars in a range of environments. The results of some of the experiments have been briefly reported previously (Burstall *et al*. 1987; O'Brien *et al*. 1993) or presented in thesis form (Thomas 1988).

MATERIALS AND METHODS

Ten experiments examining the effects of shading were carried out from 1984 to 1994. Experiments 1–5, 7, 8 and 10 were carried out at Cambridge University Farm on gravelly-sandy loam soils of the Milton Association (Soil Survey of England and Wales 1984) which had high organic matter content (3–4%). Experiments 6 and 9 were carried out on a fertile sandy loam soil near Valencia, Spain. The cultivars used were Estima (Expts 1–3), Record (Expt 4) and Maris Piper (Expts 4–10). Effects of seed tuber spacing on initiation of stolons and tubers were examined in two experiments at Cambridge in 1994 (Expt 11) and 1995 (Expt 12). The principal details of the experiments are shown in Table 1. The number of replicates was four in Expts 3 and 6 , two in Expts 11 and 12 and three in the other experiments. A split-plot design was used in Expts 8 and 12 with intensity of shading as mainplots and time of removal of shade as subplots in Expt 8 and planting date in mainplots and other treatments in subplots in Expt 12. All other experiments used randomized block designs.

The polythene used for mulching in Expt 1 was slit at emergence to allow continued plant growth. Nylon shade (or windbreak) material, differing in mesh size, was used to vary the proportion of incident radiation which was prevented from reaching the crop. The values quoted for percentage shading in the text, Tables and Figures for different shading materials are those specified by the manufacturer and refer to the percentage of total global radiation excluded. These specified values of percentage shading are higher than those calculated from *in situ* measurements using tube solarimeters, particularly for 37% shading or less. All shading materials excluded substantially more photosynthetically active radiation (PAR) than total incident radiation (for shading values specified by the manufacturers of 37, 50 and 70%, the measured reductions for total radiation measured using tube solarimeters were 26, 43 and 68% respectively and for PAR using a ceptometer were 46, 67 and 87% respectively). The shade material completely enclosed plots and was supported on posts *c*. 1·2 m above the soil surface. Treatments to be shaded throughout growth (Expts 1–3) or from emergence to the beginning of tuber initiation (Expt 2) were covered with shade material within 2 days of the date of 100% plant emergence. In Expts 1–3, for the purpose of timing the placement and removal of shade covers, the beginning of tuber initiation was defined as the date on which there was at least one tuber on all plants in a sample; the end of tuber initiation was taken to be the date of the third successive harvest in which total number of tubers in three replicates did not increase. In Expts 4–10 shade covers were placed over appropriate plots at the beginning of tuber initiation within 2 days of the first observation of tubers and removed at a specific interval thereafter. A tuber was defined as a swelling of the stolon tip > twice the diameter of its subtending stolon. The period of shading during initiation was longer in Expts 1–3 (3–4 weeks) than in subsequent experiments (5–21 days). The dates of placement and removal of shade covers for each experiment are shown in Table 2. For the purposes of data analysis the beginning and end of tuber initiation was defined as the date on which 10 and 80%, respectively, of the maximum total number of tubers was present in a treatment. Solar radiation and air and soil temperatures were monitored hourly inside and outside shade covers

Table 1. *Details of experiments*

Expt	Year	Cultivar(s)	Other treatment combinations
1	1984	Estima	Three planting dates (4 and 24 April, 9 May); two floating polythene mulch treatments (none, covered 14 days prior to planting); two shade intensities (0, 50% throughout growth from emergence)
2	1985	Estima	Three planting dates (3 and 26 April, 30 May); four shade treatments (0, 50% before, during or after tuber initiation)
3	1986	Estima	Six shade treatments (0, 50% throughout growth, 15, 25, 50 or 75% during initiation)
4	1991	Record, Maris Piper	Two planting dates (10 April, 15 May); four shade intensities (0, 37, 48 and 54% during initiation)
5	1992	Maris Piper	Three within-row spacings (45, 30 and 10 cm); three shade intensities (0, 37 and 50% during initiation)
6	1992	Maris Piper	Two within-row spacings (30 and 10 cm); two shade intensities (0 and 50% during initiation)
7	1993	Maris Piper	Two planting dates (26 March*, 21 May); two within-row spacings (30 and 10 cm); four shade intensities (0, 37, 50 and 70% during initiation)
8	1993	Maris Piper	Three shade intensities (0, 50 and 70% during initiation); two times of removal of shades (5 and 14 days after placement)
9	1993	Maris Piper	Two within-row spacings (30 and 10 cm); three shade intensities (0, 50 and 70% during initiation)
10	1994	Maris Piper	Three planting dates (14 April, 25 May, 14 July); five shading treatments (0, 37, 50 and 70% for 2 weeks and 50% for 4 weeks from the beginning of initiation)
11	1994	Estima, Maris Piper	Five seed tuber spacings (10×10, 20×20, 10×71, 20×71, 40×71 cm)
12	1995	Maris Piper, Maris Peer	Four planting dates (24 March, 28 April, 2 June, 20 July); four seed tuber spacings (10×10, 10×71, 20×71, 45×71 cm)

* Abandoned after plant emergence.

in several experiments using tube solarimeters and thermistor probes, respectively. Relative humidity and carbon dioxide concentration in the air *c*. 30 cm above the crop canopies was measured at 14.00–15.00 h in Expts 4, 5 and 8 using a Vaisala element humidity sensor and infra-red gas analyser (ADC Limited, England). There were no effects of shading on temperature, relative humidity or carbon dioxide concentration.

Seed weighing 65 ± 5 g was used in Expts 1–3; in other experiments the seed used was size graded into fractions of 25–35 mm in Expt 6, 50–65 mm in Expt 8 and into 30–35 mm in all other experiments. Experiments 1–3, 11 and 12 were planted on a flat surface; other experiments were planted in ridges. Experiments 3, 5, 6, 8, 9 and 11 were planted on 2 May, 14 May, 10 February, 12 July, 19 February and 26 April, respectively. Dates of planting of other experiments are shown in Table 1. Experiments 1–9, 11 and 12 used young seed (< 200 day-degrees > 4 °C), whilst seed used in Expt 10 had a physiological age of *c*. 500 day-degrees > 4 °C. Between plantings, seed was stored at 3–4 °C in Expts 1 and 2 and at 1–2 °C in Expts 4, 7, 10 and 12. Where within-row spacing was not a treatment, seed tuber spacing within rows was 25 cm in Expt 10 and 30 cm in all other experiments. Except where row widths were varied (Expts 11 and 12), rows were 71 and 62 cm apart at Cambridge and Valencia, respectively. Fertilizer (at the rates of *c*. 150 N, 65 P, 188 K and 41 Mg kg/ha) was distributed by hand and rotovated into the topsoil in Expts 1–3, 8, 11 and 12 and broadcast by machine prior to cultivation and ridging in other experiments. Fertilizer was applied just prior to each planting in Expts 1, 2, 10 and 12, but the entire area of Expts 4 and 7 received fertilizer prior to the first planting date. All experiments were routinely sprayed with an aphicide/fungicide mixture to control aphids and blight. The experiments at Cambridge were carried out on soils with a water-holding capacity of *c*. 80 mm to a depth of 90 cm. All experiments were irrigated to maintain soil moisture deficits of $< c$. 30 mm at initiation and $< c$. 40 mm thereafter. Irrigation water was applied by a drip system in Expts 1–3, by flooding in Expts 6 and 9, and by hose-reel and boom in other experiments.

In all experiments guarded plants (four per plot) were sampled every 2–4 days to establish the timing of onset of initiation. Subsequently, Expts 1–3, 7, 8 and 10 were sampled (4–8 plants/plot) every 3–4 days until the maximum number of tubers was produced in all treatments and thereafter at longer intervals. Experiments 4 and 5 were sampled every 5–6 days during initiation and then at 2–4 weekly intervals.

Table 2. *Dates of placement and removal of shade covers and period of shading (days) at different stages of growth for different treatments in Expts 1–10*

	Treatment		Date of		
Expt	Date of planting	Polythene mulch + or −	Placement of shade material	Removal of shade material	Period of shading (days)
1	4 April	+	22 April	29 August	129
		−	28 April	29 August	123
	24 April	+	9 May	29 August	111
		−	14 May	29 August	105
	9 May	+	29 May	29 August	92
		−	2 June	29 August	88
		Shading			
2	3 April	Before tuber initiation	5 May	25 May	20
		During tuber initiation	25 May	20 June	26
		After tuber initiation	20 June	10 September	82
	26 April	Before tuber initiation	20 May	6 June	17
		During tuber initiation	6 June	4 July	28
		After tuber initiation	4 July	10 September	68
	30 May	Before tuber initiation	15 June	30 June	15
		During tuber initiation	30 June	30 July	30
		After tuber initiation	30 July	3 October	63
3		Shading from emergence to end of growth	23 May	2 September	102
		Shading during tuber initiation	7 June	1 July	24
4	10 April	Shading during tuber initiation	7 June	24 June	17
	15 May	Shading during tuber initiation	1 July	18 July	17
5		Shading during tuber initiation	12 June	29 June	17
6		Shading during tuber initiation	24 March	7 April	14
7	26 March*	Shading during tuber	—	—	20
	21 May	initiation	23 June	12 July	
8		Shading during tuber initiation	11 August	16 August 25 August	5 and 14
9		Shading during tuber initiation	5 April	19 April	14
10	14 April	Shading during tuber	23 May	6 June	14
	25 May	initiation	27 June	11 July	14
	14 July		14 August	28 August	14

* Abandoned after plant emergence.

Experiments 6 and 9 were sampled on two occasions, 4 and 6 weeks and 17 days and 8 weeks after the beginning of initiation, respectively. Foliar ground cover was recorded weekly in Expts 1–3, 7 and 10 using a grid of 100 equal rectangles. The number of tubers on stolons of differing origin was recorded at intervals after the onset of tuber initiation in Expts 10–12. Stolons were categorized in relation to their origin and defined as follows – primary and lateral stolons are those arising from primary and associated axillary buds at a node, respectively; branch stolons are branches of primary stolons.

RESULTS

Meteorological data

The mean daily incident radiation integral during tuber initiation from February plantings in Expts 6 and 9 at Valencia was comparable to that for late April plantings at Cambridge (Table 3). The intensity of radiation during the brightest period of the day was usually higher (up to *c.* 32%) at Valencia than Cambridge. At Cambridge, daily incident radiation integrals during initiation were higher after the early April planting in 1985 than after any other planting.

Table 3. *Mean daily incident radiation integral* (MJ/m^2) *and mean intensity of radiation* (W/m^2) *from 10.00 to 15.00 h during the first week of tuber initiation in Expts 1–10*

Expt	Year	Date of planting	Radiation integral	Intensity of radiation
1	1984	4 April	18·2	528
		24 April	17·4	518
		9 May	20·0	565
2	1985	3 April	27·9	779
		20 April	14·4	481
		30 May	21·1	562
3	1986	2 May	19·9	551
4	1991	10 April	14·1	445
		15 May	17·5	584
5	1992	14 May	20·0	732
6	1992	10 February	16·9	625
7	1993	21 May	23·5	643
8	1993	12 July	18·6	584
9	1993	19 February	21·9	720
10	1994	14 April	10·1	255
		25 May	22·5	641
		14 July	15·7	488

In 1984, 1991 and 1994, incident radiation integrals during initiation at Cambridge were greater following plantings in May than for earlier plantings, but in 1985 radiation for the planting in early April was high, although it decreased substantially for the late April planting. Incident radiation integrals during initiation following July plantings in Expts 8 and 10 were similar to those prevailing following plantings in late April or early May. Over all experiments, mean daily incident radiation during initiation ranged from *c.* 10 to 28 MJ/m^2, which covers most of the range likely to be found during tuber initiation in commercial production in Europe. For the remainder of growth at Cambridge, receipts of incident radiation were similar to the long-term average in all years except in 1985, which were above average in July and August (Fig. 1).

At Valencia, mean daily air and soil temperatures during initiation were similar to those following May plantings at Cambridge but variation in temperatures at Cambridge was greater, ranging from *c.* 10 °C following early April plantings to 18–20 °C after plantings from early May onwards. Photoperiod during the shading period differed greatly between the two sites, being, on average, *c.* 33% shorter at Valencia than at Cambridge. In Expt 1, mulching the soil with polythene increased soil temperature (by up to 5 °C) compared with no mulching.

In all experiments, soil moisture supply was sufficient to allow rapid early and sustained foliage growth, which was reflected in final tuber yields which were substantially higher than the national average.

There were no statistically significant effects of shading on number of stems in any experiments, and thus effects on number of tubers were due to effects on number of tubers per stem.

The first planting date of Expt 7 was abandoned after emergence because many plants failed to emerge due to the effects of infection of the sprouts by the fungus *Polyscytalum pustulans*.

Effects on the timing of tuber initiation

In Expts 1–3 in Estima, there was no effect of shading from emergence to the beginning of tuber initiation or to the end of growth on the date of onset or cessation of tuber initiation and, consequently, on the duration of initiation (Table 4). In Expts 2 and 3, shading (by up to 75%) during the period of tuber initiation did not affect the duration of initiation. However, in Maris Piper the date of cessation of initiation was delayed and, therefore, the duration of initiation was prolonged by intense shading (50% or more) in Expts 7, 8 and 10 and, in Expt 8, by extending the period of shading from 5 to 14 days (Table 5). For unshaded treatments, the duration of tuber initiation was on average *c.* 1 week in Estima (Expts 1–3) and *c.* 5 days in Maris Piper (Expts 5, 7, 8 and 10).

Effects on number of tubers initiated

Shading by 50% from emergence throughout growth in Expts 1 and 3 decreased total number of tubers throughout most of growth compared with no shading, but effects on maximum number of tubers were small in Expt 3 (Table 6). In Expt 2, shading by 50% before the period of initiation did not affect number of tubers formed. However, in Expts 2–5 and 8–10 (Tables 5–9 and 12) and Expt 7, shading by 37% or more during the period of tuber initiation decreased number of tubers during and shortly after the shading period compared with no shading or shading at any other time. In Expt 3, there was no effect of increasing the intensity of shading above 50% (Table 6). In Maris Piper, there was little effect of increasing the intensity of shading above 37% in crops with stem densities of *c.* 150000/ha in Expts 4 and 5, but at similar stem densities in Expts 9 (Table 9) and 10, and higher densities (*c.* 300000) in Expts 5, 9 and 10 (Tables 8, 9 and 11) and Expt 7, total number of tubers during the shading period decreased further as the intensity of shading was increased to 50 and 70%. In Expt 6, there were no effects of shading on total number of tubers, 2 and 4 weeks after the end of shading. In all experiments, effects of shading on number of tubers initiated occurred very rapidly, for total number of tubers generally decreased within 2–3 days of the beginning of shading and effects of shading were usually very large within a week of its onset (e.g. Table 5).

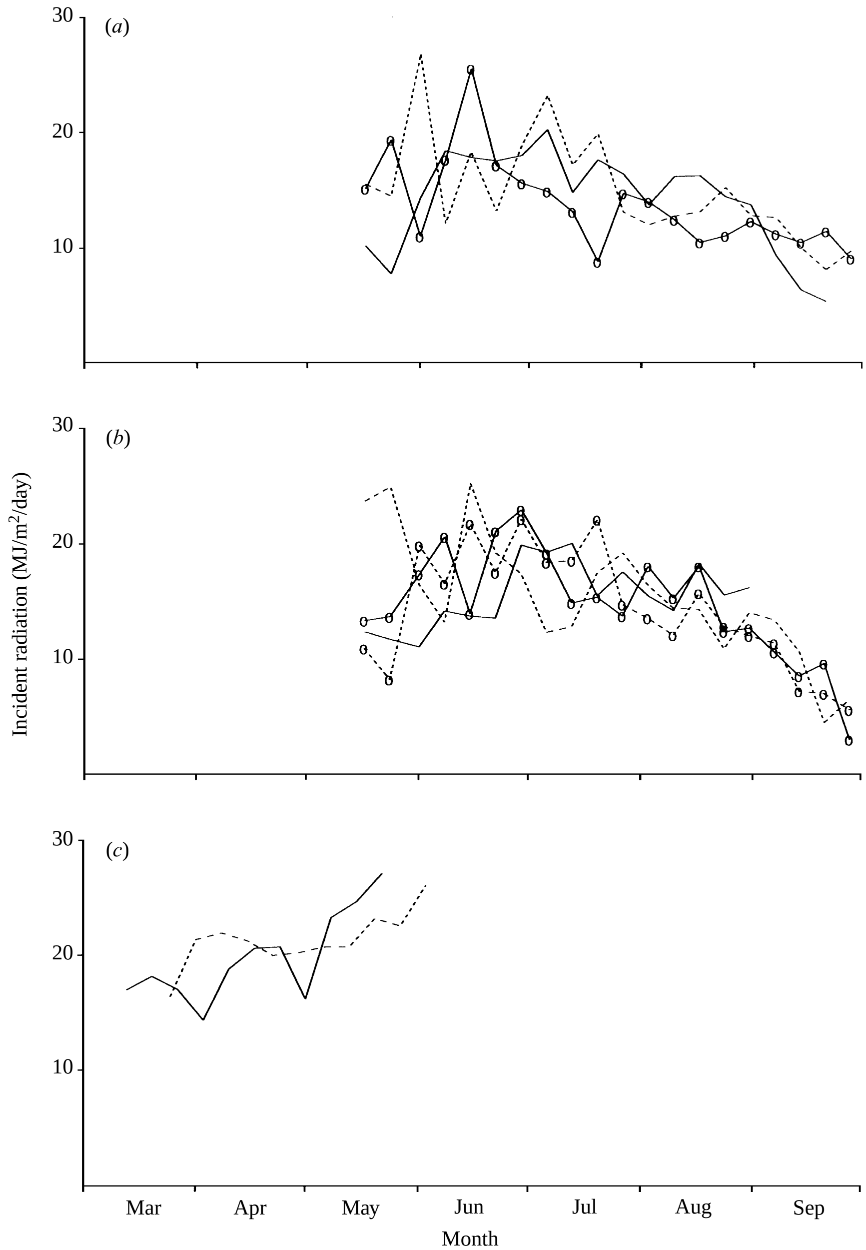

Fig. 1. Incident radiation (MJ/m^2/day) at Cambridge and Valencia. (*a*) Cambridge: 1984, —; 1985, ---; 1986, —○—. (*b*) Cambridge: 1991, —; 1992, ---; 1993, —○—; 1994, --○--. (*c*) Valencia: 1992, —; 1993, ---.

In Expts 11 and 12, effects of seed tuber spacing on initiation of stolons and tubers was similar in Estima, Maris Piper and Maris Peer. Increasing planting density did not affect the number of primary stolons per stem or the timing of onset of initiation but decreased the total number of tubers per stem (Table 10). Number of lateral and branch stolons per stem decreased with increasing planting density over the whole range, so that very few of these stolon types were present at the highest density (1×10^6/ha). The frequency of tuberization of primary stolons was not affected by planting density in either experiment, but the highest density decreased the tuberization of lateral and branch stolons in Expt 12 (Table 10) and

Table 4. *Effect of shading (mean of planting dates) on the timing of tuber initiation in Estima in Expt 2*

		Shading 50%			
	Unshaded	Before tuber initiation	During tuber initiation	After tuber initiation	S.E. (22 D.F.) (days)
Julian date of onset of initiation	162	164	163	164	1·1
Julian date of cessation of initiation	173	173	170	174	1·5
Duration of initiation (days)	11	9	7	10	1·7

Table 5. *Effect of shading intensity and time of removal of shades on the duration (days) of initiation and total number of tubers (000/ha) in Maris Piper in Expt 8*

		Time of removal of shades (days after placement)		
	Shading (%)	5	14	Mean
Duration of tuber initiation	0	3·7	3·7	3·7
	50	15·0	20·0	17·5
	70	18·1	21·2	19·7
	Mean	12·3	15·0	
	S.E. intensity of shading 0·51; time of removal of shades 0·78			
Number of tubers				
Days after onset of shading	0	594	461	528
	50	594	469	532
2	70	375	383	379
	Mean	521	438	
	S.E. intensity of shading 32·9; duration of shading 28·9			
	0	957	976	967
	50	691	746	719
5	70	516	441	478
	Mean	721	721	
	S.E. intensity of shading 72·5; duration of shading 63·5			
	0	1195	1113	1154
	50	1340	1672	1506
23	70	1668	1965	1816
	Mean	1401	1583	
	S.E. intensity of shading 121·6; duration of shading 54·7			
	D.F. intensity of shading 4; duration of shading 6			

of branch stolons in Expt 11. However, decreases in number of tubers per stem with increasing planting density were largely due to fewer lateral and branch stolons. The effects were greatest at early (March, April) than at late (June, July) plantings in Expt 12 as the number of lateral and branch stolons decreased with delay in planting from April onwards.

Effects on number of tubers retained

After the period of shading, total number of tubers in unshaded and in lightly-shaded treatments usually remained constant or decreased, whilst number of tubers in treatments which were intensely shaded (50% or more) during the period of initiation decreased more slowly, remained constant or, particularly in Maris Piper, increased, so that effects of shading on total number of tubers late in growth were usually less than effects on maximum number of tubers initiated. In Estima, the effects of shading on total number of tubers late in growth were small after the final planting date in Expts 2 and 3. In Maris Piper, increases in total number of tubers after intense shading were greatest in Expts 7–10 and following the longer period of shading in Expt 8 (Table 5). These increases occurred within a few days of removing the shade covers and the results of Expt 10 showed that they were primarily due to continued initiation of

Table 6. *Effect of shading (averaged over other treatments) on maximum number of tubers (000/ha) in Estima in Expts 1–3*

	Stage of growth									
	Emergence to the end of growth		Emergence to the beginning of initiation	During initiation				After initiation		
Shading (%)	0	50	50	15	25	50	75	50	S.E.	D.F.
Expt										
1	1166	941	—	—	—	—	—	—	39·7	22
2	1133	—	1081	—	—	798	—	1198	70·4	22
3	1268	1177	—	1347	1285	889	880	—	109·6	15

Table 7. *Effect of shading and planting date on total number of tubers at the end of the shading period and number of tubers > 10 mm at the end of growth in Maris Piper in Expt 4*

		Shading during tuber initiation (%)					
	Date of planting	0	37	48	54	Mean	S.E. (29 D.F.*)
Total number of tubers	10 April	1378	1111	1172	1279	1235	
	15 May	1195	1078	801	876	1080	
	S.E.		11.46			81·0	
	Mean	1286	1094	1132	1118		81·0
Number of tubers > 10 mm	10 April	858	661	630	687	709	
	15 May	705	620	789	581	674	
	S.E.		41·6			29·4	
	Mean	781	641	709	634		29·4

* D.F. reduced by one missing plot.

Table 8. *Effect of within-row spacing and shading on total number of tubers (000/ha) on 16 July and number of tubers > 10 mm (000/ha) on 12 August in Maris Piper in Expt 5*

		Within-row spacing (cm)				
	Shade during tuber initiation (%)	45	30	10	Mean	S.E. (16 D.F.)
Total number of tubers	0	499	715	1486	900	
	37	413	685	1242	780	
	50	452	624	1026	700	
	S.E.		66·4		38·3	
	Mean	454	674	1251		38·3
Number of tubers > 10 mm	0	435	634	1088	719	
	37	329	504	849	561	
	50	327	496	737	520	
	S.E.		36·0		20·8	
	Mean	364	545	891		20·8

tubers on terminal buds of primary stolons (Table 11). These changes in total number of tubers after the shading period were sufficiently large to negate the effects of shading on final number of tubers in Expts 7 and 9 and after the final planting date in Expt 10, reverse the effects in Expt 8 (Table 5) and also largely explain the absence of effects of shading at Valencia at both harvests in Expt 6.

For the experiments at Cambridge, effects of shading on final number of tubers > 10 mm occurred

Table 9. *Effect of within-row spacing and shading on total number of tubers (000/ha) at the end of the shading period in Maris Piper in Expt 9*

Shadow during tuber initiation (%)	Within-row spacing (cm) 30	10	Mean	S.E. (10 D.F.)
0	1181	2235	1708	
50	882	1824	1353	
70	742	1468	1105	
S.E.	101·0		71·4	
Mean	935	1842		58·3

Table 10. *Effect of seed tuber spacing (mean of cultivars Maris Piper and Maris Peer) on number of mainstems, stolons per mainstem and tubers per mainstem 42 days after emergence from the March planting in Expt 12*

	Planting density (000/ha) (Seed tuber spacing (cm)) 31·2 (45 × 71)	70·3 (20 × 71)	140·6 (10 × 71)	1000·0 (10 × 10)	S.E. (17 D.F.)
Mainstems per plant	2·59	2·66	3·22	2·83	0·32
Primary stolons	6·29	7·21	6·87	6·95	0·267
Lateral stolons	6·46	5·26	3·58	1·11	0·545
Branch stolons	6·50	5·75	2·87	0·94	0·823
Total number of stolons	19·3	18·3	13·3	9·0	1·18
Tubers on primary stolons	4·96	5·17	5·29	5·01	0·489
Tubers on lateral stolons	4·17	3·46	2·29	0·55	0·553
Tubers on branch stolons	1·50	2·00	0·92	0·37	0·275
Total number of tubers	10·6	10·6	8·5	5·9	1·02

for plantings before mid-May but generally not for later plantings. For plantings up to mid-May, effects of shading on number of tubers > 10 mm late in growth were similar to effects on maximum number of tubers (Tables 6–8, 12 and 13). Number of tubers > 10 mm in unshaded or lightly shaded treatments stabilized shortly after the end of initiation but shading by 50% or more during initiation usually delayed the date of stabilization in number of tubers > 10 mm due to more tubers already initiated growing to 10 mm in size (Fig. 2). In Expts 1 and 3, reductions in number of tubers > 10 mm due to 50% shading throughout growth compared with no shading were considerably greater than the reduction in maximum total number of tubers (Tables 6 and 13).

Effects of shading during initiation on number of tubers > 10 mm late in growth decreased with delay in planting after April in Expts 2, 4 and 10 (Tables 8, 12 and 13) and were absent after final plantings in these three experiments. In Expts 1, 2, 4 and 10, number of tubers > 10 mm, particularly in unshaded and lightly shaded treatments, decreased with delay in planting after April or early May (Fig. 2; Tables 7, 12 and 13) as a result of fewer tubers per stem. Detailed examination of mainstems from the April and July plantings in Expt 10 for number and tuberization of stolons of different types provides some understanding of the gross effects of shading and planting date on number of tubers. During the period of shading there was no change in the number of primary stolons from either planting, but the number of lateral and branch stolons increased in both plantings (Table 11). At the end of shading, the number of lateral stolons from the early planting was unaffected by shading but number of such stolons from the late planting and branch stolons from both planting dates decreased with increasing intensity of shading, especially with 50 and 70% shading. Shading had no effect on the tuberization of primary stolons for the April planting but tuberization of these stolons from the late planting decreased with increasing intensity of shading, especially to 70%. Lateral and branch stolons were more sensitive to shading, and increasing shading decreased frequency of tuberization of these stolons, particularly from the July planting. Subsequently, most primary stolons of intensely shaded treatments of the July planting tuberized (Table 11). Shading, therefore, reduced the number of tubers by a reduction in number of lateral and branch stolons, especially at the later planting, and suppression of tuber initiation on these stolons from both planting dates. As far fewer of these stolon types were produced and

Table 11. *Effect of shading and planting date on number of stolons and tubers per mainstem in Maris Piper in Expt 10** (18 D.F.)

Number of stolons	Date of planting	Onset of shading (17 DAE) (%) shading 0	37	50	70	Mean	S.E.	End of shading (31 DAE) (%) shading 0	37	50	70	Mean	S.E.	62 days after the end of shading 0	50	70	Mean
Primary	14 April	8·5	7·5	7·8	9·5	8·3		8·5	8·7	8·3	9·7	8·8					
	14 July	8·7	8·8	8·7	8·7	8·7	0·38	10·2	11·5	10·8	9·7	10·6	0·25	8·2	9·5	8·8	8·8
	Mean	8·6	8·2	8·3	9·1	8·5	0·59	9·4	10·1	9·2	9·7	9·7	0·40				
Lateral	14 April	7·0	6·8	6·5	7·8	7·0		9·8	8·3	9·5	10·2	9·5					
	14 July	0·0	0·2	0·0	0·0	0·0	0·56	6·0	6·0	4·3	2·3	4·7	0·55	3·2	1·6	2·8	2·5
	Mean	3·5	3·5	3·3	3·9	3·5	0·89	7·9	7·2	6·9	6·3	7·1	0·87				
Branch	14 April	0·0	0·7	0·5	1·3	0·6		6·2	5·3	2·7	3·2	4·4					
	14 July	0·0	0·0	0·0	0·0	0·0	0·14	4·0	0·7	1·2	0·0	1·5	0·60	0·5	0·9	0·4	0·6
	Mean	0·0	0·4	0·3	0·7	0·3	0·22	5·1	3·0	2·0	1·6	2·9	0·95				
Total	14 April	14·5	15·0	14·8	18·6	15·9		24·2	22·3	20·7	23·1	22·6					
	14 July	8·7	9·0	8·7	8·7	8·8	0·88	20·2	18·2	16·3	12·0	16·7	0·91	11·9	12·0	12·0	12·0
	Mean	12·1	12·0	11·8	13·7	12·4	1.40	22·2	20·2	15·5	17·6	19·6	1·43				
Number of tubers																	
On primary stolons	14 April	1·8	1·3	2·3	2·0	1·9		6·0	7·2	5·5	6·0	6·2					
	14 July	1·2	0·0	0·5	2·0	0·9	0·45	7·0	5·2	5·5	3·3	5·3	0·39	6·4	5·6	7·0	6·3
	Mean	1·5	0·7	1·2	2·0	1·4	0·71	6·5	6·2	5·5	4·7	5·7	0·61				
On lateral stolons	14 April	0·0	0·0	0·0	0·0	0·0		3·8	4·3	3·0	2·3	3·4					
	14 July	0·0	0·0	0·0	0·0	0·0		2·5	0·7	0·2	0·0	0·9	0·30	1·3	0·1	0·4	0·6
	Mean	0·0	0·0	0·0	0·0	0·0		3·2	2·5	1·6	1·2	2·2	0·48				
On branch stolons	14 April	0·0	0·0	0·0	0·0	0·0		1·7	1·5	0·8	0·3	1·3					
	14 July	0·0	0·0	0·0	0·0	0·0		0·7	0·2	0·0	0·0	0·2	0·16	0·1	0·1	0·2	0·1
	Mean	0·0	0·0	0·0	0·0	0·0		1·2	0·9	0·4	0·2	0·7	0·26				
Total	14 April	1·8	1·3	2·3	2·0	1·9		11·5	13·0	9·3	8·6	10·9					
	14 July	1·2	0·0	0·5	2·0	0·9	0·45	10·2	6·1	5·7	3·3	6·3	0·68	7·8	5·8	7·6	7·0
	Mean	1·5	0·7	1·2	2·0	1·4	0·71	10·9	9·6	7·5	6·0	8·5	1·07				

* Data not obtained for the intermediate planting (25 May) and only for the late planting date 62 days after the end of shading.

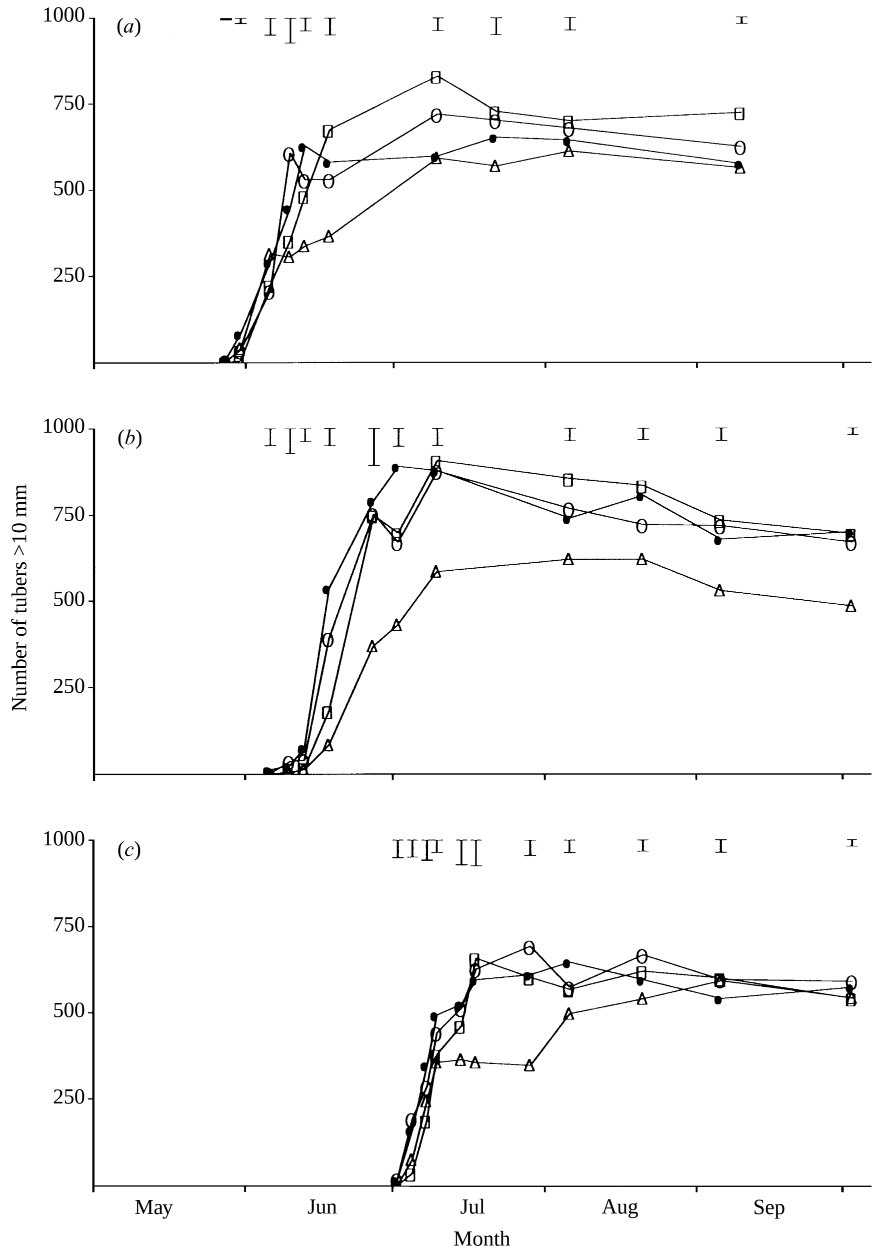

Fig. 2. Effect of shading on number of tubers > 10 mm for three planting dates of Estima in Expt 2. (*a*) Planted 3 April, (*b*) planted 26 April, (*c*) planted 30 May. No shading (○), 50 % shade before (□), during (△) and after (●) tuber initiation. Bars represent S.E. (22 D.F.).

tuberized from the July than from the April planting (Table 11) the number of tubers from this planting was largely a function of number of mainstems and number of tuberized primary stolons.

These effects of shading on stolon occurrence and tuberization are consistent with the effects of increasing density in Expts 11 and 12 and confirm the morphological changes associated with effects on number of tubers. These effects are likely to be determined by changes in the light environment and hence growth rate of the stem. Generally, shading by up to 50 % did not affect foliar ground cover during or after the shading period, so that effects of shading were a direct reduction in incident and intercepted

Table 12. *Effect of shading and planting date on number of tubers (000/ha) c. 55 days after plant emergence in Maris Piper in Expt 10*

		Shading during initiation (%)						
		0	37	50	70	50		
Number of tubers	Date of planting	For 2 weeks				For 4 weeks	Mean	S.E. (28 D.F.)
> 10 mm	14 April	947	731	762	897	612	790	
	25 May	682	478	370	466	497	499	
	14 July	391	335	347	330	262	333	
	S.E.			51·9			23·2	
	Mean	673	515	493	565	457		29·9
20–50 mm	14 April	766	624	658	618	462	627	
	25 May	546	389	284	347	373	388	
	14 July	272	253	281	209	204	244	
	S.E.			37·3			16·7	
	Mean	528	422	408	391	406		21·6

Table 13. *Effect of planting date and shading on final number of tubers > 10 mm (000/ha) in Estima in Expts 1–3*

		Stage of growth							
		Emergence to end of growth		Emergence to beginning of initiation	During initiation	After initation			
		% shading							
Expt	planting	0	50	50	50	50	Mean	S.E.	D.F.
1	4 April	847	642	—	—	—			
	24 April	878	603	—	—	—			
	9 May	690	427	—	—	—			
	S.E.	29·6							
	Mean	805	557					17·1	22
2	3 April	622	—	721	560	572	619		
	26 April	668	—	693	486	698	636		
	30 May	589	—	540	541	571	560		
	S.E.	32·8					16·4		
	Mean	626	—	651	529	614		18·9	22
3	2 May	732	489	591				83·1	15

radiation. Shading by 70% reduced ground cover during and for some time after shading compared with other shading treatments and therefore affected interception of the reduced incident radiation. Changes in intercepted radiation do not seem to affect the frequency of tuberization of primary stolons, but reduction in intercepted radiation per stem through shading or increasing density reduces frequency of tuberization first on branch stolons and, as the reduction increases, on lateral stolons. Where the number of lateral and branch stolons is low, as in late planting, the effects of shading are minimized.

Effects of shading on number of tubers > 10 mm were largely due to effects on number of tubers in size fractions below 50 mm (e.g. Table 12). In Expt 5, shading by 37% or more during initiation increased number of tubers > 50 mm at the final harvest compared with no shading due to more tubers in the 60–80 mm size fraction. There were no effects of shading on number of tubers > 50 mm in other experiments.

Further analysis of the comprehensive data of Expts 1–3 was carried out to establish any relationships between number of tubers at final harvest and maximum number of tubers initiated. Data for treatments shaded continuously from emergence in Expts 1 and 3 and shaded after initiation in Expt 2 were not included in the analyses. Linear regression analyses of the remainder of the data of Expts 1–3 indicated both total number of tubers and number of tubers > 10 mm at final harvests were dependent on the maximum number of tubers initiated. Percentage variance accounted for by linear regression ranged from 61 to 83 % in Expts 1 and 3 and for the combined data of Expts 1–3. In Expt 2, the regression accounted for only 37–41 % of the variance and in this experiment a smaller proportion of the initiated tubers were retained at final harvest than in Expts 1 and 3, particularly from treatments that initiated many tubers following the second planting date (Tables 6 and 13). Very low incident radiation for 4 days immediately after the end of initiation following the second date in Expt 2 may have been a contributory factor to the substantial reduction in number of tubers after initiation. For similar numbers of tubers initiated in Expts 2 and 3, a greater percentage of the total number of tubers was lost between the end of initiation and final harvest from treatments shaded after initiation or throughout growth (48 %) than for unshaded treatments or treatments shaded during initiation only (38 %).

Regression analyses of the data of Expts 1–3 indicated that the number of tubers lost between the completion of initiation and final harvest was dependent on the maximum number of tubers initiated. Decreases in total number of tubers after the end of initiation were due to resorption of small tubers (< 10 mm) for there was no evidence of new tuber formation after the main phase of initiation and number of tubers > 10 mm was generally constant soon after the end of initiation. Except for intensely shaded treatments (50 % or more), stabilization in number of tubers > 10 mm occurred *c.* 40–50 days after plant emergence in Expts 1–3 (Fig. 2). Regression analyses of the data indicated the number of tubers > 10 mm at final harvest was dependent on the number of tubers > 10 mm *c.* 40 days after emergence. The variance accounted for by regression was increased by taking account of differences in number of mainstems and the analysis then accounted for 65 and 69 % of the variance for all treatments and unshaded treatments, respectively. Thus, counts of the number of tubers > 10 mm early in growth reflected those at final harvest and could be used for estimation of final number of tubers.

Relationship between number of tubers and incident radiation during the period of tuber initiation

The results show that alteration of the gross radiation environment of the stem through shading or increasing density can significantly affect number of tubers and further analysis of the data attempted to link the growth of ground cover, interception of radiation and, ultimately, number of tubers. The imposition of shading causes morphological changes in leaves and stems which complicates the interpretation of the effects on intercepted radiation. Generally shading by up to 50 % did not affect ground cover and stems became taller and, although less stable than unshaded stems, remained erect throughout growth. Intense shading reduced ground cover during the shading period and for some time afterwards and also resulted in taller stems. The taller etiolated stems resulting from 70 and 75 % shading lodged after removal of shades and determination of intercepted radiation was compromised by these changes. Despite these difficulties, regression analysis was done to determine the dependence of number of tubers on intensity of radiation and integral of intercepted radiation during initiation using data for 30 cm within-row spacing in Expts 1–3 (Estima) and in Expts 4–6 and 9 (Maris Piper). The analyses were carried out with and without data from plantings after early May at Cambridge, as number of tubers decreased with delayed planting. Omission of data from such plantings in Expts 1–4 increased the variance accounted for by regression, as effects of shading on number of tubers were usually small or absent at late plantings. In order to account for seasonal variation in number of stems, all analyses were based on number of tubers per stem.

In Estima, regression analysis indicated no significant dependence of number of tubers and any aspect of the radiation environment during initiation in Expt 2 because number of tubers following very high incident radiation during initiation after the early April planting was similar to those following lower radiation at later plantings (Tables 3 and 12). Linear regression of maximum number of tubers on daily intensity, integral and intercepted radiation gave close fitting positive relationships in Expts 1 and 3, but accounted for less variance in Maris Piper, partly because sampling was not frequent enough in some experiments (e.g. Expts 6 and 9) to accurately determine maximum number of tubers. At individual sites in Expts 4–6 and 9, regression analyses of number of tubers > 10 mm per mainstem late in growth on nine parameters of the radiation environment during initiation accounted for *c.* 66–94 and 66–93 % of variance in the data at Cambridge and Valencia, respectively (Table 14). At Valencia, intercepted radiation accounted for more of the variation in number of tubers per stem than other parameters of the radiation environment but there were few differences between any other parameter at this site or between any of the nine parameters at Cambridge. For the combined data of the two sites, integral and intensity of radiation accounted for more of the variation in number of tubers per stem than intercepted radiation, but variance accounted for by regression for the combined data was much less than for each site separately. Generally, hourly integral of radiation and maximum radiation flux accounted for

Table 14. *Parameters from linear regression analyses of number of tubers > 10 mm per mainstream* (y) *on parameters of the radiation environment* (x) *during the first week of initiation in Expts 4–6 and 9*

	Site (Expt)								
	Cambridge (Expts 4 and 5)			Valencia (Expts 6 and 9)			Cambridge and Valencia (Expts 4–6 and 9)		
Parameter of radiation environment	Equation	R^2* (%)	S.E.	Equation	R^2* (%)	S.E.	Equation	R^2* (%)	S.E.
Daily total integral (MJ m^{-2})	$y = 1{\cdot}34 + 0{\cdot}2188x$	89·7	0·318	$y = 4{\cdot}49 + 0{\cdot}0728x$	66·5	0·289	$y = 2{\cdot}65 + 0{\cdot}1552x$	43·2	0·813
Daily total intercepted (MJ m^{-2})	$y = 0{\cdot}34 + 0{\cdot}6730x$	77·5	0·470	$y = 4{\cdot}62 + 0{\cdot}1842x$	91·6	0·144	$y = 3{\cdot}54 + 0{\cdot}2150x$	5·9	1·700
Daily PAR integral (MJ m^{-2})	$y = 2{\cdot}40 + 0{\cdot}3390x$	93·8	0·247	$y = 4{\cdot}87 + 0{\cdot}1107x$	75·0	0·249	$y = 3{\cdot}49 + 0{\cdot}2266x$	40·9	0·830
Daily PAR intercepted (MJ m^{-2})	$y = 2{\cdot}04 + 0{\cdot}9500x$	93·6	0·250	$y = 4{\cdot}89 + 0{\cdot}3027x$	90·6	0·153	$y = 3{\cdot}62 + 0{\cdot}5020x$	25·4	0·935
Hourly total integral (MJ m^{-2})	$y = 1{\cdot}30 + 3{\cdot}710x$	90·1	0·132	$y = 4{\cdot}45 + 0{\cdot}954x$	72·0	0·264	$y = 2{\cdot}60 + 2{\cdot}319x$	63·2	0·655
Hourly total intercepted (MJ m^{-2})	$y = 1{\cdot}96 + 7{\cdot}170x$	65·5	0·582	$y = 4{\cdot}61 + 2{\cdot}321x$	93·1	0·131	$y = 3{\cdot}08 + 4{\cdot}800x$	44·5	0·804
Hourly PAR integral (MJ m^{-2})	$y = 2{\cdot}39 + 5{\cdot}674x$	94·1	0·241	$y = 4{\cdot}86 + 1{\cdot}433x$	79·2	0·228	$y = 3{\cdot}46 + 3{\cdot}366x$	52·2	0·746
Hourly PAR intercepted (MJ m^{-2})	$y = 2{\cdot}03 + 15{\cdot}95x$	93·5	0·252	$y = 4{\cdot}88 + 3{\cdot}822x$	92·3	0·138	$y = 3{\cdot}53 + 8{\cdot}03x$	38·9	0·844
Maximum flux, (W m^{-2})	$y = 1{\cdot}99 + 0{\cdot}00531x$	93·5	0·252	$y = 4{\cdot}51 + 0{\cdot}00216x$	82·1	0·211	$y = 2{\cdot}86 + 0{\cdot}00431x$	52·8	0·743
Error D.F.		5			3			10	

* Percentage variance accounted for by regression.

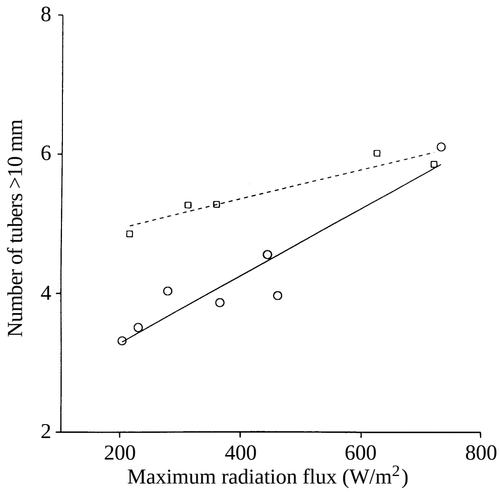

Fig. 3 Correlation between number of tubers > 10 mm per mainstem in Maris Piper (Expts 4, 6 and 9) and intensity of incident radiation (W/m^2) from 10.00 to 15.00 h during the first week of tuber initiation at Cambridge (○) and Valencia (□). Regression equations:
Cambridge, $y = 2{\cdot}32 + -0{\cdot}0048x$, R^2 (adjusted) = 0·86;
Valencia, $y = 4{\cdot}51 + 0{\cdot}0021x$, R^2 (adjusted) = 0·87.

more of the variation in number of tubers per stem than the daily radiation integral (Table 14). The mean maximum radiation flux (from 10.00 to 15.00 h) accounted for a high proportion of the variation in number of tubers > 10 mm per mainstem at individual and combined sites and the relationship between these two parameters is illustrated in Fig. 3. Linear regression of number of tubers per stem on maximum radiation flux in Expts 4–6 and 9 accounted for 94, 82 and 53% of the variation for Cambridge, Valencia and the combined data, respectively. Linear regression analysis indicated that dependence of number of tubers on aspects of the radiation environment averaged over the first 4 days of initiation were similar to those for the whole period of shading.

DISCUSSION

Effects of shading on the initiation, retention and growth of tubers in Expts 1–10 were due to changes in incident radiation alone, for there were only minimal effects of shading on temperature, relative humidity and carbon dioxide content of the air. Plentiful supply of nutrients and soil moisture ensured no confounding effects of these factors and the rapidity of effects of shading on number of tubers – within 3 days of onset of shading – precludes contributory effects of nutrients and soil moisture availability. The range in incident radiation in the experiments spans that likely to be encountered at initiation under field conditions in Europe and the results, therefore, have widespread practical implications.

The absence of effects of shading on the timing of onset of initiation in Expts 1–3 accords with the findings of Sale (1973) and disagrees with the view that initiation of tubers under field conditions is delayed in conditions of low incident radiation (Demagante & Vander Zaag 1988; Ewing & Struik 1992). The delay in attainment of maximum number of tubers in Maris Piper with intense shading in some experiments (Expts 7, 8 and 10) shows that low irradiance may delay the completion of tuber initiation in some cultivars and explain reports of delayed initiation where maximum number of tubers was the measure. The results suggest that the timing of tuber initiation in field crops would not be affected by variation in incident radiation.

In Expt 2, there was no effect of shading before or after the period of initiation on total number of tubers initiated or retained later in growth, but number of tubers was decreased by shading by > 37% during the period of initiation in all experiments. These findings agree with those in most previous reports (Gray & Holmes 1970; Struik 1986; Demagante & Vander Zaag 1988) and suggest that incident radiation affects number of tubers mainly during the period of tuber formation. The reduction was caused by the suppression of stolon and tuber growth. Incident radiation, therefore, appears to affect number of tubers as a result of changes in plant (stem) growth rate rather than changes in development as suggested by Struik (1986). The rapidity of effects of shading on number of tubers initiated in Expts 5 and 8, the effects of planting density and the increasing effect of shading with increasing planting density and, therefore, competition for light in Expt 5, tend to support the view of Slater (1963) and Perl *et al.* (1991) that abundance of assimilates is crucial in promoting initial tuber formation. The absence of effects of shading on total number of tubers initiated in Sebago reported by Sale (1973, 1976) may be due to the paucity of tubers on higher order stolons, as Cother & Cullis (1985) observed that only one tuberized stolon per node is normally present in this cultivar.

The results of Expts 1–3, 5, 7, 8 and 10 and many other experiments at Cambridge (O'Brien *et al.* 1998) show that with synchronous plant emergence the majority of tubers are usually formed within 2–7 days of the commencement of initiation, which is considerably shorter than the widely accepted period of 2–6 weeks (Krijthe 1955; Sale 1976). Consequently, there is only a brief period during which any factor can affect number of tubers, but within such a short period incident radiation can vary greatly. Table 15 shows data for total incident radiation at Cambridge for 3–7 day periods during May and June, the period during which tuber initiation normally occurs in NW Europe. Although there was relatively little seasonal variation in mean monthly radiation but substantial short-term fluctuation in incident radiation, in most

Table 15. *Mean minimum and maximum incident radiation (MJ/m²/day) for 2–7 day periods from mid-May to the end of June at Cambridge 1984–95*

Year		Period of observation 3	5	7	Mean (mid-May–June)
1984	Minimum	3·5	4·7	7·1	14·9
	Maximum	22·4	21·7	20·9	
1985	Minimum	6·9	9·4	11·3	16·8
	Maximum	29·1	29·1	28·5	
1986	Minimum	6·5	8·7	10·1	17·3
	Maximum	27·4	27·1	25·9	
1987	Minimum	8·4	10·0	11·1	15·1
	Maximum	22·1	19·6	19·4	
1988	Minimum	4·7	7·2	11·1	16·6
	Maximum	29·6	22·0	20·7	
1989	Minimum	13·7	13·7	16·0	21·6
	Maximum	30·2	28·7	27·6	
1990	Minimum	7·0	8·8	10·6	16·6
	Maximum	25·9	24·9	24·5	
1991	Minimum	5·6	7·1	7·5	13·6
	Maximum	20·8	20·0	17·9	
1992	Minimum	7·5	10·1	11·3	19·8
	Maximum	27·5	27·4	25·6	
1993	Minimum	8·5	10·2	12·3	17·5
	Maximum	27·6	25·2	24·5	
1994	Minimum	6·7	7·0	7·2	16·7
	Maximum	26·8	24·0	22·7	
1995	Minimum	7·6	8·9	8·8	16·7
	Maximum	27·8	26·2	23·2	
1984–95	Minimum	3·5	4·7	7·1	16·9
	Maximum	30·2	29·1	28·5	

years there was a 4–6-fold range in incident radiation over a 3-day period and a 2–3-fold range over a 7-day period. In treatments planted before mid-May at Cambridge at a within-row spacing of 30 cm (*c.* 47000 plants/ha) in Expts 1–5, a 50% reduction in incident radiation during the period of initiation decreased number of tubers > 10 mm during the harvesting period by *c.* 20% in Estima and Maris Piper compared with full radiation. The corresponding reduction in number of tubers for the highest planting density (*c.* 140000 plants/ha) in Expt 5 ranged from 19 to 34%. These effects and the observed variation in incident radiation over the short period of initiation suggest that solar radiation may be an important factor affecting number of tubers in temperate regions. In experiments at Cambridge, 50% of plants emerged within 3 days of the date of observation of the first emerged plants. In commercial practice, plant emergence is normally less synchronous than in experiments, resulting in a wider range of dates of onset of initiation and, therefore, an apparently longer duration of initiation. Consequently, the effects of incident radiation on number of tubers would be expected to be larger and more variable in commercial crops and it is known that large effects are sometimes found, even in crops planted from the same seed lot.

Effects of shading on number of tubers retained late in growth were sometimes different from effects on number of tubers initiated, for post-shading changes in number of tubers frequently differed between shading treatments. Number of tubers post-shading often increased in intensely shaded treatments but not in less intensely shaded or unshaded treatments, especially in the variety Maris Piper, a result similar to that found by Gray & Holmes (1970) in Maris Peer. Increases in number of tubers were generally greatest following very intense shading, extension of the shading period, late planting and in high solar input. It would seem, therefore, that very low plant growth rates during the period of initiation will decrease number of tubers but, if followed by rapid growth rates, the retention of tubers may be increased. This response would contribute to the absence of effects of shading on final number of tubers in Expts 6, 7, 9 and 10 and in the experiment reported by Gray & Holmes (1970).

The difference between sites in the dependence of number of tubers on radiation resulted from fewer tubers per mainstem from shaded treatments at Cambridge than at Valencia (Fig. 3). Differences in row width, stem density (Table 16) and chronological age of seed tubers (2–3 months) at planting between the sites were probably too small to affect number of tubers per stem (O'Brien *et al.* 1998). Meteorological data for a month post-shading, in 2 years in which significant effects of shading on number of tubers > 10 mm per mainstem were found at Cambridge but not at Valencia, show that there was little difference in mean daily air or soil temperature between the sites (Table 16). At Valencia photoperiod was, on average, 19% shorter than at Cambridge, but mean daily radiation integral was *c.* 15% higher at Valencia. The available data from Expts 5 and 6 in 1992 and 7 and 9 in 1993, which used seed of similar physiological age from a common seed lot and had similar stem densities in each year at the two sites, suggest that a greater percentage of the total population of tubers in shaded treatments was retained late in growth at Valencia (91%) than at Cambridge (67%), probably as a result of higher growth rates post-shading. In unshaded treatments, a similar proportion (80%) of the total population of tubers was retained at both sites.

The absence of effects of shading on final number of tubers > 10 mm from plantings after mid-May at Cambridge in Expts 2, 4, 7 and 10, in Expts 6 and 9 at Valencia and the reversed effects in Expt 8 and in an experiment reported by Gray & Holmes (1970) differed from effects found at normal planting dates (March to early May) at Cambridge. Date of planting

Table 16. *Mean meteorological data during the first month after the end of the shading period and mean number (000/ha) of mainstems and tubers > 10 mm at Cambridge and Valencia*

	Site, year, experiment (date of end of shading)				Mean percentage increasing (+) or decreases (−) in values at Valencia compared with Cambridge
	Cambridge		Valencia		
	1991 Expt 4 (24 June)	1992 Expt 5 (29 June)	1992 Expt 6 (7 April)	1993 Expt 9 (19 April)	
Soil temperature at 10 cm (°C)	16·4	18·8	16·9	15·8	−7
Daily integral of radiation (MJ m^{-2})	17·5	15·2	19·3	18·3	+15
Hourly integral of maximum radiation (MJ m^{-2})	1·06	0·94	1·34	1·28	+31
Photoperiod (h)	16·3	16·2	13·5	13·8	+19
Number of mainstems	220	119	115	181	−13
Number of tubers > 10 mm	709	545	645	962	+28
Number of tubers > 10 mm per mainstem	3·22	4·58	5·61	5·31	+40

appears to affect number of tubers independently of the radiation environment and also influences the effect of shading. In some experiments at Cambridge (Expts 1 and 2), the number of tubers increased slightly with delay in planting up to late April or early May mainly as a consequence of more stems being produced. With further delay in planting, number of tubers decreased in many experiments, largely due to decreases in number of tubers per stem. The results of Expt 10 suggest that reductions in number of tubers at late plantings were mainly caused by decreases in the number of lateral and branch stolons and the proportion which tuberized (Table 13), so that at such plantings the vast majority of tubers in all shading treatments were borne on primary stolons. Number and frequency of tuberization of primary stolons does not appear to be affected even by wide fluctuations in growing conditions, which explains the absence of effects of shading on number of tubers at late plantings at Cambridge and, possibly, between varieties and sites as reported by Struik (1986).

The effects of all treatments, shading, planting density and planting date on number of tubers were achieved by altering the frequency of occurrence and tuberization of the different stolons. Primary stolons were always present and invariably tuberized, but the growth and tuberization of other stolons were much more vulnerable to environmental conditions. With intense shading or at high stem densities, lateral and branch stolons could be eliminated and, when present, many of these stolon types failed to tuberize. The consistency of effects suggests that a hierarchy of stolons exists in relation to their development and growth which is based on their origin on the stem. Within this system, the likelihood of appearing, tuberizing and ultimately producing a marketable tuber is greatest for primary stolons and least for branch stolons. The variation in number of initiated tubers resulting from effects on lateral and branch stolons could also be achieved by delaying planting and this cannot be attributed to the same environmental conditions. Decreases in number of tubers and in number of lateral and branch stolons with delay in planting did not appear to be associated with any changes in temperature, incident radiation, photoperiod or sprout development at planting. The direction and rate of change in photoperiod are environmental features that change as a consequence of delay in planting. In Expt 10, daylength during the period of growth of lateral and branch stolons increased by *c.* 1·3 h after the April planting, remained relatively constant after the May planting and decreased by *c.* 1·2 h after the July planting. Large absolute changes in photoperiod can affect several aspects of plant development in some varieties, including Maris Piper (Firman *et al.* 1995; O'Brien *et al.* 1998) and it is possible that the observed changes in number of lateral and branch stolons and, consequently, in number of tubers that occurred with delay in planting were caused by the alteration in the direction of change in the photoperiod. However, the seed was increasing in chronological age between plantings and it is possible that irreversible physiological changes were occurring. As the effects were consistent, it seems that delaying planting until June/July in practice will result in fewer tubers per stem than if planting were earlier. This is a major handicap for such production, as the objective is large yields of small tubers for which large numbers of tubers are desirable. The separation of photoperiodic effects from those of seed physiology has considerable commercial significance and experiments designed to separate the effects of these factors are in progress.

Where shading during initiation reduced number of tubers > 10 mm throughout growth the reduction usually occurred in the smaller grades 10–50 mm.

This suggests a hierarchy of growth amongst tubers which was confirmed in other experiments (O'Brien *et al*. 1998). The largest tubers in any population were found on primary stolons at central or lower central nodes; most medium-sized tubers were borne on primary and lateral stolons and the majority of small tubers were found on lateral and branch stolons. This hierarchy of tuber sizes is established very early in growth and maintained throughout much of growth and is probably determined and controlled by the main shoot apex. This leads to the expectation that real differences in tuber size distribution can be created by conditions during and immediately after tuber initiation. A population of tubers borne primarily or exclusively on primary stolons would not be expected to produce the same distribution, at any yield, as the same population composed of tubers on all three stolon types. In terms of the method introduced by Travis (1987) to describe size distribution, μ (the size with most yield) would be larger and σ (the standard deviation) would be smaller for the former population than the latter.

The main commercial justification for seeking greater understanding of tuber initiation is to control number of tubers with greater precision. Such control would give more consistent and predictable size distributions and ensure increased yields of the most valuable size fractions. As Thomas (1988) suggested, such control must begin with consistent number of mainstems which bear the stolons. However, even with consistent numbers of mainstems the results suggest that the light conditions during initiation and subsequent growth can create different numbers of tubers. In many cases, the ultimate number of tubers may be similar but be derived from different stolon types. The absolute number of tubers should be greater if initiation occurs early in the season and/or in high irradiance. Both conditions occurred in Valencia in these experiments but are difficult to combine in most NW European countries. The results suggest that late planting of seed crops in many areas is likely to limit number of tubers and there is some evidence to support this view (grown from similar seed sizes and planted in Cambridge on 21 April and 19 July and in Scotland on 17 April, similar stem populations (105000–107000 mainstems/ha) were produced but the numbers of tubers per mainstem were 8·9, 5·2 and 5·6 respectively). Such broad comparisons only provide circumstantial support that the implications of this work do have practical relevance, as many factors are confounded in the husbandry of the crops being compared. However, as O'Brien *et al*. (1998) showed that many of these husbandry factors have little effect on initiation, the conclusions must be that the effects are likely to be real and justify immediate testing. If the production of consistent stem populations were achieved, there must be real expectation that number of tubers set in a particular environment in well-grown healthy crops would not vary sufficiently to confound the grower. Where the former has been achieved by the use of small seed from similar areas and production practices, the resultant tuber population at Cambridge has been reasonably consistent, particularly in the cultivar Estima (Table 17).

Table 17. *Number of mainstems and tubers (000/ha) in irrigated reference plots of two cultivars grown at Cambridge from 25–30 mm seed*

	Estima		Cara	
	Mainstems	Tubers	Mainstems	Tubers
1993	110	456	102	459
1994	115	487	103	431
1995	120	461	106	572
1996	106	373	124	298

Maximum total number of tubers is difficult to detect as peak numbers are transient and, therefore, a count of the total number of tubers initiated is of little use in assisting the prediction of effects of treatments on final number and size grading of tubers. Except for intensely shaded treatments (50% or more), number of tubers > 10 mm stabilized some 40–50 days after plant emergence in Expts 1–3 and in other experiments at Cambridge, which included a wide range of treatments and environments. This stability in number of tubers > 10 mm for much of growth allows for early prediction of number of tubers at desired harvest dates and can be used in practice for estimation of final number of tubers. The universal use in research of number of tubers larger than a specified size grade, such as 10 or 15 mm, as a measure of total number of tubers would enable valid and meaningful comparisons to be made between experimental results in published reports.

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