61

Leaf and flower initiation in potato (*Solanum tuberosum*) sprouts and stems in relation to number of nodes and tuber initiation

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SUMMARY

Experiments were conducted in controlled environment cabinets and in the field at Cambridge, UK, in 1987–90 and in Valencia, Spain 1989–90 with several varieties of potato. The initiation of leaf primordia and flowers was recorded in sprouts stored for long periods at 13 °C with constant illumination and in sprouts exposed to different photoperiods and periods of cold storage. In field experiments, the effects of a wide range of planting dates, differences in physiological age, the time at which seed tubers were sprouted and of imposing an 8 h photoperiod were investigated.

More than 40 leaf primordia were initiated in the sprouts of Home Guard and Arran Comet stored at 13 °C, but, in other varieties, fewer leaves were initiated. Flowers were initiated in the sprouts of some varieties. In field-grown plants, the number of nodes to the first flower differed between varieties and was increased by ageing sprouts before planting. Stems from physiologically old seed of all varieties had more nodes below ground than young seed but the number of aerial leaves to the first flower increased only slightly with increasing physiological age. The number of aerial leaves to the first flower was lower and less variable in Estima than in Maris Piper.

Initiation of flowers usually occurred before tuber initiation and within two weeks of emergence but was earlier in some varieties than others. There was little influence of photoperiod on the time to initiation of flowers and tubers in most experiments but, with low levels of radiation, flowering was completely inhibited in the variety Maris Piper.

INTRODUCTION

In many crops, much research has emphasized morphological changes during development and the factors influencing development rate. However, little attention has been given to development in potatoes and most studies of the crop have simply divided its life into various growth periods. Much discussion has centred on the relationship between leaf growth at tuber initiation and subsequent growth (Ivins & Bremner 1965) although Allen & Scott (1980) have seriously questioned the generality of this view of the control of the crop's growth pattern. This preoccupation with growth has ignored the potential significance of the distinct developmental sequence within the shoot which begins with the initiation of leaf primordia at bud apices, continues at sprout (or stem) apices, until temporarily ended by differentiation of floral primordia, and is resumed by further development in secondary apices. Somewhere in this sequence, tuberization occurs, but its relation to the other processes is unclear.

The morphology and growth of buds and developed sprouts in potatoes has been described by Artschwager (1918), Goodwin (1967), Krijthe (1946), Sadler (1961) and Sussex (1955). A potato tuber has an apical bud with leaf primordia arranged in a 5/13 phyllotactic spiral so that the angle of divergence between successive leaves is about 138°. As the tuber grows, older leaves from the apical bud form scale leaves over the tuber surface which subtend 'eyes' consisting of one secondary-axis and two or more tertiary-axis buds. In mature tubers, dormant apical and fully developed lateral buds consist of *c.* 12 leaf primordia (Goodwin 1967): younger lateral buds nearer the apical bud, and tertiary-axis buds, have fewer primordia. Bud growth resumes some weeks after harvest if tubers are kept at a suitable storage temperature. Little sprout growth occurs at *< c.* 4 °C but at higher temperatures the rate of sprout elongation is increased with temperature up to *c.* 25 °C (Krijthe 1962; Kirk *et al.* 1985). Sadler (1961) found that the rate of leaf production on sprouts longer than 20 mm decreases while Kirk *et al.* (1985)

suggested that in Maris Piper the rate of initiation decreased linearly with the number of leaf primordia so that the rate of initiation is effectively zero by the time 24 nodes have formed. Kirk *et al.* did not observe an inflorescence during sprouting and concluded that floral initiation did not arrest leaf initiation.

Taylor (1953) suggested that the number of nodes to the first flower was constant at *c.* 26 for a range of varieties, although Jones & Borthwick (1939) found *c.* 22 nodes to the flower in Sebago and Kirk *et al.* (1985) reported 31 nodes to the flower in Maris Piper. There is a general consensus in the literature that leaf production and flowering in the potato are increased under long days and that tuberization is favoured by short days (Driver & Hawkes 1943; Krug 1960; Steward *et al.* 1981). In much of the literature, flowering refers to the appearance of open flowers rather than to the initiation of floral buds and leaf production is loosely applied to the expansion of the leaf canopy and not to the initiation of leaf primordia or the number of expanded leaves formed. In many reports the timing of tuberization is not measured. Consequently, the general view of the effect of photoperiod on the potato may not be justified and is misleading in understanding the relationship between the two processes.

The growth and development of buds in the sprouting phase is also important in determining the subsequent growth of the potato plant. Effects of physiological age of sprouts on leaf growth patterns have been documented (Allen *et al.* 1979; O'Brien *et al.* 1983) but the understanding of these effects in terms of the developmental sequence is limited. The control of floral initiation in sprouts and field grown plants and the relationship between vegetative development, flowering and tuber initiation was studied. Attention was directed to the number of leaf primordia initiated before the first flower and to the timing of initiation of leaf primordia, flowers and tubers in relation to planting and emergence.

MATERIALS AND METHODS

Experiments were carried out in controlled environments (Expts 1–4) and in the field at Cambridge (Expts 5–9) and Valencia (Expts 10, 11). The later experiments were initiated to explain and examine the findings from Expt 1 in which flowering was observed in unplanted sprouts and Expt 5 in which variation in the number of nodes to the first flower was recorded.

The controlled temperature facilities were insulated rooms used routinely for the ageing of seed tubers or smaller cabinets (Expts 2 and 4). Temperatures of 13 °C (for ageing) and 4 °C (for restricting growth) were selected from past experience and for practical reasons (storage at < 4 °C may result in frost damage if temperature regulation is not precise). Illumination in

Expts 1–3 was from fluorescent strip lights and the light intensity was *c.* 25 W/m².

Seed tubers for all the experiments were selected by hand from commercial tubers graded 30–55 mm. For most varieties, seed tubers of *c.* 30 g were used but tubers of Estima in Expts 1, 2, 6 and 7 weighed *c.* 20 g. Only undamaged tubers were selected and any with obvious sprout damage were discarded at planting.

In all experiments, observations were made on the longest sprout or stem of each seed tuber. Sprout length, total number of nodes differentiated and development of the flower were recorded for each sample. All nodes attached to the sprout were included in the count but nodes on the tuber surface (within the 'eye') were not. The nodes counted were all attached to a distinct structure (the sprout) rather than to the eye, which may contain different numbers of tertiary-axis buds. Any primordia which formed a discernible bump on the apical dome at × 60 magnification under a binocular microscope were included. Floral development was recorded according to a key (previously used by J. N. Bean, unpublished; Figs 1, 2)
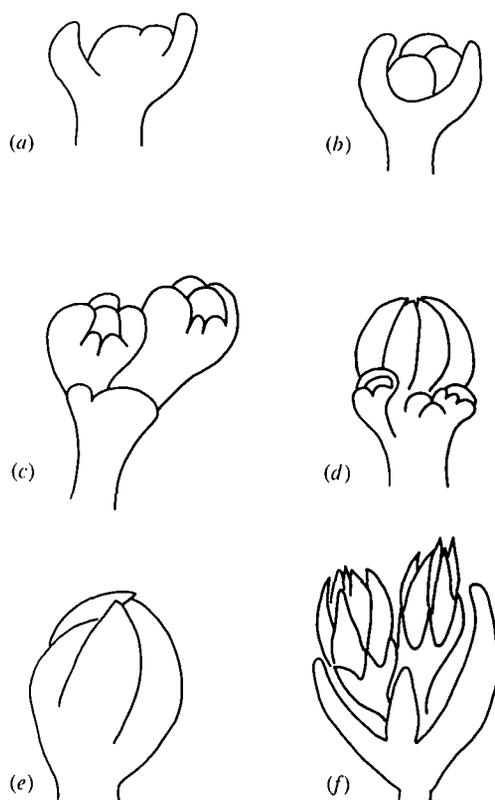

Fig. 1. Numerical key to flower development: (*a*) stage 1, apical dome swelling; (*b*) stage 2, apex dividing into separate floret lobes; (*c*) stage 3, differentiation of florets; (*d*) stage 4, development of visible floral organs; (*e*) stage 5, enlargement of flower; (*f*) stage 6, flower visible without disturbing leaves.

with stages similar to figures illustrated by Danert (1957). In the sprouting experiments (Expts 1–3), five tubers from each treatment were assessed for all samples.

Controlled-environment experiments

Experiment 1, 1987/88

Growth and development of sprouts kept at 13 °C with constant illumination were examined in the varieties Arran Comet, Cara, Désirée, Estima, Home Guard, Maris Piper and Vanessa. The seed tubers were put to sprout in December 1987, as soon as received on the farm, and were sampled at intervals for up to 10 months until sprouts ceased to grow. Seed of all varieties had mean sprout lengths 3 mm or less at the start of the experiment.

Experiment 2, 1988

The effect of three photoperiods of 8, 16 or 24 h/day on development of sprouts of Estima and Maris Piper kept at 13 °C was examined. Seed tubers which had sprouts with c. 17 nodes were transferred from a cold store (4 °C) with constant illumination by fluorescent lights into 13 °C cabinets with fluorescent lights on 26 April and sampled at intervals for 7 months.

Experiment 3, 1989

The effect of periods of cold storage on the development of sprouts of Estima was investigated by comparing the growth of sprouts at 13 °C after treatments of all combinations of 5, 10 or 15 weeks at 13 °C after breaking dormancy (12 January), followed by a period of 5, 10 or 15 weeks at 2 °C. Samples were assessed every 5 weeks and compared with untreated tubers at constant 13 °C. Tubers kept at 2 °C were also assessed to determine any growth during cold storage.

Experiment 4, 1989

The effect of photoperiods of 8 or 18 h/day on the growth of Maris Piper was examined by growing plants in pots in controlled-environment chambers (Fison's 600H). Seed of Maris Piper, which had been kept at 2 °C and had sprouts with c. 17 nodes, were planted in 175 mm diameter pots in August, and ten were placed in each of two cabinets with 8 or 18 h photoperiod, at 19 °C with maximum light intensity of 300 W/m^2 and relative humidity c. 75%. Two plants were sampled from each cabinet at intervals after emergence and the number of nodes, flower development and number of tubers assessed.

Field experiments

Experiment 5, 1987

Seed tubers of Estima and Maris Piper were planted at Cambridge on eight dates, 13 March, 13 April, 14 May, 14 June, 29 June, 13 July, 3 August and 31 August, in a randomized block design with three replicates. The soil was a light gravelly soil of the Milton Association (Soil Survey of England and Wales 1984). Tubers were planted by hand 30 cm apart in ridges 71 cm wide. At each planting date fertilizer was applied by hand at 120 kg N, 52 kg P, 150 kg K and 32 kg Mg/ha and the soil was cultivated with a hand rotavator. Tubers were pushed into ridges with the apical end uppermost for unsprouted seed and with the longest sprout facing vertically upwards for sprouted seed. After planting, ridges were hoed up to cover the seed tuber with c. 10 cm of soil. As with the other field experiments, a pre-emergence herbicide of Gramoxone + Opogard was used at each planting date and when necessary plants were sprayed to prevent blight (*Phytophthora infestans*), according to normal farm practice. Hourly measurements of soil and air temperature (using thermistors) were taken with a datalogger. Accumulated day degrees > 0 °C were calculated as the cumulative sum of daily mean temperatures > 0 °C.

Seed tubers were kept at 4 °C from receipt to planting date but after poor emergence of the unsprouted seed at the first two planting dates, a different source of Maris Piper seed tubers was used for subsequent plantings and the Estima seed tubers were placed in a greenhouse until sprouts were c. 3 mm so that any diseased or damaged sprouts could be discarded.

Emergence of plants was recorded in each plot and two plants from each plot were sampled twice a week from emergence until tuber initiation. Emergence was defined for each treatment as the date on which more than half of the plants had emerged. At each sampling, the longest stem from each plant was examined using a binocular microscope and the number of nodes below ground and to the apex (or first flower if present) was recorded. The length of the stem, stage of floral development and number of tubers present were also recorded. The date of tuber initiation was defined for each plot as the first date on which tubers more than twice the diameter of the stolon were found on any plant in that plot. The date of flower initiation was defined as that when a flower of any stage was present. At the end of the season, the number of nodes between the 1st and 2nd, and 2nd and 3rd flowers (where present) was recorded for four stems/plot at the first five planting dates.

Experiment 6, 1988

The treatments were all combinations of the varieties Cara, Désirée, Estima, Home Guard, Maris Piper and Vanessa, two physiological ages of seed; young (kept below 4 °C throughout) and old (sprouted at 13 °C to accumulate 750 day-degrees > 4 °C, then at < 4 °C between plantings) and four planting dates; 14 April, 24 May, 29 June and 9 August at Cambridge
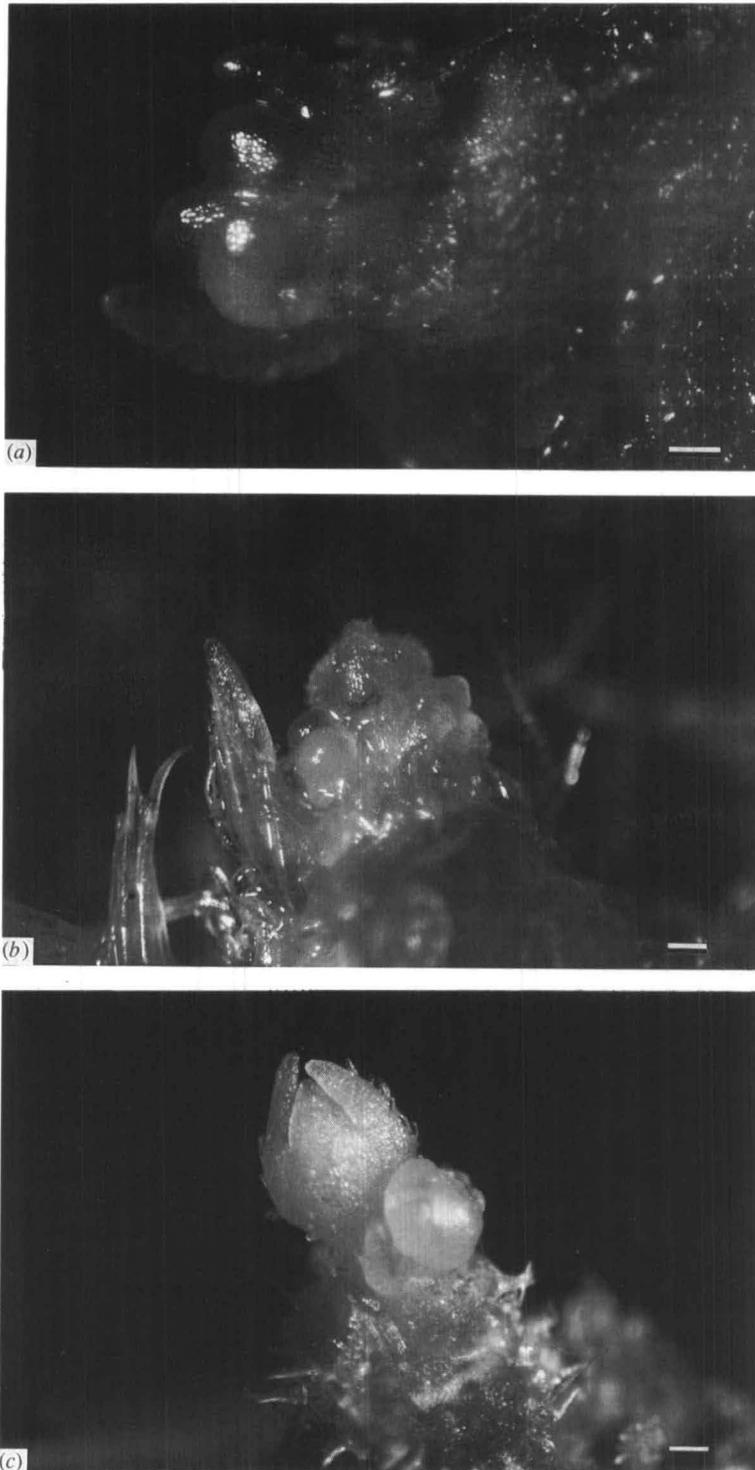
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Fig. 2. Photomicrograph of floral primordia in the potato variety Estima. (a) stage 2; (b) stage 4; (c) stage 5. Scale bar = 0·5 mm.

University Farm. The old seed of the variety Home Guard was allowed to accumulate 1128 day-degrees > 4 °C rather than 750 day-degrees. There were three replicates in a randomized block design planted in a similar way to Expt 5 with 100 kg N, 75 kg P, 188 kg K and 27 kg Mg/ha applied at each planting. The emergence of plants was recorded and two plants/plot sampled at emergence, 2 and 3 weeks after emergence. Stems were examined as in Expt 5 and, in addition, the number of below-ground nodes with stolons and branches was recorded. The number of nodes between the 1st and 2nd flower (where present) was recorded.

Experiment 7, 1988

Seed tubers of the varieties, Cara, Désirée, Estima, Home Guard and Maris Piper were sprouted at 13 °C for 45 days from three different dates; 8 January, 22 February and 7 April and otherwise kept at < 4 °C. The tubers were planted at Cambridge on 24 May (the same date as the 2nd planting in Expt 6) with three replicates in a randomized block design. Fertilizer application, recording and observations were carried out as for Expt 6.

Experiment 8, 1989

Sprouted seed of three varieties, held at 2 °C from receipt, was planted in ridges (Estima and Record) or 150 mm pots (Maris Piper) on 11 August in two blocks in the field at Cambridge. As there was only a limited number of seed tubers of Maris Piper, the use of pots enabled the size of the experiment to be minimized. One block was covered daily between 17.00 and 09.00 h with black polythene to give an 8 h photoperiod and the other block was left uncovered with the ambient photoperiod decreasing over the course of the experiment from *c.* 15 to 13 h. Samples of two plants were taken from after emergence until tuber initiation and the number of nodes and tubers were counted and the development of the flowers was assessed. Hourly measurements of soil and air temperature (using thermistors) and total solar radiation (using a Kipp solarimeter) were recorded with a datalogger.

Experiment 9, 1990

Sprouted seed tubers of the varieties Estima and Maris Piper, held at 2 °C from receipt on the farm were planted on 6 August in ridges in the field at Cambridge. Four sub-plots of each variety consisting of a single row of 12 plants spaced at 20 cm were planted by hand in two blocks. One block was covered daily with black polythene between 17.00 and 09.00 h as in Expt 8 and the other block was covered with clear polythene for the same period to reduce any differences in temperature and air movement. Over the course of the experiment, the ambient photoperiod decreased from *c.* 15 to 13 h. Samples of two plants were taken from after emergence until

tuber initiation and the number of nodes and tubers were counted and the development of the flowers was assessed. Hourly measurements of soil and air temperature and total solar radiation were recorded as in Expt 8.

Experiment 10, 1989

Unsprouted seed tubers of the varieties Estima, Maris Piper and Désirée were planted on two dates, 10 January and 23 February, in a sandy soil, near Valencia, Spain. Each treatment was planted as a single block with four rows of 25 tubers at 30 cm spacing in rows 61 cm wide. Seed tubers were kept at 4 °C between planting dates. For the first planting date, emergence was recorded and the date of tuber initiation was established by regular sampling of four plants. The number of nodes to the first flower was assessed by sampling ten plants from each plot after flowers had been initiated.

Experiment 11, 1990

Unsprouted seed tubers of the varieties Estima, Maris Piper, Record and Désirée were planted on 2 February in a sandy soil, near Valencia, Spain. Each treatment was planted as a single block with four rows of 8 tubers planted at 20 cm spacing in rows 61 cm wide. Emergence was recorded and the date of tuber initiation was established by regular sampling of four plants. The number of nodes to the first flower was assessed by sampling eight plants from each treatment after flowers had been initiated.

RESULTS

Controlled-environment Experiments (1–4)

The initiation of leaf primordia on sprouts in Expt 1 kept at a constant 13 °C differed between the varieties examined (Fig. 3). In Maris Piper (Fig. 3*a*) there was a marked reduction in the rate of initiation of primordia but in other varieties, particularly Home Guard (Fig. 3*a*) and Arran Comet, there was a linear increase in the number of nodes over a long period. Consequently, the maximum number of nodes observed on sprouts held at 13 °C was much higher in Arran Comet and Home Guard than in other varieties (Table 1) and the fewest nodes were initiated in Estima and Maris Piper. During most of the period of growth, sprouts elongated linearly in proportion to the increase in the number of nodes (Fig. 3*b*). Some sprouts were etiolated after storage, particularly in Estima. Sprouts were left for several months until they had become very dry and the seed tuber was quite shrivelled but floral initiation was only observed in some sprouts of Home Guard with *c.* 40 nodes initiated and there was no evidence that flowers occurred after a fixed number of primordia had been initiated.
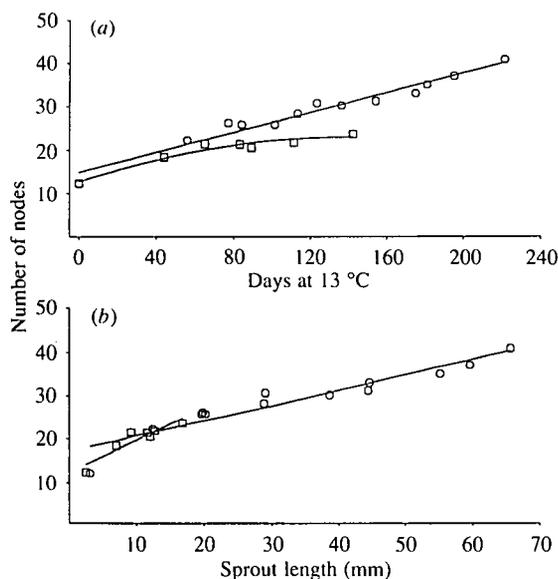
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Fig. 3. The growth of potato tuber sprouts stored at 13 °C, (a) number of nodes (b) relationship between number of nodes and sprout length. $\bigcirc$, Home Guard; $\square$, Maris Piper. Fitted lines (a) Home Guard, $y = 14\cdot9 + 0\cdot114x$ (r^2 adjusted 0·955); Maris Piper, $12\cdot7 + 0\cdot146x - 0\cdot0052x^2$ (0·918). (b) Home Guard, $y = 17\cdot1 + 0\cdot355x$ (0·885); Maris Piper $y = 12\cdot3 + 0\cdot741x$ (0·834).

Table 1. *Mean maximum number of nodes recorded on sprouts of seven potato varieties after constant storage at 13 °C in Expt 1*

Arran Comet	Home Guard	Estima	Cara	Maris Désirée	Maris Piper	Vanessa	S.E.
42·6	37·8	24·2	33·3	31·7	23·6	29·4	1·33

Table 2. *Effect of photoperiod on sprout development in two potato varieties in controlled environment chambers (Expt 2)*

	Number of nodes			Sprout length (mm)		
Photoperiod (h)...	8	16	24	8	16	24
Variety						
Estima	27·0	23·0	24·2	76	52	39
Maris Piper	24·6	29·4	28·5	123	51	42
S.E.		0·92			6·5	

Sprouts of Estima produced flowers readily visible to the naked eye when transferred from 4 to 13 °C with either a 16 or 24 h photoperiod in Expt 2 but,

with an 8 h photoperiod, flowers were only observed on one sprout out of five at the two final samples, by which time they were etiolated and shrivelled. More nodes were initiated in Estima with an 8 h photoperiod than with 16 or 24 h photoperiods though the reverse was true in Maris Piper (Table 2). In both varieties decreasing photoperiod increased sprout length. Flowers were not initiated at any photoperiod in Maris Piper but, in this experiment, sprouts had more nodes at 13 °C after cold storage than when kept at a constant 13 °C in Expt 1. The sprouts were chronologically older at the time of transfer from cold storage to 13 °C than sprouts at the start of Expt 1 and had initiated nodes during cold storage so that when transferred the mean number of nodes on sprouts was 16·8 in Estima and 17·2 in Maris Piper and sprouts did not become dehydrated (as in Expt 1) by the time flowers were observed in Estima. Therefore, the difference between results from Expts 1 and 2 may be largely the result of more prolonged growth of sprouts at 13 °C before growth became inhibited by dehydration.

In Expt 3, all treatments, including constant storage at 13 °C, initiated flowers on the sprouts. Flowers were initiated after 25 weeks at constant 13 °C whereas with cold treatments, some sprouts initiated flowers after a total of only 15 weeks at 13 °C but there was considerable variation between sprouts, particularly where sprout development was interrupted by 15 weeks at 2 °C. The mean number of nodes to the first flower was fewer for sprouts held at 2 °C for 5 weeks ($23\cdot0 \pm 0\cdot47$) than 10 weeks (25·4) but there was no effect of the number of nodes initiated before cold treatment.

In Expt 4, plants grown in an 8 h photoperiod had initiated tubers when sampled 18 days after emergence (d.a.e.) but no tubers were found on plants in the 18 h photoperiod. Both treatments had initiated tubers by 25 d.a.e. At the final sampling, neither treatment had initiated flowers although stems had up to 46 leaf primordia.

Experiment 5

At the first two planting dates, emergence of both varieties was poor, particularly for Maris Piper, due to skin spot (*Polyscytalum pustulans*) infection of young sprouts, and because too few plants emerged, data from these two plantings for emergence, flower and tuber initiation were excluded from the analysis, although dissections of plants were done to determine the number of nodes. Buds at the first two planting dates were dormant (mean sprout length < 3 mm) with c. eight nodes in both varieties, but from the third planting date, the seed tubers of both varieties had broken dormancy (see Experimental details) and the sprout length and number of nodes increased throughout cold storage although kept at 4 °C (apart from a period of a few days when the cold store

Table 3. *Effect of planting date on the number of nodes at emergence, to the first flower and below ground and on the time of emergence, flowering and potato tuber initiation in Expt 5*

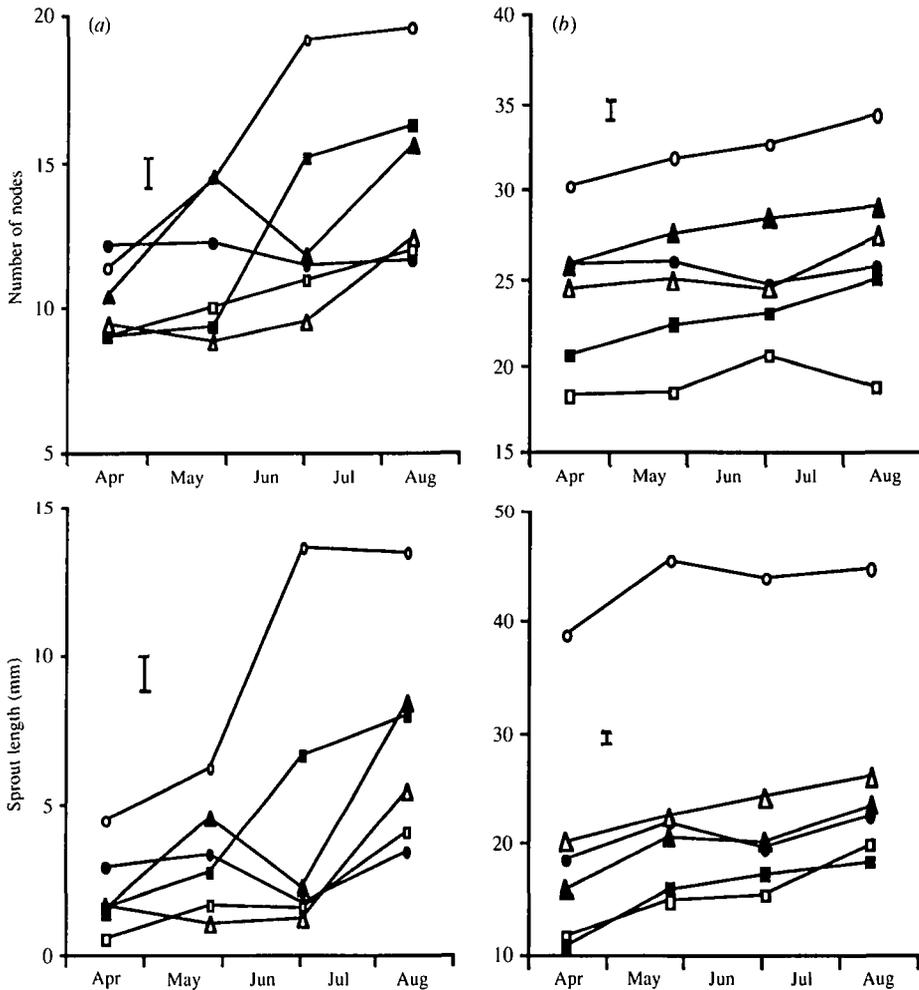| Planting Date	Number of nodes				Number of days					Day degrees > 0 °C Soil		Mean temperature (°C)			Day length* at emergence (h)
	At Emergence	To first flower	Below ground	Above ground	Planting to emergence	Planting to tuber initiation	Emergence to flower initiation	Emergence to tuber initiation	Duration of flower development	Planting to tuber initiation	Emergence to tuber initiation	Air Emergence to flower initiation	Soil Planting to tuber initiation	Soil Emergence to tuber initiation	
Estima															
13 Mar	20·5	22·6	7·6	14·9	—	—	—	—	—	—	—	—	—	—	—
13 Apr	21·1	21·7	7·4	14·3	—	—	—	—	—	—	—	—	—	—	—
14 May	19·7	22·4	7·4	15·0	27·0	51·0	3·0	24·0	16·0	747	390	12·1	14·6	16·1	17·0
14 Jun	20·6	23·2	7·0	16·2	12·0	32·0	3·0	20·0	15·0	585	411	20·0	18·3	20·6	17·1
29 Jun	21·0	23·2	7·0	15·0	10·0	29·3	3·7	19·3	12·3	550	337	18·8	18·8	17·5	16·9
13 Jul	21·8	22·1	9·1	13·0	9·7	30·7	3·3	21·0	12·0	506	341	13·9	16·5	16·2	16·3
3 Aug	20·0	21·4	9·5	11·9	11·7	32·3	0·3	20·7	9·0	539	351	19·2	16·7	17·0	15·2
31 Aug	20·8	21·8	10·1	11·7	12·0	17·7	2·3	5·7	6·7	269	84	16·7	15·3	15·0	13·3
Maris Piper															
13 Mar	22·0	27·0	8·2	18·1	—	—	—	—	—	—	—	—	—	—	—
13 Apr	21·6	25·0	7·9	17·1	—	—	—	—	—	—	—	—	—	—	—
14 May	21·6	27·2	8·2	19·1	13·7	46·0	16·3	32·3	22·0	642	478	12·7	14·0	14·8	16·5
14 Jun	23·4	29·6	9·1	20·4	12·0	31·0	10·3	19·0	13·7	567	392	18·4	18·3	20·7	17·1
29 Jun	21·8	33·3	10·3	23·0	10·0	33·0	9·0	23·0	23·0	613	400	17·6	18·6	17·4	16·9
13 Jul	22·8	33·1	9·6	23·5	12·3	35·0	20·7	22·7	7·0	582	362	14·9	16·6	16·0	16·3
3 Aug	22·8	35·4	10·0	25·4	11·0	35·7	23·0	24·7	9·3	590	413	16·9	16·5	16·7	15·2
31 Aug	23·2	33·5	11·7	21·8	13·0	29·3	15·3	16·3	13·7	424	223	13·6	14·5	13·7	13·2
S.E.	0·48	0·61	0·67	0·87	0·80	1·84	2·09	1·95	1·73	—	—	—	—	—	—

* Including civil twilight.

Fig. 4. The growth of sprouts during cold storage in Expt 6. (a) Young seed; (b) old seed. ○, Home Guard; ●, Vanessa; □, Estima; ■, Maris Piper; △, Désirée; ▲, Cara; I, s.e.

temperature rose to 7 °C). The sprouts would conventionally be classified as physiologically young but they were considerably more developed at the final planting, with about 19 nodes in Estima and 21 nodes in Maris Piper, than at earlier plantings. Thus, the sprouts had been growing slowly during cold storage in both varieties, at least 10 more leaf primordia were present at the final planting date than at the first planting date, and the sprouts were also chronologically some 5 months older.

Plants emerged within 10–13 days of planting in both varieties for all but the first three plantings (Table 3) The number of nodes at emergence was similar at all planting dates but slightly higher for Maris Piper than Estima (Table 3). Floral initiation occurred within 4 days after emergence at all planting dates in Estima but, in Maris Piper, there was more variation, with initiation of flowers occurring from

9–23 days after emergence but with no apparent trend with planting date (Table 3). Differences in the time from emergence to floral initiation between planting dates did not result from differences in air temperature.

Tuber initiation occurred about 3–4 weeks after emergence in both varieties at most plantings but took longer at the May planting and was more rapid at the latest planting, especially in Estima (Table 3). The longer interval from emergence to tuber initiation from the May planting was associated with cool soil temperatures. The thermal time (accumulated day degrees > 0 °C) from planting to tuber initiation (Table 3) was similar to values reported by Jeffries & MacKerron (1987).

The number of nodes to the first flower was not affected by planting date in Estima but in Maris Piper increased with delay in planting, with a range of

Table 4. *The effect of physiological age and planting date on the number of days from planting to emergence, nodes at emergence, nodes below-ground and nodes to the first flower in six potato varieties in Expt 6*

| | | Physiological age | | | | | | | | |
| | | Young | | | | Old | | | | |
Planting Date...		14 Apr	24 May	29 Jun	9 Aug	14 Apr	24 May	29 Jun	9 Aug	S.E.
Days from	Home Guard	30·3	19·7	12·3	13·3	21·0	16·0	8·3	10·3	
planting to	Vanessa	32·0	20·0	14·3	15·0	22·3	16·7	12·0	10·7	
emergence	Estima	39·0	22·3	18·0	14·7	24·0	18·7	11·7	9·0	
	Maris Piper	30·3	20·0	12·7	12·0	24·7	16·7	12·7	10·0	
	Désirée	34·7	22·7	21·0	14·0	20·7	16·3	11·7	10·0	
	Cara	31·7	21·0	17·0	10·7	22·3	16·3	12·0	10·7	0·77
Number of	Home Guard	21·5	22·5	21·2	23·3	33·3	33·7	37·3	37·8	
nodes at	Vanessa	20·8	—	20·2	22·5	30·3	30·5	31·3	30·0	
emergence	Estima	20·5	20·2	21·2	21·2	21·5	22·1	24·8	22·7	
	Maris Piper	20·8	21·7	22·8	27·5	26·7	28·8	27·0	30·7	
	Désirée	22·3	23·0	21·3	21·3	29·8	29·5	29·2	29·3	
	Cara	22·2	23·7	17·2	22·0	29·5	31·0	31·0	32·8	0·93
Number of	Home Guard	8·7	8·7	8·5	11·0	15·7	19·8	19·5	23·2	
below-ground	Vanessa	10·5	6·5	8·0	8·3	14·5	16·0	14·7	17·2	
nodes	Estima	5·8	7·7	7·5	7·5	9·5	9·2	11·7	10·5	
	Maris Piper	8·8	8·7	10·2	11·3	12·7	13·7	16·0	16·3	
	Désirée	8·3	7·5	7·3	8·0	14·2	13·0	11·7	17·5	
	Cara	7·8	7·7	8·2	8·3	12·2	14·3	15·8	18·0	0·76
Number of	Home Guard	25·7	27·8	28·0	29·7	35·8	37·5	39·7	39·3	
nodes to the	Vanessa	28·0	25·7	23·7	24·5	30·2	32·5	31·3	35·2	
first flower	Estima	21·5	23·7	21·2	22·5	24·3	24·8	27·2	26·8	
	Maris Piper	26·2	28·0	30·5	30·5	31·3	31·7	37·3	36·8	
	Désirée	26·0	22·8	23·7	24·5	30·7	29·7	27·2	35·3	
	Cara	26·5	24·3	24·5	25·8	30·0	32·3	34·7	35·8	0·77

c. 10 nodes (Table 3). There was a tendency for the number of nodes below ground to increase with delay in planting date in both varieties. This was associated with a slight decrease in the number of aerial nodes to the flower with delay in planting in Estima but an increase in Maris Piper (Table 3).

The development of the flower was more rapid in Estima with delay in planting but in Maris Piper was rather variable (Table 3). Floral initiation always preceded tuber initiation but the interval between the two stages was shorter in Maris Piper than in Estima especially from July and August plantings and at the final planting date floral and tuber initiation occurred within days in both varieties. At the final planting, some plants of Maris Piper which had tuberized had not initiated flowers.

The number of nodes between the 1st and 2nd flowers was not affected by planting date in either variety but was higher in Maris Piper (8·9) than in Estima (6·3, S.E. 0·18) and ranged from 6–13 in Maris Piper and 3–11 in Estima. The number of nodes between the 2nd and 3rd flowers could not be recorded on an adequate number of plants for statistical analysis as few stems produced tertiary axis flowers,

but the numbers of nodes was comparable to the number between 1st and 2nd flowers with a mean of 7·7 in Maris Piper and 5·2 in Estima.

Experiment 6

Comparisons were made between different physiological ages of seed at each planting date so that the effects of seed age and planting date, which were confounded in Expt 5 due to the gradual ageing of seed in cold store, could be separated. Seed was held at 2 °C rather than 4 °C as in Expt 5 to inhibit sprout growth but, even at this temperature, the number of nodes on sprouts at planting increased with delay in planting for both physiologically young and old seed of most varieties (Fig. 4). Dissections of young seed showed that many young buds were very dry and brittle so that in some cases, particularly with the varieties Vanessa and Désirée, sprouts did not survive and the stems which emerged in the field probably arose from tertiary-axis buds with fewer nodes than suggested by assessments at planting. In these varieties, the number of nodes at planting did not increase for later plantings.

The number of days from planting to emergence was generally less for physiologically old than young seed and decreased with delay in planting with both ages of seed (Table 4). Although old seed tubers were pushed deeper into the ridge at planting than young seed tubers, the distance from the apex of the longest sprout to the soil surface was on average 10 mm less for old than young seed due to the considerable differences in sprout length. The mean soil temperature between planting and emergence was higher with successive planting dates (for successive planting dates 11·7, 14·8, 15·6 and 17·3 °C). At emergence the total number of nodes on the longest sprout tended to increase with delay in planting in some varieties, but the difference was small in most cases (Table 4). Flowers were present in a few sprouts of Estima, Vanessa and Désirée at emergence and, by two weeks after emergence, all treatments had initiated flowers. Small tubers were present on some plants (< 50 %) of Désirée, Vanessa and Home Guard 2 weeks after emergence and, by 3 weeks after emergence, all treatments had initiated tubers except for Cara and old seed of Maris Piper at the first planting date.

The number of nodes to the first flower was increased by physiological age and delay in planting (Table 4) except for young seed of Vanessa, Désirée and Cara which had more nodes to the first flower at the earliest planting than later plantings. The number of nodes to the flower was lower in Estima than in any other variety at both physiological ages and in all other varieties, physiologically old seed at the final planting date had at least 35 nodes. The number of below-ground nodes also tended to increase with physiological age and delay in planting (Table 4) so that much of the difference in the number of nodes to the first flower was accounted for by differences in the number of below-ground nodes. Although the number of aerial leaves differed between varieties, it was relatively stable in each variety. The number of aerial nodes to the first flower was greater in Maris Piper (19·3) than Estima (15·3) as in Expt 5. The number of nodes between the 1st and 2nd flower was not affected by planting date or physiological age, but was lower in the early varieties Home Guard, Estima and Vanessa than the main crops Maris Piper, Désirée and Cara, although the difference was only about 1 node (Table 5).

Experiment 7

In Expt 6, all old seed was sprouted before the first planting date and subsequently held cold so that at each planting date, seed had been kept cold for progressively longer, whereas, in this experiment, seed was held cold for different periods after sprouting but planted at the same time. By comparing the different times at which seed tubers were sprouted at the same planting date, possible effects of the time of sprouting influencing the results of Expt 6 could be examined.

Table 5. *Number of nodes between the 1st and 2nd flower in six potato varieties in Expt 6 (mean of first two planting dates)*

Variety						
Home Guard	Vanessa	Estima	Maris Piper	Désirée	Cara	S.E.
6·6	6·4	6·5	7·9	7·0	7·4	0·19

Table 6. *Number of nodes to the first flower for sprouts aged at different times in Expt 7*

	Variety				
Time of sprouting	Home Guard	Estima	Maris Piper	Désirée	Cara
8 Jan	32·3	22·7	30·3	26·7	29·7
22 Feb	31·2	23·5	29·5	27·0	29·0
7 Apr	32·2	23·5	31·0	27·5	29·3
S.E.			0·60		

The number of nodes to the first flower was not affected by the time at which seed tubers were sprouted in any variety and for all varieties the number of nodes was intermediate between the extreme physiological ages of the treatments in Expt 2 (Table 6). As in Expt 1, all plants had initiated flowers by 2 weeks after emergence and all varieties except Cara had initiated tubers by 3 weeks after emergence.

Experiments 8 and 9

The mean values of incident radiation (total) for the duration of the experiments were 10·2 (Expt 8) and 13·8 (Expt 9) MJ/m² per day for the 8 h photoperiod and 12·8 (Expt 8) and 17·9 MJ/m² per day (Expt 9) for ambient conditions. The mean soil temperature 19 °C (Expt 8) and 22 °C (Expt 9) was similar for both photoperiods, although the mean air temperature was warmer in the 8 h treatment (18 °C) than ambient (15 °C) in Expt 8 and 19 °C for both photoperiods in Expt 9. In Expt 8, floral initiation occurred at the same time in both 8 h and ambient photoperiods in Estima (7 d.a.e.) and Record (10 d.a.e.) but, in Maris Piper, the 8 h treatment had not initiated flowers by the final sample at 36 d.a.e., whereas at the ambient photoperiod flowers were present when sampled 15 d.a.e. In Expt 9, floral initiation at both photoperiods occurred 5 d.a.e. in Estima and 15 d.a.e. in Maris Piper. The number of nodes to the first flower was similar for both photoperiods (Expt 8, Estima 23·0, Record 26·5; Expt 9, Estima 25·4, Maris Piper 31·3) and was 32·8 for Maris Piper in the ambient

Table 7. *The number of nodes to the first flower in Expt 10*

Planting date...	Estima		Désirée		Maris Piper	
	10 Jan	23 Feb	10 Jan	23 Feb	10 Jan	23 Feb
	20·8	22·0	22·7	24·3	25·2	26·0
S.E.	1·40	1·49	1·57	1·16	0·63	0·94

photoperiod in Expt 8. In Expt 8, tubers were present at 18 d.a.e. in Maris Piper and Record at both photoperiods but, in Estima, tubers were formed earlier with the 8 h photoperiod (12 d.a.e.) than at ambient conditions (16 d.a.e.). In Expt 9, tubers were present 10 d.a.e. in Maris Piper and 15 d.a.e. in Estima with the 8 h photoperiod and 17 d.a.e. in both varieties with the ambient photoperiod.

Experiments 10 and 11

At the first planting of Expt 10, 50 % emergence occurred on about 23 February for all varieties and all varieties had initiated tubers at 18 d.a.e. The daylength at emergence of the first planting date, including civil twilight, was 11·2 h and both Estima and Désirée had already initiated flowers. Flowers were formed in all varieties at both planting dates after the initiation of similar numbers of nodes (Table 7) to those found for young seed in other experiments. In Expt 11, all varieties emerged between 30 and 36 days after planting when the daylength was 11·6–11·8 h. Tuber initiation was observed 10 d.a.e. in Désirée and Record, 13 d.a.e. in Estima and 14 d.a.e. in Maris Piper and the mean number of nodes to the first flower was similar to previously recorded values in all varieties (Estima 22·6, Maris Piper 25·9, Désirée 24·2 and Record 23·7).

DISCUSSION

Although the initiation of leaf primordia in sprouts may be arrested after some time without the initiation of flowers, as found by Kirk *et al.* (1985), some varieties, like Home Guard and Arran Comet, continue to initiate primordia over very long periods of time and initiation of floral primordia and development of flowers in sprouts can occur. Conditions during sprouting may influence the course of development. Initiation of primordia was arrested in sprouts of Estima after 24 nodes in Expt 1 but in Expts 2–4, flowers were initiated. Similarly, Maris Piper initiated only 24 nodes in Expt 1 at a constant 13 °C but in Expt 2, where sprout development was interrupted by a period of cold storage, up to 29 nodes were initiated. Inhibition of growth may result

from dehydration during sprouting at low humidity and this would be more marked with small seed which had less stored water but could be reduced by sprouting at lower temperatures or increased humidity.

Large differences in the number of nodes to the first flower were found between varieties in these experiments, ranging from 20 to 40. Thus the results of Taylor (1953), showing similar numbers of nodes for a range of varieties, which led to the conclusion that there are 26 nodes to the flower in the potato, were misleading. The increase in number of nodes to the first flower with increase in physiological age indicates that any statement of the number of nodes to the inflorescence for a variety (e.g. 31·3 in Maris Piper by Kirk *et al.* 1985) is only true for the specific physiological condition of the sprout and is not necessarily constant. A near constant number of leaves to the first flower is characteristic of plants induced to flower rapidly (Holdsworth 1956) and these experiments indicate that the lowest number of nodes may be greater in varieties like Maris Piper (lowest number recorded 26) than Estima (20). Holdsworth suggested, the 'minimum number' of nodes may be reduced by starvation or other factors which retard vegetative growth, as found by Bald and Hutton (1950) who reported that the number of aerial nodes was lower in potato plants infected by leaf-roll virus than in healthy plants.

The development pattern of some varieties may be less readily manipulated by environmental conditions than others. In particular, the variety Estima showed much less variation in the number of nodes to the first flower than other varieties in all experiments. This may be true for other similar varieties as the data of Fischnich & Krug (1963) indicate that, in the variety Erstling, large differences in sprout length induced by storage at different temperatures increased the number of nodes below ground but had little effect on the total number of nodes to the first flower. The absence of any effect of time of sprouting on number of nodes to the inflorescence found in Expt 7 shows that, for a given variety, it is the number of nodes on the sprout at planting which is a major determinant of the number of nodes to the first flower and not the interval from the end of sprouting to time of planting. More nodes at planting resulted in more nodes remaining below ground but there was little variation in the number of above ground leaves to the flower. The number of leaves to the flower was fairly constant within a variety, which suggests that the number of leaves may have a role in the control of flowering, but the ability of some varieties to form flowers on sprouts, as in Expts 1–3, or when grown in darkness (Jones & Borthwick 1939; Clarke & Lombard 1942), indicates that neither normal growth nor light is an absolute requirement for flowering. Similarly, the difference between the number of nodes to the flower between planting dates in Maris Piper in Expt 5 and

the complete absence of floral primordia in this variety grown in short days indicates that the number of leaves is not fixed. More than 20 below-ground nodes were recorded for old seed of Home Guard, double that found in young seed, and thus old seed provided many more potential sites for stolon and tuber initiation on each stem.

Increase in sprout length and number of nodes during cold storage (< 4 °C) suggests that the use of day-degrees above a base temperature of 4 °C to assess physiological age is not accurate for tubers held at low temperatures for several months after dormancy break. O'Brien et al. (1983) found that use of day-degrees above a base of 4 °C as a measure of physiological age minimized variation in describing effects of physiological age on plant growth, but growth did occur in sprouts held for long periods at 4 °C in the experiments of O'Brien et al. and a lower base temperature would have been more appropriate. It is clear from this study, and the data of other workers (Krijthe 1962; Raouf 1979), that growth and development of sprouts may occur below 4 °C and more rapidly in some varieties than others. Kirk et al. (1985) calculated a base temperature for sprout growth in Maris Piper of 3·6 °C but the lowest temperature actually used was 10 °C. It is likely that the base temperature varies between varieties and is lower than 2 °C for some. The effect of using a base temperature for a particular variety which is too high is that the heat unit summation required increases as the mean temperature during the developmental period increases (Arnold 1959), the reverse is true if the base temperature used is too low. If the number of nodes is directly proportional to 'physiological age', measurement of day-degrees above a base temperature may not be entirely satisfactory because of differences between sprout growth of varieties and the reduction in growth rate during long periods of sprouting. In addition, time at which sprouting commences after a period at cold temperatures may affect the subsequent rate of growth (Wurr 1979) and influence number of nodes for a given number of accumulated day-degrees. There was some evidence from Expt 3 that interruption of sprout development by a period of cold storage may result in more rapid floral initiation than in sprouts kept at a constant 13 °C. Data relating effects of numbers of nodes at planting rather than just physiological age would be useful in order to assess whether the two are directly equivalent.

The effect of light intensity and quality on flowering appears to be more important than photoperiod, as suggested by Driver & Hawkes (1943), so that the low light intensity of controlled environment experiments may delay or completely inhibit the initiation of flowers and result in the initiation of more nodes (Expts 2, 4). In the field experiments, flowers were initiated within 2 weeks of emergence for most treatments; however in Expt 5, flowers were not

initiated until about 3 weeks after emergence in Maris Piper at some planting dates and, in this variety, the floral stage 2 weeks after emergence in Expt 6 was lower than in other varieties. Induction of flowers in some varieties such as Estima is more readily achieved than in others such as Maris Piper, where floral initiation did not occur in artificial illumination or an 8 h photoperiod with natural light in Expt 8; but even in Estima, normal flower development was prevented at an 8 h photoperiod. Flower initiation at this extreme photoperiod may be inhibited in Maris Piper due to the low total of incident radiation, because in Expt 9, where the mean incident radiation from the 8 h photoperiod was as high as the ambient photoperiod of Expt 8, flowers were initiated in Maris Piper; however Turner & Ewing (1988) found that extending a 12 h photoperiod with 4 h of dim light promoted flower production by reducing bud abortion in a range of clones, which suggests that there is a direct effect of photoperiod on floral development. The greater variation in aerial leaves to the flower in Maris Piper is associated with a requirement for high light intensity, so that when light levels are low, more leaves are initiated before flowering.

The interval from emergence to tuber initiation was usually 2–3 weeks in all experiments, irrespective of physiological age, but was always longer in Cara and was considerably shorter in Estima at the very late planting (31 August) of Expt 5. The very rapid initiation of tubers at this late planting is unlikely to have resulted from the shorter photoperiod, as the effect of photoperiod in Expts 8–11 were small, but may have been influenced by the extreme chronological age of the sprouts. For most UK potato crops, the photoperiod at emergence is unlikely to be less than 15 h and any effects of photoperiod are probably negligible. However, the use of varieties throughout the whole of Europe, including the Mediterranean area, exposes them to a much wider range of daylengths. Demagante and Van der Zaag (1988) found that tuberization in Désirée and other varieties was only a few days earlier with short daylengths (11·5–12 h) in the Philippines than when the daylength was extended to 16 h with artificial light. Results from Expts 8 and 9, in which the photoperiod was artificially shortened to 8 h, and Expts 10 and 11, grown in Spain when the daylength at emergence was less than 12 h, indicated that tuber initiation may occur at the same time or, at most, a week earlier in very short daylengths compared with daylengths up to 17 h in the UK. These observations suggest that the photoperiodic sensitivity of many varieties is of much less importance than has perhaps been assumed. Whether such photoperiodic effects extend to number of tubers is still unclear.

Time from planting and emergence to tuber initiation decreased with initial delay in planting into warmer temperatures in Expt 5 in contrast to the

contention that tuber initiation is advanced by low temperatures (e.g. Toosey 1964). Although the time from planting to tuber initiation can be quite variable, emergence to tuber initiation is less variable, which indicates that it is the post emergence period which is important in stimulating tuber initiation. The use of thermal time after the end of dormancy to predict time of tuber initiation, as suggested by Jeffries & MacKerron (1987), cannot be accurate for well-sprouted seed (which could exceed the proposed thermal time requirement before planting) and prediction of tuber initiation as occurring around 3 weeks after emergence is probably more useful in most commercial crops for applications such as irrigating for common scab control (Lapwood & Wellings 1970). The later initiation of tubers in Cara compared with the other varieties occurred despite similar floral development to other varieties 2 weeks after emergence, thus initiation seems to be delayed in Cara by a longer interval from flowering to tuber initiation rather than by later initiation of flowers.

The large variation in nodes to the flower with physiological age may be of limited importance in determining the pattern of leaf growth because the number of above-ground leaves to the flower is relatively invariant. Nevertheless there may be effects on individual leaf morphology due to acropetal variation (Humphries & French 1963; Scaramella-Petri 1963). Extreme age in varieties like Home Guard and Arran Comet can result in very large increases in the number of nodes at planting and to the flower compared with young seed, but other varieties do not readily initiate as many nodes in store and some (e.g. Estima) may flower before planting. Any factors which affect the number of above ground leaves below the first flower would be most important in determinate varieties like Estima, as these varieties are largely unable to increase leaf area by further growth of secondary axes and would only be able to compensate for reduced numbers of leaves by an increase in leaf size. Such varieties are heavily dependent on the survival and functioning of their smaller number of leaves over a considerable period if substantial yields are to be achieved. This development involves a quite different leaf growth pattern than such maincrop varieties as Maris Piper and Cara. A much reduced partitioning of assimilates into leaf growth is involved and Firman (1987) has shown that leaves in Estima may live for 90 days and Firman & Allen (1988) showed that such leaves retain much of their photosynthetic capacity over this period. Consequently Estima can produce very high yields but any damage to its leaf development can restrict ground cover permanently and lead to disappointing yields.

The results of these experiments do not support the view that tuber initiation *per se* has an overriding influence on subsequent leaf growth, rather that tuber initiation is part of a sequence which is a fixed period of time from emergence for each variety. This sequence is greatly influenced in some varieties through effects on number of underground nodes but less so in other varieties. Further study is necessary to establish how the variation in underground nodes, which provide sites for stolon and tuber formation, is related to the determination of the number of tubers which are formed and retained.

In order for a developmental key for the potato to be useful, it is necessary that there is a rigid sequence of development events. Under normal growing conditions in the UK, this is satisfied by flower initiation preceding tuber initiation but this study shows that a satisfactory key cannot be readily established because the number of nodes to flower varies and the interval between flower initiation and tuber initiation is also variable in some varieties. Keys describing the growth and development of cereals (e.g. Zadoks *et al.* 1974) are, however, extensively used although the number of leaves to the flower, as in the potato, may vary substantially (Jones & Allen 1986), therefore use of developmental markers such as flowering and the initiation of leaves may be more beneficial for understanding and monitoring the growth of potato crops than consideration of growth alone.

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