

REVIEW

A review of some studies into tuber initiation in potato (*Solanum tuberosum*) crops

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

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

INTRODUCTION

Despite the importance of potato tubers as a source of food and a means of propagation, the initiation, growth and development of tubers and the factors affecting these processes are not well understood. There are many reported studies of the effects of various factors on the initiation of tubers but, for a number of reasons, few have sought to understand the initiation of tubers under field conditions. Most reports are concerned with experiments carried out in growth-rooms, which often used very short stem sections as planting material and in which environmental conditions, especially light intensity, differed greatly from those normally prevailing during the period of initiation in the field. In almost all field experiments, the timing of initiation was not defined or properly assessed; number of tubers was recorded infrequently and maximum number of tubers was rarely, if ever, established. Despite these deficiencies, the initiation of tubers is still widely regarded as a key developmental stage in the crop's life, having profound implications for subsequent growth and development (Ewing 1990; Ewing & Struik 1992). This view was first expressed 30 years ago (Ivins & Bremner 1965; Bremner & Radley 1966) and its general acceptance has greatly influenced studies of the growth and development of the crop. During the intervening years, the study of tuber initiation has been an important aspect of research programmes at the University College of Wales (UCW) Field Station, Tenby, Pembrokeshire (1972–84) and Cambridge University Farm (CUF), Cambridge (1982–95), which have now produced sufficient data for a re-evaluation of the significance of tuber initiation in field-grown potato crops.

A reappraisal of available information is essential for effective future research and improved agronomic practice and this review is mainly concerned with the timing of tuber initiation in crops of cultivated varieties of *Solanum tuberosum* subsp. *tuberosum* L.,

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

the factors affecting the process and the influence of tuber initiation on subsequent plant growth and development. The main focus is on initiation of tubers in crops grown in N W European conditions and uses the methods and definitions derived from results of experiments carried out at UCW and CUF. Such field experiments were carried out using common methods. Treatment combinations were normally arranged in the field in random block designs but, in some experiments, split-plot designs were used to group dates of planting, mulching or shading treatments in main plots. In most experiments, there were three complete replicates, but four replicates were used if there were fewer than six treatment combinations and, in some experiments with 10 or more treatment combinations, there were two replicates. Seed was tightly graded, certified seed either sprouted in well lit trays or held unsprouted in cold stores (< 4 °C). Seed tubers were planted by hand with all fertilizer applied (at rates comparable to those used commercially) at planting. The date of 50% emergence was established by counting the number of plants emerged in each plot every 2–3 days. Samples were hand dug and, to avoid edge effects, harvested plants were guarded by at least one plant within the row and by one guard row. To establish the date of onset and cessation of tuber initiation, samples of four plants per plot were dug every 1–3 days (4–7 days in some experiments) from c. 2 weeks after emergence, until the number of tubers stopped increasing rapidly.

THE INITIATION OF TUBERS

Timing of tuber initiation – measurement and definitions

Tubers are normally initiated on stolons, which are underground branches of stems, initially recognizable as swellings just behind the stolon tip. Under certain conditions, sessile tubers may form either above or below the soil surface; these are the norm on stem cuttings (Ewing & Struik 1992). Tubers may also form on sprouts or directly on unplanted mother-tubers after prolonged storage even at low temperatures

(2–4 °C), especially in darkness or on plants that fail to emerge following planting (Madec 1956; van Schreven 1956). However, the normal sequence in field conditions is that tubers are induced and initiated after the formation of functional leaves (and possibly roots). Initiation of tubers usually commences some time after plant emergence and is thought to be complete within 2–6 weeks of that event (Smith 1931; Krijthe 1955; Moorby & Milthorpe 1975; Sale 1976). The induction of plants to tuberize occurs before initiation and this process may be closely linked to that controlling the initiation of floral organs (Chailakhyan *et al.* 1981; Steward *et al.* 1981; Martin *et al.* 1982; Firman *et al.* 1991). Induction of tuberization can be defined as a physiological change in the plant which results in the characteristic swelling of stolons. The nature of this change is not fully understood but induction clearly precedes the physical changes which are observed at initiation. After the completion of initiation, some tubers may be resorbed. Those remaining are usually referred to as being 'set' or 'retained'. In some conditions, e.g. drought followed by wet soil, further initiation of tubers may occur long after the main phase of initiation and the apical bud of tubers (previously of the stolon) may exhibit substantial growth late in the season as, for example, in some forms of second growth of tubers which may be regarded as an extension of the process of tuber initiation. This review, however, is only concerned with the normal, main phase of tuber initiation.

In order to establish the timing and significance of initiation, appropriate indicators of the beginning and end of the process are required, together with an appropriate frequency and size of samples but, surprisingly, these are generally absent in the literature. In this review, tuber initiation refers to the visible appearance of tubers rather than induction; a tuber being defined as a swelling of the stolon tip that is twice the diameter of the subtending stolon. Determination of the timing of initiation in crops requires a definition of the beginning and end of initiation and an appropriate frequency and size of sample. Several methods of estimating the date of onset of tuber initiation have been used in published reports but the majority are subject to serious inaccuracies. Estimating the beginning of initiation by back extrapolation of tuber bulking lines to zero, often referred to as 'the apparent date of initiation' was widely used by some earlier workers (e.g. Burt 1965; Bremner & Radley 1966; Slater 1968; Goodwin *et al.* 1969). This is not a satisfactory method for estimating the timing of initiation as the onset of initiation is not closely related to the onset of rapid tuber bulking (Bean & Allen 1978) and bulking rate can be influenced by many factors unconnected with initiation. Number of tubers has been widely used and is potentially a useful measurement of onset of tuber

initiation, but in controlled-environment experiments it may be unsatisfactory. Number of tubers can be a very variable character, and its peak values can be transient (Fig. 1) so that accurate measurement requires large and frequent samples which have rarely been used in field experiments and are not usually possible in controlled-environment experiments. The date of appearance of the first tubers to be initiated has also been widely used in controlled-environment experiments to assess the onset of initiation. This method has its limitations, for it shows considerable inter-plant variation both in growth-rooms and in the field (Bean & Allen 1978; Raouf 1979). In reported field experiments, only Demagante & Vander Zaag (1988*a*) and Jefferies & MacKerron (1987) defined timing of initiation. The former authors defined their measures as, '50% tuberization', which was the period from planting to the day when 50% of the sample of four representative plants had tubers. This method does not discriminate between effects on timing of emergence relative to initiation nor does it establish onset and cessation of initiation. Jefferies & MacKerron (1987) estimated the timing of onset of initiation by back extrapolation of fitted regression lines between number of tubers > 10 mm and time to zero. Their use of number of tubers > 10 mm, which involves growth, would be expected to be affected by factors such as incident radiation, which may not affect the timing of onset of initiation (O'Brien *et al.* 1998). Furthermore, in good growing conditions, a near maximum number of tubers > 10 mm can be produced within 1 week, so that weekly samples as used by Jefferies & MacKerron (1987) allow few data points for fitting regression lines.

In order to provide an appropriate and repeatable method of measuring the timing of initiation, the authors tested several methods over many seasons. In early experiments with relatively infrequent sampling (5–7 days), when the duration of initiation was thought to be long (Ali 1979; Raouf 1979; Raphael 1979), the measure chosen for the onset of initiation was the mean of the dates for all replicates in a treatment on which all plants had tubers on two consecutive dates of sampling. However this method proved largely unsatisfactory, as the duration of initiation was invariably much shorter than expected and initiation was well advanced or complete at the defined date of onset of initiation. Subsequently, in frequently sampled (1–3 days) experiments, the proportion of plants or stems having tubers and the percentage of the maximum number of tubers present were tested for estimation of the timing of initiation in a wide range of treatments. In order to exclude spuriously early or late tuber formation, various percentages of final number of tubers were assessed as the start and end point of initiation and established as the dates when 10 and 80% of the final population was present, respectively. Onset and cessation of

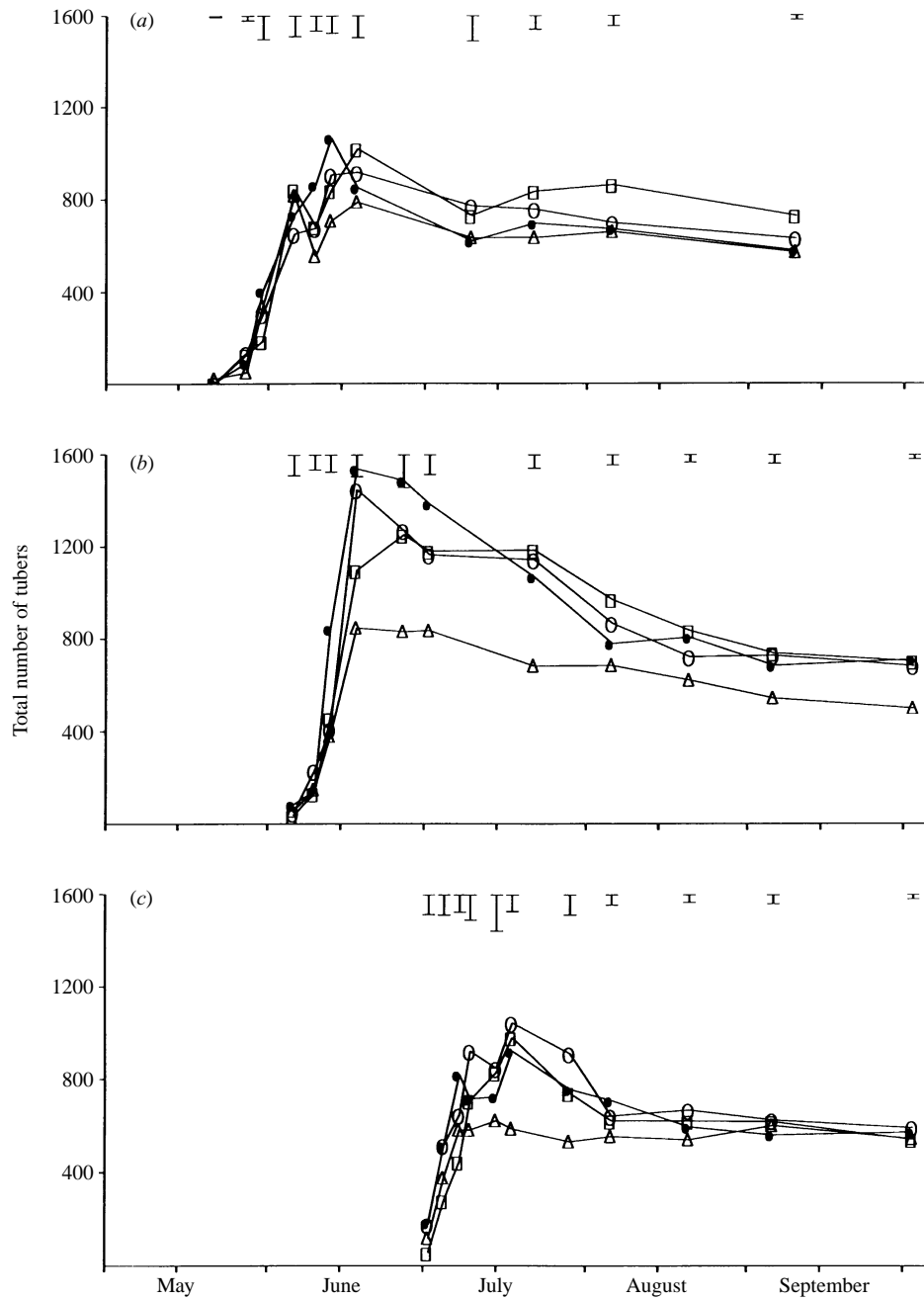


Fig. 1. Effect of shading on total number of tubers for three planting dates of Estima in Expt 2. (a) Planted 3 April, (b) planted 26 April, (c) planted 30 May. No shading (○); 50% shade before (□); during (△) and after (●) tuber initiation. Bars represent S.E. (22 D.F.). Data from Expt 2 of O'Brien *et al.* (1998).

initiation based on the percentage of all tubers present usually occurred somewhat later than estimated from the proportion of plants or stems that had tuberized, especially in physiologically old seed (Table 1). Since

the eventual number and size of tubers in crops is more directly related to the number of tubers initiated than to the number of plants or stems that tuberize, the above percentages of tubers initiated were adopted

Table 1. *Effect of physiological age and date of planting on number of days from 50% plant emergence to onset and cessation of tuber initiation and on the duration of initiation in Maris Piper assessed in different ways (CUF 1992)*

Method of estimation	Physiological age* of seed (number of day-degrees > 4 °C)	Date of planting		Mean	s.e.
		13 April	27 May		
Onset of initiation					
10% of plants tuberized	0	17	17	17.0	
	600	15	15	15.0	
Mean		16	16		1.12
S.E.		1.58		1.12	
10% of mainstems tuberized	0	19	15	17.0	
	600	15	15	15.0	
Mean		17	15		1.22
S.E.		1.73		1.22	
10% of mainstem tubers present	0	21	19	20.0	
	600	17	19	18.0	
Mean		19	19		1.40
S.E.		1.98		1.40	
Cessation of initiation					
80% of plants tuberized	0	23	21	22.0	
	600	22	25	23.5	
Mean		22.5	23.0		1.10
S.E.		1.56		1.10	
80% of mainstems tuberized	0	23	21	22.0	
	600	21	26	23.5	
Mean		22.0	23.5		1.23
S.E.		1.74		1.23	
80% of mainstem tubers present	0	25	23	24.0	
	600	25	34	29.5	
Mean		25.0	28.5		1.42
S.E.		2.01		1.42	
Duration of initiation (days)					
10-80% of plants tuberized	0	6	4	5.0	
	600	7	10	8.5	
Mean		6.5	7.0		1.01
S.E. (D.F. = 12)		1.43		1.01	

* Physiological age measured from the break of dormancy ($\geq 80\%$ of tubers with sprouts ≥ 3 mm).

for estimating the timing of initiation. This provides the basis for consistent recording of the timing of tuber initiation, providing that sampling begins early enough and is sufficiently frequent (every 2-3 days).

The timing of the different stages of plant growth and development prior to the initiation of tubers has, until recently, received little attention and, consequently, their significance and utility has not been generally appreciated. To be meaningful, the onset of tuber initiation should be related to the time of plant emergence rather than to time of planting, as emergence usually precedes initiation and the interval from planting to emergence can be extremely variable (Firman *et al.* 1992). There is little published information on the relationship between the time of

emergence and the time of initiation and in some reports it is not clear whether treatments affected emergence or initiation or both. The results of many experiments carried out by the authors show that, for any cultivar, tuber initiation commences at a similar interval after plant emergence for a wide range of husbandry and environmental conditions (e.g. Tables 1, 2, 5, 8, 9 and O'Brien *et al.* 1998). For photoperiods ranging between *c.* 13 and 17 h, this interval normally varied only from *c.* 14 to 21 days in Maris Piper, Estima, Desirée and Record and, thus, the time of onset of tuber initiation appears to be closely related to the time of plant emergence. The timing of other aspects of plant development, such as initiation of floral organs (Firman *et al.* 1991) and the appearance

Table 2. Timing of emergence and initiation and thermal time (day-degrees) to initiation in Maris Piper in two years at Cambridge University Farm

Year	Date of planting	Physiological age (number of day-degrees > 4 °C)	Accumulated thermal time					Mean air temperature 50% emergence to initiation (°C)	
			Number of days from planting to 50% emergence	Number of days from 50% emergence to initiation	In store (> 4 °C)	Planting to 50% emergence (> 0 °C)	50% emergence to initiation (> 0 °C)		D = B + C
1992	13 April	0	37	21	0	440	341	781	16.2
	27 May	600	25	17	600	285	235	520	13.8
1993	10 March	0	14	19	600	219	308	683	16.2
	3 May	600	42	19	0	355	304	523	16.0
30 June		500	36	21	500	285	203	488	10.8
		500	16	18	0	193	264	457	10.7
		500	13	18	500	148	259	407	14.7
		0	16	18	0	263	307	570	14.4
		500	14	20	500	228	342	569	17.1

of leaves (Firman *et al.* 1995), also seems to be closely related to time of emergence. Thus, plant emergence can be taken as the starting point for the timing of subsequent plant development and used in practice for timing husbandry practices such as irrigation at the time of tuber initiation. Jefferies & MacKerron (1987) suggested that timing of onset of initiation could be defined in terms of thermal time. They reported that the sum of thermal time in store (above a base temperature of 4 °C) and air temperature from planting to initiation (above a base temperature of 0 °C) required for initiation to occur in Maris Piper was *c.* 615 day-degrees. The authors found no such correlation between thermal time and timing of initiation for a wide range of physiological ages and temperatures after planting in this or any other cultivar tested (Table 2). Indeed, old seed of Maris Piper (600 day-degrees > 4 °C) approached the thermal time requirement for initiation suggested by Jefferies & MacKerron (1987) before planting but accumulated a further 400–500 day-degrees in the field before initiation occurred. In experiments at CUF, onset of initiation was advanced by ageing seed of some varieties (e.g. Home Guard and Record) only when planting was followed by a prolonged period (*c.* 2 weeks) of low temperatures (< *c.* 7 °C). Thus, thermal time from dormancy as suggested by Jefferies & MacKerron (1987) cannot be used to predict timing of initiation. Thermal time from planting might be used, but prediction of initiation on the basis of chronological time from emergence appears more accurate and useful in practice. In experiments carried out by the authors, the duration of initiation was normally *c.* 1 week (e.g. Table 1) which is considerably shorter than widely assumed (2–6 weeks, Krijthe 1955; Sale 1976). Initiation was found to be completed much more quickly (2–3 days) in warm bright weather or more slowly (up to 3 weeks) in conditions not conducive to rapid growth.

In controlled-environment experiments, the time of tuber initiation has been found to vary considerably between stems on the same plant and on individual stems (Struik *et al.* 1990; Ewing & Struik 1992). In such environments, it is likely that plant growth rates are low, the period of tuber initiation is, therefore, extended and variation in initiation occurs. In practice, tuber initiation normally occurs quickly in conditions conducive to rapid plant growth and initiation may be complete within a few days (Table 1). Under these conditions following uniform stem emergence, initiation of tubers both within and between stems could be considered to be synchronous. Considerable variation in the timing of initiation of tubers between stems can occur where there is substantial tuberization of secondary stems as well as mainstems, for secondary stems normally emerge and initiate tubers later than mainstems. In most cultivars, only a small proportion (< 10%) of the total number

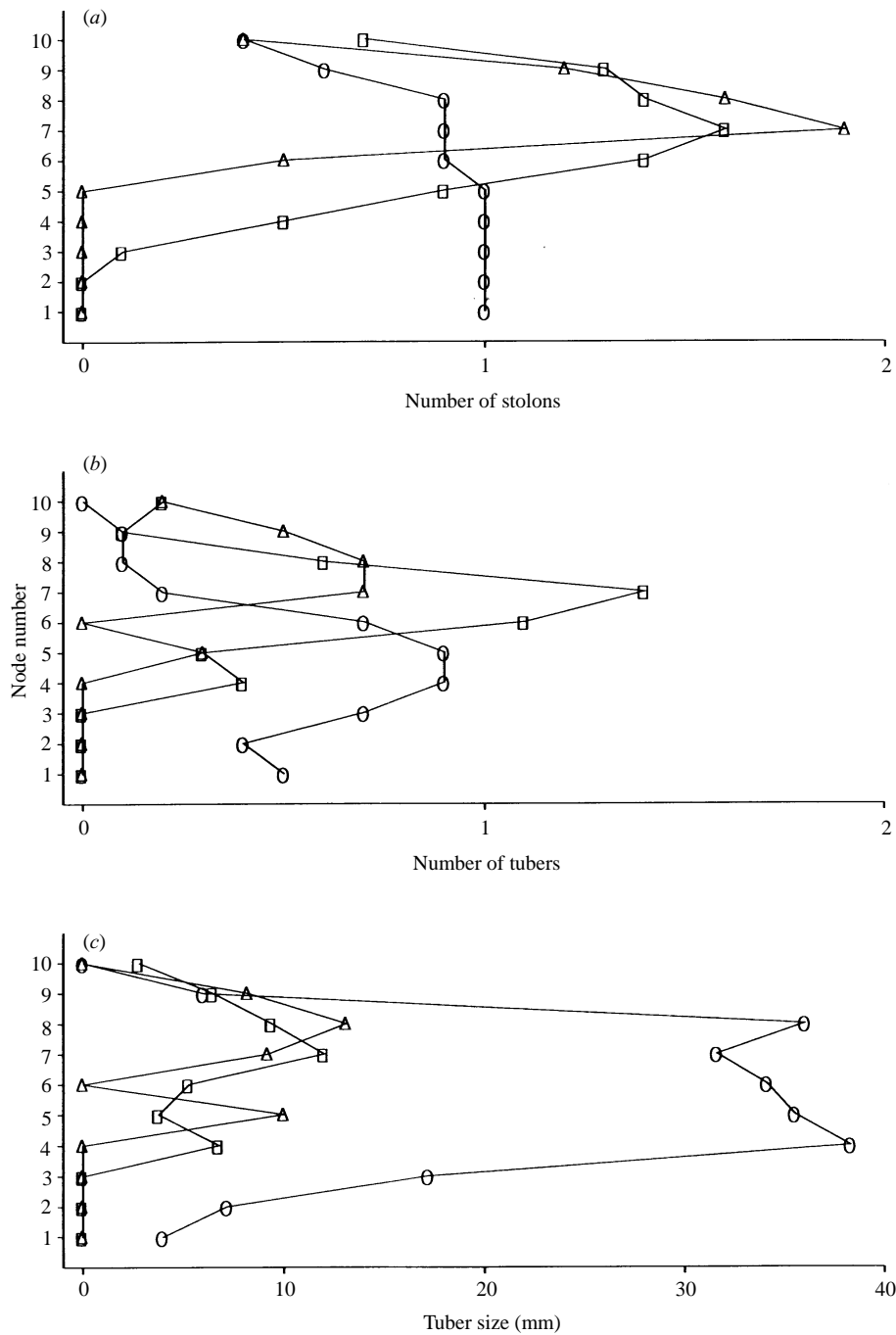


Fig. 2. The distribution of (a) stolons, (b) tubers and (c) tuber size with node position (1 = basal). Primary (○); Lateral (□); Branch (△).

and yield of tubers was borne on secondary stems. Also, the latest formed tubers are those most likely to be resorbed later in growth or to remain small

(Krijthe 1955; Ewing & Struik 1992) and, therefore, make little contribution to the final number and yield of tubers. Thus, in normal conditions of growth in

temperate regions, the production of tubers by secondary stems can be ignored in many cultivars and attention focused on the initiation and growth of tubers on mainstems. The production of secondary stems can, however, be important in affecting the number of tubers and their size distribution as each secondary stem represents the loss of a terminal tuber of a primary stolon.

The pattern of initiation of stolons and tubers along the stem axis

Stolons are normally formed exclusively on underground nodes of field-grown plants and may bear tubers. Surprisingly, the pattern of initiation and growth of stolons and tubers on the stem axis has not been elucidated. Wurr (1977) found that most stolons and tubers and the largest tubers were formed at basal nodes in Desirée, Pentland Crown and Maris Piper, whilst Krijthe (1955) and Cother & Cullis (1985) observed that most stolons and tubers and the largest tubers were generally produced at the third to the fifth node from the base of the stems. The results of experiments carried out by the authors, which used a wide range of cultivars including two of those used by Wurr (1977) support the findings of Krijthe (1955) and Cother & Cullis (1985). Stolons were categorized according to their origin: primary and lateral stolons are those arising from primary and associated axillary buds at subterranean nodes, respectively, whilst stolons originating as branches of primary stolons or secondary stems are referred to as 'branch stolons'. The pattern of distribution of stolons, tubers and tuber size along stem axes was similar in all cultivars studied and is illustrated for young seed of Desirée in Fig. 2. Uppermost nodes produced fewer stolons of all three types than nodes further down the profile and several basal nodes produced few lateral or branch stolons (Fig. 2*a*). The pattern of distribution of tubers along stem axes was similar to that of stolons, but primary stolons at basal nodes frequently did not tuberize (Fig. 2*b*), so that most tubers per node were found in the central region two to three nodes distant from the soil surface and from the base of stems. By far the largest tubers were found on primary stolons, particularly in the central region of stem axes (Fig. 2*c*). Medium-sized tubers were mostly found on primary stolons at nodes distant from the central region and on lateral and branch stolons at upper-central nodes. Small tubers predominated on lateral and branch stolons and were also found on primary stolons at upper and basal nodes. These patterns of initiation and growth of stolons and tubers were consistent between many cultivars, treatments and dates of sampling, but they may be altered, for example, by physiological ageing of seed and by disease, as found by Cother & Cullis (1985) who showed that the probability of uppermost and

Table 3. Mean length (mm) of primary stolons at different node positions in Record (CUF 1992)

Number of days after planting...	Node position (1 = basal node)						
	1	2	3	4	5	6	7
15	2.5	2.8	3.0	3.2	3.7	2.2	—
21	4.2	11.0	18.0	30.3	26.5	18.0	21.3
30	10.7	20.2	23.2	46.0	37.5	52.0	32.2

lowermost nodes producing tubers was greatly increased when stolons in the central regions of the stem were pruned by *Rhizoctonia solani*. At CUF, physiological ageing of seed increased number of underground nodes, variation in the pattern of initiation of stolons and tubers and the number of basal nodes devoid of stolons or tubers. In Wurr's (1977) experiments, several basal nodes may not have had a visible structure and, consequently, may not have been recorded, thereby accounting for the reported pattern of stolon and tuber formation. The results suggest that, in the absence of disease or other causes of disruption, there is a set and distinct pattern of distribution of stolons and tubers and tuber size along stem axes. The mechanism controlling these patterns appears to operate at the level of the node and the position of a node in the hierarchy seems to be a major determinant of number of stolons and tubers and tuber size. This control mechanism operates at a very early stage of development, for patterns of initial growth of stolons along sprout axes are similar to those found for tuber growth (Table 3).

EFFECT OF TUBER INITIATION ON SUBSEQUENT GROWTH AND DEVELOPMENT

There is widespread belief in the literature that tuber initiation is a major factor influencing subsequent plant growth and development which derives mainly from the results of field experiments reported by Ivins (1963), Radley (1963), Ivins & Bremner (1965) and Bremner & Radley (1966) and from results of many growth-room experiments using short stem sections or node cuttings recently reviewed by Ewing (1990) and Ewing & Struik (1992). The general consensus is that initiation of tubers leads to an abrupt preferential diversion of assimilate to the tubers, thereby causing either a reduction in the growth rate or cessation in growth of foliage and roots (Moorby & Milthorpe 1975; Ewing 1990; Ewing & Struik 1992). As a consequence, it is suggested that early initiation of tubers necessarily results in small plants with limited leaf areas and, consequently, low final tuber yields, whilst late initiation leads to large plants with high final tuber yields (Toosey 1964; Ivins & Bremner

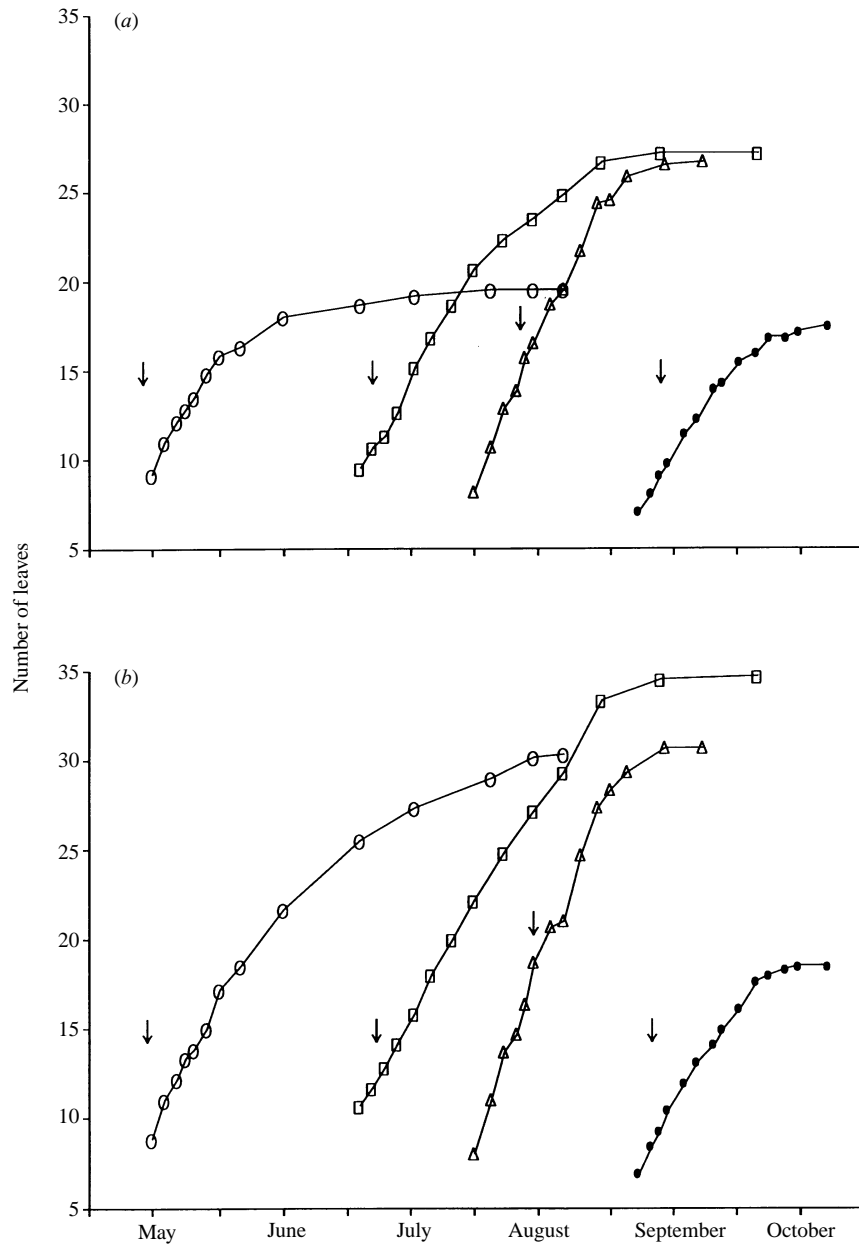


Fig. 3. Leaf appearance on the mainstem and sympodial branches in (a) Estima and (b) Maris Piper at four planting dates 13 March (○); 23 May (□); 6 July (△); 17 August (●). Date of onset of tuber initiation indicated by ↓. After Firman *et al.* (1995).

1965; Bremner & Radley 1966). Bremner & Radley (1966) used four cultivars with contrasting leaf growth and three dates of planting (March, April and May) but did not accurately record the timing of tuber initiation. They found that treatments which produced small plants around the apparent time of tuber initiation (old seed of early varieties at early

plantings) produced smaller and less persistent leaf surfaces and lower final tuber yields than treatments which produced large leaf surfaces at the apparent date of initiation (younger seed of late varieties, especially at later plantings). They concluded that the size and duration of the leaf surface is determined by plant size at the time of tuber initiation and that tuber

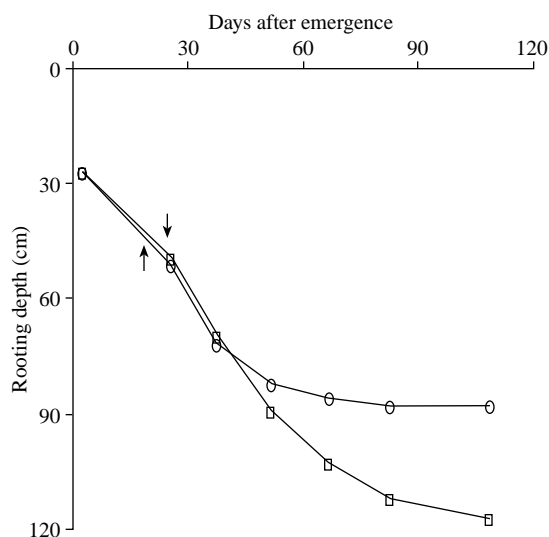


Fig. 4. Root depth for unirrigated crops at CUF in 1993. Estima (○); Cara (□). Date of onset of tuber initiation indicated by ↓. (M. A. Stalham, unpublished.)

initiation is the dominant influence on subsequent growth. The reduction or cessation in the production of leaves, axillary branches and roots following tuber induction and initiation on stem sections found in growth-room experiments (e.g. Ewing 1990; Ewing & Struik 1992) appears to reinforce the conclusions of Bremner & Radley (1966). However, the results of many subsequent field experiments show no such interruption or cessation in leaf or root growth. In contrasting cultivars grown in a wide range of environments, leaves (Fig. 3; Frier 1975; Firman *et al.* 1995) and roots (Fig. 4) are produced at a constant rate from emergence until long after the period of tuber initiation. The vast majority of aerial branches and, consequently, a major proportion of the leaf surface in many cultivars is produced after tubers have been initiated (Firman *et al.* 1995). These results show that the production of leaves and aerial branches in field-grown plants is not inhibited by the initiation of tubers, as previously suggested. The production of aerial branches and leaves in intact plants can be affected by changes in genotype, environment and husbandry practices and it is, therefore, not surprising that the pattern of growth of organs from stem sections bear little relation to that in field-grown plants.

Nonetheless, the conclusions of Bremner & Radley (1966) continue to be used in discussions of potato physiology (e.g. Haverkort & Kooman 1996) and their reconciliation with the results of more recent experiments (Bean & Allen 1978; Ali 1979; Raouf 1979; Al-Rawi 1981; Millard & MacKerron 1986; Firman 1987; Fowler 1988; Firman *et al.* 1991, 1995)

is essential. The growth and development of leaves is now known to differ greatly between cultivars and may be profoundly affected by environmental and husbandry factors. Some cultivars, such as Estima and Diana, produce very few aerial branches on the main shoot, are essentially determinate in their leaf growth and rely mainly on the leaf surface of the main shoot to intercept incoming radiation to produce their tuber yield (Firman 1987; Allen & Scott 1992). At the other extreme, cultivars such as Cara, Maris Piper and King Edward branch profusely, produce several flowers and a much larger and persistent leaf area than determinate cultivars and may be described as indeterminate in their leaf growth. For other cultivars, a gradation of determinacy prevails in between these extremes. Determinacy can be increased by advancing the physiological age of seed tubers, by low nitrogen supply and by low temperatures after planting. The combination of physiologically old seed of a determinate cultivar can lead to a very limited or no leaf surface, particularly when planting is followed by a period of cold weather (Madec 1956; Raouf 1979; Al-Rawi 1981; O'Brien 1981). Bremner & Radley (1966) used cultivars differing in physiological age and ranging from determinate (Ulster Chieftain) to indeterminate (Ulster Torch), whose leaf growth was likely to be differentially affected by the changing temperatures, physiological age and nitrogen supply as planting was delayed from March to May. Determinacy in the pattern of foliage growth may be linked to flower initiation which can occur before planting and, therefore, long before tubers are initiated (Al-Rawi 1981; Firman *et al.* 1991). However, differences in determinacy only become apparent around the time of tuber initiation, as leaf appearance ceases in determinate cultivars whilst leaves continue to emerge on sympodial and axillary branches in indeterminate cultivars for some time afterwards (Fig. 3). In Bremner & Radley's (1966) experiments, it was inevitable that Ulster Chieftain would produce small plants, for it was a determinate cultivar and the seed was physiologically old and susceptible to the restrictive effects of low temperatures on leaf growth at the March planting. Ulster Torch, by contrast, was indeterminate and physiologically younger, and so escaped any adverse effects of low temperature on its leaf development and produced larger plants and higher tuber yields. The eventual size of plants and their leaf surfaces in the cultivars used by Bremner & Radley (1966) was a consequence of differences in determinacy and was not caused by the initiation of tubers.

Bremner & Radley (1966) also concluded that plant size at the time of tuber initiation affects the partitioning of dry matter between the foliage and tubers and final yield. They argued that a greater proportion of the total plant dry weight was partitioned to tubers as plant size at initiation

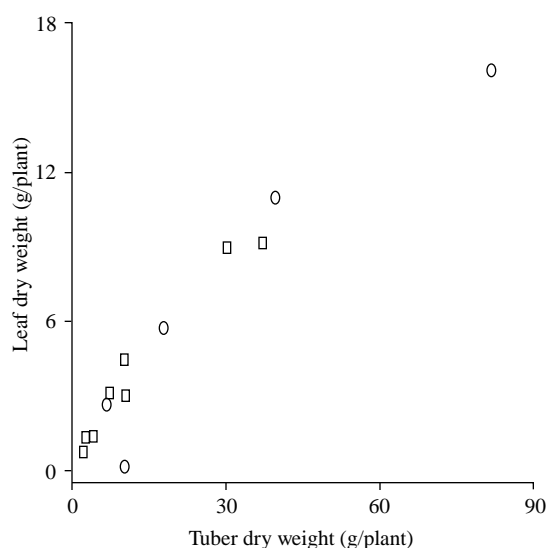


Fig. 5. Leaf dry weight (post-initiation) at different tuber dry weights in Home Guard. Young seed (○); old seed (□). Adapted from Raouf (1979).

decreased (i.e. earlier varieties and planting and older seed). Their conclusions are questionable as they did not establish the timing of tuber initiation nor foliage dry weight at initiation. Ali (1979), Raouf (1979) and Jones (1981) found very close relationships between tuber, foliage (post-initiation) and total plant dry weight which were not affected by any treatment (Fig. 5) and, therefore, no evidence that dry-matter partitioning was affected by plant size at initiation. The deduction of foliage dry weight present at initiation from the total foliage dry weight was crucial in affecting the relationships as the value for some treatments (e.g. young seed) was nearly equal to the differences in maximum foliage dry weights and, if ignored, would have resulted in a relationship which showed more foliage for any tuber dry weight. Differences in foliage dry weight per plant at initiation

between seed ages were mainly due to differences in number of stems. In the absence of 'little potato' disorder, initiation of tubers occurs around the same time after emergence on stems with similar numbers of leaves and dry weights for different physiological ages of seed and for many cultivars differing in determinacy (Ali 1979; Raouf 1979; Al-Rawi 1981).

Bremner & Radley's (1966) interpretation of the results was understandable at the time but current knowledge of determinacy and timing of tuber initiation allow different conclusions to be reached. These do not attribute any significance to initiation in the subsequent growth and development of the crop. Consequently, no relationship between plant size at initiation and final yield can be established either within or between cultivars. Bean & Allen (1978) showed that cultivars with early maturity classification usually emerged and initiated early and produced the earliest marketable tuber yield. At the end of growth, early cultivars generally had the lowest tuber yields but cultivars with high yields were found in all groups, classified as early, second early and maincrop and the largest yield occurred in the cultivar Arran Comet which was one of the first to initiate tubers. Similarly, Raouf (1979) found no correlation between plant size at initiation and final tuber yield for different physiological ages of seed which initiated tubers over a period of *c.* 3 weeks (Table 4). Tuber yields are largely determined by the extent and duration of leaf growth, which determines the amount of radiation intercepted, and these are varietal characteristics which can be influenced by sprouting and environmental conditions, but are not determined by the timing of tuber initiation nor plant size at that time, primarily because these do not vary much.

FACTORS AFFECTING TUBER INITIATION

Photoperiod

Photoperiod is regarded as an important factor affecting the timing of tuber initiation and the number

Table 4. *Effect of physiological age on timing of tuber initiation, plant dry weight at initiation and final tuber yield (t/ha) in Home Guard*

	Physiological age (number of day-degrees > 4 °C)									
	0	336	672	700	868	1036	1064	1232	1400	L.S.D.
Mean date of tuber initiation	19 June	19 June	6 June	26 May	23 May	26 May	30 May	23 May	26 May	
Plant dry weight (g/plant) at initiation	15.3	16.0	5.4	2.0	1.9	1.6	3.0	2.3	1.6	
Final tuber yield (t/ha)	42.0	40.4	32.8	40.8	25.3	28.4	35.7	36.1	29.2	10.0

From Raouf (1979). D.F. = 16.

Table 5. Effect of photoperiod on the timing of tuber initiation in two potato varieties at CUF in 1992

Number of days from 50% emergence to	Photoperiod (hours)	Variety		Mean	S.E. (D.F. = 2)
		Estima	Maris Piper		
Onset of initiation	8.0	14.0	14.3	14.2	
	16.5	14.3	19.7	17.0	
Mean		14.2	17.0		0.26
S.E.		0.50		0.43	
Cessation of initiation	8.0	20.7	21.3	21.0	
	16.5	27.0	28.3	27.7	
Mean		23.8	24.8		0.39
S.E.		0.50		0.31	
Duration of initiation (days)	8.0	6.7	7.0	6.8	
	16.5	12.7	8.7	10.7	
Mean		9.7	7.8		0.62
S.E. (D.F. = 4)		0.67		0.24	

of tubers formed. The consensus in the literature is that initiation occurs earlier in short than in long days (Wassink & Stolwijk 1953; Bodlaender 1963; Ewing 1990; Ewing & Struik 1992). Such effects have been demonstrated in many controlled-environment experiments particularly for stem cuttings. Reported effects of photoperiod on tuber initiation under field conditions are less well documented and are generally smaller and more variable than in controlled environments. Interpretation of reported effects of photoperiod under field conditions is difficult for three major reasons: (1) the quantity and/or quality of incident radiation, which may also affect initiation, usually varied with changes in photoperiod; (2) there is a wide range in sensitivity to photoperiod between cultivars, particularly between those selected and adapted to widely differing environments; (3) the timing of initiation was not accurately assessed. Usually, plants were sampled long after initiation had started in all treatments and differences in number or yield of tubers were assumed to reflect differences in the timing of initiation (Wassink & Stolwijk 1953; Krug 1960).

During the period from plant emergence to onset of tuber initiation daylength can range from *c.* 10 to 24 h world-wide and between *c.* 12 and 24 h in Europe. More than two thirds of the world's potato crop is produced at high latitudes (*c.* 45–60°) in continental Europe (FAO 1990) and tubers are generally initiated from May to July in photoperiods ranging from *c.* 15 to 18 h. Thus, tuber initiation for much of the world's potato production normally takes place in a narrow range of long days and, within this range, photoperiod would not be expected to be an important factor affecting initiation. Unfortunately, effects of photoperiod within this range have received little study. In photoperiods ranging from *c.* 12 to 17 h with similar temperatures and daily amounts of incident radiation

during initiation, the authors found no differences in the interval between the time of plant emergence and onset of initiation in Desirée, Maris Piper, Estima or Record. The first two cultivars have been shown to be sensitive to photoperiod in other environments. Demagante & Vander Zaag (1988*b*) reported earlier initiation in Desirée (*c.* 8 days) and other cultivars grown in *c.* 12 h than in *c.* 16 h days in a tropical environment. Differences in temperature between the sites used by Demagante & Vander Zaag (1988*b*) and the authors may be the major cause of the apparent variation in effects of photoperiod because combinations of high temperatures and long photoperiods have been shown to be particularly inhibitory to tuber formation in controlled environments (Gregory 1965). The authors, using normal (*c.* 16.5 h) and shortened (8 h) daylengths found effects of photoperiod on the timing of initiation which were influenced by cultivar (Table 5). Onset of initiation was advanced in Maris Piper (by *c.* 5 days) by shortening the daylength, but there were no effects on onset of initiation in Estima. Shortening the daylength resulted in earlier cessation of initiation (6–7 days) in both varieties and, therefore, a shorter duration of initiation in Estima but not in Maris Piper (Table 5). The available evidence suggests that the timing of onset of initiation in temperate regions is relatively fixed in relation to time of emergence and is not affected either by the small changes in photoperiod that may occur during the period of development of the stolons or by absolute photoperiod. The timing of completion of tuber initiation is dependent on plant growth rate, which is largely a function of temperature and irradiance and, in crops, is also unlikely to be affected by photoperiod. The possible range in photoperiod during the period of formation of stolons and tubers is potentially less in low than in high latitudes and, within any region, the available evidence suggests that photoperiod is

Table 6. *Effect of temperature (°C) and irradiance (MJ m⁻² d⁻¹) on number of tubers per plant*

Temperature		Irradiance			L.S.D.
Day	Night	3.4	7.7	11.0	
22	18	5.6	6.9	6.9	—
26	22	3.3	5.0	7.4	1.4
30	26	0.0	0.6	8.5	—

From Menzel (1985).

not important in affecting the timing of initiation of tubers in crops.

Effects of the change in direction of the photoperiod in high latitudes which occurs with extended dates of planting (e.g. March–July in the UK) of crops intended for a variety of new retail outlets have not been considered in the literature. Between the time of plant emergence and end of tuber initiation (*c.* 4 weeks), daylength at Cambridge, for example, increases by *c.* 1.6 h, remains fairly constant and decreases by *c.* 1.8 h as emergence is delayed from early May to mid-June and to mid-August, respectively. In experiments at CUF, these changes in the direction of the photoperiod did not affect the timing of initiation, but decreasing daylengths may be a factor causing fewer tubers to be initiated at late plantings (O'Brien *et al.* 1998).

Effects of irradiance

Effects of irradiance on the timing of tuber initiation have not been satisfactorily established, largely because the timing of initiation has not been defined and long sampling intervals precluded accurate assessment. There is, nevertheless, a widespread belief that the initiation of tubers is delayed in conditions of low or decreasing incident radiation (Bodlaender 1963; Menzel 1985; Ewing & Struik 1992). Menzel (1985) showed that the effect of irradiance on tuberization was influenced by temperature in the range 20–28 °C (Table 6). At the lower temperature, a near maximum number of tubers was produced even in very low irradiance (3.4 MJ/m² per day) but the combination of high temperature (28 °C) and low irradiance prevented or greatly inhibited tuberization. The results of an experiment carried out at high temperatures by Demagante & Vander Zaag (1988*b*), who used shading to change incident radiation and supplementary lighting to alter photoperiod, provide some support for Menzel's (1985) findings for field conditions. They reported that shading by up to 58% delayed initiation, particularly in long days, compared with full radiation, but effects within cultivars were not consistent between experiments or daylengths. In

Table 7. *Duration of initiation (days) for different levels of shading and (in parenthesis) amounts of incident radiation (MJ m⁻² d⁻¹) during initiation in Maris Piper (CUF 1993)*

Shading (%)				
0	37	50	70	S.E.
(15.0)	(9.5)	(7.5)	(4.5)	(D.F. = 7)
4	4	7	18	0.89

From O'Brien *et al.* (1998).

somewhat lower temperatures (15–20 °C), Sale (1973, 1976) found no effects of shading on the onset of initiation in Sebago in a narrow range of daylengths (12–13 h) in Australia and O'Brien *et al.* (1998) found no effects in Estima and Maris Piper in long photoperiods (16–17 h) in the UK. The available evidence suggests that low incident radiation (< *c.* 7 MJ/m² per day) may delay the onset of initiation in conditions of very high temperatures and long days: conditions which are uncommon in practice. The results reported by O'Brien *et al.* (1998), Gray & Holmes (1970) and Sale (1973, 1976) show that number of tubers decreases with decreasing amounts of incident radiation when plants are shaded during the period of initiation (Fig. 1). These effects occurred rapidly, within 2–3 days of the start of shading, and probably account for the contention in the literature that tuberization is delayed by decreasing irradiance.

In view of the above effects of incident radiation on number of tubers, it may be expected that reducing radiation below some critical amount would suppress growth sufficiently to delay the attainment of maximum number of tubers and consequently the date of cessation of tuber initiation. In Estima at Cambridge, O'Brien *et al.* (1998), found that reductions of up to 75% in incident radiation during the period of initiation did not delay cessation of initiation. However, in Maris Piper (O'Brien *et al.* 1998) and in experiments reported by Gray & Holmes (1970) and Struik (1986) cessation of initiation was delayed by substantial reductions in incident radiation during the period of initiation (Table 7). Shortly after removal of shade material in experiments with Maris Piper (O'Brien *et al.* 1998) and Maris Peer (Gray & Holmes 1970), total number of tubers in heavily-shaded treatments increased whilst numbers in lightly-shaded or unshaded treatments remained constant or decreased. As a result, effects of shading decreased, disappeared or even became reversed, and this occurrence may account for some of the variation in reported effects of shading in the literature. The results show that the period of tuber initiation is not

absolutely fixed in time but can be greatly extended by very low plant growth rates caused by very low irradiance: conditions which frequently prevailed in many reported controlled-environment experiments (e.g. Borah and Milthorpe (1962), < 5 MJ/m² per day; Slater (1968), < 3 MJ/m² per day). In practice, such low incident radiation would not normally occur for much of the period of initiation and the duration of initiation is probably quite constant for any cultivar in most field environments.

Effects of temperature

There is no comprehensive study in the literature of the effects of temperature on the initiation of tubers in crops grown in temperate regions. Published studies have mainly been conducted in controlled environments and have only covered a narrow range of temperatures and, consequently, the effects of temperature on initiation and cardinal values for tuber formation have not been established. Interpretation of effects of temperature on initiation of tubers in field experiments is complicated by possible interactions between temperature and other factors, such as irradiance and photoperiod and variation in responses to these factors between cultivars. Minimum temperatures for tuber formation have not been established but tubers can be formed earlier following transplanting to low temperatures of 5–7 °C from a higher constant temperature sequence (Burt 1964, 1965). Optimum temperatures for tuber formation are widely regarded as being in the range 10–17 °C (Went 1957; Bodlaender 1963; Moorby & Milthorpe 1975) whilst tuber formation is assumed to be inhibited above mean daily temperatures of *c.* 30 °C (Bushnell 1925; Gregory 1965). Night and soil temperatures are regarded as being particularly important in the tuberization process (Slater 1963, 1968). A mean night air temperature of between 12 and 15 °C has been suggested as optimum for tuber formation (Went 1957; Slater 1968) whilst Gregory (1965) suggested that mean night soil temperatures > 24 °C inhibit tuber formation. However, various authors have reported adequate tuberization at temperatures differing from those suggested as optimal or maximal (Borah 1959; Hay & Allen 1978; Midmore 1984; Khedher & Ewing 1985; Demagante & Vander Zaag 1988*a*).

It is frequently reported that tuber initiation is hastened at low temperatures (Bodlaender 1963; Slater 1963, 1968; Burt 1964, 1965; Moorby & Milthorpe 1975; Ewing & Struik 1992). Interpretation of such statements is dependent on the definition of 'low temperature' and this has been variously regarded as 6–15 °C (Burt 1964, 1965), < 15 °C (Midmore 1984) and *c.* 20 °C (Menzel 1985); a range which covers most of the temperatures experienced during initiation of tubers in crops in N W European

Table 8. *Timing of tuber initiation (days from 50% emergence) at two dates of planting of Désirée and mean soil temperature (°C) and incident radiation (MJ m⁻² d⁻¹) during initiation (CUF 1993)*

	Date of planting		S.E. (D.F. = 22)
	3 March	28 April	
Temperature...	14.7	19.6	
Radiation...	18.0	18.0	
Onset of initiation	15.6	15.1	0.47
Cessation of initiation	27.7	20.9	0.37
Duration of initiation (days)	12.1	5.8	0.32

conditions. The belief that initiation is earlier at low temperatures is based largely on the results of the experiments of Burt (1964, 1965) and Slater (1963, 1968). The former authors transplanted emerged plants from higher temperatures and using the 'apparent date of initiation' found this to be earlier at low (6–15 °C) than at high (> 15 °C) temperatures. These conclusions must be questioned, as the lower temperatures almost certainly reduced bulking rates, leading inevitably to earlier 'apparent' initiation and the direct effects of transplanting cannot be ignored. In contrast, in temperate regions, the onset of initiation has been reported to occur earlier (Burt 1964, 1965; Bremner & Radley 1966) as a result of increasing temperatures with delay in planting. Table 8 shows that the timing of onset of initiation was not affected by varying mean daily soil temperatures between emergence and onset of initiation from *c.* 12 to 19 °C as a result of mulching crops or delaying planting at Cambridge. In some experiments, however, in which mean daily soil temperatures were low after emergence (8–10 °C) following early plantings, onset of initiation was somewhat earlier at higher temperatures from later plantings, suggesting that low temperatures may indeed delay rather than hasten onset of initiation, as is widely stated in the literature. Of course, effects of date of planting cannot be ascribed to temperature alone, as other factors which may affect the timing of initiation, such as chronological and physiological age of seed, and also changes occurring when planting is delayed. The balance of the available experimental evidence suggests that temperature is not an important factor affecting the onset of tuber initiation in crops, at least in temperate regions.

Several authors have also suggested that high mean daily temperatures (> 25–30 °C), especially soil temperatures, delay initiation (Sale 1979; Sato 1981; Midmore 1984, 1992; Ewing & Struik 1992) but the evidence for this is not convincing, as the timing of onset of initiation was generally not accurately assessed. In controlled environments, mean

temperatures of $> 28\text{--}30\text{ }^{\circ}\text{C}$ have been shown to delay and even inhibit initiation in some cultivars (Sato 1981; Khedher & Ewing 1985; Nowak & Colborne 1989) but adequate initiation has been demonstrated in different cultivars in field experiments at mean temperatures of *c.* $24\text{--}28\text{ }^{\circ}\text{C}$ in hot climates (e.g. Hay & Allen 1978; Sale 1979; Demagante & Vander Zaag 1988*a, b*). In the Philippines, Demagante & Vander Zaag (1988*a, b*) found that this interval was relatively fixed at *c.* 14 days in Desirée grown at minimum temperatures ranging from *c.* 21 to $24\text{ }^{\circ}\text{C}$ and maximum temperatures between *c.* 28 and $34\text{ }^{\circ}\text{C}$, which is similar to that found by the authors for this cultivar with similar radiation integrals and daylengths at much lower temperatures (Table 8). Similarly, Hay & Allen (1978) reported an interval from emergence to the onset of initiation of *c.* 14 days for the cultivar Roslin Eburu grown in mean soil temperatures of *c.* $24\text{ }^{\circ}\text{C}$ in Malawi, which is similar to that found by the authors in many cultivars grown in temperate environments. From the limited experimental evidence available, it would seem that the interval from emergence to the onset of tuber initiation for crops grown at mean temperatures of $25\text{--}30\text{ }^{\circ}\text{C}$ in the hot tropics is similar to those grown in temperate regions with mean temperatures of *c.* $10\text{--}20\text{ }^{\circ}\text{C}$.

Although onset of initiation appears to be little affected by changes in temperature, the results of experiments at Cambridge suggest that the duration of initiation may be prolonged in moderately low temperatures ($< 15\text{ }^{\circ}\text{C}$). In experiments with Desirée, the completion of initiation was hastened by *c.* 1 week as a result of delaying planting from March to April (Table 8). During the period of initiation, the principal difference between planting dates was in mean daily temperature, which was *c.* $5\text{ }^{\circ}\text{C}$ lower from planting in March than from later plantings.

The results of several experiments at Cambridge suggest that the total number of tubers initiated is not greatly affected by varying mean daily temperatures within the range *c.* $10\text{--}20\text{ }^{\circ}\text{C}$. In hot climates, high mean daily temperatures (*c.* $25\text{--}30\text{ }^{\circ}\text{C}$) have been reported to decrease the total number of tubers retained (Sale 1979; Midmore 1983) and the authors found similar effects of very high maximum air temperatures ($30\text{--}40\text{ }^{\circ}\text{C}$) under floating polythene mulches in the UK. It is likely that the delay in onset of initiation with increasing temperature in some reports was a reflection of fewer tubers rather than an actual delay in the onset of initiation, as assessments of the timing of tuber initiation were frequently based on changes in number of tubers.

Soil moisture

Soil moisture status during the phase of stolon growth is regarded as important in affecting the timing of

tuber initiation and number of tubers (North 1960; Ivins 1963; Salter & Goode 1967; van Loon 1981; Struik & van Voorst 1986). Ivins (1963) suggested that high soil moisture status at this stage of growth delayed tuber initiation, whilst Haverkort *et al.* (1990) reported the opposite effect in pot experiments. There are few reports which show any effect of soil moisture on the onset of initiation and certainly no evidence that a plentiful supply of soil moisture delays initiation. In experiments at Cambridge, there were no effects of withholding water for different periods from planting to the end of initiation on the timing of initiation or on number of tubers initiated in the cultivar Record. Soil moisture deficits at the beginning of initiation in these experiments ranged from *c.* 10 to 40 mm and were achieved by exclusion of rainfall and irrigating as required. Number of tubers retained late in growth, however, decreased with prolonged, severe restrictions in soil moisture in some experiments as a result of increased resorption of tubers. In pot experiments in a glasshouse, MacKerron & Jefferies (1986) using a severe drought treatment (28% of available soil water) found fewer tubers at final harvests from withholding water between planting and emergence than from withholding water at any later period up to the end of the period of initiation. With very extreme drought (5% of available soil moisture), Cavagnaro *et al.* (1971) reported that withholding water between planting and emergence of crops substantially delayed both emergence and onset of initiation, shortened the duration of initiation and eventually increased number of tubers initiated compared with no water restriction. Overall, the results of field experiments suggest that stolon formation is the critical period for effects of water supply to occur and, unless soil moisture content is greatly depleted during this stage of growth, there will be no effect on the initiation of tubers. This contention is supported by the conclusions of Struik & van Vorst (1986) from controlled-environment experiments, which showed that unless the moisture environment in the immediate vicinity of the stolons is altered, number of tubers is not affected by wide fluctuations in soil moisture deficits. The occurrence of initiation at small plant sizes ($\text{LAI} < 1$) and the brief period (a few days) over which tubers are normally initiated in crops usually precludes large changes in soil moisture content and excludes this factor as a major influence on the duration of initiation or on number of tubers formed.

Effect of mineral nutrient supply

There are few published reports on effects of nutrients other than nitrogen on tuber initiation and the prevailing view is that tuber initiation is delayed with high nitrogen supply (Radley 1963; Moorby & Milthorpe 1975; Ewing 1990; Ewing & Struik 1992).

Table 9. *Effect of rate of nitrogen application (kg/ha) on timing of tuber initiation (days from 50% emergence) in Estima in 1993 (CUF)*

	Rate of nitrogen application					S.E. (D.F. = 16)
	0	60	120	180	240	
Onset of initiation	18	20	18	18	20	1.45
Cessation of initiation	27	27	25	28	29	1.54
Duration of initiation (days)	9	7	7	10	9	1.36

This contention is largely based on results of early pot experiments of Werner (1934, 1940) in glasshouses, a few field experiments (Radley 1963) and more recent experiments in a hydroponic medium conducted by Krauss and co-workers (Krauss & Marschner 1982; Krauss 1985). Werner (1934, 1940) did not assess the date of onset of tuber initiation but his results suggested that very few tubers were formed with very high nitrogen supply particularly at high temperatures in long days. Krauss and co-workers (*loc. cit.*) found no tuber formation, but uninterrupted growth of shoots, with continuous supply of nitrogen in an hydroponic solution under conditions considered favourable for tuberization (short days, low temperatures). When nitrogen was temporarily withheld from the solution, tuberization occurred and was followed by a cessation of root and shoot growth. These experiments were carried out under very low incident radiation yet the conclusions, together with those of Werner (1934, 1940), are widely considered to summarize the effects of nitrogen on tuber initiation. The experiments of Krauss (*loc. cit.*) were recently repeated with much higher light intensities in growth-chambers and few effects of nitrogen on tuberization were found (Ewing & Struik 1992). Effects of nitrogen found by Werner (1934, 1940) and Krauss (*loc. cit.*) therefore probably bear little relation to those that may pertain in crops under different husbandry and environmental conditions.

There are few published experiments which have accurately assessed effects of nitrogen on onset or cessation of initiation under field conditions. Experiments which were sampled frequently by the authors from plant emergence onwards showed that there was no effect in a range of cultivars and environments of a wide range of rates of nitrogen application on the interval from emergence to onset or end of initiation (Table 9). Raphael (1979) found no effect of applying different rates of N to the soil or to the foliage on the timing of onset or cessation of initiation in Home Guard in 2 years. These results suggest that nitrogen does not affect the timing of tuber initiation in crops under a range of husbandry and environmental

conditions. However, the authors have observed that high rates of applied nitrogen banded in ridges can delay plant emergence (Firman 1987) and consequently the period from planting to onset of tuber initiation was increased. On organic soils, the interval from emergence to onset of initiation can be substantially delayed in indeterminate cultivars such as Cara receiving high rates of applied nitrogen (240 kg/ha) where the residual soil N content alone at planting was very high – exceeding 500 kg/ha/90 cm depth. There is, therefore, some evidence from field experiments that tuber initiation may be delayed in some cultivars by the presence of very high concentrations of soil nitrogen. It is, however, likely that this effect will be found only in indeterminate varieties, such as Cara, for the partitioning of assimilate between foliage and tubers is much more stable in more determinate varieties (Gunaseena & Harris 1968; Allen & Scott 1992).

Experiments at CUF show that N can affect the number of tubers formed, particularly where the supply of soil N is very low or very high. Reductions in number of tubers frequently occurred where supplies of soil N at planting were below *c.* 70 kg/ha/90 cm depth and resulted in maximum foliar ground cover of < 60% without fertilizer N. Where N uptake from soil supplies alone or with fertilizer N produced complete ground cover, there were generally no effects on number of tubers. At the highest rates of application and where soil N exceeded *c.* 300 kg/ha/90 cm depth, the number of tubers in indeterminate varieties decreased in some experiments due to effects on partitioning of assimilates.

Effect of physiological and chronological age

Increasing physiological age of seed tubers leads to increased sprout length at planting, advances emergence and, therefore, the onset of tuber initiation (Table 4). From normal dates of planting (March to June) the authors found that the interval from emergence to the onset of initiation was not affected by a wide range of physiological ages (0–1200 day-degrees > 4 °C) in most cultivars tested (Ali 1979; Firman *et al.* 1991). However, in a few cultivars (e.g. Home Guard and Record), this interval was considerably shortened when physiologically old seed (> 600 day-degrees > 4 °C) was subjected to prolonged periods of low temperature (< 6–8 °C) after planting (Raouf 1979; Al-Rawi 1981). In these circumstances, tubers were present on several plants of old seed before or close to the time of emergence and some plants failed to emerge – exhibiting the condition known as ‘little potato’ disorder. Tuberization on plants from physiologically young seed can occur close to the time of plant emergence following very late planting (August) of chronologically old cold-stored (3–4 °C) seed (Firman *et al.* 1991). The presence

of tubers on sprouts prior to planting following prolonged storage even at low temperatures has also been observed by the authors and others (Madec 1956). Therefore, there appears to be a critical chronological and physiological age above which onset of initiation is advanced in relation to the time of emergence rather than a progression towards earlier tuberization with increasing seed age as suggested by Madec & Perennec (1962), Ewing (1990) and Ewing & Struik (1992). The abrupt change in the timing of initiation in old seed may be associated with a change from the vegetative to the floral state of the terminal shoot apex as suggested by Steward *et al.* (1981) and Firman *et al.* (1991) or with the death of the shoot apex which frequently occurs when the physiological condition leading to 'little potato' disorder is reached.

In some experiments the duration of initiation was somewhat longer for old (> 600 day-degrees > 4 °C) than for any younger seed (Table 1) but there were no effects of physiological age in the vast majority of experiments. Effects were most common in old seed of early varieties such as Home Guard and Arran Comet, which produced many secondary stems. These stems generally initiated tubers later than mainstems, which largely accounted for the delay in completion of initiation. However, delayed completion of initiation of tubers on mainstems of old seed of Maris Piper has been noted by the authors (Table 1) which may have been due to the increased number of nodes and sites for tuber production on such seed. It would appear, therefore, that the duration of initiation can be extended with the use of physiologically old seed, but effects have little practical significance as such seed would rarely be used. Very limited evidence suggests that variation in chronological age of seed does not affect the duration of initiation.

The results, overall, suggest that the physiological and chronological age of seed tubers has little influence on the timing of initiation unless extreme ages are used. This does not support the view of Madec & Perennec (1962) that the physiological condition of the mother tuber *per se* exerts a major influence on the timing of initiation of tubers under a wide range of field conditions.

Date of planting

Effects of date of planting on tuber initiation have not been considered in previous reviews of the subject. Its effects may be difficult to interpret, as all factors considered to affect initiation may also change with alteration in the date of planting. However, date of planting is an important husbandry factor and requires consideration, for crops from the same seed lot may be planted over a very long period (6–12 months). An understanding of the effects of this factor on initiation is desirable, as number of tubers is

a crucial element in the production of the specialized crops, seed, canning and scraping, which are planted over much of the season.

With delay in planting and improved conditions for growth in temperate regions, it might be expected that the timing of initiation would be hastened as stolon development and initiation of tubers involves growth. The results of experiments using a range of cultivars and environments show that date of planting does not usually affect the interval from plant emergence to onset of initiation (e.g. Table 8), which agrees with the findings of Demagante & Vander Zaag (1988*a*) and supports the general absence of effects of individual husbandry and environmental factors noted previously. However, initiation was generally completed more slowly following plantings in March or early April compared with any later plantings (Table 8). Seed was stored at 1–3 °C between planting dates and had similar sprout growth and development over the range of planting dates. The principal environmental difference between early and any later plantings was in temperature (Table 8). Growth may have been limited by moderately low mean temperatures (10–15 °C) during initiation at early plantings but there were no effects on the duration of initiation of delaying planting after late April when temperatures at initiation were between 15 and 20 °C. The duration of initiation was usually *c.* 2 weeks for plantings before mid-April and 2–7 days for any later plantings. As noted previously, onset of initiation was hastened by very late plantings (August) and overall the results suggest that the timing of initiation in temperate regions is relatively stable for normal planting dates and may be affected only by extreme planting dates.

CONCLUSIONS

The factors regarded as important in the literature in affecting the timing of tuber initiation, namely, photoperiod, temperature, irradiance, nitrogen and soil water supply appear to have little effect on the timing of initiation in plants grown under a wide range of field conditions in temperate climates. The results presented in this review show that it is only in extreme circumstances that any of these factors significantly affect the timing of initiation. Thus, for example, the duration of initiation may be extended in conditions of low irradiance and onset of initiation may be delayed by very low soil moisture supply or by very high concentrations of soil nitrogen. Such conditions do not normally prevail in commercial practice and effects of these on the timing of initiation of tubers in crops is negligible. Non-uniform emergence of plants, for whatever reason, is likely to be a far more important cause of variation in the timing of tuber initiation of field crops. The principal reasons for the discrepancies between reported concepts and actual effects found for field-grown plants have been

discussed and emphasise the confusion that can arise when results of experiments carried out in specific environments are extrapolated to very different environments. The only factors found to affect the timing of initiation (from emergence) in some cultivars in the photoperiods tested at CUF were physiological ageing of seed tubers, irradiance and date of planting. Onset of initiation was hastened in some cultivars by extreme ageing (chronological and physiological) of seed and the duration of initiation was lengthened by increasing physiological age of seed in a few cultivars, severe reductions in incident radiation and early planting. For the vast majority of commercial potato production, the available evidence from these field studies suggests that the timing of onset and cessation of tuber initiation varies very little even with substantial variation in husbandry practices and in environmental conditions. Thus, in most circumstances, the timing of tuber initiation and other stages of plant development, such as floral initiation (Firman *et al.* 1991), occur at a relatively fixed interval after plant emergence which can be readily recorded and used to predict the timing of subsequent stages of development. For any cultivar, a sufficiently accurate prediction of the timing of onset of tuber initiation can be made from a knowledge of the time of plant emergence and any husbandry treatment, for example, the timing of irrigation to control common scab, can be planned in advance.

Experimental results show that for all, except very old seed, the interval from plant emergence to the onset of tuber initiation is 2–3 weeks in many cultivars (such as Estima, Record, Desirée and Maris Piper) and slightly longer in others (e.g. Cara). In most cultivars and environments investigated, the duration of initiation was *c.* 1 week: this period was extended to *c.* 2 weeks at early plantings in some experiments but in conditions of rapid growth from mid-May onwards, initiation was usually completed within 3–4 days. Thus, the usual period over which tubers are formed in field experiments is much shorter than widely believed (2–6 weeks) and only allows a brief period for any factor to affect the number of tubers initiated. However, in commercial crops, plant emergence may not be synchronous and, consequently, the period from emergence to initiation and the duration of initiation will appear longer than in experiments. The effective duration of initiation may be even shorter than 3–4 days, for many tubers that

initiate fail to grow to a marketable size or are resorbed later in growth and there is some evidence that the majority of these tubers are the last to be initiated (Krijthe 1955).

The extension of the period of initiation in moderately low temperatures (10–15 °C) at early plantings and in low irradiance suggests that the rate of completion of initiation is affected by the rate of assimilation. The consistency in the duration of initiation at later plantings, despite substantial variation in temperature and incident radiation suggests that only low critical temperatures and irradiances are required for rapid initiation. The rapid decrease in number of tubers (within 2–3 days) resulting from shading plants (O'Brien *et al.* 1998) supports the view of Perl *et al.* (1991) of the importance of assimilate in the process of initiation and suggests that hormones do not play a major controlling role at this stage of initiation. The consistency in the interval from emergence to the onset of initiation, even in conditions of very low irradiance, suggests that hormones rather than assimilates may be important in controlling the early stages of tuber initiation (i.e. induction) as suggested by Menzel (1985) and Perl *et al.* (1991).

The stability in timing of initiation and the short period of initiation in good growing conditions suggests that the process of initiation *per se* is not an important factor affecting subsequent growth and tuber yield, at least in temperate regions. The absence of any clear relationship between tuber initiation and any aspect of leaf growth and yield supports this conclusion. However, tuber initiation is important in the establishment of a population of growing tubers from which the size distribution of final yield is ultimately derived. O'Brien *et al.* (1998), have shown that reducing radiation intercepted per stem by shading during initiation or by increasing planting density reduces the number of tubers per stem but the size of the effect of shading on number of tubers that survive at harvest is also determined by growing conditions after the end of shading. Future research must elucidate the relationship between the initiation and survival of tubers to allow more accurate prediction of number of tubers and tuber size distribution. This requires a greater understanding of stem growth and development in relation to tuberization of stolons differing in origin and nodal position and the role of husbandry and environmental factors on this.

REFERENCES

- ALI, S. M. J. M. (1979). *Effect of temperature during sprouting on growth and yield of the maincrop potato variety Desirée*. MSc thesis, University College of Wales, Aberystwyth.
- ALLEN, E. J. & SCOTT, R. K. (1992). Principles of agronomy and their application in the potato industry. In *The Potato Crop: The Scientific Basis for Improvement*, 2nd Edn (Ed. P. M. Harris), pp. 816–881. London: Chapman & Hall.
- AL-RAWI, A. W. (1981). *Effect of storage environment on the growth and development of contrasting varieties of potatoes*. PhD thesis, University College of Wales, Aberystwyth.
- BEAN, J. N. & ALLEN, E. J. (1978). The relationship between

- tuber initiation and subsequent plant growth in field grown potatoes. In *Proceedings of the 7th Triennial Conference of the EAPR*, pp. 11–12. Warsaw, Poland.
- BODLAENDER, K. B. A. (1963). Influence of temperature, radiation and photoperiod on development and yield. In *The Growth of the Potato* (Eds J. D. Ivins & F. L. Milthorpe), pp. 199–210. London: Butterworths.
- BORAH, M. N. (1959). *The effect of light intensity, length of day and temperature on growth and tuber formation in the potato*. PhD thesis, University of Nottingham.
- BORAH, M. N. & MILTHORPE, F. L. (1962). Growth of the potato as influenced by temperature. *Indian Journal of Plant Physiology* **5**, 53–72.
- BREMNER, P. M. & RADLEY, R. W. (1966). Studies in potato agronomy. II. The effects of variety and time of planting on growth, development and yield. *Journal of Agricultural Science, Cambridge* **66**, 253–262.
- BURT, R. L. (1964). Influence of short periods of low temperature on tuber initiation in the potato. *European Potato Journal* **7**, 197–208.
- BURT, R. L. (1965). The influence of reduced temperatures after emergence on the subsequent growth and development of the potato. *European Potato Journal* **8**, 104–114.
- BUSHNELL, J. (1925). The relation of temperature to growth and respiration in the potato plant. *Technical Bulletin of the Minnesota Agricultural Experimental Station*, No. 34.
- CAVAGNARO, J. B., DE LIS, B. R. & TIZIO, R. M. (1971). Drought hardening of the potato plant as an after-effect of soil drought conditions at planting. *Potato Research* **14**, 181–192.
- CHAILAKHYAN, M. KH., YANINA, L. J., DEVEDZHIAN, A. G. & LOTOVA, G. N. (1981). Photoperiodism and tuber formation in grafting tobacco onto potato. *Doklady Akademii Nauk, SSSR* **257**, 1276–1280.
- COTHER, E. J. & CULLIS, B. R. (1985). Tuber size distribution in cv. Sebago and quantitative effects of *Rhizoctonia solani* on yield. *Potato Research* **28**, 1–14.
- DEMAGANTE, A. L. & VANDER ZAAG, P. (1988a). Potato (*Solanum* spp.) in an isohyperthermic environment. II. Response to planting date. *Field Crops Research* **19**, 153–166.
- DEMAGANTE, A. L. & VANDER ZAAG, P. (1988b). The response of potato (*Solanum* spp.) to photoperiod and light intensity under high temperatures. *Potato Research* **31**, 73–83.
- EWING, E. E. (1990). Induction of tuberization in potato. In *The Molecular and Cellular Biology of the Potato* (Eds M. E. Vayda & W. D. Park), pp. 25–41. Wallingford: CAB International.
- EWING, E. E. & STRUIK, P. C. (1992). Tuber formation in potato: induction, initiation, and growth. *Horticultural Reviews* **14**, 89–197.
- FOOD AND AGRICULTURE ORGANIZATION (1990). *Bulletin of Statistics 1990, Vol 111/1*.
- FIRMAN, D. M. (1987). *Leaf growth and senescence of the potato*. PhD thesis, University of Cambridge.
- FIRMAN, D. M., O'BRIEN, P. J. & ALLEN, E. J. (1991). Leaf and flower initiation in potato (*Solanum tuberosum*) sprouts and stems in relation to number of nodes and tuber initiation. *Journal of Agricultural Science, Cambridge* **117**, 61–74.
- FIRMAN, D. M., O'BRIEN, P. J. & ALLEN, E. J. (1992). Predicting the emergence of potato sprouts. *Journal of Agricultural Science, Cambridge* **118**, 55–61.
- FIRMAN, D. M., O'BRIEN, P. J. & ALLEN, E. J. (1995). Appearance and growth of individual leaves in the canopies of several potato cultivars. *Journal of Agricultural Science, Cambridge* **125**, 379–394.
- FOWLER, J. H. (1988). *Effect of plant arrangement and density on growth, development and yield of two potato varieties*. PhD thesis, University of Cambridge.
- FRIER, V. (1975). *Some factors that influence tuber growth in the potato*. PhD thesis, University of London.
- GOODWIN, P. B., BROWN, A., LENNARD, J. H. & MILTHORPE, F. L. (1969). Effect of centre of production, maturity and storage treatment of seed tubers on the growth of early potatoes. II. Field growth. *Journal of Agricultural Science, Cambridge* **73**, 167–176.
- GRAY, D. & HOLMES, J. C. (1970). The effect of short periods of shading at different stages of growth on the development of tuber number and yield. *Potato Research* **13**, 215–219.
- GREGORY, L. E. (1956). Some factors for tuberization in the potato. *American Journal of Botany* **43**, 281–288.
- GREGORY, L. E. (1965). Physiology of tuberization in plants (tubers and tuberous roots). *Handbuch der Pflanzenphysiologie, Vol XV/1*, 1328–1354.
- GUNASENA, H. P. M. & HARRIS, P. M. (1968). The effect of the time of application of nitrogen and potassium on the growth of the second early potato, variety Craig's Royal. *Journal of Agricultural Science, Cambridge* **71**, 283–296.
- HAVERTKORT, A. J. & KOOMAN, P. L. (1996). Crop growth models help to identify ideotypes in potato breeding. In *European Association for Potato Research. 13th Triennial Conference*, pp. 51–52 (Abstract).
- HAVERTKORT, A. J., VAN DE WAART, M. & BODLAENDER, K. B. A. (1990). The effect of early drought stress on numbers of tubers and stolons of potato in controlled and field conditions. *Potato Research* **33**, 89–96.
- HAY, R. K. M. & ALLEN, E. J. (1978). Tuber initiation and bulking in the potato (*Solanum tuberosum*) under tropical conditions: the importance of soil and air temperature. *Tropical Agriculture (Trinidad)* **55**, 289–295.
- IVINS, J. D. (1963). Agronomic management of the potato. In *The Growth of the Potato* (Eds J. D. Ivins & F. L. Milthorpe), pp. 303–312. London: Butterworths.
- IVINS, J. D. & BREMNER, P. M. (1965). Growth, development and yield in the potato. *Outlook on Agriculture* **4**, 211–217.
- JEFFERIES, R. A. & MACKERRON, D. K. L. (1987). Thermal time as a non-destructive method of estimating tuber initiation in potatoes. *Journal of Agricultural Science, Cambridge* **108**, 249–252.
- JONES, J. L. (1981). *Effect of date of planting on contrasting potato varieties*. PhD thesis, University College of Wales, Aberystwyth.
- KHEDHER, M. B. & EWING, E. E. (1985). Growth analyses of eleven potato cultivars grown in the greenhouse under long photoperiods with and without heat stress. *American Potato Journal* **62**, 537–554.
- KRAUSS, A. (1985). Interaction of nitrogen nutrition, phytohormones, and tuberization. In *Potato Physiology* (Ed. P. H. Li), pp. 209–230. Orlando, FL: Academic Press.
- KRAUSS, A. & MARSCHNER, H. (1982). Influence of nitrogen nutrition, daylength and temperature on contents of gibberellic acid and abscisic acid and on tuberization in potato plants. *Potato Research* **25**, 12–21.

- KRIJTHE, N. (1955). Observations on the formation and growth of tubers on the potato plant. *Netherlands Journal of Agricultural Science* **3**, 291–304.
- KRUG, H. (1960). Zum Photoperiodischen Verhalten Einiger Kartoffelsorten I & II. *European Potato Journal* **3**, 47–79 and 107–136.
- MACKERRON, D. K. L. & JEFFERIES, R. A. (1986). The influence of early soil moisture stress on tuber numbers in potato. *Potato Research* **29**, 299–312.
- MADEC, P. (1956). La nature et les causes du boulage chez la pomme de terre. *Annales de l'Amélioration des Plantes* **6**, 151–169.
- MADEC, P. & PERENNEC, P. (1962). Les relations entre l'induction de la tuberisation et la croissance chez la plante de pomme de terre *Solanum tuberosum*, L. *Annales de Physiologie Vegetale* **4**, 5–84.
- MARTIN, C., VERNAY, R. & PAYNOT, N. (1982). Physiologie vegetale. Photoperiodisme, tuberisation, floraison et phenolamides. *Comptes Rendus de l'Academie des Sciences, Paris* **295**, 565–568.
- MENZEL, C. M. (1985). Tuberization in potato at high temperatures: interaction between temperature and irradiance. *Annals of Botany* **55**, 35–39.
- MIDMORE, D. J. (1983). Potato in tropical environments: leaf area index, light interception and dry matter accumulation. *Potato Research* **27**, 313–314.
- MIDMORE, D. J. (1984). Potato (*Solanum* spp.) in the hot tropics. I. Soil temperature effects on emergence, plant development and yield. *Field Crops Research* **8**, 255–271.
- MIDMORE, D. J. (1992). Potato production in the tropics. In *The Potato Crop: The Scientific Basis for Improvement, 2nd Edn* (Ed. P. M. Harris), pp. 728–793. London: Chapman & Hall.
- MILLARD, P. & MACKERRON, D. K. L. (1986). The effects of nitrogen application on growth and nitrogen distribution within the potato canopy. *Annals of Applied Biology* **109**, 427–437.
- MOORBY, J. & MILTHORPE, F. L. (1975). Potato. In *Crop Physiology: Some Case Histories* (Ed. L. T. Evans), pp. 225–257. London: Cambridge University Press.
- NORTH, J. J. (1960). Irrigation of farm crops. *Journal of the Royal Agricultural Society* **121**, 7–20.
- NOWAK, J. & COLBORNE, D. (1989). *In vitro* tuberization and tuber proteins as indicators of heat stress tolerance in potato. *American Potato Journal* **66**, 35–45.
- PERL, A., AVIV, D., WILLMITZER, L. & GALUN, E. (1991). *In vitro* tuberization in transgenic potatoes harboring β -glucuronidase linked to a patatin promoter: effects of sucrose levels and photoperiods. *Plant Science* **73**, 87–96.
- O'BRIEN, P. J. (1981). *Effects of seed crop treatments on the growth and yield of progeny tubers of early potato cultivars*. PhD thesis, University College of Wales, Aberystwyth.
- O'BRIEN, P. J., FIRMAN, D. M. & ALLEN, E. J. (1998). Effects of shading and seed tuber spacing on initiation and number of tubers in potato crops (*Solanum tuberosum*). *Journal of Agricultural Science, Cambridge* **130**, 431–449.
- RADLEY, R. W. (1963). The effect of season on growth and development of the potato. In *The Growth of the Potato* (Eds J. D. Ivins & F. L. Milthorpe), pp. 211–220. London: Butterworths.
- RAOUF, G. S. M. (1979). *Effects of physiological age of seed tubers in the early potato variety, Home Guard*. MSc thesis, University College of Wales, Aberystwyth.
- RAPHAEL, B. S. (1979). *Effects of foliar applications of nutrients on growth and yield of potatoes*. MSc thesis, University College of Wales, Aberystwyth.
- SALE, P. J. M. (1973). Productivity of vegetable crops in a region of high solar input. I. Growth and development of the potato (*Solanum tuberosum* L.). *Australian Journal of Agricultural Research* **24**, 733–749.
- SALE, P. J. M. (1976). Effect of shading at different times on the growth and yield of the potato. *Australian Journal of Agricultural Research* **27**, 557–566.
- SALE, P. J. M. (1979). Growth of potatoes (*Solanum tuberosum* L.) to the small tuber stage as related to soil temperature. *Australian Journal of Agricultural Research* **30**, 667–675.
- SALTER, P. J. & GOODE, J. E. (1967). Crop responses to water at different stages of growth. *Commonwealth Bureau of Horticulture, East Malling, UK* **2**, 93–97.
- SATO, K. (1981). Growth and development of potato plants influenced by combinations of air- and soil-temperatures. *Japanese Journal of Crop Science* **50**, 267–275.
- SLATER, J. W. (1963). Mechanisms of tuber initiation. In *The Growth of the Potato* (Eds J. D. Ivins & F. L. Milthorpe), pp. 114–120. London: Butterworths.
- SLATER, J. W. (1968). The effect of night temperature on tuber initiation of the potato. *European Potato Journal* **11**, 14–22.
- SMITH, O. (1931). A study of growth and development in the potato plant. *Proceedings of the American Society for Horticultural Science* **28**, 279–284.
- STEWART, F. C., MORENO, U. & ROCA, W. M. (1981). Growth, form and composition of potato plants as affected by environment. *Annals of Botany* **48**, (Supplement 2), 1–45.
- STRUIK, P. C. (1986). Effects of shading during different stages of growth on development, yield and tuber-size distribution of *Solanum tuberosum* L. *American Potato Journal* **63**, 457 (Abstract).
- STRUIK, P. C. & VAN VOORST, G. (1986). Effects of drought on the initiation, yield, and size distribution of tubers of *Solanum tuberosum* L. cv. Bintje. *Potato Research* **29**, 487–500.
- STRUIK, P. C., HAVERKORT, A. J., VREUGDENHIL, D., BUS, C. B. & DANKERT, R. (1990). Manipulation of tuber-size distribution of a potato crop. *Potato Research* **33**, 417–432.
- TOOSEY, R. D. (1964). The pre-sprouting of seed potatoes: factors affecting sprout growth and subsequent yield. Part II. Field growth and yield. *Field Crop Abstracts* **17**, 239–244.
- VAN LOON, C. D. (1981). The effect of water stress on potato growth, development, and yield. *American Potato Journal* **58**, 51–69.
- VAN SCHREVEN, D. A. (1956). On the physiology of tuber formation in potatoes. I. Premature tuber formation. *Plant and Soil* **8**, 49–56.
- WASSINK, E. C. & STOLWIJK, J. A. J. (1953). Effect of photoperiod on vegetative development and tuber formation in two potato varieties. *Mededelingen van de Landbouwhogschool Te Wageningen, Netherlands* **53** (5), 99–112.
- WENT, F. W. (1957). The experimental control of plant growth. *Chronica Botanica* **17**, 109–112.

- WERNER, H. O. (1934). The effect of controlled nitrogen supply with different temperatures and photoperiods upon the development of the potato plant. *Nebraska Agricultural Experimental Station, Research Bulletin* **75**, 1–132.
- WERNER, H. O. (1940). Response of two clonal strains of Triumph potatoes to various controlled environments. *Journal of Agricultural Research* **61**, 761–790.
- WURR, D. C. E. (1977). Some observations of patterns of tuber formation and growth in the potato. *Potato Research* **20**, 63–75.