

University of Warwick institutional repository: <http://go.warwick.ac.uk/wrap>

This paper is made available online in accordance with publisher policies. Please scroll down to view the document itself. Please refer to the repository record for this item and our policy information available from the repository home page for further information.

To see the final version of this paper please visit the publisher's website. Access to the published version may require a subscription.

Author(s): D. C. E. WURR, J. R. FELLOWS, J. M. AKEHURST, A. J. HAMBIDGE and J. R. LYNN

Article Title: The effect of cultural and environmental factors on potato seed tuber morphology and subsequent sprout and stem development

Year of publication: 2002

Link to published version:

<http://dx.doi.org/10.1017/S0021859600008431>

Publisher statement: None

---

# The effect of cultural and environmental factors on potato seed tuber morphology and subsequent sprout and stem development

---

D. C. E. WURR\*, J. R. FELLOWS, J. M. AKEHURST, A. J. HAMBIDGE AND J. R. LYNN

*Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK*

*(Revised MS received 5 July 2000)*

## SUMMARY

Seed crops of the variety Estima were grown in each of 2 years using two planting dates, two harvest dates, two plant densities and two irrigation regimes to produce seed tubers which had experienced different cultural and environmental conditions. The effects of these treatments on tuber characteristics, sprout production and stem development in the ware crop were then determined in subsequent experiments using storage regimes of 3 and 10 °C. Time of planting the seed crop affected numbers of eyes, sprouts and above ground stems in the subsequent ware crop because environmental conditions around the time of tuber initiation appeared to alter tuber shape. Cooler, wetter conditions in the 7 days after tuber initiation were associated with tubers which were longer, heavier and had more eyes, sprouts and above ground stems. In contrast, the time of harvesting the seed crop did not affect tuber shape or numbers of above ground stems and there was no interaction with tuber size. The density of the seed crop had no effect on any character measured and irrigation well after tuber initiation did not affect tuber shape, numbers of sprouts or numbers of stems. Seed production treatments, which resulted in earlier dormancy break, were associated with tubers that produced more sprouts and above ground stems, in contrast to the conventional understanding of apical dominance. Storage at 3 °C gave fewer sprouts, a lower proportion of eyes with sprouts and fewer stems than storage at 10 °C. The major effects on stem production appear to result from environmental conditions at the time of tuber initiation of the seed crop and sprouting temperature.

## INTRODUCTION

There are strong relationships between tuber yield and stem density (Bleasdale 1965; Jarvis 1977) and between tuber yield distribution in different size grades and stem density (Wurr 1974). Thus control over stem numbers is a fundamental requirement if growers are to control tuber size to meet market requirements. While it is known that the number of stems produced can be affected by the origin of seed (O'Brien & Allen 1986; Gill & Waister 1987) and cultural factors during seed production (O'Brien & Allen 1992) there seems to be little explanation of why this occurs. It is not known whether it occurs because of morphological differences between seed lots or because of inherent physiological differences in tuber dormancy and apical dominance or because of effects imposed between sprouting and stem emergence in the field.

Svensson (1966) reported that the number of eyes on a tuber of a given size differed between seed lots and this must be one potential cause of differences in sprout and stem growth. Additionally, there are many reports of agronomic factors influencing the date of dormancy break (Allen *et al.* 1992), though they concluded that appreciation of the controlling factors is poor and commercial manipulation largely unknown. This may be important because at dormancy break in suitable conditions the apical bud grows rapidly, displaying apical dominance by suppressing the growth of other buds (Allen *et al.* 1992). Thus treatment effects on dormancy break may also affect numbers of sprouts and stems.

Accordingly, the objective of this work has been to study the effects of environmental and cultural factors during seed production on tuber morphology, the date of dormancy break and numbers of sprouts and to determine the magnitude of and relationships between these effects.

\* To whom all correspondence should be addressed.  
Email: david.wurr@hri.ac.uk

## MATERIALS AND METHODS

### *Experiment 1*

In 1997 certified seed tubers (SE2) of the variety Estima were planted by hand on two occasions (18 April and 15 May) into prepared soil to which 180 kg N, 105 kg P and 200 kg K/ha had been applied and incorporated. The objective of this work was to produce progeny seed tubers under a range of cultural conditions so that eye and bud development could be compared on tubers of similar size. On each planting date there were eight plots representing all combinations of two spacings (15 and 30 cm) and four dates of defoliation at 14 day intervals. Plots were six, 76 cm rows wide and 6 m long and progeny tubers were harvested from 5 m of the four central rows. Plots were defoliated on 8 July, 22 July, 5 August and 19 August and harvested 14 days later (H1 to H4 respectively). Spray applications of pirimicarb and demeton-S-methyl were made as necessary to minimize aphid activity and cymoxanil + mancozeb + oxadixyl, chlorthalonil and fentin hydroxide to protect against blight infection. Temperatures in the air and in the potato ridges 5 cm above the seed tubers were recorded using thermistors connected to a portable data logger.

Tubers were dug by hand, cured for 14 days at 15 °C, graded into 5 mm size grades from 15 to 60 mm, re-cured for a further 14 days at 15 °C and then transferred to a cold store at 3 °C. In October, 20 tubers from each of the 16 treatments graded 35–40 mm were carefully cleaned in warm water and immediately dried. The tubers were split into two lots of ten for storage under two different temperature regimes using two replicates of five tubers each. Within each temperature regime the treatments were arranged in an incomplete block design, with each replicate comprising four blocks of four units of five potatoes. The four-level harvest-date factor was treated as two two-level pseudofactors. In one replicate the block effect was confounded with the four way interaction (planting date with density and both harvest-date pseudofactors), and two two-way interactions (planting date with one of the harvest-date pseudofactors, and density with the other harvest-date pseudofactor). In the other replicate the block effect was confounded with two three-way interactions (planting date with density and one harvest-date pseudofactor, and planting date with density and the other harvest pseudofactor), and with the two-way interaction between the two harvest-date pseudofactors.

A number of detailed measurements were then made on the tubers. The number of eyes was counted and each labelled appropriately, eye 1 being that found at the 'heel' end of the tuber closest to the point of stolon attachment. Subsequent eyes were located on the phyllotactic spiral progressing towards

the apex of the tuber. At the apical end a microscope was used to determine further distinct eyes, which were numbered, while any bud development which was not distinct was regarded as the apical cluster. The height of the main bud in the apical cluster was measured, together with tuber weight and the three major axes (length and two breadths).

Measurements were also made of the spatial location of the main bud in each eye using a purpose-built device. Tubers were held in a vertical position on a plastic disc mounted above a rotatable 360° protractor. A retractable stainless steel spike held in a collar, which slid up and down a calibrated column, determined the vertical location of each eye.

The tubers were stored at 10 °C or 3 °C throughout the winter in preparation for planting in 1998 to determine effects of seed production on numbers of stems produced. At both temperatures tubers were illuminated for 12 h daily by white fluorescent lighting once bud development started. Throughout the winter at 10 °C the length of the apical bud was measured weekly using a binocular microscope with a graticule, while at 3 °C this was done monthly. Once bud development was visible to the naked eye microscopic measurements were stopped and the length of the apical bud was measured manually every 3 to 4 weeks as it developed into a sprout.

Immediately before planting in the field the numbers and lengths of every sprout exceeding 2 mm in length were measured and recorded on individual tubers. On 12 May 1998 tubers were planted by hand 30 cm apart in 76 cm rows into prepared soil to which 180 kg N, 105 kg P and 200 kg K/ha had been applied and incorporated. Plots were 1.5 m long and one row wide. The blocking structure from storage was maintained, except that the strata of the storage temperatures and the replicates were reversed, so that the experiment was laid out as two replicates with each replicate containing two main-plots, one for each storage temperature. Each main-plot contained the four incomplete blocks of four plots described earlier. Three weeks after 80% emergence of a plot the plants in it were dug up and the number of above ground stems was counted.

### *Experiment 2*

In 1998 certified seed tubers (SE1) of the variety Estima were planted by hand on two occasions (30 April and 28 May) into prepared soil to which 180 kg N, 105 kg P and 200 kg K/ha had been applied and incorporated. At each planting date there were eight plots representing all combinations of two irrigation regimes (no irrigation and irrigation to keep the soil moisture deficit below 30 mm) and four dates of defoliation at 14 day intervals from 7 July. All tubers were planted 15 cm apart in plots the same size as those in Expt 1. Crop protection sprays were applied

and soil and air temperatures were measured as in Expt 1. The crop was harvested 14 days after defoliation (H1 to H4 respectively), cured, graded and re-cured as in Expt 1. The first harvest of the late planting failed to produce tubers of sufficient size for seed and so only 14 treatments were available for detailed studies. Eighty tubers from each plot, graded 35–40 mm, were carefully cleaned in warm water and immediately dried. Forty of these were stored at each of 3 and 10 °C in two replicates of 20 tubers arranged as a randomized block design. Eyes were counted and numbered and tuber weights and dimensions were recorded as previously, together with the vertical eye separation. Bud and sprout measurements were made as previously throughout storage and prior to planting in the field.

The seed tubers from the 14 treatments were planted by hand on 30 April 1999 in a randomized block design with two replicates, preserving the blocking structure from storage, except that again the replicate and storage-temperature strata were reversed in the field. Plots were 6 m long and one row wide. The number of stems was counted as previously.

### Experiment 3

The seed produced in Expt 2 was also used to study eye and bud characteristics on tubers of different sizes. Sixty tubers, graded 20–25, 30–35, 40–45 and 50–55 mm from all four harvests of the seed crop planted on 30 April 1998 and supplied with irrigation, were cleaned thoroughly in warm water and immediately dried. They were split into three replicates each containing 20 tubers in preparation for planting in the field in 1999. Eyes were numbered and counted and the direction of phyllotaxy recorded. The lengths of the apical bud, vertical eye separation and tuber weights and dimensions were recorded as previously. All tubers were stored at 3 °C and the length of the apical bud was measured monthly. Prior to planting the lengths of the buds in each eye were measured. Tubers were planted 30 cm apart by hand on 30 April 1999 in a randomized block design, preserving the blocking structure from storage. Plots were 6 m long and one row wide. Fourteen days after 80% emergence in each plot plants were carefully lifted and the number of stems determined.

### Statistical analysis

The data from all the experiments were subjected to analysis of variance using the Genstat 5 (Payne *et al.* 1993) computer package. In the analysis of the field components of Expts 1 and 2, the blocking structure used in the analysis was that of the field layout. In all analyses of these two experiments differences between the two storage regimes were attributed to storage

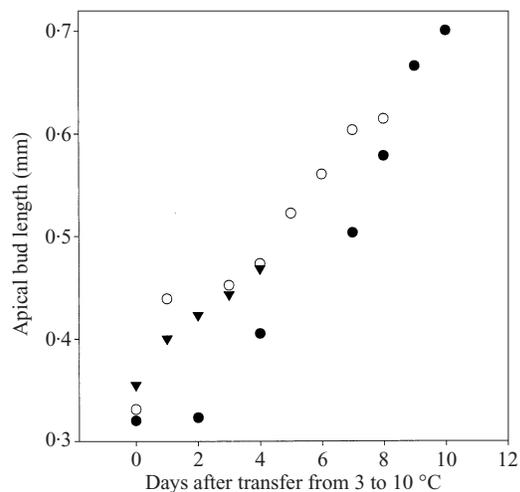


Fig. 1. Microscopic measurement of the elongation of the apical bud. ●, moved on 4 January 1999; ○, moved on 14 January 1999; ▼, moved on 18 January 1999.

temperature. In the analyses of Expt 1, information about the treatment means was combined from the unit and incomplete block strata using the method of Payne & Tobias (1992).

### Determination of date of dormancy break

To establish a standard procedure for estimation of the time of dormancy break in these experiments, three samples of ten tubers of cv. Estima were moved from 3 to 10 °C on 4, 14 and 18 January 1999 and apical bud length was measured at frequent intervals using a microscope. Figure 1 shows that the apical bud starts to elongate from about 0.3 mm. Potato tuber dormancy is usually defined as lasting from tuber initiation until a sprout 2 mm long is formed in conditions optimal for sprouting (Van Ittersum *et al.* 1992). However, Van Ittersum *et al.* (1992) found that buds grew for about 20 days to reach 2 mm in length and questioned whether this was a good criterion. Here we chose a standard value of 0.5 mm bud length as indicating that buds were definitely elongating and therefore dormancy was broken and for all data sets the time when bud length was 0.5 mm was estimated by linear interpolation.

## RESULTS

In Expt 1 there was no effect of the density of the seed crop on any character measured and so this treatment factor is subsequently ignored. In Expt 2 the analyses, and therefore the errors quoted, ignored harvest 1 in order to include data from both planting dates, because there were no tubers from harvest 1 of the

Table 1. *Effects of planting date*

Character	Expt 1				Expt 2			
	Early	Planting date		D.F.	Early	Planting date		D.F.
		Late	S.E.D.			Late	S.E.D.	
Tuber weight (g)	40.9	43.1	0.64	18	43.2	37.3	0.78	11
Tuber length (mm)	51.6	54.4	0.51	18	53.9	47.8	0.65	11
Number of eyes	6.4	7.4	0.12	18	8.1	7.4	0.08	35
Vertical separation (mm) Apex to eye 1	32.6	38.5	1.24	9	35.6	35.5	1.46	11
Vertical separation (mm) Apex to eye 2	13.6	20.7	1.19	9	13.2	15.2	2.16	11
Vertical separation (mm) Apex to eye 3	3.6	7.9	0.81	9	4.4	3.7	0.93	11
Vertical separation (mm) Apex to eye 4	1.1	2.6	0.56	9	0.9	0.6	0.41	11
Day of dormancy break*	387	377	2.5	18	335	357	2.1	11
Number of sprouts > 2 mm at planting	2.9	3.6	0.15	18	3.1	3.1	0.10	23
Percentage eyes producing sprouts > 2 mm	45.8	48.3	2.24	18	38.6	41.4	1.23	23
Number of above ground stems	3.3	3.4	0.12	18	4.0	3.5	0.09	23

\* 1 = 1 January in year of seed production.

Table 2. *Effects of harvest date*

Character	Expt 1						Expt 2					
	H1	H2	Harvest		S.E.D.	D.F.	H1†	H2	Harvest		S.E.D.	D.F.
			H3	H4					H3	H4		
Tuber weight (g)	40.7	42.9	43.1	41.4	0.91	18	(42.8)	39.1	40.2	41.4	0.95	11
Tuber length (mm)	53.6	53.0	53.4	51.8	0.74	18	(54.3)	51.1	50.1	51.4	0.79	11
Number of eyes	7.5	6.8	6.6	6.7	0.19	18	(8.6)	8.0	7.7	7.6	0.09	35
Vertical separation (mm) Apex to eye 1	38.3	37.9	32.2	33.7	2.15	9	(33.6)	35.0	34.8	36.9	1.78	11
Vertical separation (mm) Apex to eye 2	22.1	17.3	12.3	16.7	2.06	9	(11.0)	14.0	12.6	16.1	2.64	11
Vertical separation (mm) Apex to eye 3	8.6	5.5	3.6	5.5	1.40	9	(5.8)	4.5	4.0	3.7	1.14	11
Day of dormancy break*	378	384	386	379	3.5	18	(339)	344	346	348	2.5	11
Number of sprouts > 2 mm at planting	4.0	3.0	3.1	2.9	0.22	18	(3.5)	3.2	3.2	2.9	0.12	23
Percentage eyes producing sprouts > 2 mm	52.8	43.6	47.1	44.8	3.30	18	(40.5)	40.3	42.1	37.6	1.51	23
Number of above ground stems	3.2	3.4	3.5	3.3	0.17	18	(4.1)	3.6	3.8	3.7	0.11	23

\* 1 = 1 January in year of seed production.

† Numbers in parentheses are from the early planting and were not used to generate the S.E.D.s.

Table 3. *Effects of sprouting temperature*

Character	Expt 1				Expt 2			
	Sprouting temperature (°C)				Sprouting temperature (°C)			
	3°	10°	S.E.D.	D.F.	3°	10°	S.E.D.	D.F.
Number of sprouts > 2 mm at planting	2.1	4.4	0.31	18	1.3	4.9	0.10	23
Percentage eyes producing sprouts > 2 mm	29.2	64.9	4.17	18	17.5	62.4	1.23	23
Number of above ground stems	3.3	3.4	0.04	18	3.4	4.0	0.09	23

late planting. Data from harvest 1 of the early planting are included in parentheses. All the effects quoted here are significant at  $P \leq 0.05$ . There were few significant interactions and the data are presented showing main effects only.

#### *Effects of planting date – Expts 1 and 2*

In Expts 1 and 2 there were contrasting effects of the time of planting the seed crop on tuber characters (Table 1). In Expt 1 late planting produced tubers

Table 4. *Effects of tuber size*

Character	Tuber size (mm)				S.E.D.	D.F.
	20-25	30-35	40-45	50-55		
Number of eyes	5.4	7.8	9.6	10.8	0.16	30
Vertical separation (mm) Apex to eye 1	13.9	28.6	40.0	52.6	1.49	30
Vertical separation (mm) Apex to eye 2	2.5	8.8	14.6	26.3	1.31	30
Vertical separation (mm) Apex to eye 3	0.3	1.7	5.1	9.6	0.85	30
Vertical separation (mm) Apex to eye 4	0.1	0.5	1.9	4.5	0.60	30
Day of dormancy break*	417	398	377	363	5.2	30
Number of sprouts > 2 mm at planting	0.0	0.3	1.3	1.9	0.18	30
Number of above ground stems	1.8	3.3	4.2	5.5	0.13	30

\* 1 = 1 January in year of seed production.

Table 5. *Correlation coefficients between tuber, sprouting and stem characters. Values in bold indicate significance (P < 0.05)*

Expt 1 3 °C D.F. 14						
Weight	1.000					
Length	<b>0.679</b>	1.000				
Number of eyes	0.366	<b>0.777</b>	1.000			
DB	0.084	-0.225	<b>-0.601</b>	1.000		
Number of sprouts > 2 mm	-0.118	0.319	<b>0.622</b>	-0.481	1.000	
Above ground stems (AGS)	0.435	<b>0.774</b>	<b>0.706</b>	-0.420	0.376	1.000
	Weight	Length	Number of eyes	DB	Number of sprouts > 2 mm	AGS
Expt 2 3 °C D.F. 10						
Weight	1.000					
Length	<b>0.944</b>	1.000				
Number of eyes	0.575	<b>0.766</b>	1.000			
DB	-0.435	-0.536	-0.401	1.000		
Number of sprouts > 2 mm	-0.162	-0.013	0.026	<b>-0.676</b>	1.000	
Above ground stems	0.504	0.548	0.569	-0.066	-0.020	1.000
	Weight	Length	Number of eyes	DB	Number of sprouts > 2 mm	AGS
Expt 1 10 °C D.F. 14						
Weight	1.000					
Length	<b>0.866</b>	1.000				
Number of eyes	<b>0.497</b>	<b>0.755</b>	1.000			
DB	-0.248	-0.307	<b>-0.541</b>	1.000		
Number of sprouts > 2 mm	0.467	<b>0.533</b>	<b>0.728</b>	-0.287	1.000	
Above ground stems	0.491	0.337	-0.116	0.262	-0.061	1.000
	Weight	Length	Number of eyes	DB	Number of sprouts > 2 mm	AGS
Expt 2 10 °C D.F. 10						
Weight	1.000					
Length	<b>0.944</b>	1.000				
Number of eyes	0.575	<b>0.766</b>	1.000			
DB	-0.435	-0.536	-0.401	1.000		
Number of sprouts > 2 mm	0.132	0.111	0.329	0.427	1.000	
Above ground stems	<b>0.706</b>	<b>0.635</b>	0.144	<b>-0.694</b>	-0.433	1.000
	Weight	Length	Number of eyes	DB	Number of sprouts > 2 mm	AGS

DB, Day of dormancy break.

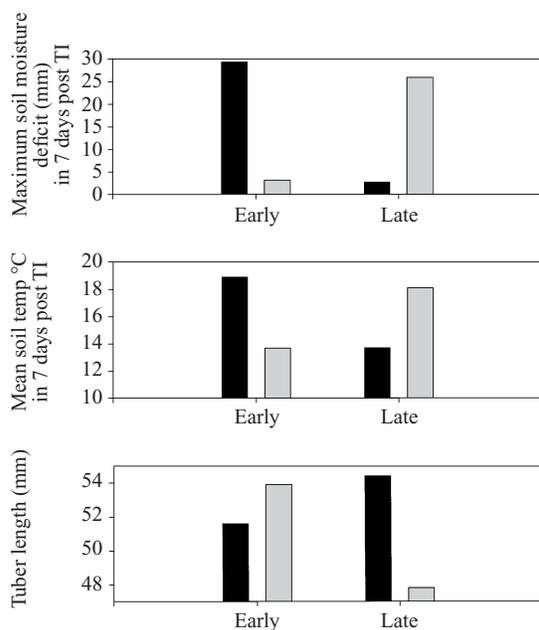


Fig. 2. The effect of planting date in 1997 and 1998 on soil moisture deficit and soil temperature immediately after seed tuber initiation (TI) and the subsequent effect on the length of tubers graded 35–40 mm. ■, 1997; ▒, 1998. TI is an estimate of the day of tuber initiation, 21 days after emergence.

which were heavier and longer and had more eyes and sprouts > 2 mm at planting than tubers from early planting. However, the reverse was true in Expt 2 with late planting resulting in tubers which were lighter and shorter, had fewer eyes, broke dormancy later, and gave fewer stems in the field, though there was no effect on the number of sprouts > 2 mm at planting. In Expt 2 early-planted seed broke dormancy 22 days before late-planted seed and reduced the proportion of eyes that produced sprouts > 2 mm at planting. In Expt 1 late-planted seed produced eyes 1 to 4 that were further from the apex than early-planted seed but there was no effect in Expt 2.

#### *Effects of harvest date – Expts 1 and 2*

In neither experiment was there a significant effect of harvest date on tuber weight or length but there were effects on numbers of eyes and sprouts > 2 mm in length at planting (Table 2). In Expt 1 numbers of eyes and sprouts > 2 mm and the proportion of eyes producing sprouts > 2 mm were significantly higher in seed from the first harvest. In Expt 2 seed from harvest 2 produced more eyes than seed from harvests 3 and 4 and harvests 2 and 3 gave more sprouts > 2 mm than harvest 4. In Expt 1 there was a significant effect on the date of dormancy break with seed from harvest 1 breaking dormancy first. There

were also significant effects of harvest date in Expt 1 on the vertical separation of eyes from the apex with harvest 1 producing eyes 1 to 3 that were further from the apex than other harvests.

#### *Effects of irrigation and storage temperature – Expts 1 and 2*

In Expt 2 irrigation did not affect tuber weight or length but did increase the number of eyes (7.9) relative to no irrigation (7.6, S.E.D. 0.08, D.F. 35) and delayed dormancy break by 18 days (day 355) relative to non-irrigated seed (day 337, S.E.D. 2.1, D.F. 11). Irrigation had no effect on the number of sprouts > 2 mm at planting or on the number of stems but did reduce the proportion of eyes giving sprouts > 2 mm at planting (irrigation 38.6%, no irrigation 41.3%, S.E.D. 1.23, D.F. 23).

In both experiments (Table 3) storage at 3 °C gave significantly fewer sprouts > 2 mm at planting, a lower percentage of eyes resulting in sprouts > 2 mm and fewer above ground stems than storage at 10 °C.

#### *Effects of tuber size – Expt 3*

In Expt 3 (Table 4) as tuber size increased so the numbers of eyes increased, eyes 1 to 4 were further from the apex, tubers broke dormancy earlier and produced more sprouts > 2 mm at planting and more above ground stems. There were no interactions between tuber size and harvest date affecting number of sprouts and above ground stems.

#### *Correlations between characters*

Correlation coefficients were calculated between seed, sprout and stem characters in Expts 1 and 2, with separate correlations for tubers stored at 3 and 10 °C because the data were discrete (Table 5). At 3 °C, tuber weight, numbers of eyes and above ground stems increased with tuber length. Tubers with more eyes broke dormancy earlier and gave increased numbers of sprouts and stems in Expt 1 while in Expt 2 earlier dormancy break was associated with more sprouts.

At 10 °C, numbers of sprouts > 2 mm increased with tuber length in Expt 1 and in Expt 2 above ground stems also increased with tuber length. Tubers with more eyes broke dormancy earlier and gave more sprouts > 2 mm in Expt 1. In Expt 2 earlier dormancy break increased the number of above ground stems.

#### *Relationships with environmental characters*

Firman *et al.* (1991) found that, over a range of planting dates, the time from emergence to tuber initiation in Estima was approximately 21 days. This information was used to estimate the time of tuber

initiation in Expts 1 and 2 from the known dates of emergence. The soil moisture deficit and the soil temperature at seed tuber depth were summarized over three weekly time periods, the first beginning at tuber initiation, in an attempt to explain why the time of planting in Expts 1 and 2 had contrasting effects on seed tuber length. Figure 2 shows that longer tubers were associated with wetter and cooler conditions in the 7 days after tuber initiation.

## DISCUSSION

Seed tubers have a variable number of buds contained in groups within eyes which are arranged in a phyllotactic spiral over the surface of the tuber (Allen *et al.* 1992). The number of lateral buds which separate from the apical bud and form distinct eyes depends upon the extent of tuber development and Allen *et al.* (1992) showed that the number of eyes on a tuber increases with size but at a decreasing rate. Allen *et al.* (1992) observed that there were at least 10 times more potential growing points on seed tubers than stems which ultimately grew. Thus in understanding the effect of various factors on numbers of stems it may be more appropriate to consider those restricting the development of stems rather than those which promote it.

Above ground stems are recognized as the best practical estimate of density in the potato crop (Allen & Wurr 1992). They develop from sprouts, which in turn grow from eyes on the tuber surface. While it is known that differences in stem density can result from differences in the sprouting regime (Allen *et al.* 1992) they can also occur as a result of seed origin (O'Brien & Allen 1986; Gill & Waister 1987). Thus seed production must influence characteristics of seed tubers, which in turn affect the number of sprouts and stems produced. The work described here has attempted to determine which those characteristics are and how they affect numbers of sprouts and stems. It has compared seed tuber weight, length, number of eyes, date of dormancy break, sprout growth and stem development on seed tubers produced at the same site in different ways and graded to a common close standard. This is inevitably an artificial comparison because it is unlikely that different batches of seed would grade out identically. However, since the number of eyes increases with tuber size it is the fairest way of comparing the effect of cultural and environmental differences on basic tuber characteristics of seed produced at one location.

The results show that the times of planting affect tuber characteristics, though in contrasting ways in the two years. There was no consistent effect of planting date per se but longer tubers were consistently heavier and produced more eyes, sprouts and stems. This suggests that differences in the environmental conditions in the two years affected tuber size, which

then resulted in subsequent effects on other tuber characteristics. Indeed, estimates of soil moisture deficit and soil temperature showed that longer tubers were associated with cooler, wetter conditions in the period around tuber initiation. This finding is supported by evidence from Martin *et al.* (1931) who reported longest tubers in years of greatest rainfall and Neumann (1925) who found elongated tubers on heaviest soils. These results therefore suggest that wetter conditions around tuber initiation may result in longer tubers, with more eyes differentiating away from the apex, and increased numbers of sprouts and stems. This could help explain why seed from different sources is known to differ in its ability to produce stems in the ware crop. Why then did irrigation during Expt 2 have no effect on tuber shape, numbers of sprouts and stems? Certainly one reason is that in the 7 days after tuber initiation the maximum soil moisture deficits observed were the same from the wet and dry treatments (3 mm – early planting; 26 mm – late planting) because they were below the 30 mm used to trigger irrigation, which was applied later.

This effect on tuber shape must have been imposed at a very early stage in tuber development because there was no effect of harvest date on tuber shape. However, there was a tendency for seed harvested earlier to have more eyes, break dormancy earlier and produce more sprouts without significantly affecting numbers of stems. The reduction in the number of eyes with later harvest is interesting. Tubers of the same size from a later harvest must have grown slower than those from an earlier harvest and this suggests that slower growing tubers differentiate fewer eyes away from the apex.

Allen *et al.* (1992) observed that few of the many reports of agronomic factors influencing dormancy break have used carefully controlled experiments. They found that dormancy was shortened by defoliation of crops with full leaf canopies while later defoliation had no effect. Our results confirm the limited nature of these effects. Thus seed tubers of the same size, harvested over a 6-week period and which have therefore grown at different rates, have a similar shape and ability to produce stems, while in contrast, different environmental conditions at tuber initiation can have a subsequent effect on stem production. Although this point was demonstrated in experiments which used just one tuber size (Expts 1 and 2), Expt 3 suggested that these effects would apply to seed tubers of all sizes since it showed that there was no interaction between tuber size, ranging from 20 to 55 mm, and harvest date.

Growing conditions and cultural practices have been shown to influence tuber dormancy (Van Ittersum 1992). Conventionally, the effect of apical dominance is regarded as restricting the numbers of buds and sprouts developing (Allen *et al.* 1992). Thus

temperatures suitable for sprout growth at dormancy break result in few sprouts because of apical dominance and this might therefore reduce stem numbers. According to Moorby (1978), the first bud to be released from dormancy and start growing is usually the apical bud. One might therefore expect that the seed production treatments we applied and which resulted in earlier dormancy break, would produce fewer sprouts. However the evidence that we collected is largely to the contrary. In Expt 1 harvest 1 gave the earliest dormancy break and the most sprouts. Furthermore, the correlation matrices showed that earlier dormancy break was associated with more eyes, sprouts and stems. In addition to this we also found that effects of storage temperatures on apical dominance did not reduce sprout and stem numbers. Thus the conventional botanical view of treatment effects on apical dominance does not necessarily apply in practice. It seems unlikely that effects on dormancy break resulting from the seed production regimes used here have a major influence on stem numbers. However, the differences in dormancy break resulting from the planting dates were not large possibly because tuber initiation of the two plantings only differed by 15 days in Expt 1 and 26 days in Expt 2. In practice the effects of planting date could be much larger creating ranges in the timing of dormancy break which will affect numbers of stems per seed tuber.

It is possible that the effect of tuber shape on other characters is purely physical with longer tubers differentiating more eyes away from the apical bud. Indeed, this hypothesis would also explain why larger tubers produce more sprouts. Although larger tubers have more eyes, these do not necessarily give more stems; instead the fact that eyes at the 'heel' end are further away from the apex may be the key factor by diluting the effect of apical dominance. Here effects of tuber size were as expected and the range of eye numbers from 5.4 (20–25 mm) to 10.8 (50–55 mm) for Estima is comparable with ranges of 6.8 to 12.2 (Pentland Crown), 7.0 to 13.4 (Majestic), 7.2 to 12.1 (King Edward) and 6.3 to 10.8 (Desiree) in studies carried out 25 years ago (Wurr & Barnes 1977).

The results reported here go some way towards explaining and quantifying effects of seed production practices on the fundamental physical characteristics of batches of seed tubers and their potential for subsequent growth. They suggest that in order to understand effects of the site of seed production on stem development more attention needs to be paid to soil conditions around the time of tuber initiation.

We thank Cambridge University Farm for providing seed and the Ministry of Agriculture, Fisheries and Food for funding this work.

## REFERENCES

- ALLEN, E. J., O'BRIEN, P. J. & FIRMAN, D. (1992). Seed tuber production and management. In *The Potato Crop. The Scientific Basis for Improvement. 2nd edition* (Ed. P. M. Harris), pp. 247–291. London: Chapman & Hall.
- ALLEN, E. J. & WURR, D. C. E. (1992). Plant density. In *The Potato Crop. The Scientific Basis for Improvement. 2nd edition* (Ed. P. M. Harris), pp. 292–333. London: Chapman & Hall.
- BLEASDALE, J. K. A. (1965). Relationships between set characters and yield in maincrop potatoes. *Journal of Agricultural Science, Cambridge* **64**, 361–366.
- 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.
- GILL, P. A. & WAISTER, P. D. (1987). Factors influencing stem number per tuber. *Potato Research* **30**, 140.
- JARVIS, R. H. (1977). An assessment of the value of different sizes of seed potatoes of maincrop varieties. *Experimental Husbandry* **32**, 102–114.
- MARTIN, W. H., BROWN, B. E. & SPRAGUE, H. B. (1931). The influence of nitrogen, phosphoric acid and potash on the number, shape and weight of potato tubers. *Journal of Agricultural Research* **43**, 231–260.
- MOORBY, J. (1978). The physiology of growth and tuber yield. In *The Potato Crop. The Scientific Basis for Improvement* (Ed. P. M. Harris), pp. 153–194. London: Chapman & Hall.
- NEUMANN, H. (1925). The effect of environmental conditions on the potato tuber (translated title). *Journal für Landwirtschaft* **73**, 7–38, abstracted in *Experimental Station Record* (1926) **54**, 638–639.
- O'BRIEN, P. J. & ALLEN, E. J. (1986). Effects of site of seed production on seed yields and regrowth of progeny tubers in potatoes. *Journal of Agricultural Science, Cambridge* **107**, 83–101.
- O'BRIEN, P. J. & ALLEN, E. J. (1992). Effects of seed crop husbandry, seed source, seed tuber weight and seed rate on the growth of ware potato crops. *Journal of Agricultural Science, Cambridge* **119**, 355–366.
- PAYNE, R. W., LANE, P. W., DIGBY, P. G. N., HARDING, S. A., LEECH, P. K., MORGAN, G. W., TODD, A. D., THOMPSON, R., TUNNICLIFFE WILSON, G., WELHAM, S. J. & WHITE, R. P. (1993). *Genstat 5 Release 3*. Reference Manual. Oxford: Oxford University Press.
- PAYNE, R. W. & TOBIAS, R. D. (1992). General balance, combination of information and the analysis of covariance. *Scandinavian Journal of Statistics* **19**, 3–23.
- SVENSSON, B. (1966). Seed tuber – stand – yield. Properties and relationships. *Växtodling* **21**, 86.
- VAN ITTERSUM, M. K. (1992). *Dormancy and growth vigour of seed potatoes*. Ph.D. thesis, Wageningen Agricultural University.

- VAN ITTERSUM, M. K., ABEN, F. C. B. & KEIJZER, C. J. (1992). Morphological changes in tuber buds during dormancy and initial sprout growth of seed potatoes. *Potato Research* **35**, 249–260.
- WURR, D. C. E. (1974). Some effects of seed size and spacing on the yield and grading of two maincrop potato varieties. I. Final yield and its relationship to plant population. *Journal of Agricultural Science, Cambridge* **82**, 37–45.
- WURR, D. C. E. & BARNES, A. (1977). The influence of some seed potato production techniques on basic tuber characteristics. *Journal of Agricultural Science, Cambridge* **89**, 285–289.