# Accumulated day-degrees as a measure of physiological age and the relationships with growth and yield in early potato varieties

By P. J. O'BRIEN\*, E. J. ALLEN\*, J. N. BEAN, R. L. GRIFFITH, SUSAN A. JONES\* AND J. L. JONES\*

Department of Agriculture (Crop Husbandry), University College of Wales, Aberystwyth

(Revised MS. received 30 March 1983)

## SUMMARY

Data from nine experiments from 1973 to 1981 which examined the effects of physiological age on sprout and field growth of early potato varieties are reported. Length of longest sprout per tuber and all aspects of field growth were related to number of daydegrees > 4 °C experienced by the seed after onset of sprout growth (measured as the appearance of a 3 mm sprout). It is, therefore, suggested that this scale is an effective measure of physiological age. In Home Guard and Maris Bard, increasing age of seed tubers resulted in earlier emergence and tuber initiation, larger early leaf areas and increased early tuber yields. As growth proceeded young seed produced the largest and most persistent leaf areas and the yields surpassed those of older seed and in some experiments yields decreased with increasing age at the final harvests.

Optimum ages for specific harvesting periods were determined from regressions of tuber yield on age. In both varieties, they decreased with delay in harvesting. However, optimum ages differed in the two varieties and the implications for production and storage of seed and testing of varieties are discussed.

## INTRODUCTION

About a quarter of maincrop potatoes and all early potatoes are sprouted before planting (Potato Marketing Board, 1968a, b). Many experiments have studied the effects of sprouting on growth and yield; generally sprouting increased yields at early harvests but as harvesting was delayed the effect decreased and was even reversed at late harvests (e.g. Younger, 1975). There is considerable variation in the results and as a consequence debate continues as to the merits of sprouting and the most desirable practices to follow. Much of the difficulty in interpretation of experimental results on sprouting is a consequence of the descriptive nature of the term 'sprouting'. This is used to cover a whole range of circumstances which allow some growth of the seed tuber to take place before planting. Sprouting is usually described as a period of time allowed for growth, and its effects are illustrated by the numbers and lengths of sprouts present at planting. Sprout growth does not commence until the end of dormancy, which is variable in time,

\* Present address: Department of Applied Biology, University of Cambridge, Cambridge. and is then determined by prevailing temperatures, light intensities and the condition of the seed tuber when first exposed to temperatures conducive to growth (Wurr, 1978a). Consequently, similar periods for sprouting can produce large differences in sprout growth, especially if temperatures are variable. As many of the factors affecting sprout growth are commonly not recorded, even within one variety, the term sprouting is unsatisfactory for comparing experiments. These variations in sprout growth are important, for Madec & Perennec (1955) have demonstrated that the amount of sprout growth at planting, which they termed physiological age, markedly altered the leaf growth pattern in the field, and suggested that effects were progressive as older and older seed was used. Although the effects reported by Madec & Perennec were quite clear and have subsequently been confirmed by other authors (Scott & Younger, 1973) the usefulness of the effects for controlling field growth has been limited by inability to measure the causal factor and consequently to produce seed of the required physiological age. No scale based on time alone can be an adequate measure of the ageing process because of the effects of temperature and the varying time of onset of sprout growth.

	No. of day- degrees > 4° C of treaments	0: 208: 432:	656; 880 0; 208; 376;	544; 792; 920 0; 184; 424; 584;	864; 1056; 1168 0; 144; 288; 432;	576; 720; 864; 1008	0; 112; 224; 336; 448; 560; 672;	, 134 0; 168; 336, 504; 672; 840
	No. of replicates	e	4	ę	ŝ		en	t
	No. of ages	, rů	9	٢	œ		œ	9
	Planting	3. iii	4. iv	9. iv	17. iv		6. iv	31.iii
Dates of	End of storage	ard 1. iii	10. iii	10. iii	3. iii		rd 30. iii	24.iii
	Entry of seed to 12 °C	Variety, Home Guard 27. x	18. xi	7. xi	12. x		Variety, Maris Bard 11. x	19. x
	Plot size	Vari 9 rowe	6-4 m 11 rows	4-62 m 7 rows	4-84 m 5 rows	4·5 m	Var 5 rows 4-95 m	5 гоwв 4.95 m
	Seed weight (g)	65-80	6580	55-70	<u> 90–100</u>	100-110 110-120	50-60 60-70	60-75
	Source of seed	1975–6 Scottish 'FS'	1976-7 Scottish 'FS'	1976–7 Once grown	1978-9 Once grown	•	1979-80 Once grown	1980-1 Once grown
	Үевг	1975-6	1976-7	1976-7	1978-9		1979-80	1980–1
	Experiment	4	ũ	9	7		œ	6

Table 1. Details of Expts 4-9

.

# P. J. O'BRIEN AND OTHERS

.

## Downloaded from http://www.cambridge.org/core. Faculty of Classics, University of Cambridge, on 24 Nov 2016 at 15:47:35, subject to the Cambridge Core terms of use, available at http://www.cambridge.org/core/terms. http://dx.doi.org/10.1017/S002185960003865X

Allen et al. (1979), noting the similarity of effect of lengthening the period of sprouting and increasing the temperature, suggested that the causal factor in physiological age was probably temperature and that a measure of age may be obtained by integration of the temperature experienced by the seed tuber during sprout growth. As physiological age was known to affect growth pattern it was further suggested that yields may be related to this measure of age. As was briefly reported good relationships were indeed found between physiological age, measured as day-degrees > 0 °C during sprout growth and yields. This paper presents the full analysis of those data and data from six experiments which tested the hypothesis that physiological age of seed tubers may be measured by accumulated day-degrees and related to growth and yields in the varieties Home Guard and Maris Bard. The analysis determined the relationship between sprout growth and temperature, the most

### THE EXPERIMENTS

appropriate scale for measurement of physiological

age and the relationship with field yields.

Data from the three experiments (Expts 1-3) reported by Allen et al. (1979) were used in these analyses. Six further experiments were carried out in which a range of physiological ages (measured as day-degrees > 4 °C) were produced. Seed tubers were put in travs in early October and placed in an illuminated, controlled-temperature cabinet set at 12 °C. When 90% of tubers had sprouts > 3 mm, dormancy was considered over, and from this time seed lots were moved at 3- to 4-week intervals to a similar cabinet set at 4 °C. A range of accumulated day-degrees were achieved with relatively small differences in number of sprouts per tuber. The details of Expts 4-9 are given in Table 1. Numbers and length of sprouts were recorded on ten randomly selected tubers in each replicate of all treatments at the end of controlled-temperature storage. Seed in all experiments was removed from controlled temperatures in Aberystwyth in anticipation of planting. In Expt 4 planting occurred within 2 days but Expts 5, 6 and 7 were out of controlled-temperature storage for 3-4 weeks as planting was delayed by persistent cold, wet weather. The seed was stored in an unheated barn and, consistent with the prevention of frost, temperatures were maintained as low as possible. Some limited sprout growth occurred during these periods on all treatments. However, no records of temperatures are available, so the day-degrees used in the analysis refer only to the period of controlled-temperature storage. The unknown day-degrees were not large, but they must be considered when comparing optimum ages derived from the different experiments. In Expts 8 and 9 seed was kept at  $4 \degree C$  for 7 days before planting at Trefloyne.

Experiments 4-8 used randomized-block designs and were carried out at Trefloyne in a similar way to Expts 1-3. In Expt 9 a split-plot design was used with two irrigation treatments as main plots. no supplementary water and trickle irrigation to maintain soil-moisture deficits below 30 mm. Water use was measured with a neutron probe on plots of 0, 504 and 840 day-degrees, and application of water for other plots determined by comparison of their leaf area indices with those of the recorded plots. Rainfall was sufficiently well distributed in May and June to maintain small soil-moisture deficits until 29 June, when 30 mm of water was applied to all irrigated plots. On 9-12 July a further 44 mm was applied to plots of 0-504 daydegrees and 26 mm to the two older treatments. Soil moisture deficits on unirrigated plots increased during July and exceeded 70 mm in all plots by final harvest. Soil-moisture deficits on irrigated plots were approximately 30 mm for most of late July and early August, but no further application of water was made. Plant spacing was 22.5 cm in 71 cm rows for Expts 4-9. Soil conditions were good in Expts 4, 6-9 but rather cloddy in Expt 5. No outbreak of potato blight was found in these experiments, and aphids were also well controlled.

Experiments 4 and 5 were sampled intensively in the early stages of growth in order to record tuber initiation in detail. Three plants per plot were dug by hand every 3 or 5 days until tuber initiation was complete and then at fortnightly intervals until final harvest in July. The date of tuber initiation was calculated as the mean of the dates for each replicate when all plants in two consecutive samples had tubers. (A tuber was defined as a swelling twice the diameter of the stolon.) Methods of sampling, division of plants and drying techniques were as previously described (Allen et al. 1979). Emergence and number of above-ground stems were recorded at approximately weekly intervals using one harvest row. Tuber yield was assessed on four occasions in Expts 4, 5 and 8, three occasions in Expts 6 and 7 and five occasions in Expt 9, using a 4.40 m length of row in Expt 4, 2.64 m in Expts 5 and 6, 2.25 m in Expt 7 and 2.03-2.7 m in Expts 8 and 9. Methods of harvesting and grading were as previously described (Allen et al. 1979).

In Expts 5-9 tubers less than 13 mm were discarded at grading but in all other experiments all tubers were counted. The weather conditions in the first 3 years, 1973-5, were given in the previous paper. In 1976 soil conditions were good but temperatures were extremely high and little rain fell after mid-May, so that growth was restricted from late June onwards. In 1977, 1979 and 1980



Number of day-degrees > 4 °C

Fig. 1. Relationship between length of longest sprout per tuber and number of day-degrees > 4 °C, Home Guard. y = 4.1 + 0.075x,  $R^{s} = 0.89$ .  $\bigcirc$ , Expt 1;  $\bigcirc$ , Expt 4;  $\bigcirc$ , Expt 5;  $\blacktriangle$ , Expt 6; ×, Expt 7;  $\triangle$ , Raouf (1979) for 1976-7.



Fig. 2. Relationship between length of longest sprout per tuber and number of day-degrees > 4 °C.  $\triangle$ , Pentland Javelin,  $y = 2\cdot8 + 0\cdot0115x$ ,  $R^2 = 0.94$ ;  $\bigcirc$ , Vanessa, Expt 3,  $y = 4\cdot1 + 0\cdot017x$ ,  $R^2 = 0.92$ .



Fig. 3. Relationships between plant emergence and number of day degrees > 4 °C in Home Guard, Expt 5.  $\bigcirc$ , 5 May;  $\square$ , 10 May;  $\triangle$ , 20 May.



Fig. 4. Relationships between plant emergence and number of day-degrees > 4 °C in Maris Bard, Expt 9.  $\bigcirc$ , 22 April;  $\triangle$ , 8 May.

rainfall was average and well distributed throughout most of the growing season but soil conditions were poorer in 1977 than in other years.

## RESULTS

The data were subjected to both analysis of variance and regression analysis using linear and quadratic functions only. Presentation of the data is in the form of relationships between measurements of sprout or field growth and age, measured as accumulated day-degrees > 4 °C. In order to determine the most appropriate method of calculating the accumulated day-degrees, various starting points and base temperatures were used and the tuber yields regressed on the various scales. No scale produced better fits to the data than number. of day-degrees > 4 °C after onset of sprout growth. and some explained considerably less of the variation in yields. Individual treatment differences are not discussed. The functions used were limited and no biological meaning can be attributed to their significance. Moreover, in certain cases the shape of the fitted curve would imply biological nonsense and specific comment is made. From the negative quadratic relationships optimum ages were derived.

## Sprout growth

In Home Guard there were poor relationships between total sprout length and accumulated daydegrees in Expts 1 and 2 and close linear relationships in Expts 4-7. However, in all experiments there were close linear relationships between length of longest sprout and accumulated day-degrees. A common regression covering all experiments and the data of Raouf (1979) was highly significant (Fig. 1). For Vanessa in both Expts 2 and 3 and Pentland Javelin in Expt 3 similar significant relationships between length of longest sprout and accumulated day-degrees were found (Fig. 2). Similar close relationships were found in Maris Bard.

#### Field growth

In Home Guard the effects of age on field growth were similar in all experiments; in Vanessa and Pentland Javelin the effects were in the same direction but much smaller in magnitude. The most detailed growth analyses were carried out in Expts 4-7 (Home Guard) and 8-9 (Maris Bard) and the effects are illustrated from these experiments.

The complete analysis of the effects of physiological age on growth and particularly partitioning of dry matter will be presented in subsequent papers. In Home Guard at the earliest samplings, the number of emerged plants increased with increased number of day-degrees experienced by the seed up to approximately 600 day-degrees and



Fig. 5. Relationships between number of above-ground stems and number of day-degrees > 4 °C in Maris Bard, Expt 8.  $\bigcirc$ , 12 June 1980,  $y = 434\cdot4 - 0.2265x$ ,  $R^2 =$ 0.93;  $\bigcirc$ , 15 June 1981,  $y = 290\cdot5 + 0.6351x - 8\cdot1 \times 10^{-4}x^2$ ,  $R^2 = 0.75$ .

greater ages had no further effect (Fig. 3). There were no effects of physiological age on final number of plants, for even the oldest seed was not affected by 'little potato' disorder. In Maris Bard effects of increasing day-degrees on plant emergence were even larger than in Home Guard (Fig. 4). The oldest seed reached 90% plant emergence almost 3 weeks before the youngest seed in both years. There were



Fig. 6. Relationship between days from planting to mean date of tuber initiation and number of daydegrees > 4 °C, Home Guard. O, Expt 4, y = 65.9 - 0.0108x,  $R^2 = 0.92$ ;  $\bigoplus$ , Expt 5, y = 50.0 - 0.0106x,  $R^2 = 0.99$ .

also large effects of treatments on numbers and types of stems. Figure 5 shows that in Expt 8 numbers of above-ground stems decreased linearly with increasing number of day-degrees while in Expt 9 numbers increased with increasing daydegrees up to 300-400 day-degrees and decreased sharply above 600 day-degrees. In both experiments numbers of secondary stems increased with increasing day-degrees up to 500-600 day-degrees and then decreased. Number of mainstems decreased with increasing age; the effect was large: seed with the maximum day-degrees had half

		Ex	periment 8 Nun	(12 June) aber of day	-degrees >	4 °C		
	0	112	224	336	448	560	672	784
Mainstems	86.9	<b>88</b> ·0	76.6	64·5	57.7	44.9	51.1	51.5
Secondary stems	13.1	12.0	23.4	35.5	<b>4</b> 2·3	55.1	<b>48</b> ·9	<b>4</b> 8·5
			xperiment ber of day	9 (6 June) •degrees >	4 °C			
	0	168	336	504	672	840		
Mainstems	87.4	65.7	51.1	35.9	$32 \cdot 8$	53.5		
Secondary stems	12.6	34.3	<b>48</b> ·9	64.1	67.2	46.5		

Table 2. Proportions of different types of stem in above-ground stems in Maris Bard

Downloaded from http://www.cambridge.org/core. Faculty of Classics, University of Cambridge, on 24 Nov 2016 at 15:47:35, subject to the Cambridge Core terms of use, available at http://www.cambridge.org/core/terms. http://dx.doi.org/10.1017/S002185960003865X



Fig. 7. Relationships between leaf area index and number of day-degrees > 4 °C in Home Guard. (a) Expt 5; (b) Expt 6. (a)  $\blacktriangle$ , 22 May, y = 0.33 + 0.01x,  $R^2 = 0.93$ ;  $\bigcirc$ , 14 June, y = 1.3 - 0.004x,  $R^2 = 0.99$ ; O, 21 June,  $y = 1.61 - 0.0012x + 6.57 \times 10^{-7}x^2$ ,  $R^2 = 0.99$ . (b)  $\bigstar$ , 15 June,  $y = 0.89 + 0.0015x - 1.52 \times 10^{-6}x^2$ ,  $R^2 = 0.99$ ; O, 30 June, y = 1.79 - 0.008x,  $R^2 = 0.93$ .

(Expt 9) or a third (Expt 8) of the mainstems produced without accumulated day-degrees. Thus secondary branching contributed substantially to above-ground stem densities at intermediate numbers of day-degrees but relatively little at the lower end of the range. The proportions of main and secondary stems are shown in Table 2. Similar effects were found in all experiments with Home Guard.

Number of days from planting to mean date of tuber initiation decreased linearly with increasing number of day-degrees of the seed in both varieties. In both Expts 4 and 5 the slope of the relationship was the same although the number of days from planting to initiation was greater in Expt 4 (Fig. 6). Consequently, plant dry weight at tuber initiation was reduced by increasing the number of daydegrees accumulated by the seed. These results suggest that age is a major determinant of the timing of tuber initiation in potatoes.

In both varieties, leaf area index (L) was initially increased by increasing number of day-degrees of the seed, but as growth proceeded leaf area index increased more rapidly from seed with limited number of day-degrees (Figs 7 and 8). Leaf area index was little affected by number of day-degrees in early June in both varieties but the areas were much larger in Maris Bard and continued to increase during June. In both varieties negative quadratic relationships (or negative linear) between L and number of day-degrees were found after June, and as growth continued fewer and fewer day-degrees were required for maximum L (Figs 7 and 8). In Home Guard L values were generally small and complete ground cover was achieved by only the youngest seed in some experiments. Maris Bard produced substantially larger leaf areas than Home Guard and complete ground cover was achieved by all treatments. However, the smallest peak leaf areas were produced by seed experiencing the largest number of day-degrees and these treatments began to senesce earlier than seed with smaller numbers of day-degrees.

After setting of tubers was completed in all treatments, effects of physiological age on number of tubers were small in Home Guard, with the older seed having slightly fewer tubers than young seed. In Expt 5 loss of tubers during growth was greater from old than from young seed. At most harvests number of tubers was unaffected by initial increases in age and thereafter decreased, so that negative linear or quadratic functions fitted the data well (Table 3). However, individual experiments differed considerably in the age beyond which total number of tubers decreased. In Expt 6 only ages above 864 day-degrees had markedly fewer tubers, while in Expts 4 and 7 decreases in numbers of tubers occurred at ages above 208 and 576 day-degrees respectively. In Expts 4 and 5 increasing seed age increased the number of tubers > 25 mm early in the season (Table 3), and this effect was found in progressively larger grades as harvesting was delayed. After the first harvest, number of tubers > 25 mm was generally un-



Fig. 8. Relationships between leaf area index and number of day degrees > 4°C in Maris Bard, Expt 9.  $\bigcirc$ , 17 May, y = 0.22 + 0.0018x,  $R^2 = 0.96$ ;  $\bigcirc$ , 28 May, y = 1.93 + 0.0045x,  $R^2 = 0.91$ ;  $\triangle$ , 6 June, y = 3.094 + $0.0043x - 5.53 \times 10^{-6}x^3$ ,  $R^2 = 0.81$ ;  $\bigcirc$ , 15 June, y = $5.05 + 0.0075x - 8.78 \times 10^{-6}x^3$ ,  $R^2 = 0.92$ ;  $\blacksquare$ , 26 June,  $y = 5.54 + 0.00028x - 6.11 \times 10^{-6}x^2$ ,  $R^2 = 0.84$ ;  $\blacktriangle$ , 22 July\*, y = 5.39 - 0.0024x,  $R^2 = 0.70$ . \* Data for irrigated treatments only.

affected by initial increases in age and then decreased with further increases in seed age. There were more tubers from Maris Bard than from Home Guard. There was considerable loss of very small tubers from most seed ages during growth. Throughout sampling in both experiments increasing the number of day-degrees of seed above 500-600 daydegrees reduced number of tubers. Seed with the greatest number of day-degrees always had few tubers and consequently numbers over specific grade sizes (> 25 mm) were increased by increasing the number of day-degrees of the seed at the first sampling but not at later harvests (Table 4). This effect was found on the first occasion that a specific grade was analysed, decreased as growth proceeded and was frequently reversed by the end of the experiment (Table 4).

## Tuber yields

In all experiments there were significant effects of physiological age at some stage of the harvesting period. Increasing age generally increased yields early in the season but decreased them at the end, and there were limited effects of age in the intervening period. The yields and regression coefficients for Expts 4–9 are shown in Tables 5 and 6. The equations for the more important relationships are given in Table 7.

#### Experiment 1

No close relationship between tuber yields and number of day-degrees could be demonstrated until final harvest, when total and saleable yields decreased linearly with increasing number of daydegrees experienced by the seed (Fig. 9).

## Experiment 2

Number of day-degrees had little effect on tuber yields in either variety, and only in Home Guard at final harvest were significant relationships found. Total and saleable yields decreased with increasing number of day-degrees up to 630 but increased slightly with more day-degrees, and consequently the curve was positively quadratic.

## Experiment 3

In both varieties, close relationships existed between total and saleable tuber yields and number of day-degrees at the first two harvests (Fig. 10). In all cases negative quadratic functions fitted the data well. At the two later harvests relationships were much poorer. These final harvests were taken during the increasingly severe drought and it was apparent that some plants were in advanced senescence as a consequence of water stress.

## Experiment 4

Close relationships between yields and number of day-degrees were found at the beginning and end of the harvesting period (Tables 5 and 7). At the first harvest, yields increased linearly with increasing number of day-degrees, but as harvesting was delayed the effect became small. However, at final harvest, yields decreased with increasing number of day-degrees up to the oldest seed which produced an increase, and a positive quadratic curve fitted the data.

## Experiment 5

Yields increased with increasing number of daydegrees at the first harvest (Table 7). Number of day-degrees had little effect on yields at subsequent harvests (Table 5).

	$R^3$	Quadratic		0.65	0-61	0.58	0-94	ł	I	0-73	I	0.72	0-89	0.79	0-86	l	I		I	66-0	0-89	78-0	26-0	1	I	0-43	0.56	0-83	0.80	18-0	
		Linear		I	1	ł	l	ł	I	1	I	1	1	ł	ļ	06-0	0.86		0-93	1	1	1	1	I	0-76	0-51	1	ł			0-85 0-82
> 25 mm		S.E.		65.4	71-3	50-7	48-7	30-7	25-9	33.6	36.2	35-6	32.5	25.1	56.9	42-0	67-5		30.2	23.8	18-3	28.2	16.8	13-2	22.1	18-9	16.6	30.6	18-2	26.3	30-1 57-7
Table 3. Effect of accumulated day-degrees on total number of tubers and number of tubers >		1008 1056 1168		1	1	I	1	I	I	I				0 489	I	1			1	1	1	1	I	I	I			331		l	11
er of		8 105		1	1	I	1	I	1	I	1	510		540	1	1	1		1	I	I	1	1	I	ł	I	34	316		 	
qum				1	1	1	1		1		1	1	1	1	738				1	1	1	I					•		1	4	689 635
u pu		) 920			۲ ۳	1		657	689	602	. 590	I	1	ł	I	4	ļ	> 25 mm ('000s/ha)	:	1	۱ ~		385	44	412	42	ł		1	I	
ers a		1 880		1437	1416	1165	722	1	l	I	1	-			 ~	1	.   	1,000	35	468	42	53	1		l	1	1	1		ן ה.	
f tub	1	864	/ha)	. 1	1	1	1	1	1	1		673	20	627	925	92	ŝ	5 mm	1	1	1	1		1	1		<b>4</b> 00	442	439	646	696 696
ber o		792	of tubers ('000s/ha)	`	ł	Ι	1	637	661	592	009	1	I	Ι						Ι	I	I	372	401	<del>1</del> 00	450	I	1	-1		
mmu	- 4° C	720	bers (	 	1		Ι	ł	I	1	ł	I		I	844	919	935	Number of tubers	1		T	1	ļ	I	I	1	I	I	1	8	679 775
otal	Number of day-degrees >	656	of tu		1326	1225	692	I	I	1	1	I	1	I	I	1	I	er of	331	433	447	479	1	l	I	ł	1		I	1	
on t	7-degr	584	Total number	I	I	Ι	ł	I	I	I	I	694	661	720	I	Ι	I	Numb	1	I	ł	I		1	I	I	419	<b>48</b> 0	£33	I	
Jree8	of day	576	otal m	I	ł	I	1	Ì	Ι	1	I	l	I	I	1004	1077	1092		I	I	ł	I	I	ł	ł	I	I	1	L	656	792 913
y-de	mber	544	Ĕ	ł	I	ļ	ł	622	684	588	610	ł	ļ	١	1	l	ł		1	ł	ł	ł	365	413	406	420	ł	ł	1	l	
sd da	ΝΠ	432		1217	1330	1084	671	I	1	I	1	I	I		1088	1077	1098		296	438	428	482	ł	I	I	I	ł	I	I	138	835 921
ulate		424		1	I	I	ł	I	l	I	1	615	665	631	I	1	ļ		I	ł	I	I	١	I	I	I	336	457	444	1	
unc		376		1	l	ł	l	645	640	618	009	I	1	l	Ι	1	l		Ι	1	ł	I	358	432	430	420	I	ļ	I	1	
of a		288		١	I	ł	I	۱	I	I	I	I	}	I	1085	1067	1098		Ι	I	I	I	ļ	1	I	I	ļ	ł		202	819 883
ffect		208		1564	1557	1376	827	704	737	736	<u>6</u> 2	ł	I	١	I	I	1		290	496	524	567	321	445	472	$\overline{500}$	l	ł	I	ł	11
3. E		184		t	I	1	ł	ļ	l	ļ	1	672	679	641	I	I	1		Ι	ł	١	I	ł	١	١	1	366	442	441	1	
able		144 184		I	1	I	I	ł	I	I	۱	I	١	ł	1081	1144	1088		I	ł	I	I	I	1	I	I	I	ł	I	200	827 896
Ĕ		0		1577	1518	1365	923	646	685	708	660	569	666						279	585	556	599	287	444	464	480	327	467	494	719	865 996
	Date of	harvest				• •											14 Aug.		21 May	2 June	17 June	9 July	14 June	29 June	11 July	1 Aug.	15 June	30 June	18 July	22 June	4 July 14 Aug.
		Experiment		4				ð				9			7				4				ð				9			2	

## P. J. O'BRIEN AND OTHERS

	r	ate of				Numbe	r of day-d	legrees >	4 °C				
		mpling	0	112	2	224	336	448	560	672	784	È	S.E.
Total		2. vi	1802		-	1900	1879	1754	1140	890	89	8	149-3
		8. vii	1455	140	<b>4</b> :	1365	1488	935	604	685	89	)1	93· <b>4</b>
> 25 m	m 1	2. vi	125	19	4	183	246	357	348	348	38	5	31.5
	1	8. vii	713	69	4	671	625	497 <sup>`</sup>	414	437	50	4	$25 \cdot 4$
> 38 m	.m 1	2. vi	0	1	2.1	2.1	12.5	$52 \cdot 1$	102-1	143.8	18	5.4	14.0
	1	8. vii	477	48	6	<b>4</b> 81	497	419	342	342	40	2	27.7
					Expe	riment 9	(1981)						
					Num	per of da	ay-degree	s > 4 °C					
	Date of sampling			0	168	336	504	672	840	Mean	s.e. <sup>1</sup>	S.E. <sup>8</sup>	S.E. <sup>3</sup>
Total	6. vi			869	898	1225	1366	1063	563	_	<b>84</b> ·1	_	—
	22. vii	Irrigat	ed	938	942	984	1100	1074	699	951	40.0		
		Unirrig	rated	1010	952	1033	1079	889	729	948	<b>4</b> 3·3	19·9	59.3
> 25 mm	6. vi			65	229	308	433	637	389	—	34.3		—
	22. vii	Irrigat	ed	671	641	690	727	745	452	663		~ ~	<b>64</b>
		Unirrig	ated	655	653	699	690	641	526	644	27.2	9.5	36.4
> 38 mm	6. vi				—		2.3	20.8	111-1	_	3.4		_
	22. vii	Irrigat	ed	484	482	495	521	507	387	479		= 0	00 F
		Unirrig	gated	489	<b>4</b> 40	468	468	475	391	455	15.3	5.3	20.5

## Table 4. Effect of number of day-degrees experienced by seed on number of tubers ('000s/ha), Maris Bard Experiment 8 (1980)

s.E.<sup>1</sup> for comparing ages at the same level of irrigation; s.E.<sup>2</sup> for comparing irrigation means; s.E.<sup>3</sup> for comparing irrigation at the same or different ages.





622



Fig. 10. Relationships between total yield and number of day-degrees > 4 °C on two harvest dates, Expt 3. (a) Pentland Javelin  $\bigcirc$ , 25 May,  $y = 1.7 + 0.019x - 1.58 \times 10^{-5}x^2$ ,  $R^2 = 0.93$ ;  $\triangle$ , 4 June,  $y = 8.9 + 0.028x - 2.55 \times 10^{-5}x^2$ ,  $R^2 = 0.75$ ; (b) Vanessa  $\bigcirc$ , 25 May,  $y = 0.16 + 0.0197x - 1.64 \times 10^{-5}x^2$ ,  $R^2 = 0.69$ ;  $\triangle$ , 4 June,  $y = 10.1 + 0.015x - 1.20 \times 10^{-5}x^2$ ,  $R^2 = 0.66$ .

### Experiment 6

At all harvest dates negative quadratic relationships were found between total and saleable yields and number of day-degrees experienced by seed. The optimum number of day-degrees decreased as harvest was delayed, and the decrease in yield caused by exceeding the optimum number of daydegrees also increased with delay in harvesting (Fig. 11).

## Experiment 7

Effects of number of day-degrees were small at the first harvest, although the oldest seed produced the highest yields. At the second harvest increasing number of day-degrees up to 576 had little effect on yields but further increases produced small increases in yields and a positive quadratic curve fitted the data (Tables 5 and 7). At the final harvest increasing number of day-degrees above 576 reduced yields and negative quadratic curves fitted the data for total yield. As a consequence of the decrease in number of tubers with increasing number of daydegrees, the yield of saleable tubers increased with increasing number of day-degrees throughout harvesting. The effect was found in the progressively larger grades which represented the saleable fraction of total yield (Fig. 12).

Table 5 also shows the optimum number of daydegrees obtained where appropriate by differentiating the equation. The optimum values for similar yields showed good agreement in the different experiments, for example first harvests in Expts 5 and 6, third harvest in Expt 4 and final harvest in Expt 5.

## **Experiment** 8

Close relationships between total and graded yields and accumulated day-degrees were found at the first two harvests. At the first harvest yields increased linearly with increasing numbers of daydegrees (Tables 6 and 7) and the effect was large. Linear functions also fitted the data well at the second harvest but the slope was less steep as a consequence of the more rapid growth of the younger seed. At later harvests there was little effect of number of day-degrees, for the initial advantages of old seed were removed by the more rapid bulking of the young seed.

#### Experiment 9

Results were similar to those of Expt 8; yields increased with number of day-degrees at the first two harvests and the size of the response was large (Tables 6 and 7). At the third harvest a significant negative quadratic relationship was found and only 600 day-degrees were required for optimum yields. At the fourth harvest, there was no effect of age in unirrigated plots; with irrigation, yields increased linearly with number of day-degrees. At the final

		S.E.		0.63	0.56	1.55	2.05	0-41	1.10	1.29	1.82	0-41	1.25	1.62	0·89	1-45	3.60		0.61	0-59	1.54	2.09	0.46	1·09	1.23	1.86	0.49	1-31	1.62	1.63	0.49	3.59
	(			1	l	I	1	I	I	l	I	11-1	14-9	17-5	1				l	ł	ł	I	1	ł	1	I	10-3	14-0	16-5	ł	I	1
		1008 1056 1168		I	1		]	l		I	l	12.0	15-1	18-1	I	1	I		l	I	1	١	l	l	1	I	11.1	14-2	17.0			I
rd		1008		1	l	I	1	۱	I	I	1	I	1	1	19-8	38-1	53-9		ļ	١	1	I	l	ļ	I	1	ł	I	I	18-7	36-9	53.2
of accumulated day-degrees on total tuber yield and tuber yield $> 25$ mm, Home Guard		920		I	l	I	I	13.0	18.1	22.8	22.0	l	I	1	1	I	I		I	l	l	I	11-4	16-8	21.7	21.0	l	1	ļ	l	1	ł
h, Hom		880		12.0	20-4	26-9	37-9	1	1		1	l	I		ļ	l	I		7.2	19-1	25.6	36-9	I		1	l	I	I	1	I	I	۱
25 mm		864		I	1	۱	I	I	۱	١	1	12-2	20-4	21-9	18-8	35-4	53-6		l	1	ł	I	I	1	١	ł	10-9	14-1	20-7	17-4	33.9	52-9
< p]		792		۱	۱	I	1	1.1-7	17.5	15.5	22.6	ĺ	ļ	١		1	l		l	l	I		10.0	16.0	18-4	21-4	1	l	I	I		l
ber yie	ပ္	720		١	I	١	1	I	I	1	I	l	١	I	18-6	34.2	58-8		۱	ł	I		ł	l	I	I	ł	1	I	17-2	32.6	57-9
and tu	Number of day-degrees $> 4$ °C	656		12-2	19.0	27.8	35.0	١	1	l	I	١	I	١	I	I	1	a)	7.7	17-8	26-7	34.2	1	١	I	I	1	l	۱	l	I	1
yield c	-degree	584	t/ha)	1	I	I	1	١	ļ		1	13.2	21-0	26.3	١	I		25 mm (t/ha)	:	I	۱	ļ		I	ł	l	11.8	19-8	24.8	١	ļ	I
tuber	of day	576	yield (t/ha)	1	1	1	1	I	l	1		1	!	١	17.8	34-4	62.0			I	1	1	l	I	۱	l	l	l	I	15-9	32.5	6-09
ı total	umber	544	tuber	I	I	I	I		17-9	22-3	24-5	١		I	١	I	1	Tuber yield >		I	ł	l	10.5	16-4	21.2	23-4	l	I	I	1	۱	l
rees on	'n	432	Total	10.0	20-4	27-1	36.0	1	1	I		۱	I	I	18.1	33.8	59-0	uber y	5.6	19-3	26.2	35.1	ł	I	I		I	I	I	16.0	32.2	57-9
ıy-degi		424		I	۱	۱	I	l	١	l	l	9.6	20-8	24.9	١	I	I	Ĥ	ł	I	I		۱	١	I	]	8.6	19-1	23.8	I	1	1
uted do		376		1	l	۱	l	11.2	19-1	21.2	24.2	!	I	1		I	Ι		I	١	I		9-3	17-9	20-1	23-2	l	١	۱	I	١	l
nmuk		288		I	I		١	I	•	١	I		I		18.9	34-4	58.4		1	1	I		١	I	1	۱	I	I	I	16.7	32.7	57.0
		208		10-3	19-1	28-4	36.0	6-6	19-4	21.6	28·8	۱	l		l	١				17.7							l	١	1	1	l	l
Effect		184		I	I	l	ł	١		۱		0.01	17.5	22-3	l	1	١		1			I	١	I	1	۱	8.5	16.0	21.1	۱	l	I
Table 5. Effect		144		I	l	I		١	1	١	!		I	I	17-9	34·1	58.2			I	1	١	I	1	1	۱	I		ł	15.5	32.1	57-0
Tal	l	. 0		6.6	19-0	26.9	39-5	8.4	16.2	20.0	22-4	9-4	17-8	22.1	18.5	33-6	59.3		2.9	17-4	25.6	38.4	5.6	14.8	18-4	21-3	8·1	16.5	21.0	16.6	31.5	57-7
	Date of	harvest		21 May	2 June	17 June	9 July	14 June	29 June	11 July	1 Aug.	15 June	30 June	18 July	22 June	4 July	14 Aug.		21 May	2 June	17 June	9 July	14 June	29 June	11 July	1 Aug.	15 June	30 June	18 July	22 June	4 July	14 Aug.
	Fronti-	ment		4				5				9			2				4				5 D				9			2		

## 624

## P. J. O'BRIEN AND OTHERS



Fig. 11. Relationships between yields > 25 mm and number of day-degrees > 4 °C in Home Guard. Expt 6.  $\bigcirc$ , 15 June,  $y = 7 \cdot 7 + 0 \cdot 007x - 3 \cdot 91 \times 10^{-6}x^{3}$ ,  $R^{2} = 0 \cdot 68$ ;  $\square$ , 30 June,  $y = 15 \cdot 4 + 0 \cdot 015x - 1 \cdot 4 \times 10^{-5}x^{3}$ ,  $R^{2} = 0 \cdot 78$ ;  $\triangle$ , 18 July,  $y = 20 \cdot 3 + 0 \cdot 015x - 1 \cdot 59 \times 10^{-5}x^{2}$ ,  $R^{2} = 0 \cdot 89$ .

harvest, on average, irrigation increased tuber yields but there was no significant effect of age at either irrigation treatment.

## DISCUSSION

If accumulated day-degrees are a measure of physiological age, they should be closely related to sprout growth, for the latter has been used as an illustration of physiological age (e.g. Toosey, 1964). Wurr (1978b) showed that total sprout length was linearly related to number of day-degrees > 0 °C from end of tuber dormancy (measured as a mean total sprout length of 2 mm) in three varieties. The same author also drew attention to the considerable variation in sprout characters used to measure sprout growth (Wurr, 1978a). In the search for general relationships between sprout growth and accumulated day-degrees it is essential that the most appropriate sprout character, the starting point for measurement and the base temperature for calculating day-degrees are determined. In Wurr's experiments seed was placed in temperatures conducive to sprout growth immediately after curing, i.e. before the end of dormancy, and relatively few sprouts grew. Using similar methods, Sadler (1961) produced data which also show a



Fig. 12. Relationships between saleable yields and number of day-degrees > 4 °C in Home Guard, Expt 7.  $\bigcirc$ , 22 June,  $y = 9.99 - 0.007x + 1.34 \times 10^{-5}x^2$ ,  $R^2 = 0.86$  (> 32 mm);  $\square$ , 4 July,  $y = 16.9 - 0.01x + 2.28 \times 10^{-5}x^2$ ,  $R^2 = 0.97$  (> 38 mm);  $\triangle$ , 14 August, y = 17.1 + 0.015x,  $R^2 = 0.83$  (> 51 mm).

good linear relationship between length of apical sprouts and number of day-degrees > 0 °C from end of dormancy. However, in the current experiments it was clear that such relationships did not always hold, and in Home Guard in Expts 1 and 2 the greatest total sprout lengths were produced by the shortest periods of sprouting which accumulated the fewest day-degrees (Tables 1 and 6 in Allen et al. 1979). This occurred because sprouting was delayed by storage at low temperatures and many more sprouts eventually grew when tubers experienced temperatures conducive to growth. However, in Home Guard a common linear relationship between length of longest sprout per tuber and accumulated day-degrees was found for all experiments and for the data of Raouf (1979) (Fig. 1) and similar relationships were found in Vanessa and Pentland Javelin (Fig. 2) and Maris Bard. It would seem, therefore, that length of the longest sprout per tuber is the sprout character directly determined by the temperatures experienced by seed. The absolute lengths achieved at any temperature will also be affected by the light environment, so that widespread use of sprout lengths as practical measures of age is precluded by the wide range in light conditions prevailing in commercial stores.

Wurr (1978b) suggested that the production of

	Data of					• •										
Experiment		0	112	168	224	336	448	504	560	672	784	840	Mean	8.E. <sup>1</sup>	S.E. <sup>2</sup>	S.E. <sup>3</sup>
						Tote	ul tuber	Total tuber yield (t/ha)	1 <b>8</b> )							
œ	12. vi	8.4	10.2		8.8 8	11-9	15.6	1	17-4	18.8	21-1	ł	1	96-0	I	1
	1. vii	36-5	38-2	]	35.7	40-9	44.5	1	43·1	45.1	46.4	I	Ι	1.72	I	l
	18. vii	<b>51-4</b>	53.1	1	56.6	59-7	50-8		54.2	55-5	56.0	ł	1	2.30	l	ļ
	19. viii	74.0	64.8	1	65.2	71.3	68.6		69.2	66-5	72-4	I	l	4-52	I	ι
6	6. vi	4·5	I	7.0	I	10-4	I	12.9	I	16-1	I	16.8	I	0.64	I	I
	15. vi	12-1		17-0		22-7	Ι	23-8	l	28-7	١	28.1	l	0.82	I	l
	26. vi	30.1	I	34.3		38.8	1	38.4	I	42-2	I	38.0	I	1.38	Ι	l
		60.7	1	60-7	ł	58.8	١	60.5	İ	62.8	1	60.7	60.7	1	000	
	I,	62.6	1	61-7	I	64.2	1	0.99	I	67.7	I	66.3	64.8	04.1	0.28	RQ. 1
	26. viii I <sub>0</sub>	59.5	I	64-7	1	61-1	1	6.09	I	63.5	1	67.4	62.9	10.0	20	000
	I	71.9	ł	72-6	1	69-5	I	71.5	I	6-69	ł	66.2	70-2	2.30	0Z-1	87.2
						Tuber		25 mm (t/ha)	(t/ha)							
œ	12. vi	2.6	4·6	1	4.2	6.4	11.6	I	15.3	17-4	20.2	I	I	1.24	1	l
	1. vii	34.6	35-9		33.9	39-0	42.6	١	42-2	44.5	45.7	Ι	1	1.78	I	ļ
	18. vii	49-9	51.6		54-7	57-7	49-7	Ι	53.5	55.0	55.1	١	ł	2.23	ł	ł
	19. viii	73.2	64.2	ł	64·3	70.3	67.7	ł	68.6	66.1	71-6	I	Ι	4.52	I	l
6	6. vi	1.2	1	4.0	١	5.7	I	8·0	Ι	13.2	l	15-6	ł	0.60	1	l
	15. vi	9-3	I	15.0	I	21.3	١	22.2	1	27.5	I	27.3	Ι	0.84	I	l
	26. vi	28.5	ł	33.0	١	37-2	I	36-6	l	40.5	1	37-3	Ι	1.48	I	l
		59-4	١	59.6	1	57.3	I	58.9	I	61.8	ł	60-0	59-5		1000	
	I,	61.7	1	60·8	ł	63·1	١	$64 \cdot 6$	I	66.1	I	65.5	63-6	C+• I	12.0	69.T
	26. viii I <sub>0</sub>	58.8	1	63-6	I	60.1	1	59-7	I	62.8	1	66·8	62.0			000
	I,	71-4	1	71.5	J	68.5	I	70-6	ł	0.69	ł	65.8	69-5	2.40	1.23	£6.£

Table 6. Effect of accumulated dav-derrees on (a) total tuber vield and (b) tuber vield > 25 mm (t/ha). Maris Bard

## Downloaded from http://www.cambridge.org/core. Faculty of Classics, University of Cambridge, on 24 Nov 2016 at 15:47:35, subject to the Cambridge Core terms of use, available at http://www.cambridge.org/core/terms. http://dx.doi.org/10.1017/S002185960003865X

## P. J. O'BRIEN AND OTHERS

## Physiological age in potatoes

				Number of
	Date of			day-degrees for
$\mathbf{Experiment}$	harvest	Regression equation	$R^2$	maximum yield
		Total yields		
4	21 May	y = 9.7 + 0.0027x	0.73	
1	9 July	$y = 39.4 - 0.017x + 1.76 \times 10^{-5}x^{2}$	0.90	
5	14 June	$y = 8.4 + 0.009x - 4.68 \times 10^{-6}x^{2}$	0.93	968
6	15 June	$y = 8.9 + 0.008x - 4.8 \times 10^{-6}x^{2}$	0.61	833
	30 June	$y = 16.8 + 0.015x - 1.44 \times 10^{-5}x^{2}$	0.80	521
	18 July	$y = 21 \cdot 4 + 0 \cdot 015x - 1 \cdot 65 \times 10^{-5}x^2$	0.89	455
7	4 July	$y = 34 \cdot 2 - 0 \cdot 004x + 7 \cdot 19 \times 10^{-6} x^{2}$	0.82	
	14 Aug.	$y = 58 \cdot 1 + 0 \cdot 0105x - 1 \cdot 50 \times 10^{-5}x^2$	0.64	350
8	12 June	$y = 7 \cdot 3 + 0 \cdot 0172x$	0.94	_
	1 July	y = 35.9 + 0.0138x	0.85	
9	6 June	$y = 4 \cdot 8 + 0 \cdot 0155x$	0.98	—
	15 June	y = 13.8 + 0.0198x	0.92	
	26 June	$y = 29.8 + 0.0345x - 2.83 \times 10^{-5}x^2$	0.91	610
		Yields $> 25 \text{ mm}$		
4	21 May	$y = 2 \cdot 9 + 0 \cdot 006x$	0.89	
	9 July	$y = 38 \cdot 2 - 0 \cdot 106x + 1 \cdot 67 \times 10^{-5} x^2$	0.88	<u> </u>
5	14 June	$y = 5.5 + 0.012x - 6.54 \times 10^{-6}x^2$	0.94	915
6	15 June	$y = 7 \cdot 7 + 0 \cdot 007x - 3 \cdot 91 \times 10^{-6} x^2$	0.68	897
	30 June	$y = 15 \cdot 4 + 0 \cdot 015x - 1 \cdot 4 \times 10^{-5}x^2$	0.78	535
	18 July	$y = 20 \cdot 3 + 0 \cdot 015x - 1 \cdot 59 \times 10^{-5}x^2$	0.89	472
7	22 June	$y = 16.5 - 0.003x + 5.41 \times 10^{-6}x^2$	0.82	
	4 July	$y = 32 \cdot 3 - 0 \cdot 004x + 7 \cdot 46 \times 10^{-6} x^2$	0.84	
8	12 June	y = 0.88 + 0.024x	0.95	<u> </u>
	1 July	y = 33.6 + 0.0159x	0.89	—
9	6 June	y = 0.67 + 0.0173x	0.97	
	15 June	$y = 11 \cdot 3 + 0 \cdot 0218x$	0.93	
	26 June	$y = 28.5 + 0.0323x - 2.512 \times 10^{-5}x^2$	0.92	643
	22 July	y = 61.3 + 0.0067x (irrigated plots)	0.68	

## Table 7. Regression equations for total yields and yields > 25 mm (y)and physiological age (x) in Expts 4-9

a mean total sprout length of 2 mm should be taken as the beginning of accumulation of day-degrees, and as this is easily recorded it can be used effectively in practice. The use of mean length of longest sprout of 3 mm in these experiments was found to be satisfactory and easy to record and may be easier for varieties with deep eyes. It is better to describe the starting point (however defined) as the onset of sprout growth, so avoiding any further confusion over the term dormancy, for the onset of sprout growth may occur following cold storage, long after natural dormancy or rest period (Emilsson, 1949) has ended.

If all sprouting periods were of the same duration, differing only in temperature, the choice of base temperature would not be important. However, both duration and temperature vary in practice and the implications must be considered. If initial sprout growth is followed by long periods of cold storage at 0-4 °C it is illogical to accumulate daydegrees above a base temperature of 0 °C when little

or no growth is occurring, and similar conditions after the end of dormancy but prior to visible sprout growth would not be counted. It would be better to accumulate day-degrees over the base temperature for growth so that periods of lower temperature would not add to the total of daydegrees or to sprout lengths. However, the base temperatures for growth have not been accurately determined in any varieties. In the current work a temperature of 4 °C has been used as the base as the coldest cabinet was maintained at this temperature and only limited growth occurred. There is some evidence from subsequent experiments that some growth can occur at this temperature in some varieties including Home Guard (Raouf, 1979) and it seems probable that the base temperature for growth does vary with variety. In the absence of substantial data on this aspect of sprout growth, 4 °C was taken as the most convenient and justified base temperature.

The results suggest a general pattern of effects

of age on yield of Home Guard and Maris Bard during the harvesting period. At early harvests increasing age increased yields, but in all experiments these early benefits were eventually reduced and in Home Guard replaced by reductions in vields at later harvests. In the middle of the harvesting period age often had little or no effect on yields. This consistent pattern was not always shown in the functions which fitted the data best. In Expt 7 the initial positive effects of age and at later harvests in Expts 2 and 4 the negative effects of increasing age were both best represented by positive quadratic functions. With relatively few data points individual regressions are vulnerable to such vagaries. Neither of the deviations from the suggested linear relationships is likely to occur in reality, and their occurrence should not obscure the importance of the pattern of effects and the general significance of this measure of age. The data support the use of accumulated day-degrees as a measure of physiological age and indicate that optimum ages can be determined for specific periods of harvesting. The effects on yields of Home Guard early in the season were small in tonnage but are of considerable value, for prices are approximately £300 per tonne at this time. In Maris Bard the effects were very large and thus the differences found are of considerable economic significance, and improved control of seed age at planting would markedly affect returns to growers.

Recognition of temperature as the dominant factor in the effects of pre-planting environment on growth is not new, for the period from the end of dormancy to tuber initiation, called the incubation period, has long been considered important by Continental authors (Reust & Munster, 1975). The incubation period is reduced in time as temperature is increased with suggests that it may be a fixed number of day-degrees for individual varieties. As its duration usually exceeds the period allowed for storage before planting it is of little practical significance. Moreover, it cannot discriminate between the many stocks of an individual variety which have progressed to some extent through their incubation period and has not been directly related to field growth pattern.

The results suggest that the effects of age on yields change with time of harvest, and the data on field growth indicate the reasons. As increasing age produced earlier emergence and tuber initiation, its effects on early tuber yields (when yields are low) were generally beneficial in all varieties. However, increasing age also produced smaller peak leaf areas and earlier senescence, so that growth rates of old seed were lower than young seed. Consequently, the relationship between yield and age changed as growth proceeded and younger seed gradually overtook old seed, and eventually

in 1973 in Home Guard a negatively linear relationship between yield and age existed at final harvest. Generally, these relationships were clearly demonstrated in Home Guard for the effects of age on plant size, especially L, were most marked. However, in 1974 when soil conditions were ideal and no serious moisture stress occurred, effects of age on plant size were small in this variety and relationships between age and yields were also poor. This would suggest that water supply may influence the effects of age on yield and how they change with time. In all other years in which some degree of water shortage occurred, old seed of Home Guard usually produced lower yields than young seed after the first harvest. In Maris Bard effects of age on early yields were very large in both years but by the end of the season there were again no effects.

This explanation of the effects of age on growth and yield leads to the general relationships shown in Fig. 13. It is suggested that the effect of age on yield changes progressively from early to the final harvest and the rate of change is determined by (a) the magnitude of the effects of age on plant size and leaf area and (b) prevailing moisture and light conditions. The absence of moisture stress may minimize the effects of age during much of the season if plants of similar leaf area are produced from seed of different ages. Old seed of Home Guard may be particularly susceptible to moisture stress for there is evidence that it produces small



Fig. 13. Suggested relationships between tuber yield and physiological age (number of day-degrees > 4 °C) for harvests throughout the season. \_\_\_\_, \_\_\_\_, \_\_\_\_, \_\_\_\_, \_\_\_\_\_, Progressively later harvests.

root systems (O'Brien, 1981) and such seed may be of short-lived usefulness in some varieties especially in dry seasons. As Scott & Wilcockson (1978) have shown that tuber yield is proportional to the amount of radiation intercepted by crops, the yields produced by seed of different ages at any time are likely to be determined by the amount of radiation intercepted. The change in the relationship between age and yield is likely to be influenced by the rate at which the increased light interception from larger but later L values of younger seed nullifies the advantage in light interception achieved by old seed early in growth. A bright May followed by a dull June would prolong the advantage of old seed. It is likely that light interception is the dominant factor in the growth of tubers, for Raouf (1979) has shown that age does not influence drymatter partitioning after tuber initiation, a result quite contrary to much previous work (e.g. Bremner & Radley, 1966). Thus, absence of good relationships between accumulated day-degrees and yield is to be expected at some stage in growth. In the early varieties grown here this occurs during June-July, but in maincrops it may be in August and September, close to final harvest. It may happen that any increased yields caused by increasing age in early varieties occur before commercially acceptable yields are reached. Thus detection of effects of age requires several harvests, the timing of which is crucial to the results.

The magnitude of the effects of age on yield and the numbers of day-degrees involved are likely to be specific to individual varieties. Thus the correct combination of storage period and temperature is specific to an individual variety and a time of harvesting. At times in the harvesting season the yields of many varieties grown at their optimum age will be insufficient to be commercially attractive; thus the ideal type of variety testing would be to compare varieties each grown from seed of the optimum age. As these changes would change with time it is clearly a difficult task, but it should be appreciated that the yields of varieties are influenced by age, and this must be taken into account in organizing variety testing.

For the early potato grower, the significance of these results is that several types of seed may be required if yields are to be maximized throughout the harvesting period. The range of seed may be achieved either by manipulating age within a variety or by the use of different varieties. The use of only one type of seed of Home Guard would probably produce economic returns throughout but would not achieve maximal yields and returns throughout the harvesting period. In areas which begin harvesting later than Pembrokeshire, yields must approach those in Pembrokeshire as prices fall with time, and the type of growth pattern exhibited by the oldest seed of Home Guard and probably Maris Bard is inappropriate. As such seed would frequently result from storing Home Guard at ambient temperatures it is not surprising that this variety is unpopular in areas outside the south-west.

The data for Home Guard and Maris Bard suggest that seed of 800-1000 day-degrees is necessary for earliest harvests. From Expts 1-3 Vanessa and Pentland Javelin appear to be too young from all storage regimes to be commercially acceptable. After about 2 weeks of harvesting, seed of 500-600 day-degrees is required for maximal yields in Home Guard and the yield decrease caused by exceeding this age can be considerable. At this time yields of Vanessa and Pentland Javelin are more similar to Home Guard, and seed of approximately 600 daydegrees is required. Seed of the oldest age is still, acceptable in Maris Bard. At even later harvests the optimum seed age for Home Guard decreases still further and Raouf (1979) has shown that in seed crops of Home Guard little or no accumulation of day-degrees is necessary for maximum yields in August. Similar changes occurred in Maris Bard but at a slower rate, so that there was little advantage in ageing seed for final harvests. There was, however, no clear evidence of any substantial disadvantage from old seed at late harvests. The growth pattern of young seed of Maris Bard was similar to that generally described for maincrop varieties, and the variety is clearly suitable for harvesting at high yields throughout the season if seed of appropriate age is used.

Optimum seed ages, as demonstrated in these experiments, should become the definitive objective of seed production and storage. The age of seed at planting is determined by the onset of sprout growth, which may be a function of the end of dormancy or delivery of seed and the temperatures prevailing during the period of sprout growth. Table 8 shows the variation in age of seed at planting resulting from variation in date of onset of sprout growth and ambient temperatures. Many, as yet unpublished, data show that 19 October is approximately the mean date on which 3 mm sprouts are produced in Home Guard and the range is about 18 days either side of this date, once-grown local seed having an earlier end to dormancy than imported Scottish seed. For Maris Bard, the first week in November is earlier than dormancy can be broken in ambient conditions without chemical treatment; much seed of this variety does not begin to sprout until December. Data on temperatures prevailing in commercial stores are limited, and as they may be below the base temperature of 4 °C at times, calculation of day-degrees from means of maximum and minimum temperatures is not strictly justified (Williams &

	1 October	19 October	4 November	13 December
Year	(150)	(132)	(116)	(89)
1960-1	781.5	640.2	501.1	340.5
1961-2	687.0	563.6	399.0	261.0
1962-3	$325 \cdot 5$	270.6	62.4	0
1963-4	714.0	616.4	412.9	226.0
1964-5	658.5	563·6	404.8	217.5
1965-6	738-0	628.3	415.3	324.0
19667	753.0	607.2	483.7	360.0
1967-8	649.5	521.4	374.7	256.3
1968-9	682.5	604.6	346.8	$253 \cdot 5$
1969-70	720.0	601.9	345.7	202.5
1970-1	768.0	660-0	589.3	301.5
1971 - 2	793-5	683.8	462.8	327.6
1972-3	790-0	671.9	488.4	346.5
1973-4	780.0	662.6	503.4	351.0
1974-5	802.5	693·0	578.8	445.5
1975-6	778.5	704.9	497.6	371.6
1976-7	624.0	421.4	367.7	217.5
1977-8	720.0	630.9	389.8	$265 \cdot 5$
1978-9	643.5	541.2	314.4	118.5

Table 8. Number of day-degrees > 4 °C from four dates of onset of sprout growth to 1 March assuming store temperatures are 2 °C above ambient. Data from Aberporth, Dyfed

MacKay, 1970). The data in Table 8 assume store temperatures to be 2 °C above ambient and have been calculated from mean temperatures for Aberporth for the period 1960-79. They are likely to be conservative estimates of age at planting as temperatures in glasshouses, especially in February and March, are likely to be more than 2 °C above ambient. From the earliest end of dormancy Home Guard usually achieves a seed age by 1 March close to that appropriate for harvesting in the first 2 weeks of the season. It is clearly possible that it will become too old for all except the earliest harvest and this may well occur in some circumstances, for example in home-produced seed having a very early end to dormancy. This consistency in age at planting is probably the major reason for the variety's popularity and the use of once-grown seed; without any effort on the part of growers the seed is usually appropriate for the earliest harvests, those growers not wishing to harvest early preferring other varieties. In Maris Bard, the seed is unlikely ever to achieve the optimum age for early harvests in unheated stores. Further, in many years it will accumulate so few day-degrees that its yields will be primarily influenced (i.e. restricted) by the age of seed achieved by planting.

The recording of temperatures in store would give growers an indication of the age of their seed even if they are unable to control the temperatures in their stores. As many stores are stacked to a considerable height (5 m) consideration of the variation in temperature within the store may be justified. The temperatures in stores are not constant throughout storage and it is clearly important to know if the differences in the sequence of temperature leading to the same total number of daydegrees have any effects on sprout and field growth. The data of Wurr (1979) suggest little effect on field growth.

The relationships between seed age and yields help to explain why disputes continue as to the merits of different sources of seed (e.g. Goodwin et al. 1969) and the methods to be practised in producing seed. As each source of seed or method practised produces a different period of dormancy and no attempt is made to control storage temperatures over seasons the comparisons are between different ages of seed. As harvest dates also differ between years of experiments it is not surprising that such comparisons produce no consistent effect and do not indicate any causal factors. All such comparisons must be made in relation to the ages of seed produced, which can now be measured if the onset of sprout growth and store temperatures are recorded. Any experimental programme can remove the effect of annual variation in age by manipulating storage temperatures in order to produce seed of the same number of day-degrees in each year.

The effects of age on number of tubers affected tuber grading and were of considerable importance for both ware and seed production. The reduction in number of tubers with old seed ensured that individual tubers were larger and number of saleable tubers (above an increasing minimum size) increased with age throughout growth in several experiments. Such effects are disadvantageous for the production of closely graded fractions of yield as in seed production. The increased tuber size from old seed may become a disadvantage at the end of the season for the tubers may become too large and have an increasing tendency to quality defects such as mis-shapes and second growth. The work reported was part of research programmes supported by the Potato Marketing Board and the Agricultural Research Council. The authors thank Miss J. Amies for help in preparation of the manuscript.

### REFERENCES '

- ALLEN, E. J., BEAN, J. N., GRIFFITH, R. J. & O'BRIEN, P. J. (1979). Effects of length of sprouting period on growth and yield of contrasting early potato varieties. Journal of Agricultural Science, Cambridge 92, 151– 163.
- 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.
- EMILSSON, B. (1949). Studies on the rest period and dormant period in the potato tuber. Acta Agricultura Suecana 3, 189-284.
- 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.
- MADEC, P. & PERENNEC, P. (1955). The possibility of sprouting seed potatoes and their consequences (translation). Annaues de l'Amélioration des Plantes 4, 555-574.
- O'BRIEN, P. J. (1981). Effects of seed crop treatments on the growth and yield of progeny tubers of early potato cultivars. Ph.D. thesis, University College of Wales, Aberystwyth.
- POTATO MARKETING BOARD (1968a). Survey of Early Potatoes.
- POTATO MARKETING BOARD (1968b). Survey of Maincrop Potatoes.
- RAOUF, G. S. M. (1979). Effects of physiological age of seed tubers in the early potato variety Home Guard. M.Sc. thesis, University College of Wales, Aberystwyth.
- REUST, W. & MUNSTER, J. (1975). The period of incubation and its importance (translation). *Revue Suisse Agricole* 7, 185-187.

- SADLER, E. M. (1961). Factors influencing the development of sprouts on the potato. Ph.D. thesis, University of Nottingham.
- SCOTT, R. K. & WILCOCKSON, S. J. (1978). Application of physiological and agronomic principles to the development of the potato industry. In *The Potato Crop*: the Scientific Basis for Improvement (ed. P. M. Harris), pp. 678-704. London: Chapman & Hall.
- SCOTT, R. K. & YOUNGER, A. (1973). The growth, development and yield following different pretreatment of seed potatoes. Proceedings of the Fifth Triennial Conference of the European Association for Potato Research, Norwich, pp. 113-114.
- TOOSEY, R. D. (1964). The pre-sprouting of seed potatoes: factors affecting sprout growth and subsequent yield. Part I. Field Crop Abstracts 17, 161-168.
- WILLIAMS, C. D. V. & MACKAY, K. H. (1970). Tables of daily degree-days above or below any base temperature. Canada Department of Agriculture, Publication 1409.
- WURR, D. C. E. (1978a). Studies of the measurement and interpretation of potato sprout growth. Journal of Agricultural Science, Cambridge 90, 335-340.
- WURR, D. C. E. (1978b). The effects of the date of defoliation of the seed potato crop and the storage temperature of the seed on subsequent growth. I. Sprout growth. Journal of Agricultural Science, Cambridge 91, 737-745.
- WURB, D. C. E. (1979). The effect of variation in the storage temperature of seed potatoes on sprout growth and subsequent yield. *Journal of Agricultural Science, Cambridge* **93**, 619–622.
- YOUNGER, A. (1975). The significance of sprouting and irregular spacing on potato production. Ph.D. thesis, University of Nottingham.