

Appearance and growth of individual leaves in the canopies of several potato cultivars

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SUMMARY

Leaf appearance of contrasting potato cultivars was examined in field experiments at Cambridge, UK, between 1985 and 1990. Three experiments examined the effects of N fertilizer on the appearance and growth of leaves. Four experiments examined leaf appearance over a wide range of planting dates and in two of these experiments different physiological ages of seed were compared.

Linear regression of rate of appearance of main-stem leaves on air temperature indicated a strong dependence of rate of leaf appearance on temperature in the cultivar Maris Piper with a phyllochron of *c.* 31 K d/leaf but in Estima variation in rate of leaf appearance was only partly explained by differences in air temperature. The phyllochron of main-stem leaves in Estima and Home Guard was shorter for old seed than young seed but there was little effect of seed age in four other cultivars. The phyllochron of main-stem leaves was longer without N fertilizer than with N but the difference in the phyllochron between rates of applied N was small. Leaf appearance on sympodial branches was slower and more variable than on the main-stem. Growth of branches differed between cultivars, particularly with no N fertilizer. In the determinate cultivars Estima and Diana there was restricted growth of branches but in the indeterminate cultivar Cara, significant leaf area was contributed by branches. The duration of leaf appearance and longevity of individual leaves is discussed in relation to N, temperature and cultivar.

INTRODUCTION

The importance of the leaf canopy in determining crop productivity has long been recognized in classical growth analysis (Watson 1952). The effects of husbandry and environment on productivity are determined by effects on canopy size, morphology and duration so that greater understanding of the components and processes creating the functional leaf canopy is needed for continuing improvements in potato production.

The leaf canopy in potato crops may comprise leaves from main-stems, secondary stems and axillary branches (Allen 1978). The initiation of new leaves does not cease with the appearance of the first flower on the main-stem but continues on sympodial (reaching above the first flower) and axillary branches. Cultivars differ in the degree to which they branch and the extent of sympodial branches is indicative of the degree of determinacy in their growth habit. Controlled environment studies have shown that mineral nutrients, especially nitrogen, increase the number of leaves on branches and individual leaf size (Fernando 1958; Humphries & French 1963; Vos & Biemond 1992). Borah & Milthorpe (1962) found that

leaf appearance was more rapid with increasing light intensity and more rapid at 20 °C than 15 or 25 °C whilst Kirk & Marshall (1992) reported that the rate of leaf appearance increased linearly with increase in temperature over the range 9–25 °C. Some studies of field-grown plants have examined effects of the environment on leaf appearance and leaf size (e.g. Jefferies 1989) but detailed information on the effects of agronomic treatments on the composition of the canopy is lacking, particularly in relation to different potato cultivars.

A close linear relationship between the number of emerged leaves and thermal time has been reported in many crop plants including wheat (Gallagher 1979) and sugarbeet (Milford *et al.* 1985). Buds with leaf initials are present in potato seed tubers and may have developed considerably before planting. With physiologically old seed, all of the primordia below the first flower can be initiated before planting (Firman *et al.* 1991) but the influence of differences in the number of initiated primordia on leaf appearance and growth is not known. The size and longevity of potato canopies differs considerably between crops (Allen & Scott 1992) but the influence of environmental factors on the formation and structure of canopies is not well

understood. This study investigated the development and longevity of canopies of different potato cultivars grown with a range of agronomic treatments.

MATERIALS AND METHODS

Seed tubers for all experiments were selected by hand from commercial seed and were sprouted in illuminated stores or held in cold store (< 4 °C). For experiments with more than one planting date, tubers were held in cold store between consecutive plantings. The experiments were planted at Cambridge University Farm and planting dates and other treatments are listed in Table 1. All experiments were planted by hand in ridges 71 cm wide at recommended spacings (MAFF 1982). Experiment 2 was a split-plot design with planting dates in main plots but other experiments were randomized block designs. Experiment 1 was replicated in four blocks, Expt 6 in eight blocks and all other experiments had three blocks. All experiments were irrigated throughout growth with an overhead sprinkler system. Air temperature in the field was recorded hourly.

The appearance of leaves was investigated by

regular observations of two (four in Expt 4) tagged plants in each plot (only two replicates were tagged in Expts 1–3). The number of emerged leaves (> 10 mm) on one main-stem per plant was recorded soon after emergence and observations were usually repeated every 3–7 days. The first record of the number of leaves was made after the sprout had unfurled so that several leaves were already present. In Expts 1, 2, 3 and 6, appearance of leaves was also recorded on successive sympodial branches with leaves numbered in acropetal sequence. A sympodial branch was defined as a branch which developed from the highest node below the flower (this position was not fixed as branches do not develop at all nodes) and branches arising from nodes below this were classified as basal axillary branches. The rate of leaf appearance to the first flower was calculated by linear regression of the number of leaves against time and thermal time (above a base of 0 °C) for each plot and effects of treatments on the phyllochron were assessed by analysis of variance. The phyllochron for leaves on the sympodial branches was calculated by the same method until the appearance of the penultimate leaf. The duration of leaf appearance was calculated from plant emergence to the appearance of the final leaf. In

Table 1. *List of treatments and details of the field experiments with potatoes*

Experiment	Year	Planting date	Cultivar	Nitrogen (kg/ha)	Physiological age (Kelvin days > 4 °C)
1	1985	19 April	Estima, Pentland Crown	0, 90, 180	—*
2	1986	14 March 11 April 12 May	Estima, Pentland Crown	0, 90, 180	—*
3	1986	11 April	Cara, Diana, Estima, Maris Piper, Pentland Crown, Pentland Dell	0, 90, 180	—*
4	1987	13 March 13 April 14 May 14 June 29 June 13 July 3 August 31 August	Estima, Maris Piper	120	0
5	1988	14 April 24 May 29 June 9 August	Cara, Désirée, Estima, Home Guard, Maris Piper, Vanessa	100	0 or 750 (1128 for Home Guard)
6	1988	18 April 17 May	Estima	136	210 or 580
7	1990	13 March 23 May 6 July 17 August	Estima, Maris Piper, Désirée, Record	150	0

* Seed allowed to sprout in ambient store (up to first planting in Expt 2).

Table 2. Effect of nitrogen on (a) the total number of leaves produced on the main-stem and sympodial branches and (b) the phyllochron (Kd/leaf) for main-stem and (c) the phyllochron for sympodial branch leaves in Expts 1-3

	Planting date	Cultivar	N applied (kg/ha)			S.E.	(D.F.)	
			0	90	180			
(a)	Expt 1	19 April	Estima	20.3	20.5	22.8	0.80	(5)
			Pentland Crown	26.5	28.0	28.8		
	Expt 2	14 March	Estima	18.0	21.0	27.0	0.97*	(15)
			Pentland Crown	25.0	27.5	31.8		
		11 April	Estima	17.5	22.0	25.8		
			Pentland Crown	26.0	28.0	29.3		
	12 May	Estima	22.3	25.3	26.3			
		Pentland Crown	23.8	26.8	27.0			
	Expt 3	11 April	Estima	17.8	19.0	24.8	1.33	(17)
			Pentland Crown	24.8	26.3	28.0		
			Maris Piper	22.5	25.8	32.0		
			Cara	27.0	30.3	31.0		
			Diana	18.0	19.8	24.0		
			Pentland Dell	23.8	24.5	29.0		
(b)	Expt 1	19 April	Estima	33.0	33.7	36.0	5.27	(5)
			Pentland Crown	45.5	39.5	37.2		
	Expt 2	14 March	Estima	39.1	37.7	33.7	3.7*	(15)
			Pentland Crown	44.1	37.1	34.3		
		11 April	Estima	55.6	34.5	37.8		
			Pentland Crown	47.6	38.7	36.4		
	12 May	Estima	46.1	36.1	37.7			
		Pentland Crown	44.6	46.0	39.4			
	Expt 3	11 April	Estima	33.0	36.7	34.7	5.36	(17)
			Pentland Crown	50.4	40.3	34.2		
			Maris Piper	54.0	31.4	29.7		
			Cara	38.7	32.7	31.9		
			Diana	49.0	42.9	39.1		
			Pentland Dell	33.3	35.4	29.0		
(c)	Expt 1	19 April	Estima	85	94	129	20.4	(5)
			Pentland Crown	91	85	86		
	Expt 2	14 March	Estima	102	259	91	47.9*	(15)
			Pentland Crown	101	86	74		
		11 April	Estima	154	99	75		
			Pentland Crown	77	81	68		
	12 May	Estima	117	78	61			
		Pentland Crown	68	81	56			
	Expt 3	11 April	Estima	168	150	98	28.3	(17)
			Pentland Crown	83	73	42		
			Maris Piper	78	84	56		
			Cara	74	62	65		
			Diana	175	128	76		
			Pentland Dell	78	84	66		

* S.E. for comparisons at the same planting date.

† S.E. for comparisons between planting dates.

Expts 2-3, the length of every fifth leaf (numbered acropetally) was measured weekly on tagged plants and the date when the leaf became senescent (> 50% of the leaf yellow) was noted. Leaf area was estimated

from leaf length using previously established relationships (Firman & Allen 1989).

Leaf area index was calculated from harvests of four plants from each plot at intervals during growth

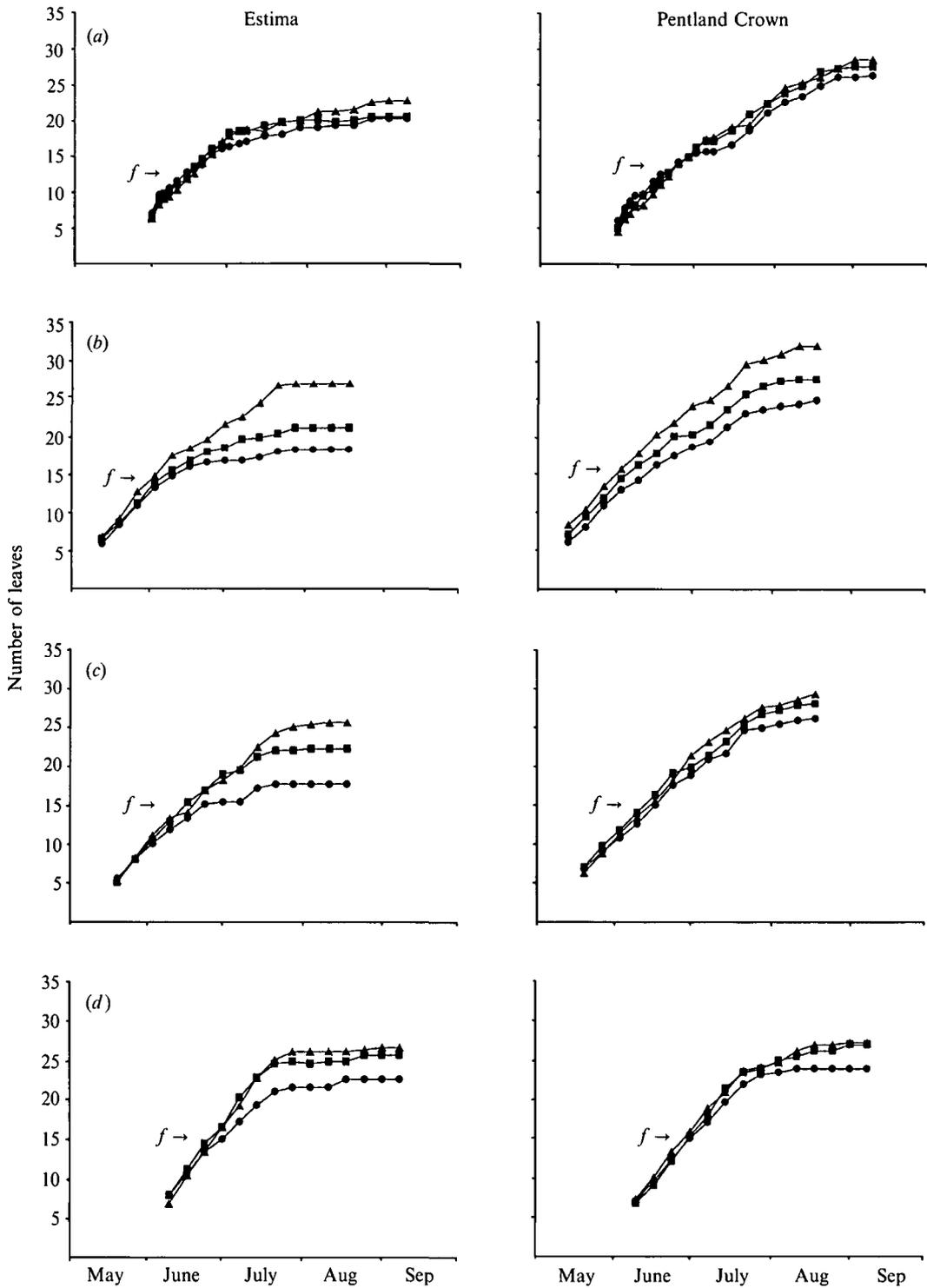


Fig. 1. Leaf appearance on the main-stem and sympodial branches in Estima and Pentland Crown at three levels of N fertilizer in Expts 1 and 2. (a) Expt 1; (b) Expt 2 first planting; (c) Expt 2 second planting; (d) Expt 2 third planting. ●, 0 kg N/ha; ■, 90 kg N/ha; ▲, 180 kg N/ha. Position of first flower indicated by *f*.

in Expts 1–3. Harvest dates were 55, 69, 83, 97, 118, 145 and 166 days after planting (DAP) in Expt 1; 74, 102, 130, 158, and 186 days after the first planting in Expt 2; and 53, 81, 109 and 137 DAP in Expt 3. Leaves were stripped from the petioles and divided into three fractions; main-stem leaves (below the first flower), sympodial branch leaves and basal axillary branch leaves. Leaf area of each fraction was estimated by punching out from the leaf sample (which included the midrib) 50 discs of known area which were dried and weighed separately from the main sample.

RESULTS

Number of leaves and rate of leaf appearance

The number of leaves on the main-stem (i.e. to the first flower) was not affected by N in Expts 1–3 but differed between cultivars in Expt 3 with fewest main-stem leaves in Diana (12.3 ± 0.82), intermediate numbers in Estima (14.1), Pentland Dell (14.6) and Pentland Crown (15.1) and most in Cara (17.3) and Maris Piper (17.7). The number of leaves produced on sympodial branches was increased by N application in Expts 2 and 3 but there was little effect of N in Expt 1 (Table 2*a*, Fig. 1*a*). The difference in number of leaves between application of 90 and 180 kg N/ha was small in Pentland Crown and Cara. In Estima, the effect of N on number of leaves in Expt 2 was greater after the first two plantings than after the final planting (Table 2*a*, Fig. 1*b–d*). In Expt 7, there were fewer leaves after the early planting than after the two subsequent plantings in all cultivars, but the number

of leaves was least after the final planting (Table 3*a*, Fig. 2).

The appearance of leaves up to the first flower was approximately linear with time in all experiments and the appearance of leaves on sympodial branches usually continued at a slower rate (Figs 1–2). Linear regressions of rate of leaf appearance on mean air temperature were calculated from treatment combination means from all experiments (180 kg N/ha treatments only in Expts 1–3) for Estima and Maris Piper, cultivars for which the most information was available. The rate of leaf appearance on the main-stem increased linearly with increase in mean air temperature between *c.* 11–19 °C in both cultivars (Fig. 3) but the variance accounted for by linear regression was less in Estima (38.1%) than in Maris Piper (68.2%). Estimates for the phyllochron (Kelvin days/leaf above an assumed base of 0 °C) obtained by fitting regression equations in which the constant was constrained to zero were 30.8 K d/leaf for Maris Piper and 34.3 K d/leaf for Estima. The number of leaves on sprouts at emergence was not recorded (this could only have been established destructively) but extrapolating fitted lines gave estimates of 3–7 leaves which is about the number of leaves (> 10 mm) that would be expected to be present in an unfurled sprout at emergence.

There was no significant effect of applied N on the rate of leaf appearance in Expt 1 but the phyllochron was longer with no applied N than with N in Expts 2 and 3 (Table 2*b*). In Expt 4, the phyllochron was similar over a wide range of planting dates in both Estima and Maris Piper (Table 4) and in Expt 5 the

Table 3. *Effect of planting date on (a) the total number of leaves produced on the main-stem and sympodial branches and (b) the phyllochron (K d/leaf) for main-stem and (c) the phyllochron for sympodial branch leaves in Expt 7*

Cultivar	Date of planting				S.E.	(D.F.)
	13 March	23 May	6 July	17 August		
(a)						
Estima	19.5	27.2	26.7	17.5	1.39	(30)
Maris Piper	30.3	34.7	30.7	18.5		
Désirée	27.5	31.0	31.8	20.5		
Record	22.5	27.7	27.0	15.2		
(b)						
Estima	29.5	49.0	32.7	36.9	3.78	(30)
Maris Piper	28.2	39.9	27.5	36.9		
Désirée	33.9	28.9	27.0	30.9		
Record	37.9	42.9	36.8	54.2		
(c)						
Estima	116	71	41	—	18.4	(22)
Maris Piper	62	50	39	—		
Désirée	146	62	38	—		
Record	125	65	50	—		

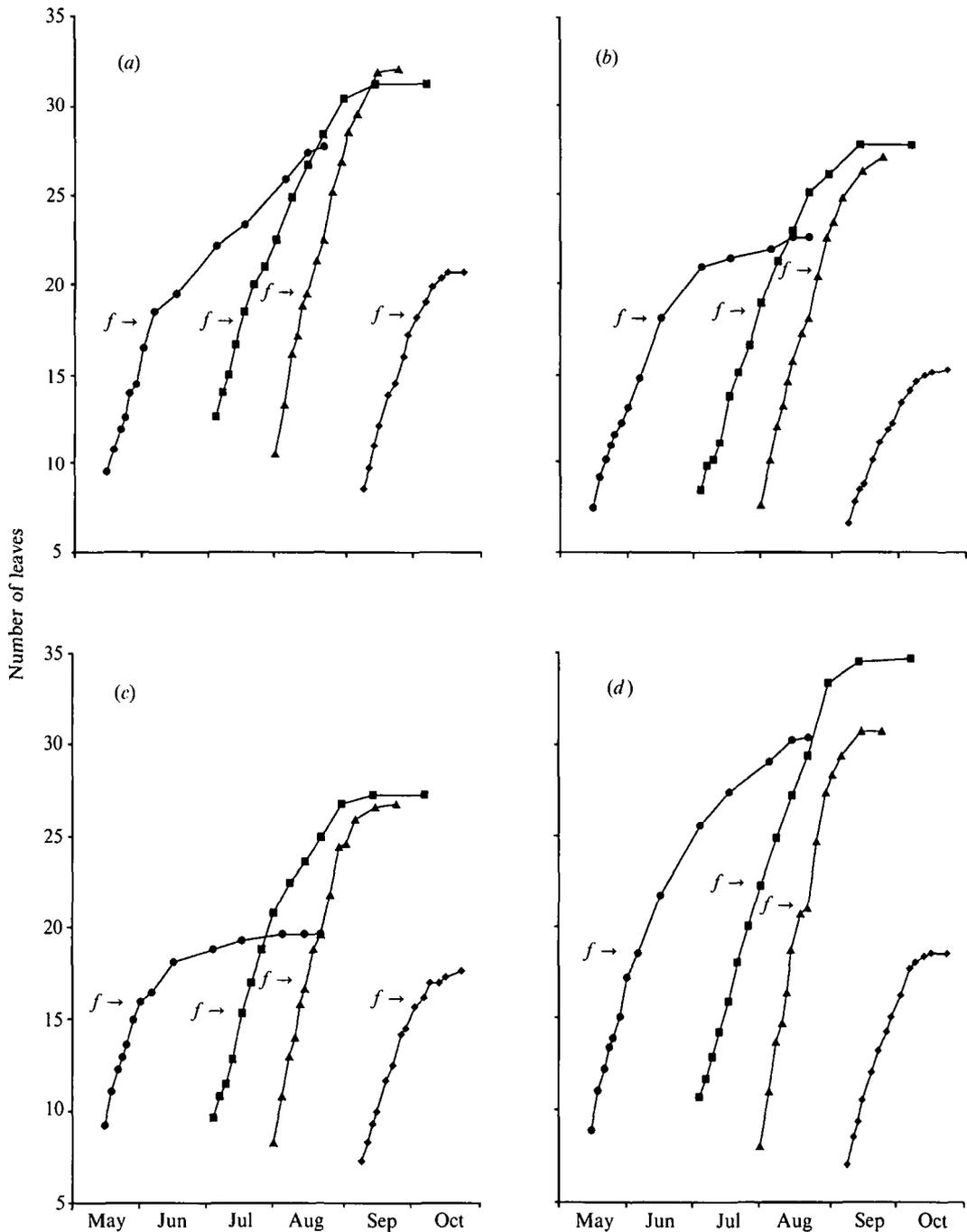


Fig. 2. Leaf appearance on the main-stem and sympodial branches in (a) *Désirée*, (b) *Record*, (c) *Estima* and (d) *Maris Piper* at four planting dates in Expt 7. ●, 1st planting; ■, 2nd planting; ▲, 3rd planting; ◆, 4th planting. Position of first flower indicated by *f*.

phyllochron was similar over a range of planting dates for young seed but was shorter after the third planting than after other plantings for old seed (Table 5). In Expt 7, the phyllochron was longer after the

second and final plantings than after the first and third plantings except in *Désirée* (Table 3). In both Expts 5 and 7 the phyllochron differed between cultivars (Tables 3 and 5) with a relatively short

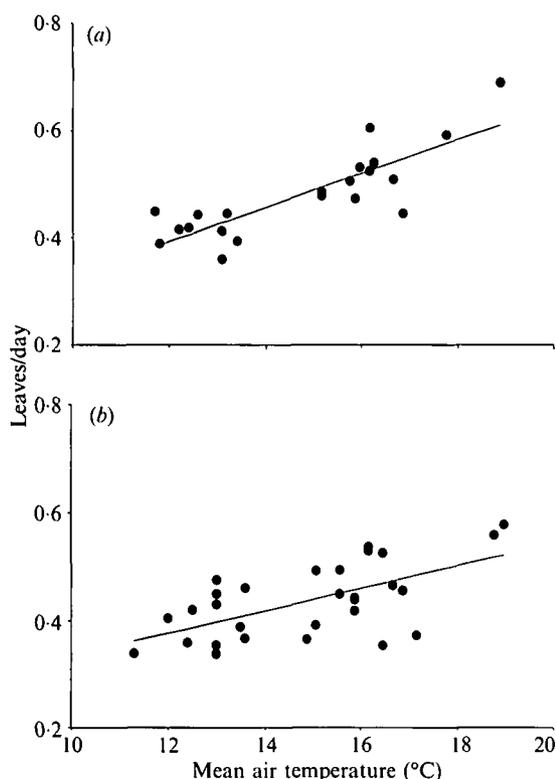


Fig. 3. The relationship between rate of leaf appearance of main-stem leaves and mean air temperature in (a) Maris Piper and (b) Estima. Fitted lines, $y = bx + c$; Maris Piper, $b = 0.0318 \pm 0.0048$, $c = 0.011 \pm 0.071$; Estima $b = 0.0214 \pm 0.0050$, $c = 0.117 \pm 0.075$.

Table 4. Effect of planting date on the phyllochron of main-stem leaves (K d/leaf) in Estima and Maris Piper in Expt 4

Planting date	Estima	Maris Piper	S.E. (30 D.F.)
13 March	33.3	31.6	1.96
13 April	30.3	30.1	
14 May	32.1	33.6	
14 June	33.8	30.6	
29 June	35.9	33.2	
13 July	30.7	32.1	
3 August	31.1	30.7	
31 August	29.4	25.6	

phyllochron for Maris Piper in both experiments. In Expt 5, the phyllochron was shorter for old seed than young seed in Home Guard and Estima but not in other cultivars (Table 5). In Expt 6 with Estima, there was also a shorter phyllochron for old seed ($29.1 \text{ K d/leaf} \pm 1.10$) than for young seed (34.3).

The phyllochron for leaves on sympodial branches

was more variable than for main-stem leaves as growth of branches differed considerably between plants. The phyllochron for leaves on sympodial branches in Expt 1 was much longer than for main-stem leaves (Table 2*b, c*). There was no statistically significant difference in the phyllochron for sympodial branch leaves between N treatments in Expts 1–3 but the phyllochron tended to decrease with increase in applied N in Expts 2 and 3 particularly in Estima and Diana (Table 2*c*). The phyllochron of sympodial branch leaves was longer in Estima and Diana than in other cultivars in Expt 3 particularly with low N (Table 2*c*). The phyllochron for sympodial leaves tended to decrease with delay in planting in Expt 2 although differences were not significant whereas in Expt 7 the phyllochron for sympodial branch leaves decreased with delay in planting in all cultivars (Table 3*c*, Fig. 2). After the final planting in Expt 7 there was little development of sympodial branches.

Duration of leaf appearance

There was no statistically significant effect of N on the duration of leaf appearance in Expts 1–3 but duration of appearance in Estima tended to increase with increase in N in Expt 1 and after the first two plantings in Expt 2 (Table 6). Duration of appearance was on average shorter in Estima than Pentland Crown in Expts 1–2 with leaves emerging for over 100 days in many cases in Pentland Crown. In Expt 3, leaves appeared over a longer period in Cara, Maris Piper and Pentland Crown than in the other cultivars (Table 6). In Expt 7, duration of leaf appearance decreased with delay in planting in Désirée and Record and decreased after the second planting in Estima and Maris Piper with leaf appearance restricted to < 40 days in all cultivars after the final planting (Table 7, Fig. 2). The duration of leaf appearance was longer for Maris Piper and Désirée than for Estima and Record after the first two plantings but after later plantings there was little difference between cultivars (Table 7).

The thermal duration of leaf appearance (K days after emergence) varied from < 500 K days after the final planting in Expt 7 to > 1800 K days for Pentland Crown in Expt 1 (Tables 6–7). In Expt 2, the thermal duration of leaf appearance was similar for all plantings (Table 6) whereas in Expt 7 thermal duration decreased with delay in planting after the second planting and was significantly shorter after the first planting than after the second one in Estima (Table 7).

Individual leaf area and longevity

Individual leaf areas of the 10th leaves were usually greater than those of the 5th or 15th leaves with progressive reductions in the area of more apical leaves. There was little effect of N on the area of the

Table 5. *Effect of seed age on the phyllochron of main-stem leaves (K d/leaf) in six potato cultivars after four planting dates in Expt 5*

Planting date	Seed age	Home	Vanessa	Estima	Maris	Désirée	Cara
		Guard			Piper		
14 April	Young	41.8	29.3	38.9	31.9	35.3	30.4
	Old	37.1	33.5	34.9	30.0	37.0	36.1
24 May	Young	35.3	32.0	34.7	31.1	33.6	31.9
	Old	31.2	31.3	30.7	30.3	39.5	36.5
29 June	Young	40.4	31.6	38.0	30.1	37.8	32.6
	Old	27.6	29.1	31.8	27.0	27.3	29.3
9 August	Young	44.4	31.2	39.2	32.2	34.8	34.2
	Old	35.0	33.8	35.7	31.5	35.4	34.1
S.E. (94 D.F.)				1.95			

Table 6. *Effect of nitrogen on the duration of leaf appearance (from plant emergence) in Expts 1-3*

Expt	Planting date	Cultivar N applied (kg/ha)...	Time (d)			Thermal time (K d)		
			0	90	180	0	90	180
			Expt 1	19 April	Estima	81	83	97
		Pentland Crown	108	108	97	1840	1840	1670
	S.E. (5 D.F.)		6.5			117		
Expt 2	14 March	Estima	67	82	90	1020	1300	1420
		Pentland Crown	110	96	99	1740	1510	1560
	11 April	Estima	64	70	95	1020	1150	1530
		Pentland Crown	94	94	97	1510	1510	1570
	12 May	Estima	88	95	83	1450	1550	1360
		Pentland Crown	77	100	91	1280	1630	1490
	S.E. (15 D.F.)	Same plantings	9.5			150		
		Different plantings	8.8			139		
Expt 3	11 April	Estima	85	85	76	1260	1200	1270
		Pentland Crown	78	79	76	1280	1340	1300
		Maris Piper	78	75	78	1240	1380	1320
		Cara	78	86	82	1360	1360	1215
		Diana	64	67	67	1240	1260	1220
		Pentland Dell	80	83	80	1040	1105	1110
	S.E. (17 D.F.)		4.5			77		

Table 7. *Effect of planting date on the duration of leaf appearance (from plant emergence) in Expt 7*

Cultivar	Planting date				S.E.	(D.F.)
	13 March	23 May	6 July	17 August		
(a) Time (d)						
Estima	70	77	45	39	4.1	(30)
Maris Piper	91	88	44	34		
Désirée	98	86	51	38		
Record	86	74	49	37		
(b) Thermal time (K d)						
Estima	960	1340	810	510	69	(30)
Maris Piper	1340	1500	810	440		
Désirée	1490	1490	910	500		
Record	1270	1290	860	490		

Table 8. Effect of nitrogen on individual leaf area (cm²) in Expts 2-3

N applied (kg/ha)...		Leaf number														
		5			10			15			20					
		0	90	180	0	90	180	0	90	180	0	90	180			
Planting date	Cultivar															
Expt 2																
14 March	Estima	107	106	132	132	236	337	19	93	96	5	5	76			
	Pentland Crown	58	63	122	130	142	269	84	105	215	28	70	108			
11 April	Estima	93	162	149	130	256	277	24	96	109	0	9	67			
	Pentland Crown	61	66	103	137	147	237	104	149	223	56	102	134			
12 May	Estima	161	199	172	214	302	301	85	162	118	6	52	113			
	Pentland Crown	79	90	86	149	248	247	95	204	234	35	113	176			
S.E. (15 D.F.)		Same planting			18.9			26.5			20.4			20.4		
		Different plantings			17.7			28.2			22.2			20.8		
Expt 3																
11 April	Estima	245	254	248	289	262	323	46	41	125	0	1	27			
	Pentland Crown	104	100	103	148	151	180	83	115	144	47	52	103			
	Maris Piper	84	150	217	105	221	297	47	139	243	19	41	122			
	Cara	67	126	138	106	210	255	83	144	191	43	83	129			
	Diana	128	206	184	102	193	214	45	59	161	6	2	84			
	Pentland Dell	111	147	197	153	153	229	81	68	133	24	31	64			
S.E. (17 D.F.)		34.0			37.9			26.5			17.6					

5th and 10th leaves after the final planting in Expt 2 but, in general, leaf area increased with increasing rate of N (Table 8). The increase in leaf area with N application was greater in the more apical leaves, particularly in Estima and Diana in which substantial expansion of the 20th leaves only occurred with the application of 180 kg N/ha. With high N application, the 5th and 10th leaves were larger in Estima than in other cultivars in both Expts 1 and 2, whereas at the most apical leaf positions, leaf area was greater in Maris Piper and Cara than in the other cultivars.

Maximum leaf longevity in Expts 2 and 3 was > 100 d or 1800 K d with the 10th and 15th leaves showing greater persistence than the 5th and 20th leaves in most cases (Table 9). Application of N decreased the longevity of the 5th leaf in each cultivar in both Expts 2 and 3. Longevity of the 10th and 15th leaf was not affected by N in Expt 2 but in Expt 3 it was reduced by N in all cultivars except Estima and Diana (Table 9). Longevity of the 5th leaf was similar in Estima and Pentland Crown in Expt 2 and in Expt 3 there was little difference between cultivars in the longevity of the 5th leaf. In Expt 2, the 20th leaf was more persistent with increase in N application and apical leaves were more persistent in Pentland Crown than Estima particularly after the first planting (Table 9). Similarly, in Expt 3, the more apical leaves were shorter lived in Diana and Estima than in other cultivars particularly at low N (Table 9). Longevity of the 5th, 10th and 15th leaves was not significantly affected by planting date in Expt 2 but that of the 20th

leaf was less after the final planting than after earlier plantings in Pentland Crown.

Leaf area index

The total leaf area index (LAI) increased with rate of N application at most harvests in all cultivars in Expts 1-3 but the trend of increase and decline in LAI was similar at all rates of N (Figs 4-6). In Expt 1 the LAI on the main-stem remained relatively stable for a period of over 50 days in all treatments (Fig. 4). The sympodial branches contributed a large proportion of the LAI from the branches but the LAI on basal axillary branches was often greater. At later harvests, the LAI on branches resulted in greater total LAI in Pentland Crown than in Estima in all Expts (Figs 4-6). In Expt 3, LAI at late harvests was greatest in the cultivar Cara and least in Estima, Diana and Pentland Dell. With no applied N, Estima produced very little LAI on branches whereas in Pentland Crown and Cara, a large fraction of total LAI at later harvests was from branches. In Expt 3, the branch LAI produced with 90 kg N/ha resulted in full canopy cover (LAI of *c.* 3) in Pentland Crown, Cara and Maris Piper but not the other cultivars. In Expt 3, the branch LAI produced by Cara with no applied N was greater than with 90 kg N/ha in other cultivars at 109 and 137 days after planting, and with 90 kg N/ha Cara produced at least as much branch LAI as other cultivars with 180 kg N/ha (Fig. 6). The LAI

Table 9. *Effect of nitrogen on individual leaf longevity in Expts 2-3*

N applied (kg/ha)... Planting date Cultivar		Leaf number											
		5			10			15			20		
		0	90	180	0	90	180	0	90	180	0	90	180
<i>(a) Time (d)</i>													
Expt 2													
14 March	Estima	68	53	46	68	70	68	63	67	65	39	35	60
	Pentland Crown	86	49	44	97	86	81	98	95	77	89	82	77
11 April	Estima	77	60	53	65	65	79	49	54	78	35	39	72
	Pentland Crown	77	54	46	91	103	81	75	93	98	74	88	91
12 May	Estima	63	46	46	74	89	46	60	72	67	49	63	65
	Pentland Crown	63	51	47	86	74	81	84	81	72	67	81	86
S.E. (15 D.F.)		Same planting			11.1			6.8			5.0		
		Different plantings			11.4			7.6			5.3		
Expt 3													
11 April	Estima	72	51	61	70	74	75	61	67	68	20	28	58
	Pentland Crown	93	72	51	117	105	88	102	96	98	65	91	65
	Maris Piper	86	61	46	95	82	75	95	86	96	88	54	102
	Cara	70	54	47	95	81	63	112	102	72	63	93	63
	Diana	86	67	67	70	72	79	53	67	74	52	16	53
	Pentland Dell	77	82	51	77	103	74	74	93	82	49	91	65
S.E. (17 D.F.)		8.6			5.9			7.4			9.9		
<i>(b) Thermal time (K d)</i>													
Expt 2													
14 March	Estima	1080	790	650	1150	1180	1140	1110	1180	1140	650	600	1030
	Pentland Crown	1390	720	620	1700	1420	1330	1560	1540	1320	1350	1290	1290
11 April	Estima	1270	950	830	1130	1130	1330	890	970	1350	540	670	1100
	Pentland Crown	1240	860	700	1500	1650	1360	1270	1490	1530	1130	1330	1410
12 May	Estima	1120	830	830	1250	1070	830	960	1160	1070	760	990	1000
	Pentland Crown	1120	920	860	1400	1220	1320	1300	1250	1150	960	1170	1240
S.E. (15 D.F.)		107			127			97			77		
		103			158			106			82		
Expt 3													
11 April	Estima	1170	790	970	1190	1250	1260	1090	1170	1190	330	460	970
	Pentland Crown	1500	1170	800	1800	1670	1460	1580	1520	1580	940	1380	1010
	Maris Piper	1410	990	700	1540	1380	1270	1500	1430	1560	1280	900	1570
	Cara	1140	870	740	1530	1340	1060	1750	1620	1250	950	1440	1020
	Diana	1410	1090	1090	1200	1240	1330	880	1160	1230	810	250	820
	Pentland Dell	1290	1370	800	1320	1660	1250	1250	1470	1360	790	1190	1300
S.E. (17 D.F.)		150			82			109			147		

produced on branches with no N fertilizer was less in Estima than Pentland Crown in all Expts and greater in Cara than any other cultivar in Expt 3.

DISCUSSION

The linear dependence of rate of leaf appearance on air temperature found in this study is consistent with results from other crop plants (Gallagher 1979; Milford *et al.* 1985) and the phyllochron for Maris Piper (*c.* 31 K d/leaf), estimated from all the field experiments, was similar to the figure obtained in

controlled environments by Kirk & Marshall (1992). The relationship between air temperature and rate of leaf appearance was less close for the cultivar Estima than for Maris Piper. Some of the variation in the rate of leaf appearance in Estima can be attributed to differences in sprout development at planting as seed age was found to affect the phyllochron directly in Estima in Expts 5 and 6. Estimates of rates of leaf appearance may also be more variable for Estima than Maris Piper as there are fewer leaves on the main-stem in Estima so that the linear phase is shorter.

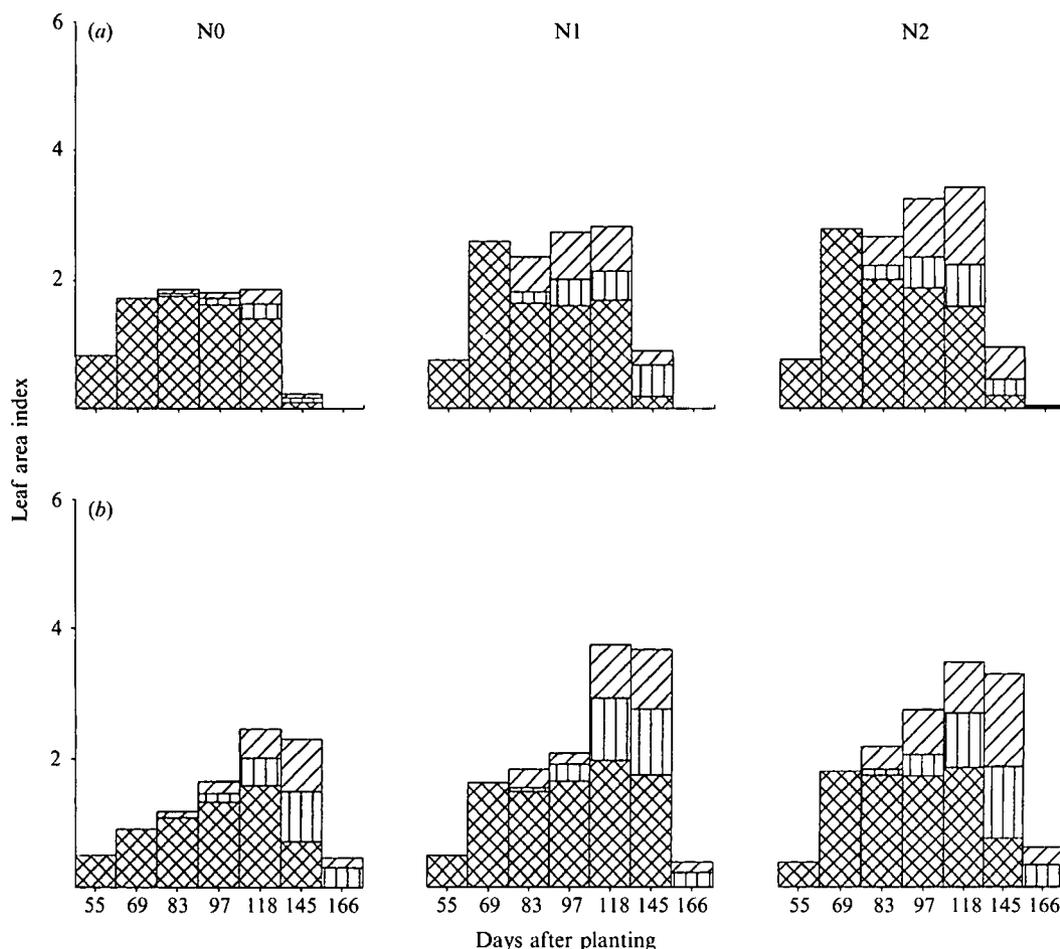


Fig. 4. Leaf area index distribution on main-stems, basal axillary and sympodial branches in (a) Estima and (b) Pentland Crown at three rates of N fertilizer at sequential harvests in Expt 1. \otimes , main-stem; \parallel , basal axillary branches; \diagup , sympodial branches.

The phyllochron of main-stem leaves was up to 15 K d longer with no N fertilizer than with applied N but there was little difference in phyllochrons between rates of applied N so that N is unlikely to be important in determining rates of leaf appearance on the main-stem in well fertilized crops. Similarly, whilst seed age reduced the phyllochron in Home Guard and Estima, the small increase in rate of leaf production is less important than other effects of seed age on plant growth. A reduction in the phyllochron with increase in seed age in Home Guard and Estima suggests that, in these cultivars at least, the initiation of leaf primordia in young seed is a limitation to the rate of leaf appearance and that in old seed the nodes present in the sprout enable faster rates of leaf appearance.

The increase in the phyllochron found after the second and final planting in Expt 7 suggests that other

factors can affect rates of leaf appearance. Jefferies (1989) has reported effects of water-stress on the phyllochron in potato but it is unlikely that soil moisture deficits sufficient to affect leaf appearance would occur in irrigated crops in the relatively short period from plant emergence to appearance of the first flower. After the second planting, leaf appearance occurred during a period over which the maximum air temperature exceeded 28 °C on several days and it is likely that these high temperatures were supra-optimal, resulting in an increase in the phyllochron. The high temperatures may have induced water-stress which was independent of soil moisture deficit. The phyllochron in the cultivar Désirée did not appear to be affected, which is consistent with the reported heat tolerance of this cultivar (Demagante & Van der Zaag 1988). A reduction in incident radiation during the short days in autumn may have contributed to the

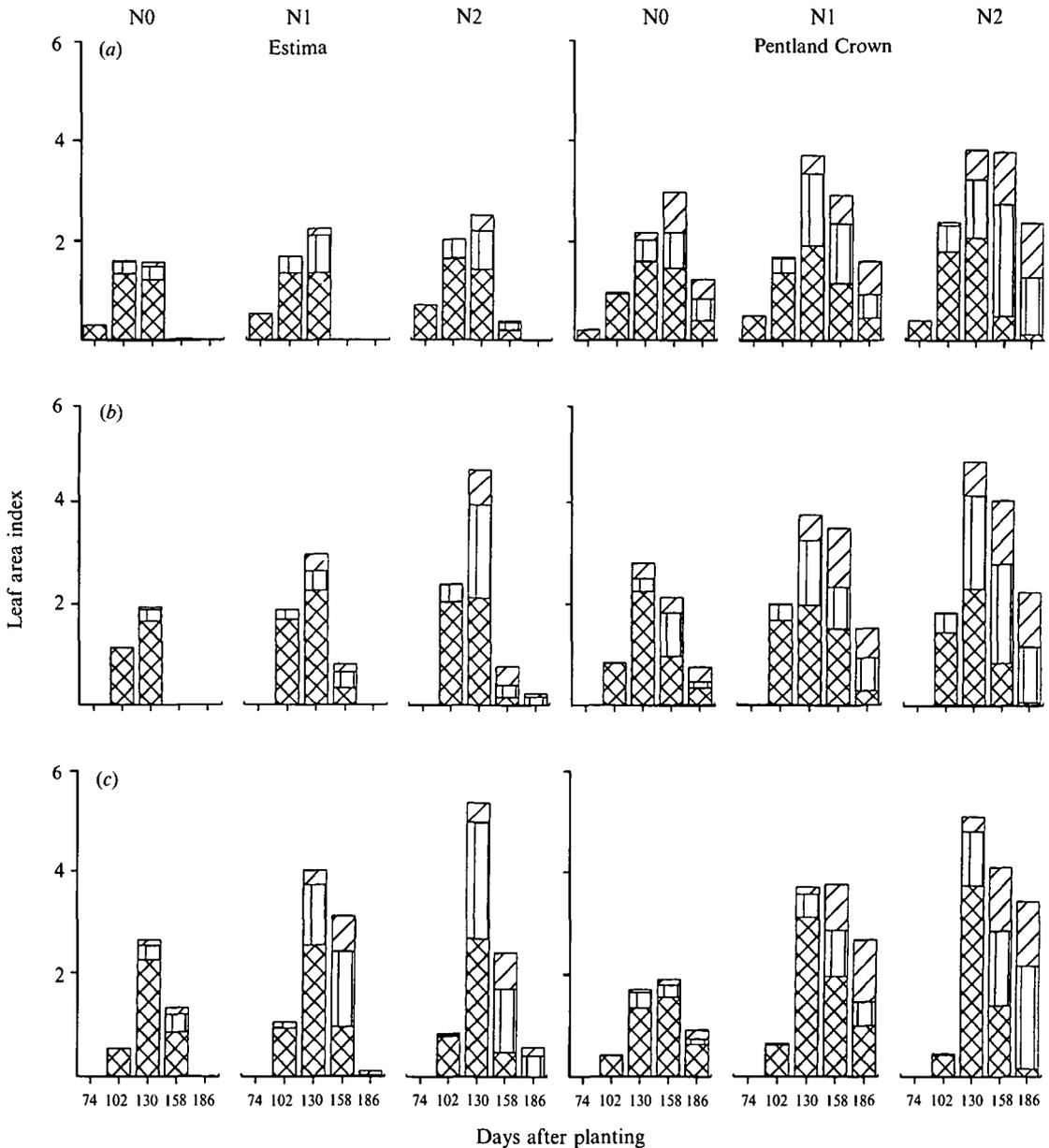


Fig. 5. Leaf area index distribution on main-stems, basal axillary and sympodial branches in Estima and Pentland Crown at three rates of N fertilizer at sequential harvests in Expt 2. (a) first planting; (b) second planting; (c) third planting. ▣, main-stem; ▤, basal axillary branches; ▥, sympodial branches.

increase in the phyllochron after the final planting in Expt 7 (*cf* Borah & Milthorpe 1962) and appearance of the later formed leaves may have been adversely affected by low night temperatures (min 2.9 °C) but a direct effect of the decreasing photoperiod on leaf appearance after this planting is also possible.

The appearance of leaves in Estima and Diana was markedly different from that in other cultivars; the rate of leaf appearance to the first flower was

comparable but the appearance of leaves on sympodial branches was much slower so that the final number of leaves which emerged was reduced. With low rates of N, Estima and Diana were almost completely determinate with very little axillary branch growth whereas in Pentland Crown and Cara, the number of leaves on the sympodial branches was only slightly reduced. However, the area of individual leaves, especially the most apical, was increased by

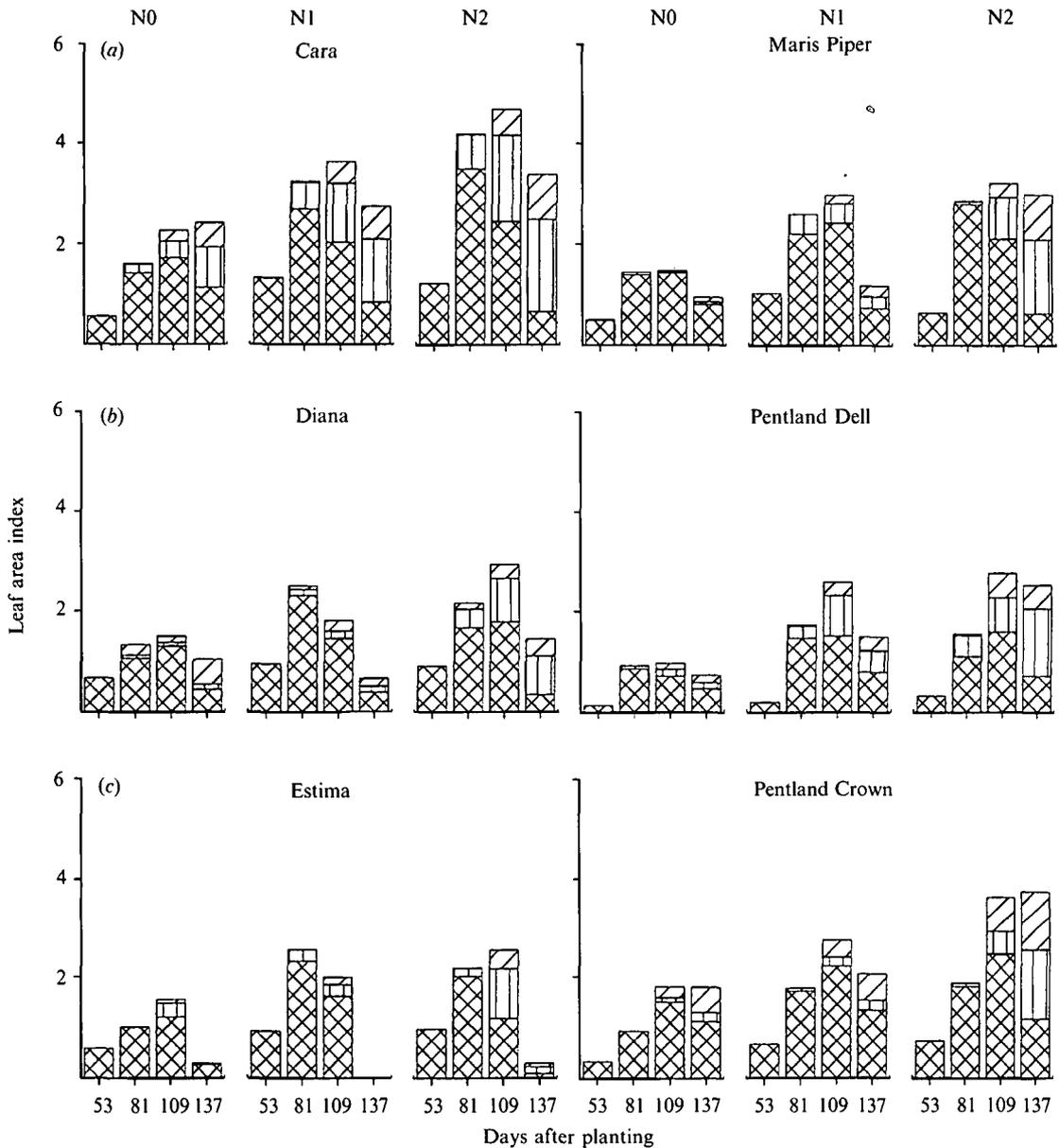


Fig. 6. Leaf area index distribution on main-stems, basal axillary and sympodial branches in six potato varieties at three rates of N fertilizer at sequential harvests in Expt 3. ☒, main-stem; ▨, basal axillary branches; ▩, sympodial branches.

application of N in all cultivars. As indeterminate cultivars with no N fertilizer produced larger canopies than more determinate cultivars in the same conditions and the increase in number and size of leaves with N was less marked than in more determinate cultivars, indeterminate cultivars should require less N fertilizer to achieve and maintain complete canopy cover. Indeterminate cultivars would, therefore, be expected to have a lower N-requirement for optimum

yield than determinate cultivars. A series of N experiments comparing Estima and Cara support this hypothesis (J. H. Fowler, unpublished).

The number of leaves on the main-stem in Expt 2 was least for the most determinate cultivars Diana and Estima and greatest for the indeterminate cultivars Maris Piper and Cara. Whilst the number of below-ground nodes is increased with increase in physiological age, the number of leaves on the main-

stem is relatively stable within a cultivar (Firman *et al.* 1991) so that number of leaves could provide a marker for leaf growth characteristics of cultivars. The relationship between number of main-stem leaves and growth characteristics deserves study but a strict association should not be expected.

There was a longer phyllochron for sympodial branch leaves than for main-stem leaves in all experiments, ranging from *c.* 40 K d/leaf after the third planting in Expt 7 to over 100 K d/leaf in many cases. Milford *et al.* (1985) found that, in sugarbeet, later leaves appeared at a slower thermal rate and suggested that this could be partly explained by differences in availability of N. In potato the average rate of appearance of sympodial leaves might be expected to be lower than for the main-stem leaves irrespective of any difference in N availability, as the appearance of these leaves results from the differentiation of successive apical meristems. The relatively long phyllochron of sympodial compared with main-stem leaves may result in part from differences in N availability but the reduction in phyllochron observed with delay in planting date suggests that the temperature during differentiation and early growth of sympodial leaves is important in determining the subsequent rate of leaf appearance.

Differences in LAI between cultivars and nitrogen rates were mainly caused by the extent of leaf expansion on branches. The continued expansion of more apical leaves on sympodial branches enabled the leaf cover to persist longer in indeterminate cultivars like Cara and Pentland Crown than in the more determinate cultivars Estima and Diana. The results indicate that longevity of the canopy is strongly influenced by the successive production of new leaves rather than differences in leaf longevity between cultivars or rate of N. Individual leaf longevity can, however, be influenced by cultivar and N because of differences in mutual shading. In these experiments, longevity of basal leaves was reduced by application of N where large canopies were formed whereas Vos & Biemond (1992) found that longevity was increased by N in pot plants. It is likely that effects of N on mutual shading which influence leaf longevity in the crop canopy are not apparent in spaced pot plants.

Although the longevity of the canopy is strongly influenced by the successive production of new leaves, a persistent canopy can result from a gradual turnover of long-lived leaves, as found in Expt 1, and this pattern of growth is potentially the most efficient for tuber yield because less photosynthate is used in the production of stem and leaves. As N is unlikely to limit the rate of leaf photosynthesis in potatoes grown on many arable soils (Firman & Allen 1988), there may be no reduction in yield from a persistent canopy grown with low N application. The value of persistent leaf cover is dependent on the growing season; in the UK, the progressive reduction in incident radiation

during autumn limits the advantages of prolonged canopy persistence.

The results of Expts 1–3 indicate that effects of N on the duration of leaf appearance are limited, particularly in indeterminate cultivars in which leaves continue to appear for long periods with no additional N fertilizer. In Expt 7, growth on sympodial branches differed between planting dates, resulting in differences in the number of leaves and the duration of leaf appearance. After the final planting in Expt 7 the early cessation of leaf appearance may be attributable to low night temperatures in October but the minimum air temperature (2.9 °C) was no lower than that experienced in May by the early plantings in this and other experiments which continued to produce leaves. It is possible that the short, decreasing photoperiod (< 12 h) during growth after this late planting inhibited growth of sympodial branches. Inhibition of sympodial branch growth at short photoperiods is consistent with the observation that canopy duration is reduced by short photoperiods (Demagante & Van der Zaag 1988). There is no evidence that the growth of a predetermined succession of sympodial branches is the normal growth pattern in potato but appearance of more than three orders of sympodial branch is unusual even where potatoes are grown in long days. Appearance of leaves may often cease on first or second order sympodial branches, particularly in determinate cultivars such as Estima and Diana, but these cultivars can produce higher order sympodial branches.

Early planting in cool temperatures has been observed to restrict canopy size particularly for old seed (Allen 1977; Jones & Allen 1983) and the restricted appearance of leaves after the early planting in Expt 7 (mean air temperature during appearance of leaves on the main-stem was *c.* 12 °C) compared with appearance after the two subsequent plantings (main-stem leaf appearance at *c.* 16 and 19 °C) is consistent with this. Following early planting dates, the residual available soil N is usually low, which may add to direct effects of low temperatures to restrict leaf growth. Data collected from crops grown on N-rich fen peat soils in East Anglia (Allen & Scott 1992) where potatoes are usually planted relatively late into a warm environment, show that both stem length and individual leaf size of these crops are greater than for crops grown on mineral soils but number of leaves to the first flower is unchanged. The luxuriant leaf canopies observed in these fenland crops, which begin growth under conditions of high available soil N and relatively high soil and air temperature, also indicates the importance of conditions during the early stages of growth in determining canopy development. Low temperatures and low soil N during early growth appear to restrict the later growth of sympodial branches particularly in determinate cultivars. In Estima, little growth above the first flower was

observed after the early planting in Expt 7 whereas after the two subsequent plantings there were c. 8 additional leaves produced on sympodial branches. In Expt 2 it was also found that more leaves were produced in Estima after the later planting. The results show that thermal duration of leaf appearance can be reduced by low temperatures early or late in growth and can be increased by N application in determinate cultivars. Other factors such as physiological age can affect canopy duration but details of effects on the duration of leaf appearance are not well documented and there is very little information for leaf appearance on basal axillary branches.

Garner & Allard (1923) found that, in cultivars where tuber formation could be prevented by artificially long days, vegetative growth could be prolonged almost indefinitely, but in tuberized field crops vegetative growth is not indefinite even under favourable conditions of long days, near optimal temperatures and sufficient fertility. The role of a storage sink in influencing senescence in a manner comparable to monocarpic senescence has been found in many indeterminate plants (Leonard 1962) and a similar influence on vegetative growth may be exerted by potato tubers although there is no conclusive evidence for this. The contention that the initiation of tubers is an important stage in determining subsequent leaf growth (Milthorpe 1963) is less likely. In many cultivars tuber initiation occurs 2–3 weeks after emergence within a wide range of temperatures and

photoperiods (Firman *et al.* 1991) so that differences in plant development at tuber initiation are small. There was no indication in these experiments that the rate of leaf appearance changed at tuber initiation and variation observed in the subsequent rate and duration of leaf appearance was not attributable to differences in the timing of tuber initiation.

This study has indicated the extent to which the growth of sympodial branches can be affected by nitrogen and temperature in contrasting cultivars. In practice, growth of main crop potatoes in the UK is often limited by onset of unfavourable conditions in autumn but in more temperate climates, delay in senescence could be beneficial. The advantages of the efficient partitioning of modern early potato cultivars (Thomson 1987) would also be extended to later harvests if leaf duration in these cultivars could be prolonged. Better control of senescence in potato would improve the utilization of the growing season and benefit harvesting, as the condition of the haulm and tuber skin strength are important practical considerations. The effects shown in these experiments suggest that manipulating leaf growth to suit individual circumstances through choice of cultivar and use of N fertilizer is achievable and should enable increases in yield and improvements in quality.

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REFERENCES

- ALLEN, E. J. (1977). Effects of date of planting on growth and yield of contrasting potato varieties in Pembrokeshire. *Journal of Agricultural Science, Cambridge* **89**, 711–735.
- ALLEN, E. J. (1978). Plant density. In *The Potato Crop* (Ed. P. M. Harris), pp. 278–326. London: Chapman and Hall.
- ALLEN, E. J. & SCOTT, R. K. (1992). Principles of agronomy and their application in the potato industry. In *The Potato Crop* (Ed. P. M. Harris), pp. 816–881. London: Chapman and Hall.
- BORAH, M. N. & MILTHORPE, F. L. (1962). Growth of the potato as influenced by temperature. *Indian Journal of Plant Physiology* **5**, 53–72.
- DEMAGANTE, A. L. & VAN DER ZAAG, P. (1988). The response of potato (*Solanum* spp.) to photoperiod and light intensity under high temperatures. *Potato Research* **31**, 73–83.
- FERNANDO, L. H. (1958). *Studies on the leaf growth, effect of mineral nutrients and the interdependence of the leaves of a plant*. PhD thesis, University of London.
- FIRMAN, D. M. & ALLEN, E. J. (1988). Field measurements of the photosynthetic rate of potatoes grown with different amounts of nitrogen fertilizer. *Journal of Agricultural Science, Cambridge* **111**, 85–90.
- FIRMAN, D. M. & ALLEN, E. J. (1989). Estimating individual leaf area of potato from leaf length. *Journal of Agricultural Science, Cambridge* **112**, 425–426.
- 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.
- GALLAGHER, J. N. (1979). Field studies of cereal leaf growth. I. Initiation and expansion in relation to temperature and ontogeny. *Journal of Experimental Botany* **30**, 625–636.
- GARNER, W. W. & ALLARD, H. A. (1923). Further studies in photoperiodism, the response of the plant to relative length of day and night. *Journal of Agricultural Research* **23**, 871–920.
- HUMPHRIES, E. C. & FRENCH, S. A. W. (1963). The effects of nitrogen, phosphorus, potassium and gibberellic acid on leaf area and cell division in Majestic potato. *Annals of Applied Biology* **52**, 149–162.
- JEFFERIES, R. A. (1989). Water-stress and leaf growth in field-grown crops of potato (*Solanum tuberosum* L.). *Journal of Experimental Botany* **40**, 1375–1381.
- JONES, J. L. & ALLEN, E. J. (1983). Effects of date of planting on plant emergence, leaf growth, and yield in contrasting potato varieties. *Journal of Agricultural Science, Cambridge* **101**, 81–95.
- KIRK, W. W. & MARSHALL, B. (1992). The influence of

- temperature on leaf development and growth in potatoes in controlled environments. *Annals of Applied Biology* **120**, 511–525.
- LEONARD, E. R. (1962). Interrelations of vegetative and reproductive growth with special reference to indeterminate plants. *Botanical Review* **28**, 353–410.
- MILFORD, G. F. J., POCOCK, T. O. & RILEY, J. (1985). An analysis of leaf growth in sugar beet. II. Leaf appearance in field crops. *Annals of Applied Biology* **106**, 173–185.
- MILTHORPE, F. L. (1963). Some aspects of plant growth. In *The Growth of the Potato. Proceedings of the 10th Easter School in Agricultural Science, University of Nottingham* (Eds J. D. Ivins & F. L. Milthorpe), pp. 3–16. London: Butterworths.
- MINISTRY OF AGRICULTURE, FISHERIES AND FOOD (1982). Seed rate for potatoes grown as maincrop. *Short Term Leaflet* **653**.
- THOMSON, A. J. (1987). The effect of fertilizer treatments on a range of old and new early-maturing potato varieties. In *The Production of New Potato Varieties: Technological Advances* (Eds G. J. Jellis & D. E. Richardson), pp. 165–167. Cambridge: Cambridge University Press.
- VOS, J. & BIEMOND, H. (1992). Effects of nitrogen on the development and growth of the potato plant. 1. Leaf appearance, expansion growth, life spans of leaves and stem branching. *Annals of Botany* **70**, 27–35.
- WATSON, D. J. (1952). The physiological basis of variation in yield. *Advances in Agronomy* **4**, 101–145.