

Development in barley (*Hordeum sativum*)

By J. L. JONES* AND E. J. ALLEN†

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

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SUMMARY

Four experiments are reported which studied the effects of date of sowing on the development of winter and spring barley. The first three experiments (1979–80, 1980–1, 1982–3) were carried out at Trefloyno, Tenby and used the varieties Sonja (winter) and Jupiter (spring). The final experiment (1983–4) was carried out in Cambridge using the varieties Igri (winter) and Triumph (spring). A wide range of dates of sowing (August–June) was used and there were considerable differences in temperature between seasons.

In both Sonja and Igri, delaying sowing from August to mid-February reduced the number of mainstem leaves but further delay in sowing increased the number of leaves. In Jupiter, delaying sowing until late October had little effect but further delay consistently reduced the number of leaves. In Triumph, delaying sowing reduced final number of leaves over the whole range (October–May).

In all experiments rate of leaf emergence was characterized by long periods when leaves emerged linearly with time, despite considerable variation in temperature. The only consistent changes in rate of leaf emergence occurred shortly after each equinox, rates slowing in the autumn and increasing in the spring. Rates of leaf emergence were similar in different seasons and sites for similar periods despite differences in temperature.

Initiation of spikelet primordia proceeded linearly with time for most dates of sowing. For winter varieties rates of spikelet initiation increased with delay in sowing provided emergence occurred before the spring equinox. Further delay in sowing decreased the rate of spikelet initiation. In contrast in Jupiter and Triumph the rate increased with each delay in sowing. During periods of low temperature, rate of spikelet initiation slowed but frequently increased to faster rates in succeeding increasing temperatures. Such increasing temperatures had no effect on rate of initiation of later-sown treatments which had not experienced the low temperatures. Effects on spikelet initiation were found when no effects on leaf emergence could be detected.

Initiation of spikelet primordia in all varieties appeared to begin when a fixed number of leaves (different in some varieties) had emerged and end when a fixed number of leaves were left to emerge. Delaying sowing in winter varieties until February and in Jupiter over the whole range reduced the number of leaves emerging during spikelet initiation and was the developmental mechanism through which large differences in date of sowing became small differences in date of anthesis (and grain maturity).

Attempts to relate development to temperature were unsuccessful and the major influence on development appeared to be daylength. Number of emerged mainstem leaves was the most consistent measure of development over sites, seasons and varieties and for winter varieties was influenced by the direction of change of daylength at emergence. Two positive linear relationships between number of leaves and daylength at emergence were found for the periods from summer to winter solstice and from spring

* Present address: Cambridge University Farm, Huntingdon Road, Cambridge.

† Present address: Department of Applied Biology, University of Cambridge, Pembroke Street, Cambridge, CB2 3DX.

equinox to summer solstice. The slope of the latter relationship was greater than the former. For the period from winter solstice to spring equinox a negative linear relationship between number of leaves and daylength at emergence was found. In Triumph number of leaves decreased with decreasing daylength in the autumn and decreased further with increasing daylength. The effects in Jupiter were less clear but there was evidence of the effect of both daylength at emergence and direction of change on number of leaves.

In view of the control of number of leaves exercised by daylength, close negative linear relationships between time from sowing to anthesis and date of sowing were found. The significance of the results for relating agronomic practice to development is discussed.

INTRODUCTION

Many experiments have sought explanations of the effects of temperature and daylength on the development of barley (Kirby & Ellis, 1980; Kirby, Appleyard & Fellowes, 1982; Russell *et al.* 1982). None have satisfactorily separated the effects of these two closely-associated factors and Ellis & Russell (1984) recently concluded that 'although it should be possible to predict the course of barley development on an empirical basis from the temperatures during the period of growth knowing the sowing date, there is still much about the effects of photoperiod that is not understood'. The method used most frequently for study of development is variation in date of sowing, often using winter and spring varieties, which if repeated over a number of seasons may result in the repeatable factor (day-length) occurring at a range of temperatures and plant growth stages. While in many experiments the range of dates of sowing has been great, relatively few sowings have been made and the large intervals between sowings have restricted the interpretation of the results and no complete explanation of the effects of daylength and temperature has emerged. In this paper the results of a series of experiments are reported in which sowings were made frequently over many months in several seasons using a winter and a spring variety. The experiments began at Trefloyne in S.W. Wales where winters are relatively mild, and, if sowings can be made in the wetter environment, emergence is reasonably rapid and a succession of emerging crops can be achieved. From the results of these experiments and data from earlier experiments at Trefloyne a hypothesis of the controlling factors in development was derived and tested in concluding experiments in Cambridge using two different varieties and sowings throughout the year.

THE EXPERIMENTS

Experiments 1-3

These experiments were carried out in 1979-80, 1980-1 and 1982-3 at the University College of Wales Field Station, Trefloyne, Tenby on Old Red

Sandstone soils of the Pembroke Series (described in the Soil Survey Record, 1974). While treatments and timings of operations differed between years, the basic husbandry methods of each experiment were essentially the same. Each experiment followed a crop of potatoes and the land was ploughed as soon as possible in late summer or early autumn. Subsequent preparations involved cultivating the whole experimental area with spring-tine harrows immediately after ploughing and lightly rotovating individual plots just before drilling. A fertilizer dressing of 27 kg P and 53 kg K/ha was applied to each plot by hand prior to rotovating. In all experiments plots were 6.1 m long and 1.8 m wide and were arranged in three randomized blocks. The seed was sown in rows 15 cm apart, with a single unit Stanhay push drill. Different combinations of belts and plates were used in an attempt to sow 200-250 seeds/m². Number of emerged plants was recorded once the individual rows were visible. Between sowing and emergence each plot was sprayed with a methabenzthiazurane herbicide. Occasionally, however, it was also necessary to make a spring application of a MCPA and mecaprop herbicide. Anthesis was recorded as the time when 50% of the ears displayed anthers. There was relatively little disease in Expts 1 and 2, but where control was thought necessary triadimefon or proconazole fungicides were used.

Experiment 1, 1979-80

There were 14 treatments comprising all combinations of two varieties Sonja (winter) and Jupiter (spring) and seven dates of sowing, 9, 27 October, 4 December, 3 March, 4, 17 and 30 April. Seventy-five kg N/ha was applied to the October sowings of both varieties in early spring (Table 1). All other sowings received 75 kg N/ha at about GS 15 (Tottman & Makepeace, 1979). Two or three plants per plot were taken at weekly intervals for dissection and observation of mainstem apical development. The total number of mainstem leaves was estimated from these data.

Table 1. Date and plant growth stage at application of 75 kg N/ha (Expt 1)

Date of sowing	Date of N application	Growth stage	
		Sonja	Jupiter
9. x	22. ii	18, 25	18, 23
27. x	13. iii	17, 24	17, 23
4. xii	22. iv	16, 24	16, 24
3. iii	6. v	15, 23	15, 23
4. iv	16. v	15, 25	15, 24
17. iv	23. v	15, 25	15, 24
30. iv	3. vi	15, 24	15, 24

Experiment 2, 1980-81

There were 17 treatments comprising all combinations of the two varieties Sonja and Jupiter and seven dates of sowing, 22 August, 12 September, 3, 31 October, 16 February, 19 March, 2 April, as well as three additional sowings of Jupiter on 14 and 27 April and 11 May. The August and September sowings of Jupiter failed to survive the winter. 75 kg N/ha was applied to all surviving autumn sowings on 2 February and to all spring sowings at GS 14. In view of very heavy rainfall in March (199 mm) it was decided to make a further application of nitrogen and an additional 37.5 kg N/ha was applied to all autumn sowings on 1 April and to all spring sowings at GS 18 (Table 2). The emergence of mainstem leaves was recorded in all sowings by observing 10 plants per plot every 3-7 days and tagging the leaves with coloured wire loops as they appeared. A leaf was regarded as emerged and was tagged once the tip of the next leaf could be observed. Two or three plants per plot were taken weekly and dissected to record mainstem apical development.

In addition to the above treatments, single plots of both varieties were sown on 11 June. Leaf development was recorded in these plots by tagging

ten plants and mainstem apices were regularly dissected.

Experiment 3, 1982-3

Some data on plant development were obtained for this season from a demonstration area of Sonja sown on 10 September and three treatments of an adjacent date of sowing and fungicide experiment on the same variety sown on 22 September, 15 October and 1 December. In the demonstration area 20 plants were randomly selected and their mainstem leaves tagged as they emerged. In the experiment, ten plants were selected and tagged in the control treatment (no fungicide) in two replicates. Plants were harvested frequently and their apical development recorded. Unfortunately, this work ceased at the end of March but it was possible to estimate the final number of emerged leaves from the tagged leaves and by reference to the records of the apical dissections.

Experiment 4, 1983-4

This experiment was carried out at the Department of Applied Biology Field Station, University of Cambridge, on a soil of the Milton series described as a sandy clay loam derived from river gravel overlying gault clay (Seale & Hodge, 1976). The experiment followed a crop of oil-seed rape and the land was ploughed and spring-tine harrowed in early September. Each plot was lightly rotovated immediately before drilling. A fertilizer dressing of 25 kg N, 27 kg P and 52 kg K/ha was applied to each plot by hand before rotovating. The plots were 6 m long and 2.1 m wide and were arranged in three randomized blocks. The seed was sown in rows 15 cm apart, with a Bean single-row push drill, aiming to sow 200-250 seeds/m². A methabenzthiazurane pre-emergence herbicide was applied to the autumn sowings while all plots were treated with a bromoxynil, ixoxynil, mecoprop,

Table 2. Date and plant growth stage at application of 75 kg N/ha and 37.5 kg N/ha (Expt 2)

Date of sowing	Date of N application	75 kg N/ha		37.5 kg N/ha		
		Growth stage		Date of N application	Growth stage	
		Sonja	Jupiter		Sonja	Jupiter
22. viii	2. ii	19, 27	—	1. iv	19, 33	—
12. ix	2. ii	19, 26	18, 25	1. iv	19, 32	19, 34
3. x	2. ii	17, 24	16, 23	1. iv	19, 25	19, 33
31. x	2. ii	14, 22	14, 21	1. iv	18, 25	19, 22
16. ii	24. iv	14, 22	14, 21	29. v	18, 25	18, 22
19. iii	7. v	14, 22	14, 21	5. vi	18, 25	18, 22
2. iv	20. v	14, 22	14, 21	8. vi	18, 25	18, 22
14. iv	29. v	—	14, 21	19. vi	—	18, 22
27. iv	5. vi	—	14, 21	26. vi	—	18, 22
11. v	9. vi	—	14, 21	1. vii	—	18, 22

Table 3. *Weather conditions*

Month	Mean temperature (°C)				Rainfall (mm)				Mean day/length Tenby and Cambridge *(ca. 52° N)
	1979-80 (Tenby)	1980-1 (Tenby)	1982-3 (Tenby)	1983-4 (Cambridge)	1979-80 (Tenby)	1980-1 (Tenby)	1982-3 (Tenby)	1983-4 (Cambridge)	
September	—	14.4	14.6	14.5	—	104	161	70	12.7
October	11.1	9.6	10.1	10.9	175	162	161	32	10.7
November	8.3	6.7	8.8	7.0	114	103	170	45	8.9
December	6.8	7.4	6.1	5.9	171	107	195	36	7.8
January	3.6	6.0	6.8	3.9	91	54	97	57	8.3
February	6.8	4.6	3.5	3.4	150	87	55	42	9.9
March	5.6	8.2	6.6	4.9	137	199	98	31	11.8
April	8.7	8.3	6.3	7.8	32	46	79	14	13.9
May	11.0	11.4	9.4	9.5	36	109	121	76	15.6
June	12.8	12.8	12.5	14.7	98	44	52	49	16.6
July	14.2	15.1	16.7	16.6	64	35	7	15	16.2
August	15.2	16.0	—	18.0	106	19	—	61	14.7

* Selected tables and conversions used in agrometeorology and related fields (Canada Department of Agriculture, 1974).

linuron herbicide at an appropriate growth stage in the spring. Disease was kept to a minimum in all sowings with a propiconazole fungicide. There were 20 treatments comprising all combinations of the two varieties Igrı (winter) and Triumph (spring) and nine dates of sowing, 20 September, 11, 31 October, 21 November, 1 December, 19 January, 13 February, 9, 19 March as well as two additional sowings of Triumph on 3 April and 11 May. Fifty kg N/ha was applied to all autumn-sown plots in early February and to all subsequent sowings at GS 15. A further 50 kg N/ha was applied to all plots at GS 31. Leaf emergence was recorded by the method described in Expt 2 and the mainstem apices of two plants per plot were dissected regularly.

Single plots of both varieties were also sown in May and June for observation of leaf development. Only the Triumph sown on 9 May, however, survived repeated attacks of mildew, from which data are included in the results.

Weather (Table 3)

1979-80

The gradual decrease in air temperatures during the autumn was checked by a period of very mild weather in late November and early December. Mean air temperatures were at their lowest, between 2 and 3.5 °C, over a period of 5 weeks from mid-December to mid-January, after which they increased steadily, although there was a cold period in March. The autumn and winter were wet, with over 50 mm of rainfall per week being recorded several times and over 80 mm during the 1st week of February. April and May were dry, but the following months were wet.

1980-1

In general the autumn was cooler, but the winter and early spring warmer than in the previous season, with mean temperatures falling below 4 °C over a 2-week period in February. The winter was not as wet as in the previous season, although over 180 mm of rain fell during a 3-week period in March. May was wet but the remainder of the season was dry.

1982-3

With the exception of some very cold weather in February the autumn and winter were relatively warm, but temperature was slower to rise in the spring than in the earlier seasons. Apart from a dry period in February, this was a very wet season.

1983-4

In general, the autumn was warmer and the winter colder in Cambridge than in the previous seasons at Tenby. Nevertheless, there were several weeks throughout the winter when the mean air

Table 4. Date of 50% plant emergence and number of plants per m² (Expts 1-4)

Date of sowing	Date of 50% emergence		Number of plants	
	Sonja	Jupiter	Sonja	Jupiter
Experiment 1				
9. x	16. x	16. x	144	139
27. x	9. xi	9. xi	148	134
4. xii	20. i	20. i	120	96
3. iii	28. iii	28. iii	105	96
4. iv	15. iv	16. iv	172	196
17. iv	28. iv	28. iv	144	191
30. iv	12. v	12. v	158	201
s.e.			17.8	
Experiment 2				
22. viii	29. viii	29. viii	162	179
12. ix	18. ix	18. ix	215	239
3. x	14. x	14. x	215	204
31. x	17. xi	17. xi	179	188
16. ii	16. iii	16. iii	131	219
19. iii	2. iv	2. iv	162	225
2. iv	13. iv	13. iv	198	232
14. iv	—	24. iv	—	219
27. iv	—	9. v	—	232
11. v	—	18. v	—	230
s.e.			19.0	
(11. vi)	(16. vi)	(16. vi)		
Experiment 3				
10. ix	16. ix	—	—	—
22. ix	2. x	—	170	—
15. x	27. x	—	239	—
1. xii	29. xii	—	232	—
s.e.			13.7	
Experiment 4				
	Igri	Triumph	Igri	Triumph
20. ix	26. ix	26. ix	231	173
11. x	24. x	24. x	242	184
31. x	12. xi	10. xi	193	164
21. xi	21. xii	19. xii	149	141
1. xii	30. xii	28. xii	162	87
19. i	3. iii	18. ii	216	171
13. ii	23. iii	18. iii	111	200
9. iii	30. iii	27. iii	—	—
19. iii	10. iv	7. iv	—	—
3. iv	—	20. iv	—	—
11. v	—	21. v	—	—
s.e.			23.2	
(9. v)	—	(19. v)		

temperature was well above 5 °C, although temperature was slower to rise in the spring than at Tenby. This was by far the driest season with less than half the rain falling in most months than in the three seasons at Tenby.

RESULTS

The number of plants and date of 50% plant emergence are given in Table 4. Experiment 1 produced fewer plants than subsequent experiments.

Table 5. Grain yields at 85% moisture content (t/ha) (Expts 1 and 2)

Date of sowing	Sonja		Jupiter
	Experiment 1		
9. x	8.05		6.76
27. x	6.79		8.11
4. xii	6.33		6.13
3. iii	6.47		7.01
4. iv	3.09		6.68
17. iv	0.60		5.74
30. iv	—		3.80
s.e.	0.352		
Experiment 2			
22. viii	2.97 (BYDV)	Winter killed	
12. ix	3.09 (BYDV)	Winter killed	
3. x	8.46		5.78
31. x	7.91		6.21
16. ii	6.59		7.60
19. iii	4.96		6.95
2. iv	3.83		7.17
14. iv	—		5.82
27. iv	—		5.21
11. v	—		4.46
s.e.	0.361		

The spring varieties produced very few plants for some dates of sowing, notably December and March sowings of Jupiter in Expt 1 and the December sowing of Triumph in Expt 4. These sowings were made in the most difficult soil conditions and the winter varieties produced more plants. There were only small differences between dates of sowing in other experiments and the importance of the differences in number of plants was greatest in relation to tillering and growth. Table 5 summarizes the grain yields for Expts 1 and 2. In Sonja the two earliest sowings were infected with barley yellow dwarf virus and produced low yields. The highest yields were produced by the early October sowing in both years and yields decreased with delay in sowing. The effect of delaying sowing became more severe after the end of February. In Jupiter, the August and September sowings in Expt 2 died in December and January respectively. In Expt 1 sowing in late October produced the highest yield. Earlier sowing and later sowings up to early April produced similar yields and yields decreased sharply with further delays in sowing. In Expt 2 sowings in October produced relatively low yields compared with sowings in February and March and further delay again reduced yields considerably.

Final number of mainstem leaves

In Sonja in Expts 1-3 delaying sowing from August to mid-February reduced the final number of mainstem leaves but further delay in sowing increased the number of leaves (Table 6). In Jupiter,

Table 6. *Final number of leaves per mainstem (Expts 1-4)*

Date of sowing	Number of leaves	
	Sonja	Jupiter
	Experiment 1	
9. x	13.8	11.0
27. x	12.8	11.2
4. xii	11.0	10.5
3. iii	11.0	9.5
4. iv	13.0	9.0
17. iv	14.5	8.8
30. iv	15.5	8.3
s.e.	0.25	
	Experiment 2	
22. viii	17.7	10.0
12. ix	16.0	11.0
3. x	14.5	10.9
31. x	12.9	11.3
16. ii	9.9	9.9
19. iii	13.0	9.4
2. iv	14.0	9.3
14. iv	—	9.1
27. iv	—	8.4
11. v	—	8.5
s.e.	0.18	
(11. vi)	(19.3)	(8.0)
	Experiment 3	
(10. ix)	(16.4)	—
22. ix	15.9	—
15. x	14.3	—
1. xii	11.8	—
s.e.	0.20	
	Experiment 4	
	Igri	Triumph
20. ix	15.7	12.4
11. x	13.6	12.0
31. x	12.4	11.8
21. xi	11.4	11.0
1. xii	11.3	10.8
19. i	10.1	10.3
13. ii	10.0	9.7
9. iii	10.6	9.9
19. iii	10.9	9.8
3. iv	—	9.4
11. v	—	8.8
s.e.	0.18	
(9. v)	(8.6)	

delaying sowing until late October had little effect but further delay to early May consistently reduced the number of leaves. In Expt 2, the magnitude of the reduction in number of leaves with delayed sowing was much greater in Sonja than Jupiter. In both varieties, there was close agreement in number of leaves from comparable dates of sowing in the two seasons. In Sonja, the number of leaves was consistent with numbers found by Kirby *et al.* (1982) and Patel (1979) for several dates of sowing.

In Expt 4 Igri produced slightly fewer leaves

than found previously in Sonja while Triumph produced more than Jupiter. The effects of date of sowing were similar to those found in Tenby. In Igri delaying sowing into February reduced final number of leaves and further delay produced a small increase in number of leaves. In Triumph delaying sowing reduced the final number of mainstem leaves over the whole range.

Rate of leaf emergence

Figures 1 and 2 show that in Expts 2 and 3 leaf emergence in all sowings of both varieties was characterized by long periods when leaves emerged linearly with time, despite considerable variation in temperature. For example, in Expt 2 the low February temperatures had no effect on the rate of emergence of leaves. There were, however, changes in the rate of leaf emergence of both varieties in the early autumn and early spring, around each equinox. The rate of leaf emergence in both varieties decreased after the autumn and increased after the spring equinox.

In Expt 4 in both Igri and Triumph rate of leaf emergence was again linearly related to time for long periods and changes in rate occurred shortly after the equinoxes (Figs 3 and 4). Both varieties had a slightly greater change in rate of emergence after the autumn equinox and slightly slower rate of emergence of leaves between the equinoxes than the comparable variety at Tenby. Although temperatures in Cambridge were lower than experienced in Tenby from December onwards, they were similar in Cambridge and Tenby from September to November so these differences in effect do not appear to be related to temperature and probably represent a small difference between varieties. The changes in rate of leaf emergence around the equinoxes frequently occurred when temperatures were changing consistently but temperatures were decreasing from high values (13–15 °C) in September and increasing from low values (5–10 °C in Tenby and 5 °C in Cambridge) in March. Moreover, there was a delay in the persistent rise in spring temperatures, in both years in Tenby and in Expt 4 in Cambridge. In Tenby in neither year was the mean temperature in April higher than in March. Thus, there was no sustained rise in temperature to drive the increased rate of leaf emergence which was always detected by mid-April.

The number of changes in rate of leaf emergence for any sowing was dependent on the date of plant emergence but in the period between equinoxes rate of leaf emergence appeared to be similar in all sowings. Irrespective of the position of the leaves actually emerging, rate of leaf emergence appeared fixed and largely unaffected by variation in temperature. Winter temperatures in Cambridge were much lower than in Tenby but the rates of leaf

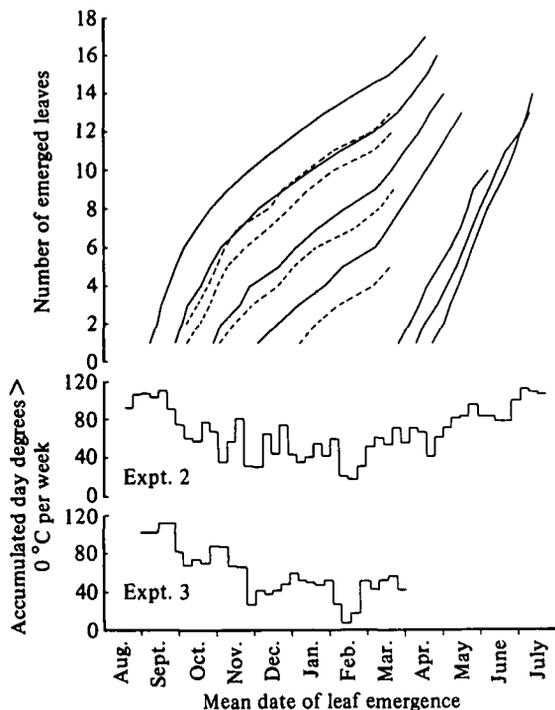


Fig. 1. Relationships between number of emerged main-stem leaves and mean date of leaf emergence for Sonja in Expt 2 (---), and Expt 3 (—), with accumulated day degrees > 0 °C per week.

emergence were similar. Where sufficient data existed the rates of leaf emergence were estimated for individual sowings of each variety in Expts 2, 3 and 4 by linear regressions on time for various periods and the results are shown in Tables 7 and 8. At Tenby, rates of leaf emergence from comparable dates of sowing were similar in the 2 years and in both varieties. However, rates of leaf emergence in the period between the equinoxes increased slightly with delay in sowing, as found by Kirby *et al.* (1982). This may be a consequence of the smaller number of leaves emerging during the period from later sowings which reduced the accuracy of the regressions. A similar increase in rate of leaf emergence with delay in sowing was found in Sonja after the spring equinox in Expt 2. The earlier sowings had very few leaves emerging (3–4) and again the accuracy of the regressions may be impaired. In Expt 4 date of sowing had only small effects on rate of leaf emergence between the equinoxes and after the spring equinox in both varieties.

Initiation of spikelet primordia

Rate of initiation

Figures 5–7 show the relationship between number of spikelet primordia and time for all

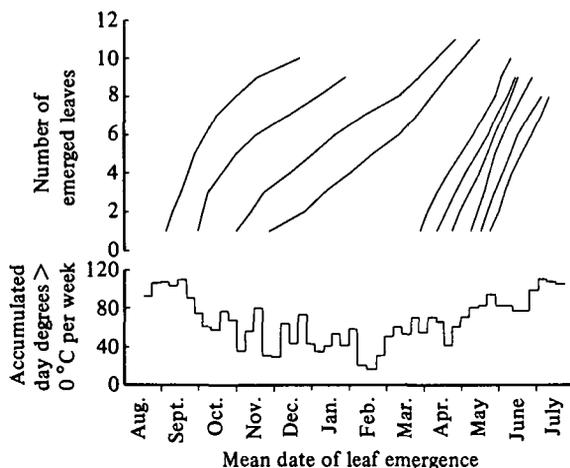


Fig. 2. Relationship between number of emerged main-stem leaves and mean date of leaf emergence for Jupiter in Expt 2, with accumulated day degrees > 0 °C per week.

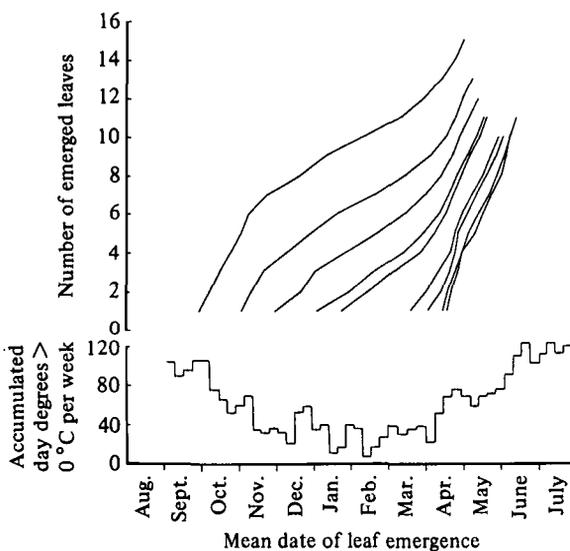


Fig. 3. Relationships between number of emerged main-stem leaves and mean date of leaf emergence for Igri in Expt 4, with accumulated day degrees > 0 °C per week.

sowings. In most sowings of all varieties the number of spikelet primordia increased linearly with time. Where direct comparison of similar dates of sowing in Sonja and Jupiter was possible, rates of initiation were similar in the two Tenby experiments. However, there were several examples of the rate of spikelet initiation changing appreciably and these effects were generally associated with large reductions in temperature. The most notable ex-

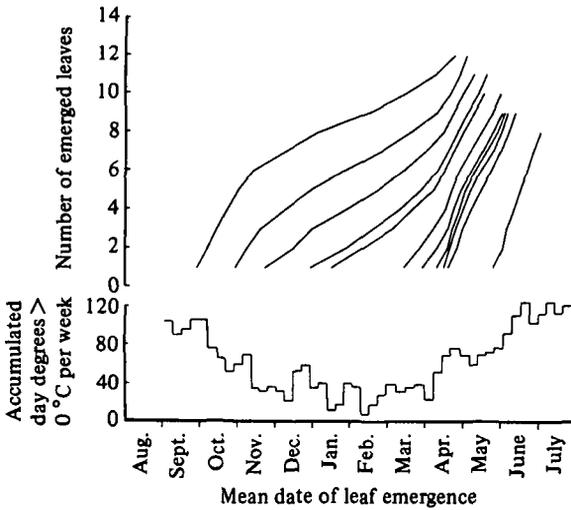


Fig. 4. Relationships between number of emerged main-stem leaves and mean date of leaf emergence for Triumph in Expt 4, with accumulated day degrees > 0°C per week.

Table 7. Rate of leaf emergence in Expts 2 and 3 calculated from linear regressions

Date of sowing	Rate of leaf emergence (number of leaves/day)				
	Sept.	Oct.- Nov.	Nov.- Mar.	Mar.- Apr.	Mar.- June
Sonja (Expt 2)					
22. viii	0.196	0.079	0.046	0.090	—
12. ix	—	0.093	0.046	0.088	—
3. x	—	0.097	0.050	—	0.093
31. x	—	—	0.054	—	0.099
16. ii	—	—	—	—	0.127
19. iii	—	—	—	—	0.139
2. iv	—	—	—	—	0.152
Jupiter (Expt 2)					
22. viii	0.164	0.069	—	—	—
12. ix	—	0.078	0.041	—	—
3. x	—	0.083	0.048	0.064	—
31. x	—	—	0.049	0.076	—
16. ii	—	—	—	—	0.116
19. iii	—	—	—	—	0.125
2. iv	—	—	—	—	0.147
14. iv	—	—	—	—	0.159
27. iv	—	—	—	—	0.141
11. v	—	—	—	—	0.144
Sonja (Expt 3)					
10. ix	—	0.119	0.047	—	—
22. ix	—	0.110	0.053	—	—
15. x	—	—	0.054	—	—
1. xii	—	—	0.053	—	—

ceptions were the two very early sowings of Jupiter in Expt 2, whose rate of initiation slowed markedly in October and November, respectively. Neither

Table 8. Rate of leaf emergence in Expt 4 (calculated from linear regressions)

Date of sowing	Rate of leaf emergence (number of leaves/day)			
	Oct.- Nov.	Nov.- Mar.	Mar.- Apr.	Apr.- June
Igri				
20. ix	0.112	0.037	0.058	0.116
11. x	0.116	0.042	0.058	0.145
31. x	—	0.046	0.067	0.135
21. xi	—	0.042	0.100	0.136
1. xii	—	0.047	0.090	0.144
19. i	—	—	—	0.137
13. ii	—	—	—	0.150
9. iii	—	—	—	0.152
19. iii	—	—	—	0.152
Triumph				
20. ix	0.111	0.030	0.049	—
11. x	0.100	0.040	0.059	0.116
31. x	—	0.044	0.070	0.128
21. xi	—	0.045	0.067	0.108
1. xii	—	0.048	—	0.124
19. i	—	—	—	0.124
13. ii	—	—	—	0.126
9. iii	—	—	—	0.141
19. iii	—	—	—	0.144
3. iv	—	—	—	0.139
11. v	—	—	—	—

change was clearly associated with any change in temperature and was probably associated with the approach of final number of spikelets. Neither of those sowings survived the winter as they were close to ear emergence before the end of the occurrence of low temperatures. In Expt 1 the rate of initiation of the first two sowings of both Sonja and Jupiter decreased during the prolonged period of low temperatures in January but subsequently increased when temperatures rose in February. These effects on rate of spikelet initiation occurred without any observed effects on rate of leaf emergence and suggest that spikelet initiation may be more affected by change in temperature than leaf emergence. Any restrictions on rate of initiation by low temperatures may subsequently be at least partially compensated for by increases in rate as temperatures rise. In the third sowing of Jupiter in Expt 1 the rate increased dramatically as temperatures increased. The first sowing of Triumph in Expt 4 also had a slowing of rate of initiation in the autumn. In all other sowings the rate of spikelet initiation proceeded linearly with time and was not affected by increases in temperature in the spring which for later sowings were large during May. Thus, the rate of initiation of spikelets appeared fixed at onset for most sowings. Where number of spikelet primordia increased linearly with time, the

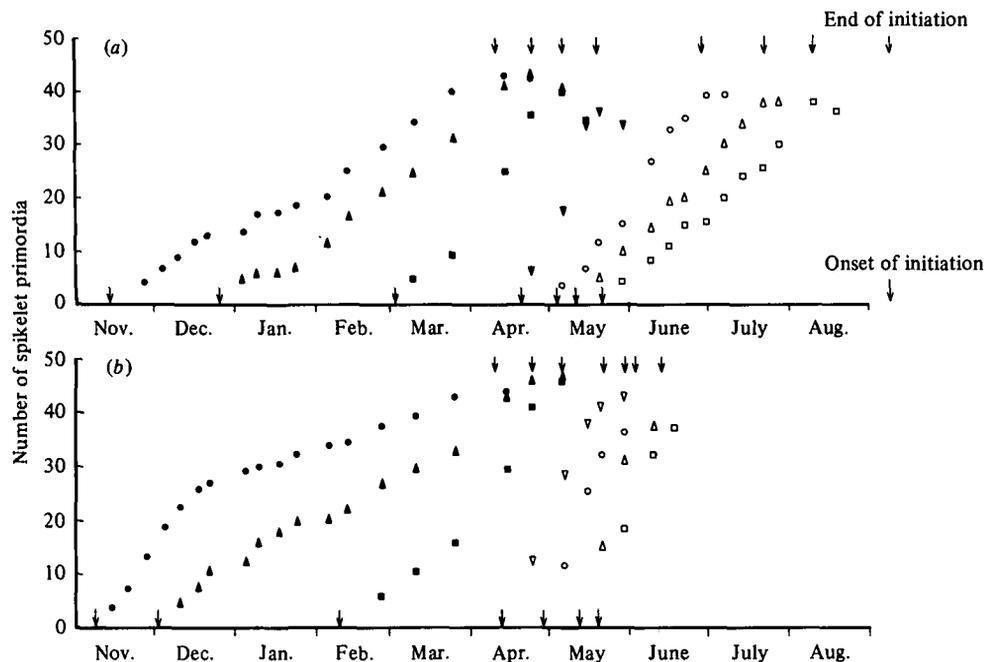


Fig. 5. The relationships between number of spikelet primordia per mainstem and time in (a) Sonja and (b) Jupiter in Expt 1. Times of onset and end (maximum number of primordia) of initiation are indicated by arrows (sowing date, ●, 9. x, ▲, 27. x, ■, 4. xii, ▼, 3. iii, ○, 4. iv, △, 17. iv, □, 30. iv).

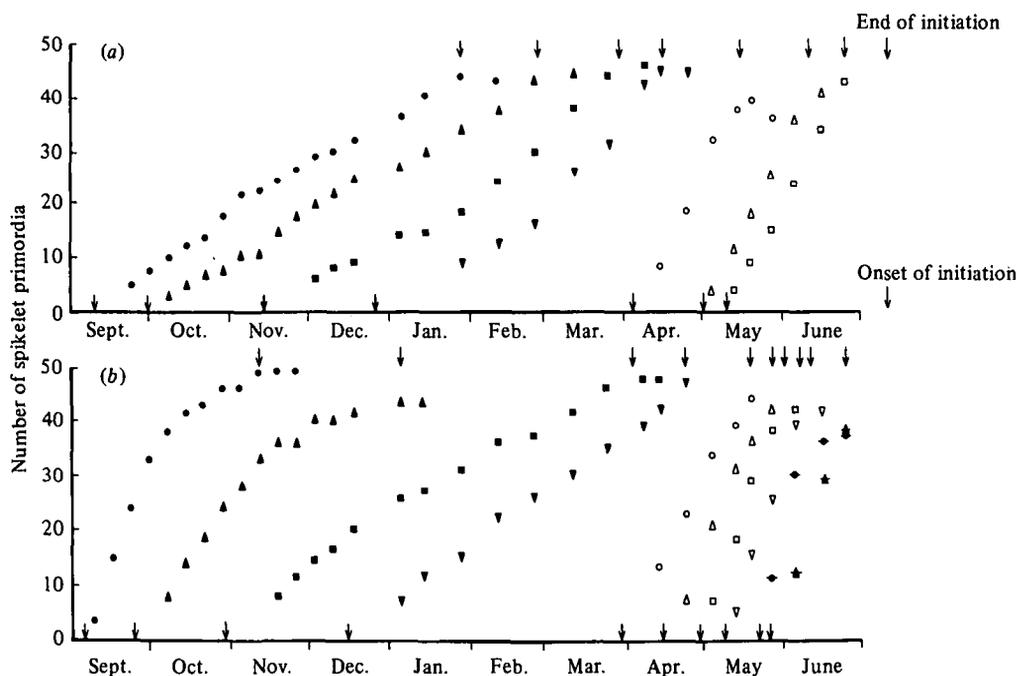


Fig. 6. The relationships between number of spikelet primordia per mainstem and time in (a) Sonja and (b) Jupiter in Expt 2. Times of onset and end (maximum number of primordia) of initiation are indicated by arrows (sowing date, ●, 22. viii, ▲, 12. ix, ■, 3. x, ▼, 31. x, ○, 16. ii, △, 19. iii, □, 2. iv, ▽, 14. iv, ●, 27. iv, ▲, 11. v).

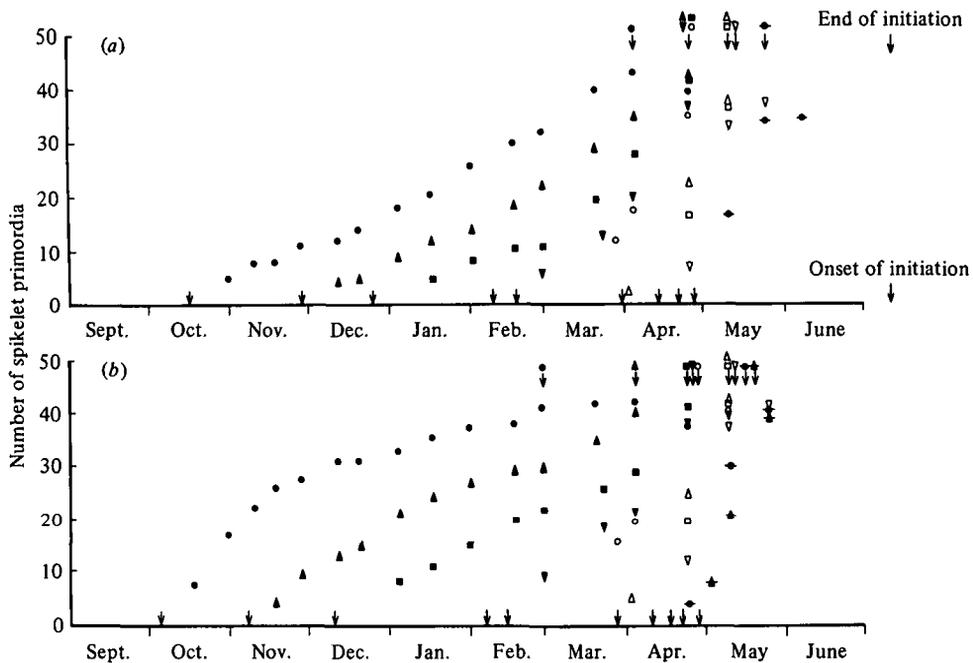


Fig. 7. The relationship between number of spikelet primordia per mainstem and time in (a) Igri and (b) Triumph in Expt 4. Times of onset and end (maximum number of primordia) of initiation are indicated by arrows (sowing date, ●, 20. ix, ▲, 11. x, ■, 31. x, ▼, 21. xi, ○, 1. xii, △, 19. i, □, 13. ii, ▽, 9. iii, ●, 19. iii, ▲, 3. iv).

timing of onset of initiation could be estimated by extrapolation of linear regression lines. Where changes in rate of initiation occurred linear regressions were fitted to separate sections of the data where no changes in rate were apparent. In these latter cases linear regressions for the initial phase of spikelet initiation allowed an estimate of onset to be obtained in all cases except the second sowing of Sonja in Expt 1 and the fifth sowing of both varieties in Expt 4. In the former case the initial rate of initiation was severely restricted but subsequently increased to a very high rate. The use of either regression gave an onset before emergence or after spikelets were first observed; the date was therefore estimated as 10 days before the first observation of spikelets. In the latter case, extrapolation of the linear regressions indicated that Igri and Triumph began spikelet initiation on 8 and 14 March respectively. However, both varieties had produced a number of spikelets at the first apical dissection of this sowing on 28 March and since the rate of initiation in the previous sowing of both varieties increased sharply with the rapid rise in temperatures in March, it is probable that the same occurred in the fifth sowing and that the dates of onset of spikelet initiation were in mid-February. Consequently it was estimated that Igri began

initiation on 18 February and Triumph on 14 February. These dates have been used in the analysis of the data and any values calculated using these dates are presented in parentheses in the Tables and as † in the Figures. The dates of onset of spikelet initiation and maximum number of spikelets (determined by visual inspection of the data) are shown by arrows in Figs 5–7. The mean rates over the period between these two estimated dates are shown in Tables 9 and 10 together with the maximum number of spikelets, number of emerged and unemerged leaves at the onset and end of initiation respectively and the number of leaves which emerged during spikelet initiation. Allowing for the difficulties in calculation, the results were consistent for the three seasons and showed that in Sonja and Igri delaying sowing increased the mean rate of spikelet initiation provided emergence occurred before the spring equinox. Further delay in emergence decreased the mean rate of spikelet initiation. In contrast, in Jupiter and Triumph the mean rate of initiation increased with each delay in sowing.

Maximum number of spikelets

Maximum number of spikelets was reduced by late sowing in both Sonja and Jupiter but over long

Table 9. Mean rate of initiation of spikelet primordia, maximum number of spikelet primordia, number of leaves emerged at the onset and un-emerged at the end of initiation and the number of leaves which emerged during initiation in Expts 1 and 2

Date of sowing	Mean rate of initiation of spikelet primordia (no. of spikelets/day)		Max. no. of spikelet primordia		No. of emerged leaves at onset of spikelet initiation (estimated)		Approx. no. of leaves to emerge at end of spikelet initiation		No. of leaves which emerged during spikelet initiation	
	Sonja	Jupiter	Sonja	Jupiter	Sonja	Jupiter	Sonja	Jupiter	Sonja	Jupiter
9. x	0.289	0.281	42.7	42.7	2	1	4	3	8	7
27. x	0.379	0.322	45.5	46.3	2	1	4	4	7	7
4. xii	0.620	0.532	39.7	46.3	2	1	3	3	6	7
3. iii	1.241	1.074	36.0	40.8	2	1	4	4	5	5
4. iv	0.715	1.177	39.3	36.5	3	1	4	3	6	5
17. iv	0.529	1.865	38.1	37.3	3	1	6	4	6	4
30. iv	0.460	1.554	37.7	37.3	3	1	6	3	7	4
Experiment 1										
22. viii	0.314	0.727	44.0	48.7	1	1	5	2	12	7
12. ix	0.297	0.422	44.5	43.5	1	1	5	3	10	7
3. x	0.313	0.301	43.8	47.5	2	1	5	2	8	8
31. x	0.396	0.366	43.2	47.2	2	1	4	2	7	8
16. ii	0.976	0.880	40.0	44.0	2	1	3	3	5	6
19. iii	1.020	0.995	40.8	41.8	3	1	4	2	6	6
2. iv	0.949	1.267	42.7	41.8	3	2	4	3	7	4
14. iv	—	1.413	—	41.5	—	1	—	3	—	5
27. iv	—	1.800	—	36.0	—	2	—	3	—	3
11. v	—	1.300	—	37.7	—	1	—	4	—	4

Table 10. Mean rate of initiation of spikelet primordia, maximum number of spikelet primordia, the number of leaves emerged at the onset and unemerged at the end of initiation and the number of leaves which emerged during initiation of spikelets (Expt 4)

Date of sowing	Mean rate of initiation of spikelet primordia (no. of spikelets/day)		Max. no. of spikelet primordia		No. of emerged leaves at onset of spikelet initiation		Approximate no. of leaves to emerge at end of spikelet initiation		No. of leaves which emerged during spikelet initiation	
	Igri	Triumph	Igri	Triumph	Igri	Triumph	Igri	Triumph	Igri	Triumph
20. ix	0.250	0.278	42.8	40.8	3	2	4	3	9	7
11. x	0.285	0.270	42.5	40.2	3	2	3	4	8	6
31. x	0.340	0.299	41.5	41.0	2	1	3	3	7	8
21. xi	0.483	0.488	36.7	39.5	2	2	3	3	6	6
1. xii	(0.522)	(0.541)	35.0	40.0	(2)	(2)	4	3	(5)	(6)
19. i	0.922	0.966	37.8	42.5	2	2	3	3	5	5
13. ii	1.352	1.393	36.5	41.8	2	2	3	4	5	4
9. iii	1.695	1.628	37.3	40.7	2	2	3	4	4	4
19. iii	1.183	1.752	34.3	40.3	3	3	4	4	4	3
3. iv	—	1.786	—	39.3	—	2	—	—	—	—
11. v	—	—	—	—	—	—	—	—	—	—

periods date of sowing had little effect. The results for Igri and Triumph in Expt 4 were similar to those found in Tenby (Table 10).

Timing of spikelet initiation

Tables 9 and 10 show that in Sonja and Igri initiation of spikelets began when there were usually two or three emerged leaves and ended when approximately four leaves remained to emerge. In the spring varieties the results were even more consistent. In Jupiter initiation of spikelets generally began when there was one emerged leaf and ended when there were approximately three leaves to emerge. In Triumph the numbers were two and three or four leaves respectively. Allowing for the accuracy of the methods of calculation the results suggest that the beginning of spikelet initiation occurred at the same number of emerged leaves irrespective of date of sowing, site or season and terminated when a fixed number of leaves remained to emerge. However, the number of leaves which emerged during initiation changed markedly especially in spring varieties as a consequence of the changes in number of mainstem leaves.

Duration of development phases

Tables 11 and 12 summarize the duration of the main developmental periods, including maximum number of spikelets to anthesis for Expts 1, 2 and 4. In winter varieties, delaying sowing until December increased the period from emergence to onset of spikelet initiation but further delay reduced the length of this period. Delaying sowing to March reduced the period of spikelet initiation and further delay increased the duration of this period. The period from the end of spikelet initiation to anthesis was generally reduced by delayed sowing although over the period from October to March the effect was small. In spring varieties delaying sowing after October reduced the duration of emergence to onset of spikelet initiation and of spikelet initiation. As in the winter varieties both periods increased with first delays in sowing where sowing began in August. The period from maximum number of spikelets to anthesis was affected only by sowings in September and early October when the period was lengthened compared with later sowings. The period was little affected by dates of sowing from late October to April. These effects were derived from the effects on individual processes already reported. The relative consistency of the final developmental phase in spring varieties was an inevitable consequence of a similar number of leaves emerging at a similar rate in all sowings. Only those sowings which experienced this phase during the equinox showed large differences. Although there was some variation in the duration of the com-

Table 11. Durations (days) of main developmental periods in Expts 1 and 2

Date of sowing	Sowing to emergence		Emergence to onset of spikelet initiation		Spikelet initiation		End of spikelet initiation to anthesis	
	Sonja	Jupiter	Sonja	Jupiter	Sonja	Jupiter	Sonja	Jupiter
Experiment 1								
9. x	7	7	29	23	148	152	36	40
27. x	13	13	47	23	120	144	26	33
4. xii	47	47	43	20	64	87	28	35
3. iii	25	25	23	15	29	38	31	36
4. iv	11	12	19	12	55	31	29	36
17. iv	11	11	13	14	72	21	—	39
30. iv	12	12	9	7	82	24	—	40
Experiment 2								
22. viii	7	7	12	8	140	67	102	—
12. ix	6	6	12	7	150	103	77	—
3. x	11	11	26	14	141	158	54	54
31. x	17	17	39	29	110	129	44	45
16. ii	28	28	19	15	41	50	36	41
19. iii	14	14	29	13	40	42	33	36
2. iv	11	11	27	16	45	33	27	39
14. iv	—	10	—	15	—	29	—	36
27. iv	—	12	—	13	—	20	—	36
11. v	—	7	—	8	—	29	—	28

Table 12. Durations (days) of main developmental periods in Expt 4

Date of sowing	Sowing to emergence		Emergence to onset of spikelet initiation		Spikelet initiation		End of spikelet initiation to anthesis	
	Igri	Triumph	Igri	Triumph	Igri	Triumph	Igri	Triumph
20. ix	6	6	20	9	171	147	50	82
11. x	13	13	35	14	149	149	35	58
31. x	12	10	43	30	122	137	40	40
21. xi	30	28	50	49	76	81	46	47
1. xii	29	27	75	71	42	51	49	51
19. i	44	40	27	28	41	44	39	39
13. ii	39	34	21	23	27	30	39	46
9. iii	21	18	22	21	22	25	40	44
19. iii	22	19	17	15	29	23	32	43
3. iv	—	17	—	8	—	22	—	38
11. v	—	—	—	—	—	—	—	—

ponent stages from similar sowings in different years, the variation in time from sowing (or emergence) to anthesis was small for comparable sowings and Figs 8 and 9 show that close relationships existed between the times for sowing to anthesis and date of sowing.

DISCUSSION

Although there were some exceptions the results showed consistency of effects of date of sowing from year to year and site to site in spite of differences in temperatures. There was therefore the opportunity of separating the effects of temperature and daylength in the control of development. The

results were therefore examined for relationships between the rates and durations of the component parts of development and measures of the two environmental factors and data were sought from the literature to extend the range of conditions.

In Figs 10 and 11 the final number of main-stem leaves in Sonja and Jupiter for both years has been plotted against daylength at emergence. In Sonja, two separate lines were apparent which distinguished between the phases of decreasing and increasing daylength. Close, positive, linear regressions were fitted to each relationship and the slope of the line for the period of increasing daylength from spring equinox onwards was slightly greater than for decreasing daylength from summer

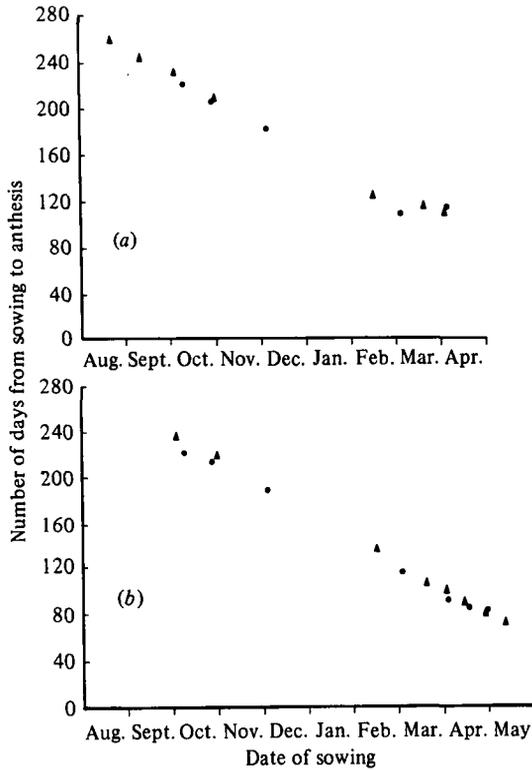


Fig. 8. Relationship between number of days from sowing to anthesis and date of sowing in (a) Sonja and (b) Jupiter. ●, Expt 1; ▲, Expt 2.

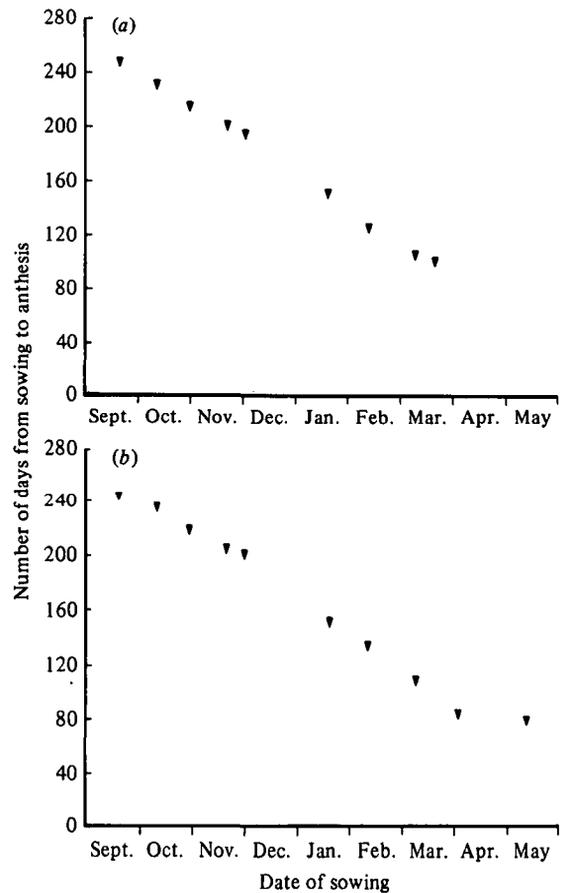


Fig. 9. Relationship between number of days from sowing to anthesis and date of sowing in (a) Igri and (b) Triumph in Expt 4.

to winter solstice. The minimum change in number of mainstem leaves occurred between the winter solstice and spring equinox (8 and 12 h daylength) and a third, close negative linear relationship was found for sowings emerging at this time (Fig. 12). In Jupiter, a single relationship was found ($R^2 = 0.80$) in which number of mainstem leaves decreased linearly with increasing daylength at emergence (Fig. 11). The two earliest sowings in Expt 2 (*) appeared to deviate from the relationship, but the range in number of leaves was small and no other data for sowing at this time were found to establish the validity of this possibility. Sowing would rarely be done at this time in practice and for sowings from October onwards a closer negative relationship existed ($R^2 = 0.91$) which was fundamentally different from that found in the winter variety.

Published data for Sonja (Kirby *et al.* 1982; Patel, 1979) which report final number of mainstem leaves and allow estimation of date of emergence, all conformed closely to the general relationship found at Trefloyne (Fig. 12). The results for Igri (Fig. 13) were in complete agreement with the general relationships obtained for Sonja and as

there was little difference between varieties in either number of leaves or rate of change with daylength, close overall relationships existed for both varieties (Fig. 14). In Triumph there were two quite distinct relationships, for number of leaves decreased with decreasing daylength from 12 to 8 h and then decreased further with increasing daylength (Fig. 13). Thus, in this spring variety there was also evidence of sensitivity to absolute length and direction of change, as found in the two winter varieties although the relationships were distinct. There are many reports in the literature of final number of leaves in spring barley but they cover a large number of varieties and substantial differences in effects of daylength were found. A selection covering four varieties was used and the results are shown in Fig. 15. In some varieties, notably Proctor, there was little effect of daylength at emergence on final number of leaves over a consider-

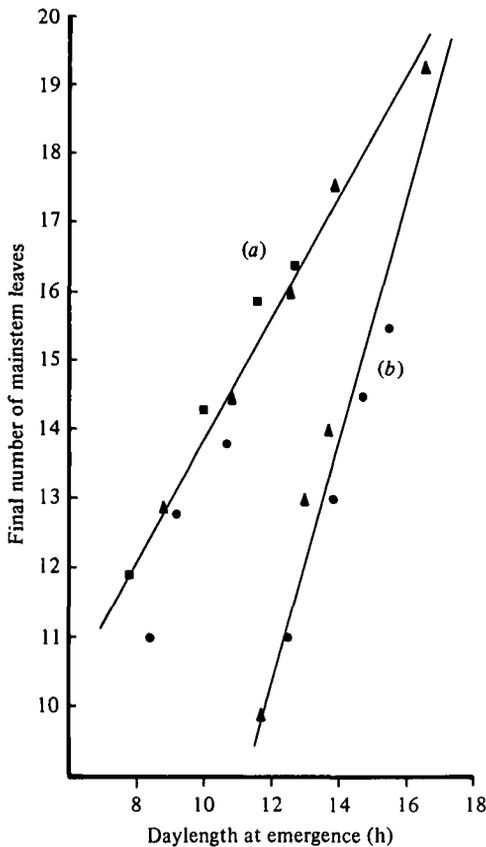


Fig. 10. Relationships between final number of mainstem leaves and daylength at crop emergence in Sonja. ●, Expt 1; ▲, Expt 2; ■, Expt 3. Regression equations: (a) autumn emergence, $y = 5.187 + 0.869x$, $R^2 = 0.97$; (b) spring emergence, $y = -10.580 + 1.742x$, $R^2 = 0.93$. (See Appendix Table 1 for key to data.)

able range. The data for Proctor reported by Scott & Dennis-Jones (1976) give nine leaves for all sowings except the final, which had eight, and there is no way of establishing the error in this estimate. As a consequence the points probably deviate from the current results by a greater amount than in reality. In others (e.g. Hassan and possibly Armelle; Patel, 1979) there was little effect of daylength over the range 10–12 h but further increases in daylength reduced the final number of leaves. Number of mainstem leaves decreased in Maris Mink and Golden Promise (Kirby & Ellis, 1980) with increasing daylength but all daylengths exceeded 14 h. None of the relationships between number of mainstem leaves or daylength was the same as found in spring sowings of Jupiter and there appeared to be different groups of spring barleys, all of which were distinct from the winter barleys.

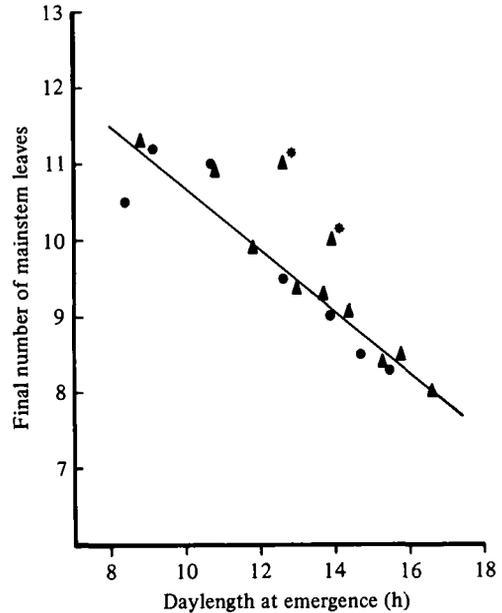


Fig. 11. Relationship between final number of mainstem leaves and daylength at crop emergence in Jupiter. ●, Expt 1; ▲, Expt 2. Regression equation (excluding *): $y = 14.773 - 0.407x$, $R^2 = 0.91$.

The data for Triumph did not conform completely with any particular group (Fig. 13). The final number of leaves decreased with decreasing daylength from 12 to 8 h for autumn sowings and then decreased further with increasing daylength for all sowings which emerged after the shortest day. There was, therefore, some similarity of effects of daylength in autumn sowings of Jupiter and Triumph and both varieties showed similar rates of decrease in final number of mainstem leaves with increasing daylength in sowings which emerged after the shortest day (Fig. 16). There would, therefore, seem to be considerable differences between varieties of spring barley in their response to daylength, especially when sown out of the normal season.

The results suggest that in winter and spring barley the number of mainstem leaves is determined by daylength at emergence and that the emerging plant is sensitive to the direction of change as well as absolute length. The three linear relationships allow complete seasonal adjustment by a winter variety to daylength at emergence, producing the maximum number of leaves in mid-summer and the minimum in mid-winter. When relationships between final number of mainstem leaves and various measures of temperature were sought no clear separation of effects according to photoperiod was found in the winter varieties and,

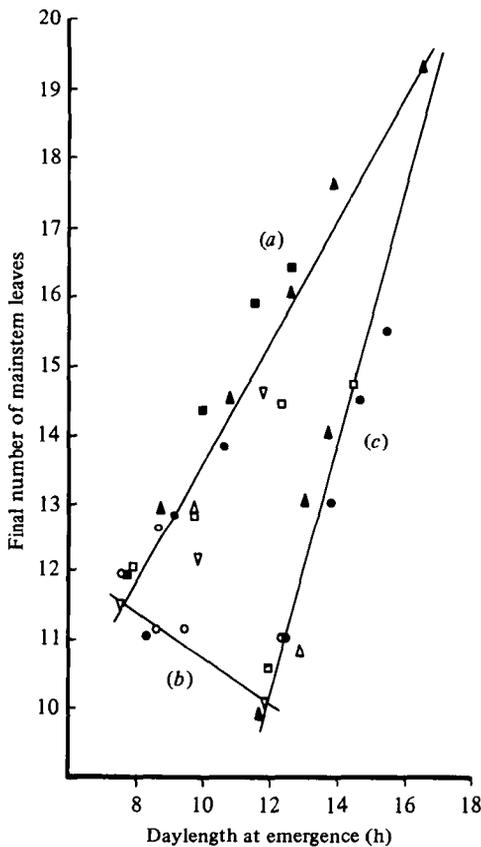


Fig. 12. Relationships between final number of mainstem leaves and daylength at crop emergence in Sonja. ●, Expt 1; ▲, Expt 2; ■, Expt 3; ○, 1976-7, △, 1977-8 (Patel, 1979); □, 1979-80, ▽, 1980-1 (Kirby *et al.* 1982). Regression equations: (a) $y = 4.834 + 0.871x$, $R^2 = 0.91$; (b) $y = 14.126 - 0.345x$, $R^2 = 0.91$; (c) $y = -10.850 + 1.757x$, $R^2 = 0.94$. (See Appendix Table 1 for key to data.)

as Fig. 17 shows, overall there was only a weak linear relationship between final number of leaves and mean temperature at emergence. Very large differences in number of leaves occurred with similar temperatures at emergence. In the spring varieties no relationships with temperature were found (Fig. 17).

The results for rate of leaf emergence were also at variance with published reports for barley (Kirby *et al.* 1982) and wheat (Hay & Tunnicliffe Wilson, 1982; Hay & Abbas Al-Ani, 1983) which argue that this is a positive, linear function of temperature. Although there were close, positive, linear relationships between number of emerged leaves and number of day-degrees (calculated from mean daily air temperatures) above any base temperature from 0 to 5 °C for all sowings, some

systematic variation remained. For example, for the sowing on 12 September in Expt 2 (Fig. 18) the data points follow the same course as seen in Fig. 1, where the data were plotted against time. For sowings whose rate of leaf emergence changed with time, the use of accumulated day-degrees was not effective in removing the systematic change in rate. Thus, acceptance of the apparently overwhelming statistical relationship is questioned if the data are scrutinized. For the sowing of 12 September in Expt 2, the number of day-degrees accumulated between emergence of successive leaves is shown in Table 13 and reveals a large range of values. Comparison of the range of accumulated day-degrees per leaf and the value obtained from regression analysis can be seen for all sowings of Sonja from Expt 2 in Table 14. The data show that the base temperature used had little effect on the variation in number of day-degrees per emerged leaf. In barley, the results which have been used to suggest that rate of leaf emergence is related to temperature have been obtained by destructive means. Such data frequently include negative changes in number of leaves as well as increases and the partitioning of this variation through varying base temperatures is suspect in establishing the effects of temperature. Where data have been obtained by non-destructive means, as in wheat by Hay & Tunnicliffe Wilson (1982) the sensitivity of the accumulated day-degree scale must be appreciated. As the data in Table 13 show, large differences in number of day-degrees per emerged leaf may be completely missed by plotting the small number of leaves against the much larger number of day-degrees which is heavily weighted by the time component. Thus, accepting the high coefficient of determination (R^2) at face value is unjustified, for a quite massive change in number of day-degrees for several consecutive leaves would be necessary to deviate from the general relationship. It is probable that any general control mechanism(s) for leaf emergence would operate in all seasons and sites and allow unification of different sets of data. However, the data of Hay & Abbas Al-Ani (1983) for wheat show different rates of leaf emergence per day-degree in different seasons.

There are also several published reports which support the suggestion that rate of leaf emergence is controlled by daylength. The data of Kirby & Riggs (1978) show a linear emergence of leaves with time for spring barley grown in an unheated glasshouse and if periods of non-emergence of leaves (caused by very low temperatures) are omitted from the data of Kirby *et al.* (1982) the rates of leaf emergence are linear with time and do conform with rates and timing of changes found in the reported experiments. The major effects of tempera-

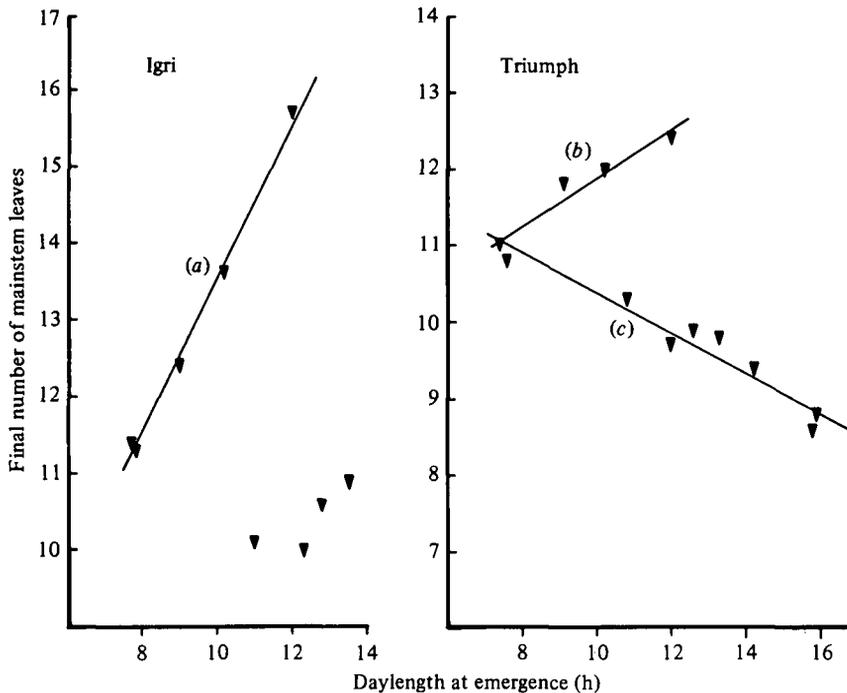


Fig. 13. Relationships between final number of mainstem leaves and daylength at crop emergence in Igri and Triumph in Expt 4. Regression equations: (a) $y = 3.431 + 1.012x$, $R^2 = 0.99$; (b) $y = 8.764 + 0.311x$, $R^2 = 0.88$; (c) $y = 12.999 - 0.260x$, $R^2 = 0.91$. (See Appendix Table 1 for key to data.)

ture appear to be through virtual cessation of emergence at very low temperatures, which occur only in some seasons and on the size of individual leaves.

Interpretation of effects of environmental factors on number of leaves may also be affected by the extent of inter-plant variation which would be influenced by emergence. The data in Figs 1–4 represent the mean dates on which individual leaves emerged on 30 (20 in Expt 3) plants of each sowing and are terminated by the number of leaves which emerged on all plants. In these experiments in almost all sowings of all varieties the majority of plants produced the same final number of leaves and, as Fig. 19 shows, presentation of data for individual plants does not alter the basic pattern. Clearly, however, any large spread in emergence is likely to produce effects on final number of leaves which may affect the determination of successive developmental stages within the crop, especially where a small number of plants is used. In this respect it is to be expected that late sowings would be more variable than earlier sowings particularly if large differences in soil conditions occurred between sowings and affected emergence. There was some indication of this in Expt 4. The slope of the lines in Figs 10 and 11 provide an estimate of

the change in daylength necessary to cause a change in number of leaves. In autumn-sown Sonja a change of 1.15 h is required to alter the average number of leaves by one while in Jupiter sown between October and May the required change is 2.46 h. Such an effect in Sonja requires emergence to occur over no more than 19 days in September–October if all plants are to have the same number of leaves. Many crops, particularly on lighter soils, will achieve this but more recent observations even on light soil in Cambridge suggest many crops do not and therefore from early in their life are composed of plants at different stages of development.

The relationships in Fig. 10 also allow the effects of latitude to be considered in relation to the whole of the U.K. Table 15 shows the final number of leaves predicted for autumn-sown Sonja at a range of extreme sites. Northerly sites would be expected to have 0.5–1.0 more leaves than southerly sites from very early dates of emergence (August or September); similar numbers of leaves from emergence in early October and increasingly fewer leaves from later emergence. Such differences are likely to be important in the practical effects of date of sowing on yields as they would influence the timing of all developmental stages, particularly anthesis, which in relation to prevailing weather conditions

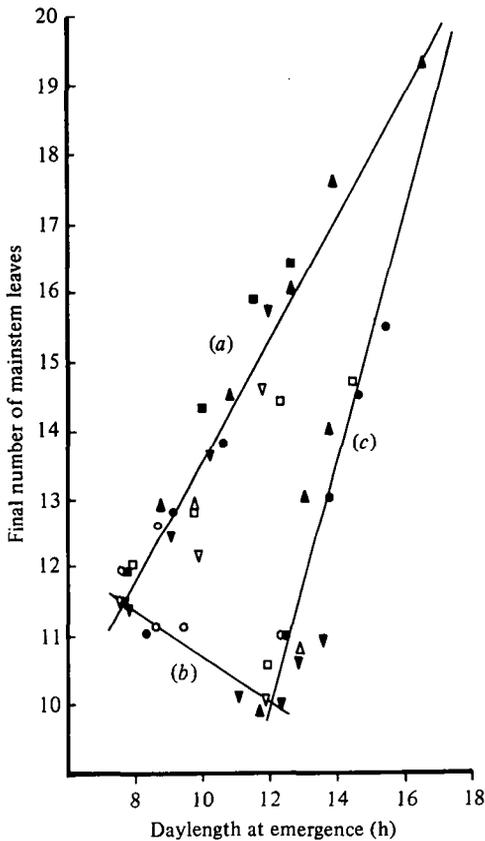


Fig. 14. Relationships between final number of mainstem leaves and daylength at crop emergence in Sonja and Igri. ●, Expt 1; ▲, Expt 2; ■, Expt 3; ▼, Expt 4; ○, 1976-7, △, 1977-8 (Patel, 1979); □, 1979-80, ▽, 1980-1 (Kirby *et al.* 1982). Regression equations:

$$(a) y = 4.628 + 0.889x, R^2 = 0.92;$$

$$(b) y = 13.972 - 0.333x, R^2 = 0.93;$$

$$(c) y = -11.650 + 1.799x, R^2 = 0.90.$$

(See Appendix Table 1 for key to data.)

may be moved into more favourable (as from very early sowing in Scotland) or less favourable (as from early sowing in S.W. England) conditions.

The results relating to changes in number of leaves also have significance for understanding vernalization. Spring sowings of winter barley varieties produced an increasing number of leaves and the failure of sowings made after mid-April to produce an emerged ear by August was primarily the lack of time for the large number of leaves to emerge. In all cases, including sowings in June at Tenby and Cambridge, the ear developed as expected. If left into the autumn, ears would probably have emerged but the plants did not survive, principally due to mildew infection. Many of these sowings experienced few if any days with tempera-

tures in the effective range for vernalization -3 to $+13$ °C (Chujo, 1966) before the apex began reproductive rather than vegetative differentiation. The increasing number of leaves in winter barley from spring sowings is often regarded as a delayed or unsatisfied vernalization requirement (Ellis & Russell, 1984) but the onset of reproductive development apparently occurred at the same number of mainstem leaves in all sowings. Figure 14 shows that the changes in number of leaves in late spring and early summer sowings were entirely consistent with the overall effect of daylength and the large number of leaves could not emerge before the end of the summer when the experiments were terminated. There is a need for detailed information for the effects of low temperatures and daylength on all aspects of leaf initiation, growth and emergence. Similarly, the mechanism of differences between varieties requires study, for the ear developed normally in all late sowings of winter varieties and the failure to produce emerged ears appeared to be simply that too many leaves were produced to allow ear emergence within the available season. Kirby & Appleyard (1984) stated that low temperatures reduced the number of leaves and hence if applied to imbibed seeds before spring planting may allow winter varieties to come into ear within the season. However, there was no obvious systematic deviation with date of sowing from the relationships between number of leaves and daylength in Fig. 14 and therefore the significance of such effects of temperature in relation to field crops is by no means clear. Early autumn sowings made in relatively high temperatures appeared to be unified through daylength with subsequent sowings which were made and began reproductive development in low temperatures.

In view of the relationships between number of leaves and rate of leaf emergence and daylength a close relationship between duration of development, i.e. emergence to anthesis, and time was to be expected. Data from all other published (Patel, 1979) and unpublished experiments at Trefloyno and many other reports from the literature conform closely with the general relationship (Fig. 20). Previous use of the term 'thermal time' (Evans & Hough, 1984) and attempts to relate the durations of developmental phases to photothermal time (barley, Gallagher, Biscoe & Dennis-Jones, 1983; wheat, Weir *et al.* 1984) must be treated with caution. The validity of the controlling mechanisms was by no means established and both attempts largely avoided the variation in number of leaves, the most variable and important character in the process of development as our unpublished data and those of Kirby, Appleyard & Fellowes (1985) show that number of leaves in wheat and barley varies with date of sowing. The emergence of mainstem

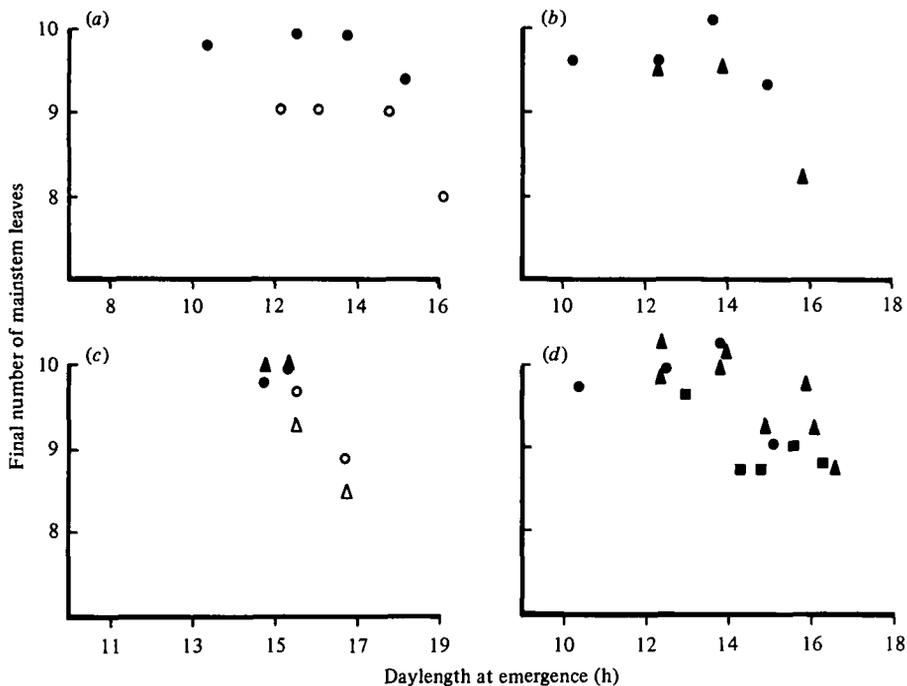


Fig. 15. Relationships between final number of mainstem leaves and daylength at crop emergence in a range of spring varieties. (a) Proctor, ●, 1976 (Patel, 1979); ○, 1975 (Scott & Dennis-Jones, 1976); (b) Hassan, ●, 1976, ▲, 1977 (Patel, 1979); (c) Golden Promise, ●, 1976, ○, 1977; Maris Mink, ▲, 1976, △, 1977 (Kirby & Ellis, 1980); (d) Armelle, ●, 1976, ▲, 1977, ■, 1978 (Patel, 1979).

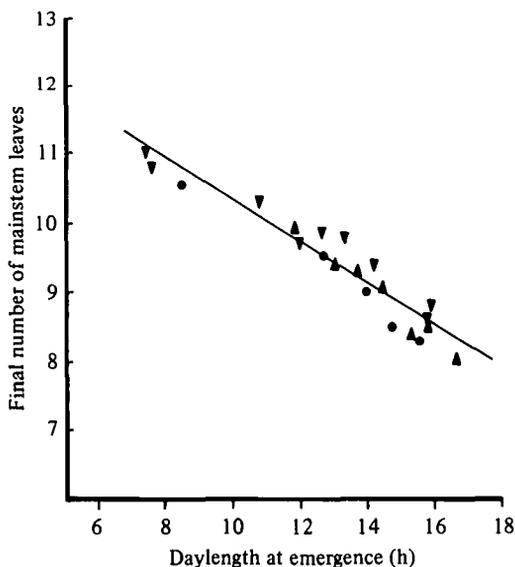


Fig. 16. Relationship between final number of mainstem leaves and daylength at crop emergence in Jupiter and Triumph emerging after the shortest day. ●, Expt 1; ▲, Expt 2; ▼, Expt 4. Regression equation: $y = 13.385 - 0.306x$, $R^2 = 0.88$.

leaves appears the fundamental and easily recognizable characteristic which documents the development of barley across sites and seasons. The apical development is closely linked to leaf emergence and so long as growing conditions, primarily temperature, are satisfactory the two processes proceed in unison. However, changes in rate of apical development occur if conditions deteriorate while leaf emergence may be unaffected. Subsequently, the rate of apical differentiation may increase considerably with increasing temperatures and presumably restore the 'normal' relationship between leaf emergence and apical differentiation, the increasing temperatures producing no effect on the rate of spikelet initiation of treatments which have not experienced low temperatures.

As Figs 21 and 22 show, rate of spikelet initiation decreased with initial increases in number of leaves emerging during spikelet initiation in Sonja, Igri and Triumph and then remained constant. In Jupiter the rate of initiation decreased with increasing number of emerging leaves over the whole range. The initial emergence of tillers usually occurs at emergence of the third or fourth leaf (Kirby & Riggs, 1978; Baker & Gallagher, 1983) and the occurrence of the maximum number of spikelets is

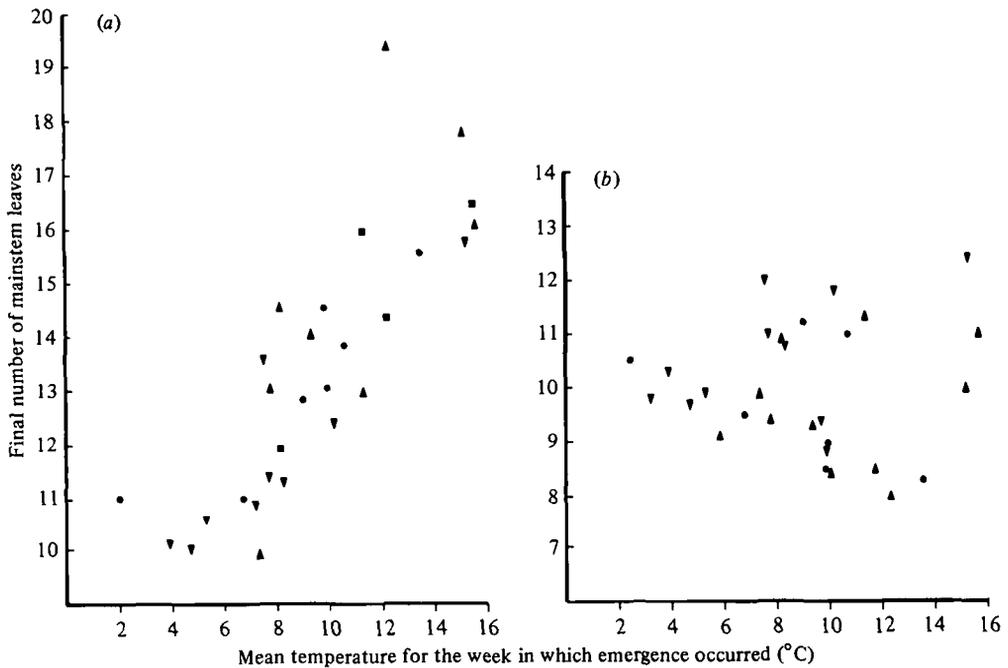


Fig. 17. Relationships between final number of mainstem leaves and mean air temperature during the week of emergence in (a) Sonja and Igri and (b) Jupiter and Triumph. ●, Expt 1; ▲, Expt 2; ■, Expt 3; ▼, Expt 4.

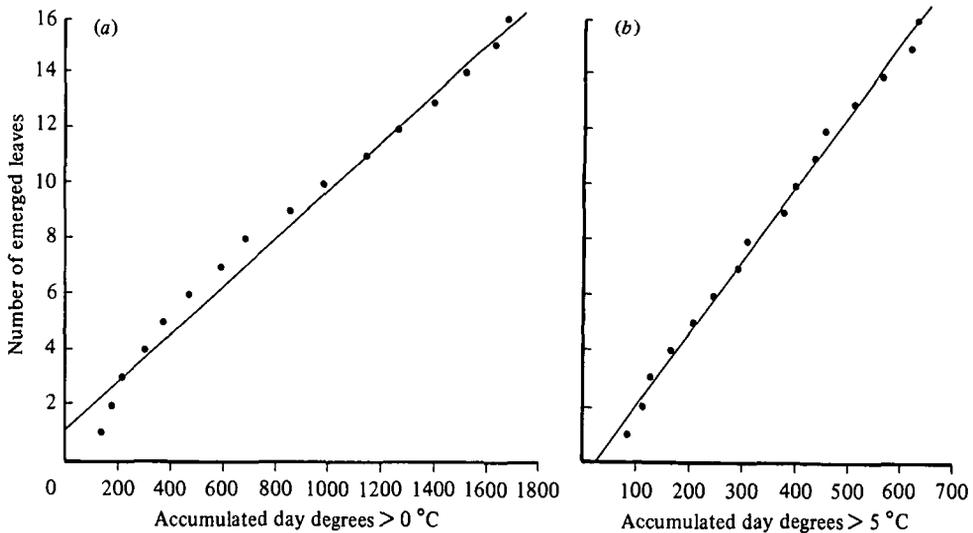


Fig. 18. Relationships between number of emerged leaves and accumulated day degrees (a) $> 0^{\circ}\text{C}$ and (b) $> 5^{\circ}\text{C}$ in Sonja (Expt 2) sown on 12 September. Regression equations:

$$(a) y = 0.112 + 0.009x, R^2 = 0.98.$$

$$(b) y = 0.686 + 0.026x, R^2 = 0.99.$$

Table 13. Number of day-degrees per emerged leaf for sowing on 12 September of Sonja, winter barley, Expt 2

Number of emerged leaves	Day-degrees > 0 °C/ emerged leaf	Accumulated day-degrees > 0 °C	Day-degrees > 5 °C/ emerged leaf	Accumulated day-degrees > 5 °C
1*	147.3	147.3	92.3	92.3
2	42.4	189.7	22.4	114.7
3	37.7	227.4	17.7	132.4
4	92.6	320.0	37.2	169.6
5	74.8	394.8	39.8	209.4
6	88.3	483.1	38.8	247.7
7	127.3	610.4	47.3	295.0
8	85.7	696.1	19.2	314.2
9	169.3	865.4	65.9	380.1
10	132.3	997.7	23.0	403.1
11	164.4	1162.1	39.4	442.5
12	111.7	1273.8	16.1	458.6
13	142.4	1416.2	57.4	516.0
14	124.5	1540.7	54.5	570.5
15	105.2	1646.4	50.7	621.2
16	58.3	1704.7	13.3	634.5

* From emergence.

Table 14. Number of day-degrees per emerged leaf (Expt 2)

Date of sowing	Accumulated day-degrees per leaf					
	> 0 °C		> 4 °C		> 5 °C	
	Regression value	Actual range	Regression value	Actual range	Regression value	Actual range
22. viii	116	47-172	58	28-85	43	18-67
12. ix	115	38-169	52	22-85	38	13-66
3. x	108	53-151	45	25-61	33	16-49
31. x	100	68-129	43	23-64	33	14-47
16. ii	77	56-159	48	28-111	40	18-99
19. iii	83	58-156	59	34-108	50	23-96
2. vi	77	31-117	56	23-81	48	21-72

Calculated from the linear regressions of number of emerged leaves on number of accumulated day-degrees and the range of actual accumulated day-degrees per leaf in Sonja.

Table 15. Predicted number of leaves produced in autumn-sown Sonja, winter barley at four sites in the United Kingdom

	Date of emergence					
	1. viii	1. ix	1. x	1. xi	1. xii	1. i
Penzance (ca. 50 °N)	18.5	17.0	15.4	13.7	12.5	12.2
Cambridge and Tenby (ca. 52° N)	18.7	17.1	15.4	13.6	12.2	12.0
Aberdeen (ca. 57° N)	19.4	17.4	15.3	13.2	11.4	11.1
Orkney (ca. 59° N)	19.7	17.5	15.3	12.9	11.1	10.7

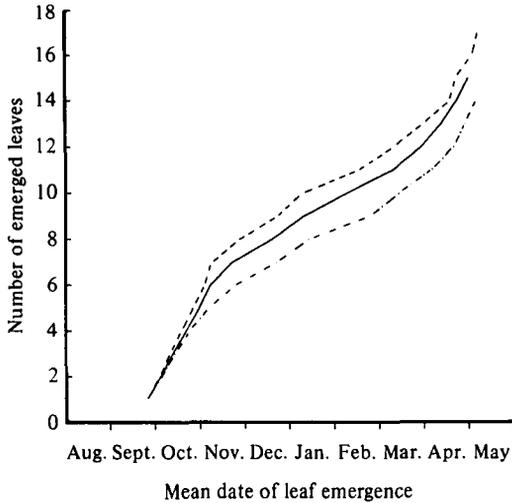


Fig. 19. Relationships between number of emerged mainstem leaves and mean date of leaf emergence in Igri (Expt 4) sown on 25 September. Single plant with 17 leaves (—); single plant with 14 leaves (---); mean of 30 plants (— · —) averaging 15.7 leaves.

associated with maximum number of tillers (Kirby & Jones, 1977) so there is considerable evidence that the timing and control of leaf emergence, tillering and spikelet initiation are linked. The significance of the changes in number of emerging leaves during the tillering period is that total number of tillers is likely to be influenced as the number of primary tillers is potentially changed. This may be a contributing factor, together with improved growing conditions, in the greatly increased number of tillers produced by May and June sowing of the winter varieties. This effect was so great that it was difficult to keep crops sown at this time free from mildew even with repeated spraying. The reverse effect was found in delaying sowings of spring varieties as the reduction in number of leaves was associated with fewer tillers, as reported by other authors (Cannell, 1969).

The results suggest a fundamental role of daylength in the control of development in barley. The wide range of dates of sowing and relatively short intervals between sowings have allowed the whole effect to be established and the results for varieties grown outside their normal season were crucial to the interpretation of the data. The direct effect of daylength is on rate of leaf emergence and final number of leaves and the reproductive phases appear to be related to the emergence of leaves. These effects are most effectively summarized by consideration of the changes over the whole season of 12 months. Figures 23–25 present the results from Expts 1, 2 and 4 and other experiments at Trefloyne for final number of mainstem leaves, rate

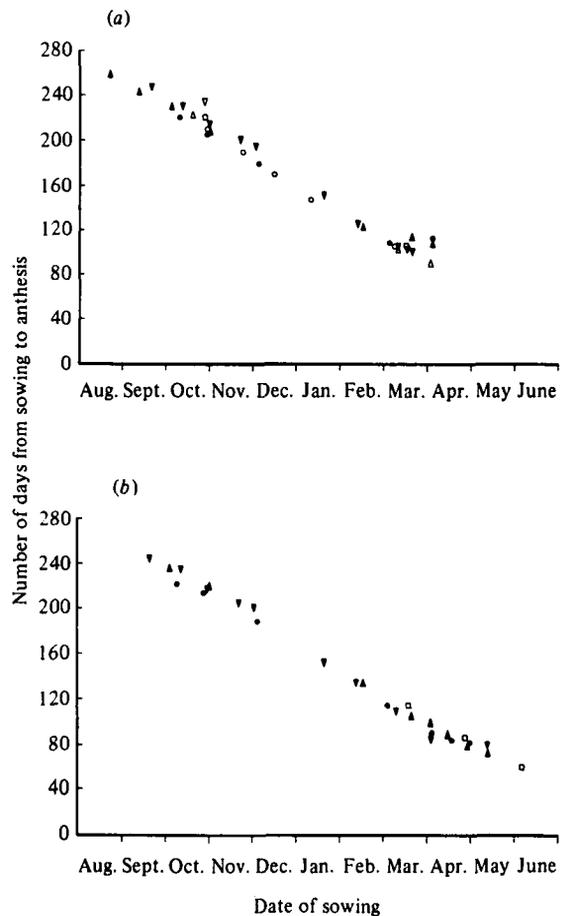


Fig. 20. Relationship between number of days from sowing to anthesis and date of sowing in (a) winter varieties, Sonja, \circ , 1976–7; \triangle , 1977–8 (Patel, 1979); \square , 1978–9; \bullet , Expt 1, 1979–80; \blacktriangle , Expt 2, 1980–1; Igri, ∇ , 1978–9; \blacktriangledown , Expt 4, and (b) spring varieties, Jupiter, \square , 1978–9; \bullet , Expt 1; \blacktriangle , Expt 2; Triumph, \blacktriangledown , 1983–4.

and duration of spikelet initiation plotted against time of emergence. It is immediately apparent that in the winter varieties and Jupiter there is a close relationship with time of emergence in all three variables. There is a seasonal direction to the effects which ensures that over 12 months the value of any variable returns to the starting value as a consequence of response to the direction of change and absolute value of daylength.

The concentration of interest on apical development as the key to understanding development,

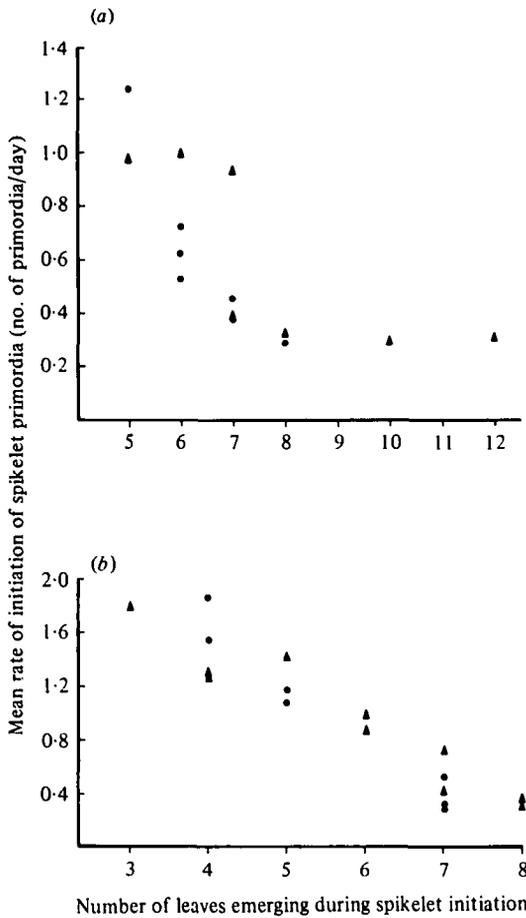


Fig. 21. Relationships between the mean rate of spikelet initiation and the number of leaves emerging during the period of initiation in (a) Sonja and (b) Jupiter, ●, Expt 1; ▲, Expt 2.

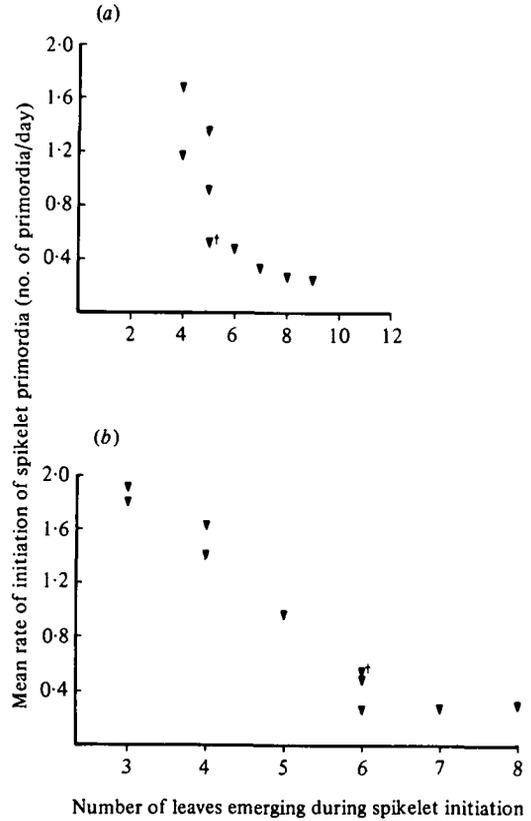


Fig. 22. Relationship between the mean rate of spikelet initiation and the number of leaves emerging during the period of initiation in (a) Igri and (b) Triumph in Expt 4.

and the relationships with growth (and finally yield) is at least partially misconceived. It appears from these results to be potentially less consistent and therefore more difficult to interpret than leaf emergence which forms the initial part of the growth stage keys (Tottman & Makepeace, 1979); the difficulty with using leaf emergence is that some reference plants with regular tagging of leaves are required to be sure of the number of leaves per plant once leaf loss begins. The important task is to increase understanding of the relationship between apical development and leaf emergence for the wide range of conditions and agronomic treatments used in practice.

In the short term the results enhance our ability to predict development from which more effective agronomic management should result. The timing of the critical phase of spikelet survival (from

maximum number of spikelets to anthesis) is determined by emergence of a specific number of leaves and within a variety can be altered only by changing the number of leaves through time of sowing. The timing of developmental stages may also be changed through breeding. Winter barley passes through similar developmental stages earlier than wheat and its earlier anthesis and maturation are likely reasons for its generally lower yields from comparable autumn sowings. Delaying anthesis would be achieved by increasing final number of leaves and thereby ensuring that the period of spikelet survival occurred in more favourable conditions (higher irradiance). If agronomic limitations did not occur with this displacement of development, such a genetic change in number of leaves may be an effective means of raising yields from early (September–October) sowings. The delay in development would, however, shorten the period of spikelet survival as the similar number of leaves emerging in this period would emerge more

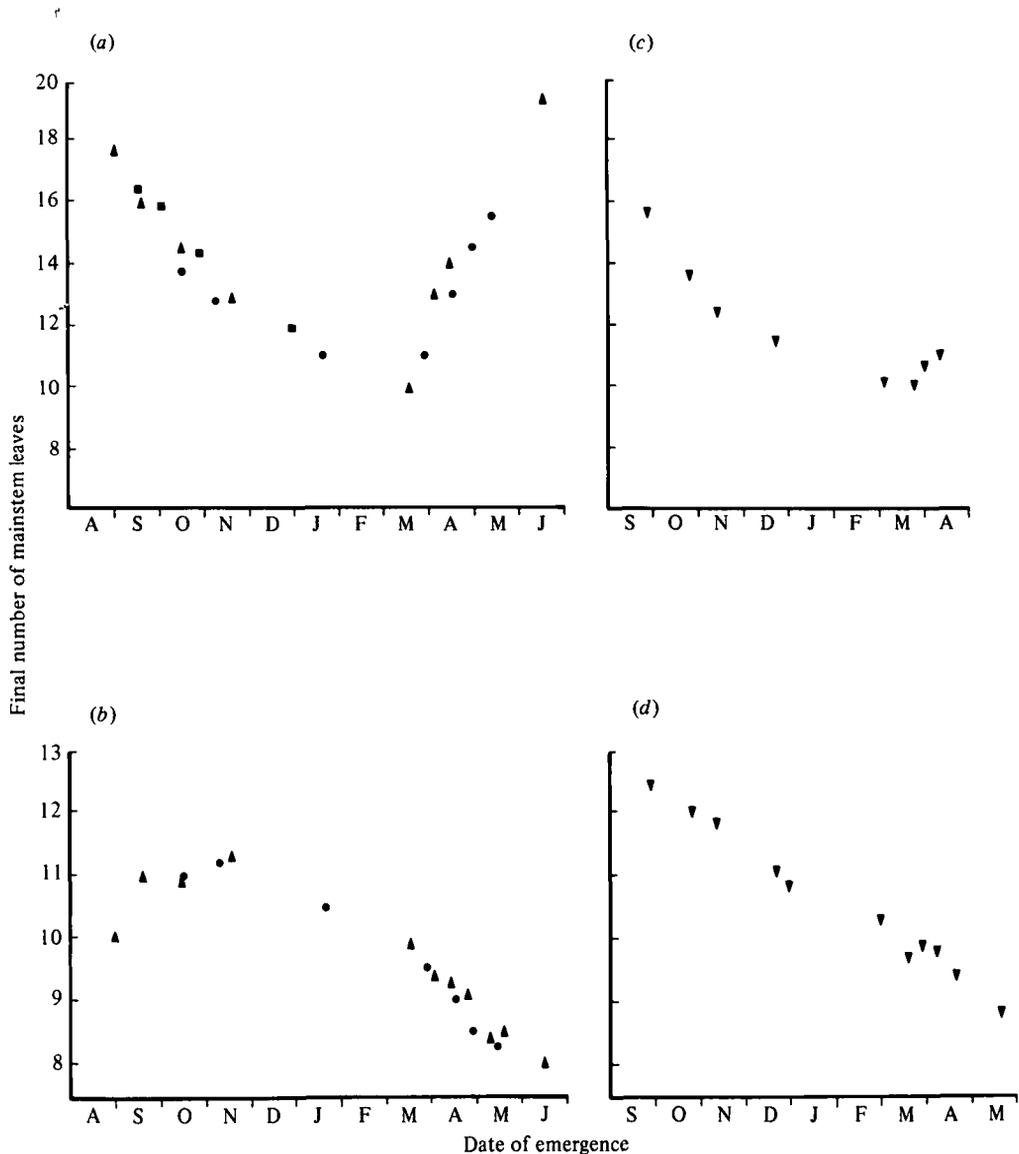


Fig. 23. Relationship between final number of mainstem leaves and date of crop emergence in (a) Sonja, (b) Jupiter, (c) Igri, (d) Triumph. ●, Expt 1; ▲, Expt 2; ■, Expt 3; ▼, Expt 4.

rapidly as all would emerge at the faster rate of the longer days. The latter feature restricts the potential advantage of delayed sowing as a means of delaying anthesis. The delaying of anthesis from September–October sowings by extra leaves on the mainstem should ensure greater dry-matter pro-

duction and retention of tillers and spikelets. The authors have found a similar basic pattern of development in wheat (unpublished) so similar changes may be effective in increasing total dry-matter production in this species and thereby grain yield. However, the potential improvement from

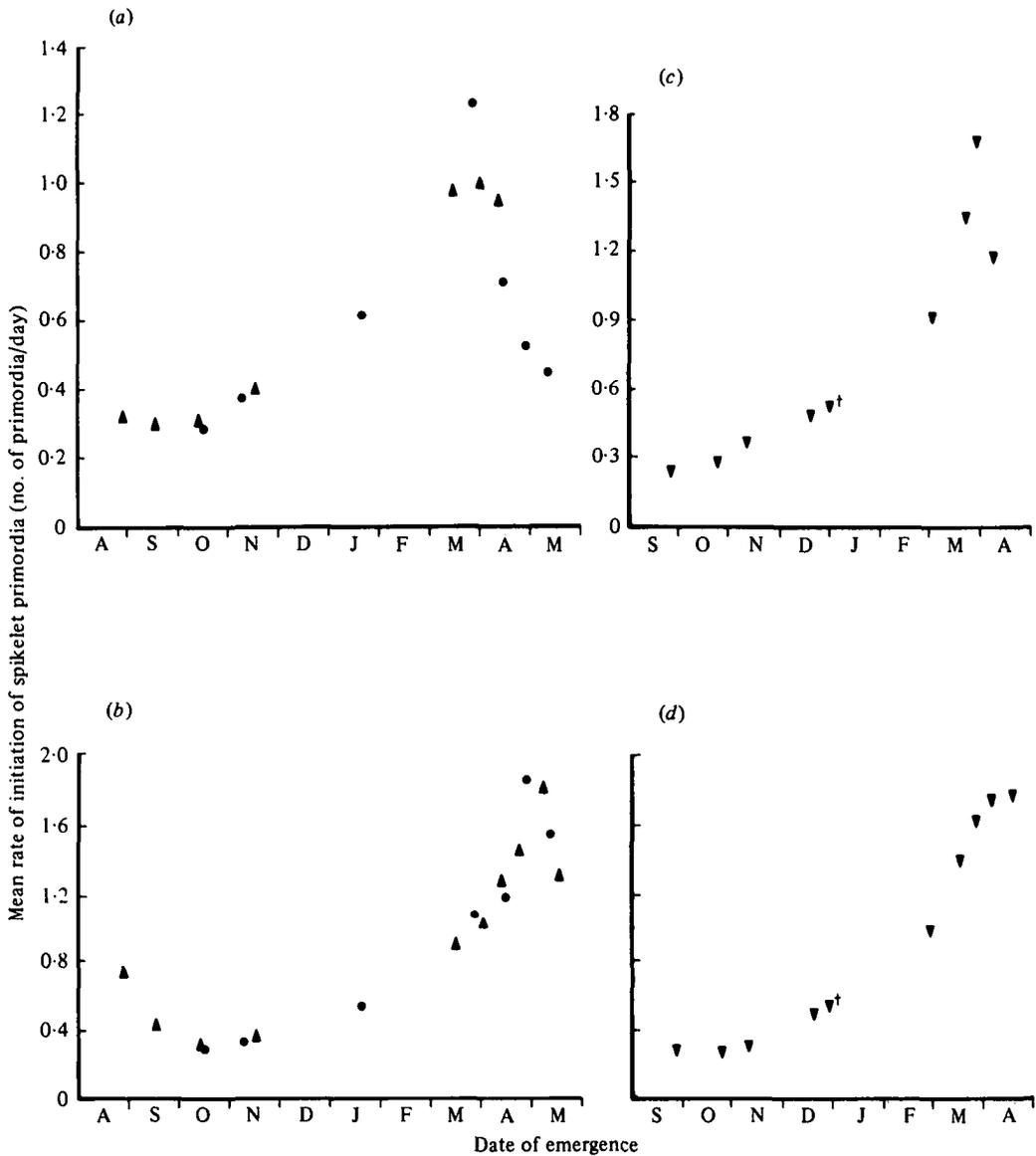


Fig. 24. Relationship between mean rate of spikelet initiation and date of crop emergence in (a) Sonja, (b) Jupiter, (c) Igri, (d) Triumph. ●, Expt 1; ▲, Expt 2; ▼, Expt 4.

delaying anthesis in wheat may be more limited in view of the already later occurrence of this stage. There may also be agronomic advantages from study of the differences in spring barley varieties in their developmental responses to daylength for the most suitable developmental patterns for the

range of environments in which the crop is grown throughout the U.K. may be identified. There is clearly a need to establish the variation in developmental pattern within both winter and spring genotypes with regard to the characteristics identified here.

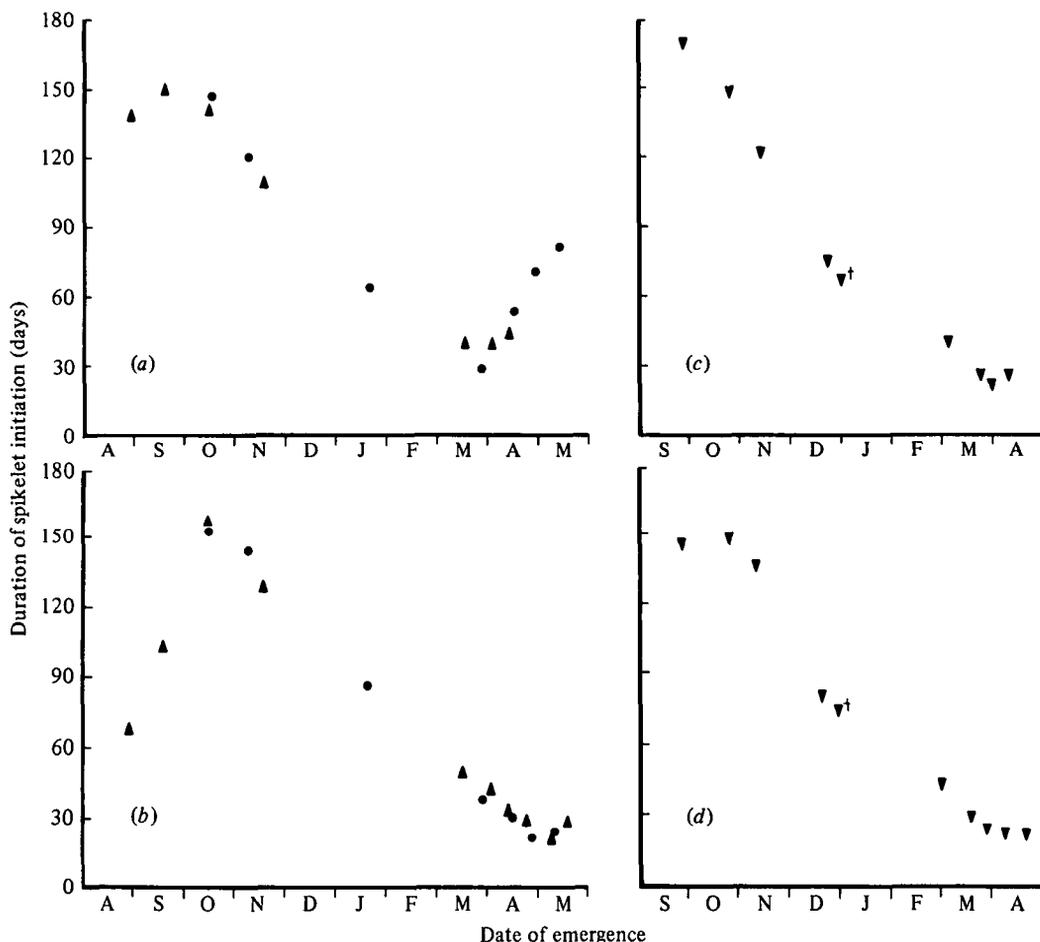


Fig. 25. Relationship between duration of spikelet initiation and date of crop emergence in (a) Sonja, (b) Jupiter, (c) Igri, (d) Triumph. ●, Expt 1; ▲, Expt 2; ▼, Expt 4.

REFERENCES

- BAKER, C. K. & GALLAGHER, J. N. (1983). The development of winter wheat in the field. 1. Relation between apical development and plant morphology within and between seasons. *Journal of Agricultural Science, Cambridge* **101**, 327–335.
- CANADA DEPARTMENT OF AGRICULTURE (1974). Selected tables and conversions used in agrometeorology and related fields. Publication 1522.
- CANNELL, R. Q. (1969). The tillering pattern in barley varieties. II. Effect of temperature, light intensity and daylength on the frequency of occurrence of the coleoptile node and second tillers in barley. *Journal of Agricultural Science, Cambridge* **72**, 423–435.
- CHUJO, H. (1966). Differences in vernalisation in wheat under various temperatures. *Proceedings of the Crop Science Society of Japan* **35**, 177–186.
- ELLIS, R. P. & RUSSELL, G. (1984). Plant development and grain yield in spring and winter barley. *Journal of Agricultural Science, Cambridge* **102**, 85–95.
- FRANKS, S. A. & HUGHES, M. (1984). The effects of several husbandry factors on the growth and yield of winter sown barley at four sites in each of three years. *Journal of Agricultural Science, Cambridge* **103**, 555–560.
- GALLAGHER, J. N., BISCOE, P. V. & DENNIS-JONES, R. (1983). Environmental influences on the development, growth and yield of barley. In *Barley: Production and Marketing* (ed. G. M. Wright and R. B. Wyn-Williams), pp. 21–49. Agronomy Society of New Zealand Special Publication No. 2.
- HAY, R. K. M. & ABBAS AL-ANI, M. K. (1983). The physiology of forage rye (*Secale cereale*). *Journal of Agricultural Science, Cambridge* **101**, 63–70.
- HAY, R. K. M. & TUNNICLIFFE WILSON, G. (1982). Leaf appearance and extension in field-grown winter wheat plants: the importance of soil temperature during vegetative growth. *Journal of Agricultural Science, Cambridge* **99**, 403–410.
- KIRBY, E. J. M. & APPELYARD, M. (1984). Cereal plant development and its relation to crop management.

- In *Cereal Production. Proceedings of the 2nd International Summer School in Agriculture* held by the Royal Dublin Society in cooperation with the W. K. Kellogg Foundation (ed. E. J. Gallagher), pp. 161–173. London: Butterworth.
- KIRBY, E. J. M., APPELEYARD, M. & FELLOWES, G. (1982). Effect of sowing date on the temperature response of leaf emergence and leaf size in barley. *Plant, Cell and Environment* 5, 477–484.
- KIRBY, E. J. M., APPELEYARD, M. & FELLOWES, G. (1985). Effect of sowing date and variety on main shoot leaf emergence and number of leaves of barley and wheat. *Agronomie* 5 (2) 117–126.
- KIRBY, E. J. M. & ELLIS, R. P. (1980). A comparison of spring barley grown in England and in Scotland. 1. Shoot apex development. *Journal of Agricultural Science, Cambridge* 95, 101–110.
- KIRBY, E. J. M. & JONES, H. G. (1977). The relations between the main shoot and tillers in barley plants. *Journal of Agricultural Science, Cambridge* 88, 381–389.
- KIRBY, E. J. M. & RIGGS, T. J. (1978). Developmental consequences of two-row and six-row ear types in spring barley. 2. Shoot apex, leaf and tiller development. *Journal of Agricultural Science, Cambridge* 91, 207–216.
- PATEL, J. C. (1979). Effects of date of sowing on contrasting barley varieties. Ph.D. thesis. University College of Wales, Aberystwyth.
- RUSSELL, G., ELLIS, R. P., BROWN, J., MILBOURN, G. M. & HAYTER, A. M. (1982). The development and yield of autumn- and spring-sown barley in south east Scotland. *Annals of Applied Biology* 100, 167–178.
- SCOTT, R. K. & DENNIS-JONES, R. (1976). The physiological background of barley. *Journal of the National Institute of Agricultural Botany* 14, 182–187.
- SEALE, R. S. & HODGE, C. A. H. (1976). Soils of the Cambridge and Ely District. *Soil Survey Special Survey* No. 10.
- SOIL SURVEY RECORD (1974). No. 24. 1. Soils in Dyfed II (Pembroke Haverfordwest).
- TOTTMAN, D. R. & MAKEPEACE, R. J. (1979). An explanation of the decimal code for the growth stages of cereals, with illustrations. *Annals of Applied Biology* 93, 221–234.
- WEIR, A. H., BRAGG, P. L., PORTER, J. R. & RAYNER, J. H. (1984). A winter wheat crop simulation model without water or nutrient limitations. *Journal of Agricultural Science, Cambridge* 102, 371–382.

Appendix Table 1. Points included in regression lines where more than one regression is presented in a Figure

Figure	Regression line	Dates of sowing
10	a	●, 9. x. 79, 29. x. 79; ▲, 11. vi. 81, 22. viii. 80, 12. ix. 80, 3. x. 80, 31. x. 80; ■, 10. ix. 82, 22. ix. 82, 15. x. 82, 1. xii. 82.
	b	●, 3. iii. 80, 4. iv. 80, 17. iv. 80, 30. iv. 80; ▲, 16. ii. 81, 19. iii. 81, 2. iv. 81, 11. vi. 81.
12	a	○, 29. x. 76, 22. xi. 76; △, 8. x. 77; □, 12. ix. 79, 17. x. 79, 21. xi. 79; ▽, 18. ix. 80, 15. x. 80, 12. xi. 80; ●, 9. x. 79, 29. x. 79; ▲, 11. vii. 81, 22. viii. 80, 12. ix. 80, 3. x. 80, 31. x. 80; ■, 10. ix. 82, 22. ix. 82, 15. x. 82, 1. xii. 82.
	b	○, 14. xiii. 76, 10. i. 77; ▽, 12. xi. 80, 17. ii. 81; ●, 4. xii. 79; ▲, 16. ii. 81.
	c	○, 7. iii. 77; △, 9. iii. 78; □, 19. ii. 80, 14. iv. 80; ▽, 17. ii. 81; ●, 3. iii. 80, 4. iv. 80, 17. iv. 80, 30. iv. 80; ▲, 16. ii. 81, 19. iii. 81, 2. iv. 81, 11. vi. 81.
13	a	▼, 20. ix. 83, 11. x. 83, 31. x. 83, 21. x. 83, 1. xii. 83.
	b	▼, 20. ix. 83, 11. x. 83, 31. x. 83, 21. x. 83, 1. xii. 83.
	c	▼, 1. xii. 83, 19. i. 84, 13. ii. 84, 9. iii. 84, 19. iii. 84, 3. iv. 84, 11. v. 84, 9. v. 84.
14	a	○, 29. x. 76, 22. xi. 76; △, 8. x. 77; □, 12. ix. 79, 17. x. 79, 21. xi. 79; ▽, 18. ix. 80, 15. x. 80, 12. xi. 80; ●, 9. x. 79, 29. x. 79; ▲, 11. vi. 81, 22. viii. 80, 12. ix. 80, 3. x. 80, 31. x. 80; ■, 10. ix. 82, 22. ix. 82, 15. x. 82, 1. xii. 82; ▼, 20. ix. 83, 11. x. 83, 31. x. 83, 21. xi. 83, 1. xii. 83.
	b	○, 14. xii. 76, 10. i. 77; ▽, 12. xi. 80, 17. ii. 81; ●, 4. xii. 79; ▲, 16. ii. 81; ▼, 21. xi. 83, 1. xii. 83, 19. i. 84, 13. ii. 84.
	c	○, 7. iii. 77; △, 9. iii. 78; □, 19. ii. 80, 14. iv. 80; ▽, 17. ii. 81; ●, 3. iii. 80, 4. iv. 80, 17. iv. 80, 30. iv. 80; ▲, 16. ii. 81, 19. iii. 81, 2. iv. 81, 11. vi. 81; ▼, 13. ii. 84, 9. iii. 84, 19. iii. 84.