Apex and ear development in relation to the number of grains on the main-stem ears in spring barley (*Hordeum distichon*)

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SUMMARY

Apex and ear development in nine spring barley genotypes were studied at two sites in southern Spain in 1988. The genotypes were grouped into medium and early types, depending on the time from sowing to anthesis. Medium genotypes had significantly more spikelet primordia than early ones at both sites. Spikelet mortality was similar between genotypes and sites, resulting in a higher final number of grains/ear in the medium than the early genotypes.

There was a positive correlation between the maximum number of spikelet primordia and the duration of three stages of apical development: lemma-, stamen- and awn-primordia. Negative correlations were observed between spikelet mortality and the duration of certain developmental phases of the ear.

INTRODUCTION

A cereal plant develops through a series of phases, whose timing depends on genetic and environmental factors. Observation of the shoot apex or developing ear of a plant leads to the precise identification of its stage of development. In recent years, numerous attempts have been made to predict the development of barley according to empirical criteria such as temperature and photoperiod (Ellis & Russell 1984; Jones & Allen 1986). Three mathematical models have been constructed relating the duration of development phases to temperature and/or daylength (Wright & Hughes 1987). This information is useful in comparative studies between genotypes and environments as well as in the timing of cultivation operations, all of which can lead to significant increases in yield (Kirby & Appleyard 1984; Wright & Hughes 1987).

In barley, the final number of grains/ear depends both upon the duration and mean rate of spikelet initiation and the proportion of spikelets that survive to set grain. The first of these two factors has been extensively studied, and may be manipulated by changing the photoperiod or by the application of gibberellins (Dale & Wilson 1979; Nicholls 1982; Cottrell *et al.* 1983). A relationship between the maximum number of spikelet primordia and the duration of the spikelet initiation phase has also been reported (Kitchen & Rasmusson 1983). There is much less data available on spikelet survival, although it is well known that most losses occur from the awn-primordium stage (maximum number of spikelet primordia) to anthesis (Ellis & Kirby 1980; Russell *et al.* 1982; Ellis & Russell 1984; Jones & Allen 1986). During this period, the stem and rachis develop rapidly, suggesting that demand for assimilates during these processes is substantial and that spikelet abortion could be the result of this intense competition for metabolites (Gallagher *et al.* 1976; Kirby 1977; Ellis & Kirby 1980; Cottrell *et al.* 1985). Jones & Allen (1986) have also suggested that the timing of the critical phase of spikelet survival is determined by the emergence of a specific number of leaves, which can only be altered in any particular variety by changing the number of leaves through times of sowing.

In this study, the development of the apex and ear of the main stem was analysed in relation to the final number of grains/ear in nine spring barley genotypes.

Table 1. *Mean values of maximum and minimum temperatures, rainfall and sunshine hours during crop development of spring barley at Montes and Colomera, Southern Spain*

	December 1987		January 1988		February 1988		March 1988	
	Montes	Colomera	Montes	Colomera	Montes	Colomera	Montes	Colomera
Temperature (°C)								
Maximum	11·3	14·1	10·1	12·4	12·1	14·4	15·3	19·9
Minimum	2·1	4·5	0·9	2·7	−0·5	1·6	1·4	4·6
Rainfall (mm)	154	66	81	48	40	21	34	11
Sunshine (%)	40	44	36	48	58	64	60	69

	April 1988		May 1988		June 1988	
	Montes	Colomera	Montes	Colomera	Montes	Colomera
Temperature (°C)						
Maximum	16·4	20·9	18·4	24·2	28·0	35·0
Minimum	3·0	6·4	5·2	9·2	9·8	14·8
Rainfall (mm)	70	49	50	32	20	1
Sunshine (%)	60	68	64	70	70	75

Table 2. *Mean and standard error values for duration of development stages in nine genotypes of spring barley in Spain in 1988*

		Days from					
		Sowing to maturity		Sowing to anthesis		Anthesis to maturity	
Genotype		Montes	Colomera	Montes	Colomera	Montes	Colomera
Zaida		170·3	155·5	135·0	120·0	35·3	35·5
	S.E.	0·6	1·0	0·6	0·9	0·6	0·6
Beka		170·3	155·8	134·0	120·0	36·3	35·8
	S.E.	0·8	0·7	0·6	0·7	0·6	0·8
2		170·8	157·0	137·8	121·5	33·0	35·5
	S.E.	0·5	0·5	0·3	0·5	0·3	0·5
3		172·3	158·5	140·3	122·8	32·0	35·7
	S.E.	0·5	0·6	0·8	0·7	0·8	0·8
2–3		172·3	158·0	141·0	123·0	31·3	35·0
	S.E.	1·0	0·9	1·0	0·9	0·9	0·5
1		160·8	150·0	124·3	113·8	36·5	36·2
	S.E.	0·5	1·1	0·3	0·8	0·3	0·9
1–2		162·2	150·3	127·0	113·8	35·2	36·5
	S.E.	0·9	0·9	0·5	0·8	0·8	0·5
1–3		163·0	151·0	127·5	115·3	35·5	35·7
	S.E.	0·5	0·9	0·7	1·0	0·9	0·8
1–2–3		162·0	151·3	128·0	116·3	34·0	35·0
	S.E.	0·9	0·5	0·6	0·3	0·5	0·5
Medium		171·2	157·0	137·6	121·5	33·6	35·5
	S.E.	1·0	0·8	0·7	1·0	0·7	0·6
Early		162·0	150·7	126·7	114·8	35·3	35·9
	S.E.	0·8	0·6	0·8	0·9	0·6	0·7
Total		167·1	154·2	132·8	118·5	34·3	35·7
	S.E.	1·9	1·1	1·2	1·3	0·9	1·0

Table 3. *Duration in days of development stages of nine genotypes of spring barley in Spain in 1988*

Genotype	Development stages									
	Vegeta-tive	Double ridge	Triple mound	Glume prim-ordium	Lemma prim-ordium	Stamen prim-ordium	Awn prim-ordium	White anther	Green anther	Yellow anther
					Montes					
Zaida	61·0	30·1	3·0	3·0	5·2	5·0	10·8	7·6	7·3	2·0
Beka	61·0	30·2	3·0	3·0	5·1	6·0	12·1	6·6	5·0	2·0
2	61·0	27·9	3·0	4·0	6·9	6·0	12·3	6·5	8·2	2·0
3	61·0	28·1	3·0	4·0	5·1	6·0	11·0	11·9	8·2	2·0
2–3	63·0	25·0	3·0	3·0	8·3	7·0	14·2	9·5	6·0	2·0
1	61·0	24·1	3·0	3·0	2·0	3·0	8·9	8·0	8·3	3·0
1–2	63·0	19·3	3·0	4·0	6·1	3·0	11·0	8·2	7·4	2·0
1–3	61·0	25·2	3·0	3·0	3·0	3·0	10·1	10·1	7·1	2·0
1–2–3	63·0	23·0	2·0	3·0	3·0	3·0	9·2	10·6	9·2	2·0
Medium	61·4	28·3	3·0	3·4	6·1	6·0	12·1	8·4	7·0	2·0
Early	62·0	22·9	2·8	3·3	3·5	3·0	9·8	9·2	8·0	2·3
Total	61·7	25·9	2·9	3·3	5·0	4·7	11·1	8·7	7·4	2·1
					Colomera					
Zaida	54·0	16·8	3·0	2·0	4·2	7·1	10·9	10·1	8·9	3·0
Beka	55·0	15·1	4·0	3·0	6·1	7·2	13·2	7·7	6·7	2·0
2	55·0	16·8	3·0	2·0	5·9	6·0	12·1	9·8	8·9	2·0
3	55·0	17·9	3·0	2·0	5·1	6·0	11·8	10·0	10·0	2·0
2–3	55·0	19·0	4·0	3·0	5·1	7·2	13·1	7·8	6·8	2·0
1	55·0	13·8	3·0	2·0	3·0	5·2	10·1	11·0	8·8	2·0
1–2	55·0	12·9	3·0	2·0	3·0	5·1	10·0	10·8	10·0	2·0
1–3	55·0	16·1	3·0	2·0	3·1	4·0	9·8	11·1	9·2	2·0
1–2–3	54·0	17·2	3·0	3·0	3·9	6·0	10·8	8·1	8·2	2·0
Medium	54·8	17·1	3·4	2·4	5·3	6·7	12·2	9·1	8·3	2·2
Early	54·8	15·0	3·0	2·3	3·3	5·1	10·2	10·2	9·0	2·0
Total	54·8	16·2	3·2	2·3	4·4	6·0	11·3	9·6	8·6	2·1

MATERIALS AND METHODS

The experiments were carried out at two contrasting sites in Granada, southern Spain: Montes (1000 m above sea level) and Colomera (600 m above sea level) (Table 1). According to FAO classification (1977), the soils of both areas are calcic cambisols, in association with calcareous regosols in Montes and with chromic luvisols in Colomera. Both soils contain similar quantities of sand, loam, clay, organic matter and organic N, although the soil at Montes is higher in assimilable P and assimilable K than at Colomera.

Nine spring barley (*Hordeum distichon*) genotypes were tested: Zaida, a variety bred by 'La Cruz del Campo S.A.' in southern Spain and well adapted to the area; Beka, another variety well adapted to semi-arid Mediterranean conditions; three single mutants: genotypes 1 and 3, obtained from Beka by irradiation with gamma rays (as described by Molina-Cano 1982), and genotype 2 obtained by Molina-Cano in exactly the same way and at the same time as genotypes 1 and 3; three double mutants, obtained by crossing genotypes 1, 2 and 3 in all combinations, excluding reciprocals (recombinants 1–2, 1–3 and 2–3), selected in F_2 and selected for apparent homozygosity in F_3; and one triple mutant (1–2–3), obtained by crossing recombinants 1–2 and 1–3, also selected in F_2 and selected for apparent homozygosity in F_3. The experimental design at both sites consisted of randomized blocks with four replicates. The plots were 10 m long and 1·2 m wide with 6 rows, 20 cm apart.

All the genotypes were sown to produce 350 viable plants/m^2, on 20 December at Montes and on 22 December at Colomera. Each plot received 45 kg P_2O_5/ha, 45 kg K_2O/ha and 24 kg N/ha at sowing and 30 kg N/ha at the beginning of tillering (in mid-February in Colomera and at the end of February in Montes). The whole of each crop was harvested in mid-July in Colomera and at the end of July in Montes.

Twenty samples per plot were taken at each site, starting when the first leaf unfolded and repeated every 3–4 days until anthesis (awn tips just visible in 50% of the plants) and then every 7 days until maturity (when 75% of the glumes of the primary ear had turned yellow in 50% of the plants). At each sampling, ten homogeneous plants per plot were

examined to establish their development (Kirby & Appleyard 1986) and growth stages (Zadoks *et al.* 1974). The following data were recorded from the main stems of five plants selected from each group of ten plants: (*a*) maximum number of spikelet primordia; (*b*) number of florets at anthesis; (*c*) number of grains/ear at maturity; and (*d*) number of grains/ear at harvest.

RESULTS

Duration of period from sowing to maturity

The genotypes with the early-heading allele matured significantly faster than the other genotypes at both sites (Table 2). The genotypes were thus divided into two groups: early (1, 1–2, 1–3 and 1–2–3), which matured from sowing in 160·8–163 days at Montes and 150–151·3 days at Colomera; and medium (Zaida, Beka, 2, 3 and 2–3), which matured from sowing in 170·3–172·3 days at Montes and 155·5–158·5 days at Colomera. We also noted that the differences in the period from sowing to maturity between the two groups of genotypes at both sites (9·2 days at Montes and 6·1 days at Colomera) resulted from the differences in duration from sowing to anthesis (10·9 days at Montes and 6·7 days at Colomera) (Table 2). During the period from anthesis to maturity, there was no difference between genotypes. The greater delay between sowing and maturity at Montes than at Colomera (12·9 days) was also the result of a longer period from sowing to anthesis (14·3 days) (Table 2).

Duration of apex and ear development stages

Table 3 shows that the length of the vegetative stage of the apex of the main stem was similar for all genotypes at Montes (61–63 days) and Colomera (54–55 days). The double-ridge stage was significantly shorter in the early than in the medium genotypes (5·4 days less at Montes and 2·1 days less at Colomera). At Montes the double-ridge stage lasted on average 9·7 days longer than at Colomera. The triple-mound and glume-primordium stages were similar at both sites for all genotypes. The following stages, lemma-primordium, stamen-primordium and awn-primordium were similar in length at both sites, although their duration was longer for the medium than the early genotypes. During the remaining stages to anthesis (white anther, green anther and yellow anther) there were no statistical differences either between sites or genotypes.

Maximum number of spikelet primordia and spikelets lost

At both sites the maximum number of spikelet primordia was significantly higher in the medium than the early genotypes (Table 4). Mortality from the awn-primordium stage until harvest was similar in

Table 4. *Mean and standard error values of main-stem development characters in five medium and four early genotypes of spring barley in Spain in 1988*

Site	Genotype group		Maximum number of spikelet primordia	Number of florets at anthesis	Number of grains/ear at maturity	Number of grains/ear at harvest	Spikelet losses from awn primordium to anthesis	Floret losses from anthesis to maturity	Grain losses from maturity to harvest	Spikelet losses from awn primordium to harvest
Montes	Medium		39·5	28·3	27·0	26·2	11·2	1·3	0·8	13·3
		S.E.	0·39	0·42	0·43	0·45	0·42	0·22	0·22	0·46
	Early		35·7	26·4	25·1	24·1	9·3	1·3	1·0	11·6
		S.E.	0·32	0·25	0·38	0·40	0·38	0·27	0·18	0·43
Colomera	Medium		38·9	30·6	28·5	27·5	8·3	2·1	1·0	11·4
		S.E.	0·29	0·40	0·40	0·40	0·30	0·38	0·20	0·35
	Early		36·5	25·9	25·3	24·2	10·6	0·6	1·1	12·3
		S.E.	0·22	0·32	0·22	0·27	0·33	0·22	0·23	0·33
Montes			37·8	27·5	26·1	25·1	10·3	1·3	0·9	12·5
		S.E.	0·41	0·30	0·33	0·33	0·33	0·17	0·15	0·36
Colomera			37·8	28·5	27·0	26·0	9·3	1·5	1·0	11·8
		S.E.	0·28	0·47	0·36	0·37	0·29	0·26	0·15	0·25

Table 5. *Correlation coefficients between the maximum number of spikelet primordia and the duration of development stages of spring barley in Spain in 1988*

Site	Development stages									
	Vegetative	Double ridge	Triple mound	Glume primordium	Lemma primordium	Stamen primordium	Awn primordium	Lemma + stamen + awn primordium	Sowing to awn primordium
Montes ($n = 9$)	0·11	0·43	0·34	0·20	0·91	0·93	0·97	0·98	0·95
Colomera ($n = 9$)	0·23	0·54	0·73	0·53	0·95	0·78	0·99	0·97	0·95
Combined ($n = 18$)	0·02	0·25	0·45	0·22	0·90	0·80	0·96	0·97	0·56

both groups of genotypes and sites, so at harvest the medium genotypes had significantly more grains per main-stem ear than the early genotypes. There were no statistical differences between sites, however, either in the maximum number of spikelet primordia or in losses, and so the final number of grains/ear did not differ between sites. The number of spikelets lost from the awn-primordium stage until harvest was 12·5 (33·1%) in Montes and 11·8 (31·2%) in Colomera. The majority of these losses were spikelets at the top and bottom of the ear, and occurred between the end of the awn-primordium stage and anthesis (10·4 and 9·3 spikelets lost in Montes and Colomera, respectively) (Table 4).

Relationships between the duration of development stages, the maximum number of spikelets and their losses

Table 5 shows that the maximum number of spikelet primordia was closely related to the length of time from sowing to the awn-primordium stage at each site taken separately, but when the data for both sites were combined, this correlation coefficient was considerably reduced. This suggests that the dependence of the maximum number of primordia upon the time between sowing and the awn-primordium stage was different at each site. Nevertheless, when the maximum number of primordia was correlated with the duration of each individual stage of development (Table 5) it was clear that the maximum number of spikelet primordia was closely and positively correlated with the duration of the lemma-, stamen- and awn-primordia development stages, both for each individual stage and for all three as a whole, in each site independently and in both combined.

We calculated the relationships between the number of spikelets lost and the duration of the following stages: white anther; green anther; yellow anther; days from anthesis to maturity; and days from maturity to harvest. The correlation coefficients thus obtained were, on the whole, negative and not statistically significant. This was expected, as the length of the stages after awn-primordium and spikelet loss in all these phases were similar at both sites and among all the genotypes.

DISCUSSION

Takahashi & Yasuda (1970) maintain that at least three physiological factors are responsible for determining earliness in barley: (1) spring and winter growth habit (i.e. vernalization requirement); (2) photoperiodic response (i.e. sensitivity to short days); and (3) minimal vegetative growth (i.e. number of leaves necessary for ear formation, which is earliness in a narrow sense). Our nine genotypes were of spring habit. It is also well known that, in a Mediterranean

climate, barley genotypes respond relatively uniformly to short days (Yasuda 1982). Thus, the differences between the early and medium genotypes from sowing to maturity seem to be due to differences in the minimum vegetative growth necessary for the formation of ears. It is almost certainly for this reason that the number of days from sowing to maturity was similar in early and medium genotypes at either site (9·2 days at Montes and 6·3 days at Colomera).

The differences between the early and medium genotypes from sowing to maturity depended wholly on differences during the period from sowing to anthesis, as after this time no appreciable differences were seen. At Montes, the phase from sowing to anthesis was on average 14·3 days longer than at Colomera, while no significant difference was observed from anthesis to maturity. These observations agree with those of other authors that the most important differences in the duration of the life cycle of barley genotypes occur in the period from sowing to anthesis (Takahashi & Yasuda 1970; Yasuda 1982).

The differences in the length of time from sowing to anthesis between the early and medium genotypes could be attributed to unequal durations of the double-ridge, lemma-primordium, stamen-primordium and awn-primordium stages. Nevertheless, between sites, the differences between the time from sowing to anthesis occurred primarily in the first two phases of apex development, i.e. the vegetative and double-ridge stages. According to Kirby *et al.* (1985), genotype, environment and weather all influence differences in the length of the double-ridge and awn-primordium stages. Our results agree only partly with these conclusions, as the duration of the double-ridge stage did indeed depend both on genotype and site, whereas the duration of the awn-primordium stage depended only on genotype. Furthermore, under our experimental conditions there were variations in the duration of the lemma-primordium and stamen-primoridum stages according to genotype.

The maximum number of primordia was far higher on the medium genotypes at both sites, probably because of the longer period of spikelet initiation in these genotypes. Ellis & Kirby (1980) have suggested that spikelet primordia have the potential to form larger grains if they are initiated more slowly and over a longer period, presumably because there is less competition for limited resources between the organs of the plant. The main resource which is limited is the assimilate produced by photosynthesis, and its availability depends on both the rate and duration of photosynthesis (Russell *et al.* 1982).

The incidence of spikelet abortion was similar between genotypes and sites, the main losses occurring during the period from the awn-primordium stage to anthesis. This agrees with the observations of Ellis & Russell (1984) and Cottrell *et al.* (1985), who found similar spikelet losses in two-rowed barley planted at different times in different years and at different sites. This similarity in spikelet abortion in the various genotypes is remarkable, and suggests that it may be under genetic rather than environmental control. If this is so, some spikelet death is inevitable, and increasing the number of grains/ear by reducing spikelet abortion may not be feasible (Cottrell *et al.* 1985). Spikelet formation at the top and bottom of the ear coincides with the maximum elongation rate of the stem and the ear, which could well lead to great competition for assimilates, thereby causing the death of some of the developing spikelets.

Russell *et al.* (1982) have indicated that in barley the maximum number of spikelet primordia initiated sets a limit to the number of grains/m^2, but grain yield depends more on the number of surviving primordia. In their study, the number of grains/m^2 was related to the photosynthetically active radiation (PAR) absorbed, thus plants with earlier anthesis absorb less PAR, with a consequent reduction in the number of grains/m^2. Jones & Allen (1986) have also indicated that delaying anthesis would ensure that the period of spikelet survival coincided with more favourable conditions (higher irradiance). In hot, dry climates such as southern Spain, however, irradiance is never a limiting factor at anthesis, usually in April, and so delay in the onset of anthesis would probably lead to a shortening of the grain-filling period due to the heat and shortage of rain during May, June and July. This in turn would produce lighter grains and also possibly an increase in spikelet abortion.

The close relationship between the maximum number of spikelet primordia and the length of the various apex development phases indicates that in southern Spain the duration of the lemma-primordium, stamen-primordium and awn-primordium stages was responsible for the differences in the maximum number of primordia between the two groups of genotypes. The close relationship observed between the maximum number of primordia and the time that elapses between sowing and the end of the awn-primordium stage is in fact somewhat deceptive, as the duration of the three stages mentioned above forms only part of the sum of all the other development stages (which are similar within each site, but differ between sites). It is for this reason that we have obtained high correlation coefficients between the maximum number of primordia and the time between sowing and the awn-primordium stage at each site taken individually, but when the results for both sites are pooled, the correlation coefficient is considerably lower. Kitchen & Rasmusson (1983) have obtained good correlations between the duration of the spikelet initiation period and the maximum number of spikelet primordia in ten barley varieties of diverse phenotypes and origins; the main difference with our findings is

that their researches did not divide the spikelet initiation phase into its five constituent stages: triple-mound; glume-primordium; lemma-primordium; stamen-primordium; and awn-primordium, and thus they could not determine exactly which of these stages had the most influence on the correlations obtained.

The negative relationships found between spikelet losses and the duration of development phases after the awn-primordium stage seem to suggest that when the spikelets grow for longer, mortality tends to be lower, which accords with Ellis & Kirby's (1980) findings. We suspect that these results may be related to the increase of temperature after anthesis in southern Spain, affecting spikelet abortion in some genotypes more than in others, although further investigation is needed.

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