Available online at www.sciencedirect.com
SCIENCE DIRECT®
Field Crops Research 81 (2003) 109–119
Field Crops Research
www.elsevier.com/locate/fcr

Yield stability and development in two- and six-rowed winter barleys under Mediterranean conditions

Luis F. García del Moral[a,*], M. Belén García del Moral[b], José L. Molina-Cano[c], Gustavo A. Slafer[d]

[a]*Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain*
[b]*Departamento de Biología Vegetal y Ecología, Escuela Politécnica Superior, Universidad de Almería, Carretera de Sacramento s/n, La Cañada de San Urbano, 04120 Almería, Spain*
[c]*Centre UdL-IRTA, Alcalde Rovira Roure 177, 25198 Lleida, Spain*
[d]*Departamento de Producción Vegetal e IFEVA, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina*

Received 20 February 2002; received in revised form 15 October 2002; accepted 23 October 2002

Abstract

Under the irregular weather that characterises Mediterranean environments, to increase yield stability in cereal crops represents an important objective for agricultural progress. In this study, a series of field experiments were conducted with two- and six-rowed barley cultivars under Mediterranean conditions (southern Spain) to determine their differences in yield stability and to identify the influence that initiation and mortality of both the spikelet and tiller could exert on yield differences. Yield stability differed markedly in two- and six-rowed cultivars. The yield of two-rowed cultivars was more responsive to environmental changes than that of the six-rowed cultivars, which consistently showed more stable behaviour, outyielding the two-rowed barleys in the lowest yielding environments. Two-rowed cultivars had far more spikes per m^2 than did six-rowed cultivars, while the latter consistently had more grains per spike, with a lower average grain weight. Yield differences among environments, for both groups of cultivars, were more associated with changes in number of grains per unit of land area than to differences in individual grain weight. Six-rowed cultivars, as expected, produced virtually threefold more spikelets per spike than the two-rowed cultivars. Although there was a large difference between two- and six-rowed cultivars in spikelet abortion, the proportion of abortion was fairly stable across environments. Two-rowed cultivars consistently tillered at a higher rate (0.11 tillers per day) than the six-rowed barleys (0.07 tillers per day), though the magnitude of the difference in tillering was more affected by the environment than was the difference in spikelet initiation. Under Mediterranean conditions the constitutive capacity of six-rowed cultivars to have a reduced tillering rate, even under favourable growing conditions, as compared with that of two-rowed cultivars could be a useful strategy to save resources that may be more efficiently used during the critical phases for yield determination. This explains their higher yield stability when compared with two-rowed cultivars.

Keywords: Two- and six-rowed winter barleys; Yield stability; Yield components; Apical development; Tiller production and mortality

1. Introduction

Under growing conditions worldwide, the main target when growing crops is to maximise net benefits

* Corresponding author. Tel.: +34-958-243253; fax: +34-958-248995.
E-mail address: lfgm@ugr.es (L.F. García del Moral).

0378-4290/02/$ – see front matter
PII: S0378-4290(02)00215-0

mainly through increasing yields. However, in regions with irregular weather, such as the Mediterranean regions of southern Spain (Ramos et al., 1995), in which the variability among sites and years can severely affect the yield of cereal crops, to increase yield stability is also an important objective for agricultural progress (Slafer and Kernich, 1996).

Barley is one of the major crops grown in Andalusia, the southernmost region of continental Spain, strongly dominated by Mediterranean weather. Barley has been grown traditionally in western Andalusia, where the weather is warm and only small spring cereals are valuable. Eastern Andalusia, particularly the province of Granada, has several growing areas of relatively high altitude, in which the use of winter barleys might be attractive to farmers.

Although exceptions can be found, it has been consistently shown that yield in barley is more frequently associated with changes in number of grains per unit area than to individual grain weight (see reviews by Feil, 1992; Smith et al., 1999; Abeledo et al., 2002), as the post-anthesis source-strength, in most conditions, hardly limits cereal grain growth (Slafer and Savin, 1994; Richards, 1996), even under stress conditions (Slafer and Miralles, 1992). When comparing either responses to changes in environmental conditions or cultivars (within the same spike morphology), differences in grain number per unit area in barley are, in turn, far more frequently related to the number of spikes per m^2 than to the number of grains per spike (Ramos et al., 1982, and other examples in Abeledo et al., 2002), thus yield in barley being strongly related to tillering and tiller-survival capabilities of the cultivars. However, the environmental conditions under which the crop is grown may determine limits to the extrapolation of this general behaviour. Barley cultivars, as well as those of most cereals, produce a large number of tillers in early phases of development. A variable, but frequently high, proportion of them do not progress to produce a fertile spike, senescing during stem elongation (García del Moral et al., 2002 and references therein). Under many environmental conditions, ranging from stress-free to moderate stresses, abundant tillering may constitute a good strategy to maximise growth and yield as the resources used to produce tillers that may eventually senesce do not normally appear to be essential to growth during stem elongation. However in Mediterranean regions, with the crop undergoing progressively drier conditions, tillering capacity may result in yield limitations associated with the magnitude of the stress in any particular year/site.

Therefore, responsiveness to environmental changes may be related to the tillering capacity of the cultivars, while yield stability would be improved in cultivars of restricted tillering. In general, two-rowed barley cultivars possess a clearly higher ability to tiller than their six-rowed counterparts (Kirby and Riggs, 1978; Le Gouis et al., 1999) even under semi-arid conditions (García del Moral et al., 1984; Hadjichristodoulou, 1985), and this would be even more marked in winter than in spring types (García del Moral and García del Moral, 1995). In other words, under Mediterranean environments characterised by terminal drought with a large degree of variation in magnitude between sites and years, such as those commonly found in eastern Andalusia, two-rowed cultivars may be, in general, more responsive to environmental variation, while six-rowed cultivars may exhibit higher yield stability.

Only very few comparisons of two- and six-rowed cultivars are available in the literature and most of these were conducted in environments quite different from those characteristic of the Mediterranean region (e.g. in northern France, Le Gouis, 1992; Le Gouis et al., 1999; Germany, Maidl et al., 1996; Canada, Jedel and Helm, 1995) or under controlled conditions (Kirby and Riggs, 1978).

Yield responsiveness in the Mediterranean conditions of southern Spain may thus be, at least partially, associated with the more freely tillering capacity of two-rowed cultivars, and consequently yields of six-rowed cultivars may be more stable in these environments, particularly if winter barleys are more widely grown. In this study, a series of field experiments were conducted with two- and six-rowed barley cultivars at Granada to determine whether these contrasting groups differ in their yield stability and to what degree the differential patterns of initiation and mortality of spikelet and tiller may underlie any yield differences.

2. Materials and methods

2.1. General conditions

An agronomic study was carried out under conventional field conditions comprising five experiments in

Table 1
Details of sowing dates, and average temperatures and accumulated rainfall for the growing periods in each experiment

Site/year	Sowing date	Temperature (°C)	Rainfall (mm)	Days to anthesis
Montes/1989	9 November 1988	4.87	231.8	163
Montes/1990	31 October 1989	5.45	412.3	167
Montes/1991	31 October 1990	4.77	295.3	180
Chimeneas/1990	10 January 1990	11.14	139.6	113
Chimeneas/1991	19 November 1990	9.48	148.4	161

the Mediterranean environment of Granada in southern Spain. The experiments consisted of the comparison of two- and six-rowed cultivars of winter barley, of commercial interest in the cereal-growing region of eastern Andalusia, conducted at two sites during three consecutive growing seasons in one site and during two of these seasons in the other (Table 1).

The sites were chosen for their strong difference in yielding capacity for cereals: Montes (37°29′N latitude and 1000 m altitude) and Chimeneas (37°08′N latitude and 650 m altitude). The difference in altitude is crucial in determining not only that Montes is considerably cooler and wetter than Chimeneas throughout the growing season, but also that it has a much steadier rise in temperature during the spring (Fig. 1). Both sites have silty clay, loamy soils; classified as Calcicerollic Xerocrept (FAO, 1977).

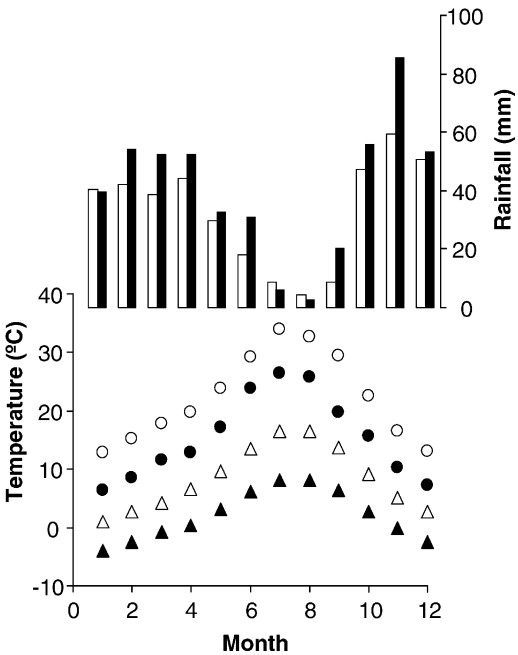

Fig. 1. Average (25 years) monthly maximum (circles) and minimum (triangles) temperature and accumulated rainfall at the two sites where the study was performed: Montes (1000 m asl, closed symbols and bars) and Chimeneas (650 m asl, open symbols and bars) in eastern Andalusia (37°N).

All experiments were performed at a sowing rate of 350 plants per m^2 and received NPK fertilisers as usual in the region, so that the variability of yield and associated traits were caused mainly by changes in water and thermal conditions across sites and years, which also differed in sowing dates (Table 1).

2.2. Treatments and design

Treatments in each experiment consisted of six cultivars of winter barley, three with two-rowed and the other three with six-rowed spikes. The two-rowed types were Finesse, Melusine and Alpha, while the six-rowed types were Barberousse, Plaisant and Hâtif de Grignon. All six are commercial French varieties of promising performance in eastern Andalusia. These cultivars were chosen as they satisfied the priorities of a breeding program of the biggest malting house in the region (Grupo Cruzcampo S.A., Seville, Spain), which funded the study, to introduce winter cultivars in an area strongly dominated by the cultivation of two-rowed spring barleys.

In previous comparisons the two-rowed French winter cultivars, Finesse, Melusine and Alpha, performed better than many of the most widely grown spring cultivars of SE Spain. In fact, in parallel with this study, García del Moral and García del Moral (1995) showed that the 2-rowed winter barleys included in this paper did yield more than three of the most popular two-rowed spring barleys in eastern Andalusia (Pallas, Zaida and Kym).

Each experiment was designed as four randomised complete blocks, with cultivars allocated to plots of 6 rows, 20 cm apart, and 10 m long. To minimise border effects, a single row in between plots was sown with a common border (cultivar Hassan, a two-row barley).

2.3. Measurements and analyses

For the determination of the dynamics of spikelet initiation, five plants per plot were sampled at random every 3–4 days, from the first-leaf-unfolded stage to the initiation of awn primordia (Kirby and Appleyard, 1987) on the most advanced spikelets when spikelet initiation ceased (Wych et al., 1985; García del Moral et al., 1991, 2002; Kernich et al., 1995). The main-shoot apex of each of these plants was dissected and the number of spikelet primordia recorded. In addition, the number of shoots on the plants of two 50 cm long sections taken at random from inner rows was counted, at intervals of about 15 days, throughout crop development until harvest. Heading time was recorded when awn tips started to emerge through the sheaths of the flag leaves in 50% of the plants.

At harvest, after the crop completely senesced, yield and yield components were determined. For this purpose, two 50 cm long sections taken at random from inner rows (the same as above) were sampled and the yield components (number of spikes per unit land area, number of grains per spike and individual grain weight) were measured. To determine yield, each plot was combine harvested and yield was corrected to 12% moisture level.

To assess yield stability, we adopted the linear-regression method as suggested by Yates and Cochran (1938) and rediscovered by Finlay and Wilkinson (1963). This methodology uses the regression coefficient (slope) of each cultivar on the average yield of all cultivars evaluated in different environments as a measure of a cultivar's yield responsiveness, and conceptually a reciprocal of yield stability, interpreted as: (a) slope < 1, indicating higher stability, under-responsiveness; (b) slope $= 1$, average stability, average responsiveness; and (c) slope > 1, lower stability, higher responsiveness, adapted to high-yielding environments.

Data were analysed with conventional statistical techniques of ANOVA and the least significant differences (at 5% level of significance) were calculated to test significance of treatment differences (Steel and Torrie, 1982). The relationship between variables was estimated by regression analyses.

3. Results

The experiment covered a large range of variation within the Mediterranean conditions of Granada. The two sites, differing in altitude, contrasted markedly in temperature, and water availability varied notably among years at the high altitude site, Montes (Table 1). There was no major variation in rainfall between the 1990 and the 1991 growing seasons at Chimeneas, but substantial variation in overall performance resulted from the differences in sowing date between years which, jointly with the differences in average temperatures, brought about a much shorter growing season in 1990 than in 1991 (Table 1). Consequently, the range of yields (averaged across cultivars for each environment) in which the performance of the two- and six-rowed cultivars were compared was 2.26–5.47 Mg ha^{-1}.

3.1. Yield stability

Analyses of variance for grain yield and its components are shown in Table 2. Within main effects, environment had the strongest influence on grain yield, grains per m^2 and spikes per m^2 while genotypic effects were more pronounced for grain per spike and grain weight. The observed variability for all characters attributed to genotype was broken down into differences between row type (two- and six-row) and within each row type. In all cases, this variability was attributed to differences between two- and six-rowed barley cultivars (Table 2).

The occurrence of genotype by environment interaction was revealed for all the traits studied (Table 2). However, lack of such interaction was observed within each row type, while differences between two- and six-rowed barleys for grain yield, grains per spike and grain weight changed from one environment to another. Thus, the genotype-by-environment interaction in our study was caused more by overall differences between cultivars when considered in bulk than when they were grouped in row class.

Table 2
Partition of sum of squares and mean squares from the combined analyses of variance for grain yield and yield components for two- and six-rowed types of barley grown in five environments for 3 years

Source of variation	d.f.	Grain yield		Grains per m^2		Spikes per m^2		Grains per spike		Grain weight	
		SS	MS	SS ($\times 10^8$)	MS ($\times 10^7$)	SS ($\times 10^5$)	MS ($\times 10^4$)	SS	MS	SS	MS
Env (E)	4	166.82	41.71***	19.32	48.29***	11.34	28.34***	2462.18	615.55***	925.98	231.50***
Rep/E	15	8.77	0.58***	1.33	0.89**	0.37	0.25	279.94	18.66	156.24	10.42
Genotypes (G)	5	21.19	4.24***	1.14	2.28***	11.88	23.77***	3936.79	787.36***	1936.26	387.25***
Tow-row barleys (T)	2	3.95	1.97	0.31	1.57	2.86	14.32	270.52	135.26	83.28	41.64
Six-row barleys (S)	2	0.71	0.36	0.68	3.41	0.69	3.43	5.17	2.59	250.60	125.30
T vs. S	1	16.53	16.53***	0.15	0.15	8.33	8.33***	3661.10	3661.10***	1602.38	1602.38***
G × E	20	33.80	1.69***	5.33	2.67***	4.15	2.07***	1426.06	71.30***	605.11	30.26***
T × E	8	9.98	1.25	1.80	2.25	1.12	1.40	299.54	37.44	251.12	31.39
S × E	8	6.96	0.87	1.34	1.68	0.57	0.72	770.60	96.44	64.91	8.11
(T vs. S) × E	4	16.86	4.22***	2.19	0.55	2.46	0.62	355.92	88.98***	289.08	72.27***
Pooled error	75	13.75	0.18	2.60	0.35	2.18	0.29	1566.50	20.89	561.96	7.49

There was a noticeable difference between two- and six-rowed barley cultivars in their responsiveness to more favourable environmental conditions (Fig. 2). The coefficients of regression of yield, averaged for all cultivars within each group, and environmental index (mean site grain yield) was 1.27 and 0.73 for the two- and six-rowed cultivars, respectively. This level of interaction implied that the trend, and the actual yields, crossed over (Fig. 2). Thus, the six-rowed cultivar, on the average, out-yielded the two-rowed barleys in the lowest-yielding environment.

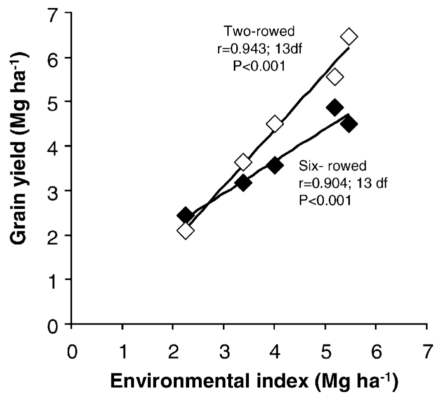

Fig. 2. Relationship between yield of the two- (open symbols) or six-rowed barley (closed symbols), averaged across cultivars within each type, and the environmental index (calculated as the average of yield of all cultivars grown in each experiment). Lines were fitted by linear regression before averaging the data of cultivars for each spike type ($n = 15$).

Individual cultivars, within each group, also differed significantly in their responsiveness (Table 3). However, each of the three two-rowed cultivars included in the present study were more responsive than each of the three six-rowed cultivars, which exhibited perceptibly less variable and hence more stable yields (Table 3). Furthermore, the newer the cultivar within each group, according to their respective dates of inscription in the National List (data not presented), the more responsive.

The crossover of the linear trends was even more marked when comparing the extreme cultivars than for the average within each group. Melusine, the two-rowed cultivar with the highest yield in the best environmental condition of this study, exhibited also the lowest yield in the poorest environment, while the opposite was true for H. Grignon, one of the six-rowed cultivars (Table 3).

In fact, there was a clear positive trend between the coefficient of regression (of the relationship between yield of individual cultivars and environmental index) and the maximum yield recorded for each cultivar in the study (Fig. 3). The trend represented not only yielding differences between cultivars of different spike morphology, but also among cultivars of each group, thus showing the effect of accumulation in the newer cultivars of genes that positively affected grain

Table 3
Parameters of the regression (coefficients of regression, CR, with its standard error, S.E., and correlation, *r*) for the relationship between yield of individual cultivars in each environment and average yield of all cultivars in these environments (environmental index) for two- (Melusine, Finesse, Alpha) and six-rowed cultivars (Plaisant, Barberousse, H. Grignon) grown at two sites and in three seasons in southern Spain

Cultivar	CR[a]	S.E.	*r*	Observed yields (Mg ha^{-1})		
				Minimum	Maximum	Mean
Melusine	1.52	±0.23	0.968	1.470	6.787	3.876
Finesse	1.24	±0.13	0.984	2.128	6.279	4.468
Alpha	1.06	±0.20	0.949	2.664	6.290	4.354
Plaisant	0.93	±0.24	0.910	2.271	5.359	3.666
Barberousse	*0.66*	±0.12	0.956	2.526	4.879	3.632
H. Grignon	*0.59*	±0.13	0.939	2.513	4.743	3.474

[a] Values in italics are significantly different from unity at $P < 0.05$. Cultivars with values in italics are considered stables.

yield or, in other words, the temporal effect of plant breeding on yield increase.

3.2. Yield components

There were two sources of yield differences: (i) between yields of two- and six-rowed cultivars and (ii) responses to environmental changes within each group. To fulfil the objective of the study, we focused on the causes of the differential yields between environments to understand the reasons for differential yield stability between barleys of different spike morphology. However, the differences between yields of two- and six-rowed cultivars in particular environments were largely consistent with the literature: two-rowed cultivars had far more spikes per m^2 than six-rowed cultivars, while the latter consistently had more grains per spike, with a lesser average grain weight. Averaging across cultivars of the same spike morphology, the ranges exhibited by two-rowed barleys were 374–743 spikes per m^2, 18.6–23.5 grains per spike and 29.9–41.1 mg per grain; while the corresponding ranges for six-rowed cultivars were 338–515 spikes per m^2, 26.1–37.6 grains per spike and 25.8–33.4 mg per grain.

Yield differences among environments, for both groups of cultivars, were more associated with changes in number of grains per unit of land area than with differences in individual grain weight. The correlation coefficients between yield and number of grains per m^2 (Fig. 4a) were higher than the corresponding coefficients between yield and individual grain weight (0.83^{***} and 0.11 for the two- and six-rowed cultivars, respectively), although this correlation was statistically significant for the two-rowed barleys only.

Differences in number of grains per m^2 were, in turn, related more to the number of spikes per unit land area (Fig. 4b) than to differences in number of grains per spike within each cultivar. The constitutive difference between two- and six-rowed cultivars in the number of grains per spike is evident in that the data points corresponding to six-rowed cultivars are always higher than those corresponding to two-rowed barleys (Fig. 4b). The correlation coefficients for the relationship between number of grains per m^2 and number of grains per spike were 0.47 and 0.66^{**} for the two- and six-rowed cultivars, respectively.

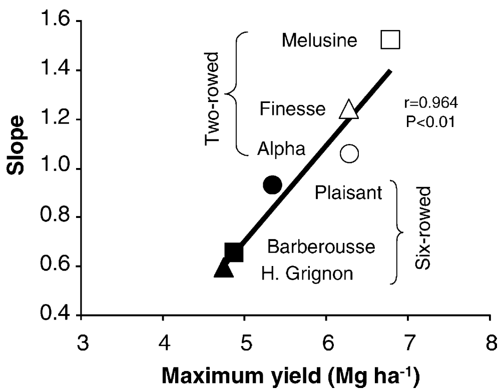

Fig. 3. Relationship between the slope of the Finlay and Wilkinson (1963) regressions (Table 2) and the maximum yield recorded in the study for each cultivar. Cultivars are identified and the two- and six-rowed forms are represented with open and closed symbols, respectively. The line was fitted by linear regression.

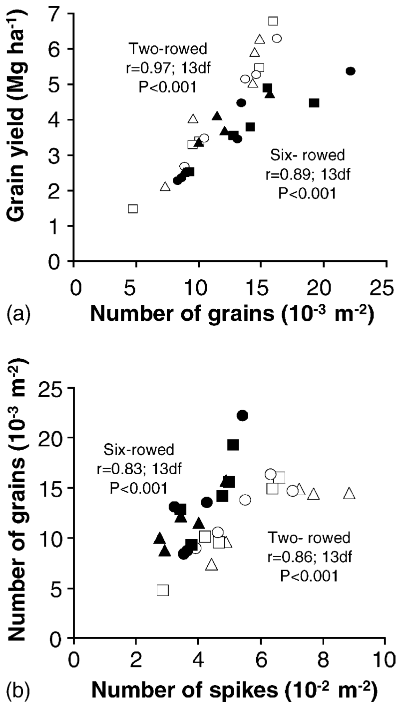

Fig. 4. Relationship between yield and the number of grains per unit of land area (a), and between the latter and the number of spikes per unit of land area (b). Symbols stand for the two- (open symbols) or six-rowed (closed symbols) cultivars (for symbols of each cultivar please see inset in Fig. 3). Lines were fitted by linear regression.

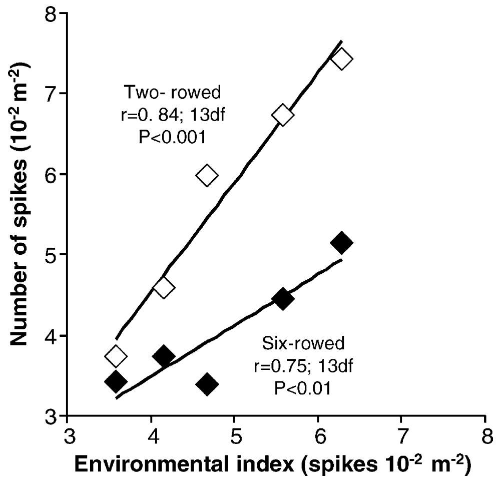

Fig. 5. Relationship between the number of spikes per unit of land area of the two- (open symbols) or six-rowed barley (closed symbols), averaged across cultivars within each type, and the environmental index (calculated as the average of spikes per m^2 of all cultivars grown in each experiment). Lines were fitted by linear regression before averaging the data of cultivars for each spike type ($n = 15$).

The response of the number of spikes per m^2 to the environmental index reflected a trend similar to that of yield (Fig. 5). In fact, yield was very closely associated with the number of spikes per m^2 ($r = 0.85^{***}$ for two-rowed cultivars and $r = 0.77^{***}$ for six-rowed cultivars).

3.3. Developmental differences

Although differences in time to heading are critical for better adaptation in Mediterranean environments, cultivars included in this study were known to be well adapted to the region, and consequently no major

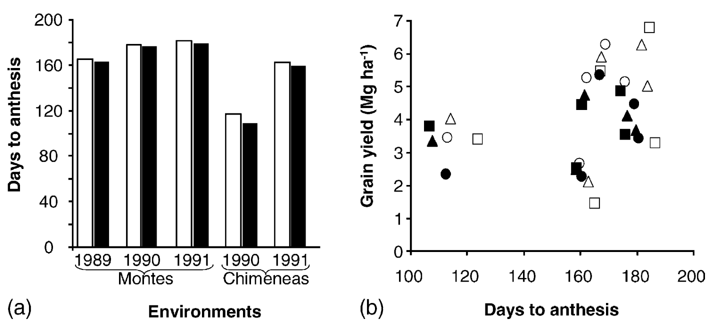

Fig. 6. Duration of the period from sowing to anthesis in each of the five experiments, averaged across cultivars of the same spike type (a), and relationship between grain yield of each cultivar in each environment and duration (b). Open and closed symbols or bars stand for two- and six-rowed cultivars, respectively (for symbols of each cultivar in (b), please see inset in Fig. 2).

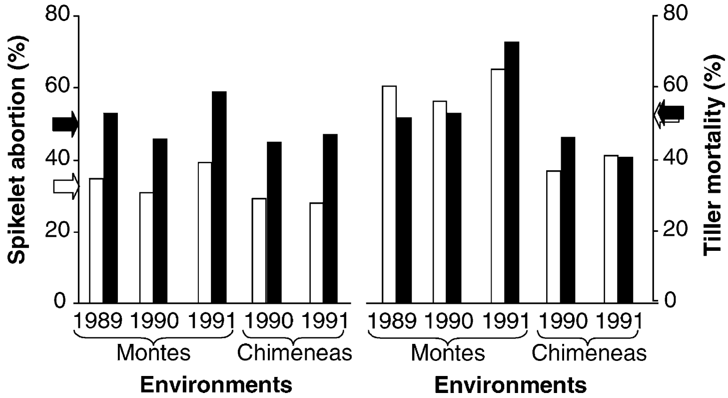

Fig. 7. Proportion of spikelet abortion on the main-shoot spikes (left half) and tiller mortality (right half) in each of the five experiments, averaged for cultivars of two- (open bars) and six-rowed spikes (closed bars). The arrows on the ordinates indicate the overall average of spikelet abortion and tiller mortality reached in the whole study for two- (open arrows) and six-rowed barley (closed arrows). In both cases the proportion was estimated as $(SN_{max} - SN_{final})SN_{max}^{-1}$ and $(TN_{max} - TN_{final})TN_{max}^{-1}$, where SN_{max}, SN_{final}, TN_{max} and TN_{final} stand for maximum number of spikelet primordia (at awn initiation), final number of fertile spikelets per spike, maximum number of tillers (at the end of tillering) and number of spike-bearing tillers at maturity.

differences were observed in time to heading between two- and six-rowed cultivars (Fig. 6a). In fact, differences among growing environments were not related to the length of the cycle either ($r = 0.37$ for two-rowed cultivars and $r = 0.34$ for six-rowed cultivars) (Fig. 6b). Therefore, characteristics making two- and six-rowed barleys respond differently to changing environments, in this set of adapted winter cultivars, it must be related to the generation or survival processes occurring during the pre-flowering development of the crop.

There was a large difference between two- and six-rowed cultivars in spikelet abortion (Fig. 7, left), but the proportion of abortion was fairly stable across environments. Consequently, this trait did not account for the differences in yield stability between cultivars of two- and six-rowed spikes.

On the other hand, tiller mortality was quite variable among environments (Fig. 7, right). However, the differential tiller mortality among environments could not explain the differences in yield stability between two- and six-rowed cultivars. Firstly, there were no clear differences among these two groups of cultivars in tiller mortality. Secondly, the relationship between yield and tiller mortality was non-significant ($r = 0.31$) for the six-rowed cultivars, although it was significant for the two-rowed barleys ($r = 0.68^{**}$). Thirdly, and most importantly, these relationships were positive (that is, the trend was: the higher the mortality, the higher the yield), implying that the factor responsible for yield responsiveness capacity of two-rowed cultivars was also simultaneously, though not strongly, producing the conditions for higher tiller mortality.

Therefore, the major constitutive difference between cultivars of two- and six-rowed spikes, explaining differences in yield stability/responsiveness in this study, was necessarily related to early developmental features. Six-rowed cultivars, as expected, produced almost threefold more spikelets per spike than the two-rowed cultivars (Fig. 8, bottom panels). The rate of spikelet initiation strongly differed between these cultivars immediately after triple mound when the development of two- and six-rowed varieties begins to differ (Bonnett, 1966), and the development of the lateral spikelets markedly slows down in two-rowed barleys (Fig. 8, bottom panels). Consequently, while two-rowed cultivars, averaged across genotypes and environments, initiated ca. 40 spikelet primordia in the main-shoot apex at awn initiation, the six-rowed barleys had by then initiated ca. 107 spikelet primordia.

The counterpart of this was evidenced with tillering (Fig. 8, top panels), which occurred to a large degree simultaneously with spikelet initiation in this study. Two-rowed cultivars consistently tillered at a higher

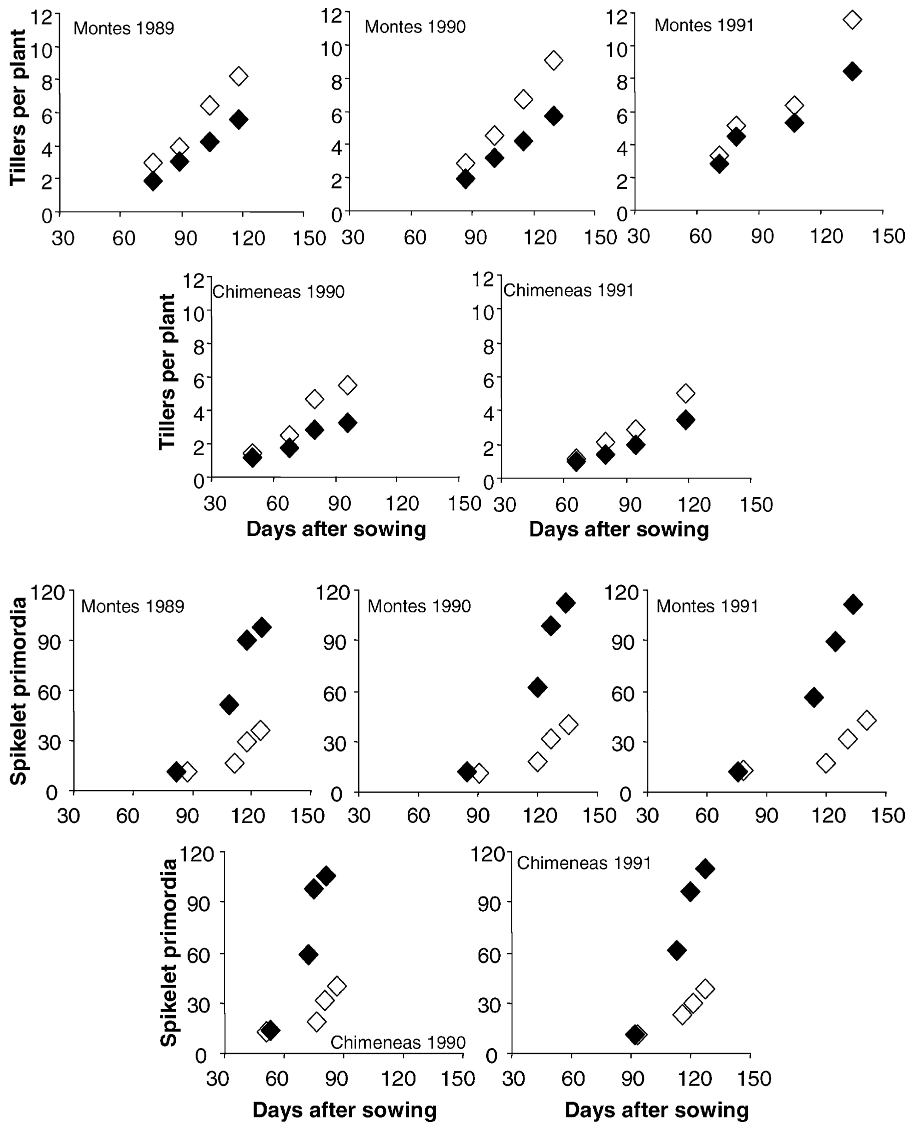

Fig. 8. Number of spikelet primordia on the main-shoot apex (bottom panels) and tillers per plant (top panels), counted at different times from double ridge to awn initiation (when the maximum number of spikelet primordia are found) averaged for cultivars of two- (open symbols) and six-rowed spikes (closed symbols) for each of the five field environments (inset each panel) in which the study was conducted.

rate than did the six-rowed barleys (averaged across environments and cultivars, the rates were 0.11 and 0.07 tillers per day), though the magnitude of the difference in tillering was more affected by the environment than was the difference in spikelet initiation (Fig. 8). The maximum number of tillers varied accordingly between cultivars of these groups, the values were ca. 8 and 5 for two- and six-rowed barleys, respectively.

4. Discussion

The yields across the range of environments explored were somewhat higher than those normally found within the range of other experiments in Andalusia. This was apparently due to the better growth conditions of relatively lower temperatures in the Province of Granada compared with those of western Andalusia, and that winter cultivars were grown. The range was sufficient to compare the behaviour of these two groups of cultivars under mild to moderate stress conditions (Slafer and Araus, 1998).

Yield stability was markedly different in two- and six-rowed cultivars. Even though a large degree of variation was found between cultivars of each group, the yield of all two-rowed cultivars was more responsive to environmental changes than that of the six-rowed cultivars, which consistently showed more stable behaviour. Although there are no reports available in the literature of this differential behaviour under Mediterranean conditions (regardless of differences in general adaptation given by timing of anthesis, making the crop match its development with seasonal rainfall pattern; see e.g. González et al., 1999; Villegas et al., 2000), the results were far from surprising. In fact, they were in line with the hypothesised behaviour.

Two-rowed cultivars, with intrinsically higher ability to tiller, consistently produced a higher number of tillers than did the six-rowed cultivars and then generated the crop structure capable of using resources that could become available under good growing conditions. In these circumstances, the amount of resources used to produce ultimately unproductive tillers does not challenge the availability of resources for later growth of the canopy. It actually improves the ability of the canopy to capture available resources (probably due to better radiation interception and soil exploration) during critical stages of immediate pre-anthesis development, when the number of grains, which will later become the main yield component, are being determined (Miralles et al., 2000). However, the opposite occurs under poorer environmental conditions. Under such conditions, the inherent higher tillering ability of two-rowed cultivars resulted in use of scarce resources to produce a canopy structure with limited additional resources to capture. Under these circumstances the constitutive capacity of six-rowed cultivars of reduced tillering rate, even under favourable growing conditions, compared with that of two-rowed cultivars becomes a useful trait to save resources that may be more efficiently used during the critical phases of yield determination.

Acknowledgements

We thank Grupo Cruzcampo S.A. (Seville, Spain) for funding the study, Dr. Felipe Roca de Togores for his contribution to the choice of cultivars used in the study and useful advice and support during the experiments, and Dr. J. Marinetto, J.M. Asensio and A. Boujenna for technical assistance. GAS acknowledges the support from the University of Granada (Grupo de Investigación AGR0123 and Plan Propio de Investigación) and from the Faculty of Agronomy, University of Buenos Aires, while participating in this study. Contribution of Grupo Andaluz de Investigación AGR0123. We also wish to thank Dr. Y. Rharrabti for help with statistical analysis and Dr. Nesbitt for correcting the English version of the text.

References

Abeledo, L.G., Calderini, D.F., Slafer, G.A., 2002. Physiological changes associated with breeding progress. In: Slafer, G.A., Molina-Cano, J.L., Savin, R., Araus, J.L., Romagosa, I. (Eds.), Barley Science: Recent Advances from Molecular Biology to Agronomy of Yield and Quality. Food Product Press, New York, pp. 361–380.

Bonnett, O.I., 1966. Inflorescences of maize, wheat, rye, barley and oats: their initiation and development. Illinois Agriculture Experimental Station, Urbana-Champaign, 105 pp.

FAO, 1977. Guías para la clasificación de perfiles de suelos. FAO, Rome, 73 pp.

Feil, B., 1992. Breeding progress in small grain cereals. A comparison of old and modern cultivars. Plant Breed. 108, 1–11.

Finlay, K.W., Wilkinson, G.N., 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14, 342–354.

García del Moral, M.B., García del Moral, L.F., 1995. Tiller production and survival in relation to yield in winter and spring barley. Field Crops Res. 44, 85–93.

García del Moral, L.F., Ramos, J.M., Recalde, L., 1984. Tillering dynamics of winter barley as influenced by cultivar and nitrogen fertilizer: a field study. Crop Sci. 24, 179–181.

García del Moral, M.B., Jimenez Tejada, M.P., García del Moral, L.F., Ramos, J.M., Roca de Togores, F., Molina-Cano, J.L., 1991. Apex and ear development in relation to the number of grains on the main-stem ears in spring barley (*Hordeum distichon*). J. Agric. Sci. 117, 39–45.

García del Moral, L., Miralles, D.J., Slafer, G.A., 2002. Phasic and foliar development. In: Slafer, G.A., Molina-Cano, J.L., Savin, R., Araus, J.L., Romagosa, I. (Eds.), Barley Science: Recent Advances from Molecular Biology to Agronomy of Yield and Quality. Food Product Press, New York, pp. 243–267.

González, A., Martín, I., Ayerbe, L., 1999. Barley yield in water stress conditions. The influence of precocity, osmotic adjustment and stomatal conductance. Field Crops Res. 62, 23–34.

Hadjichristodoulou, A., 1985. The stability of number of tillers of barley varieties and its relation with consistency of performance under semi-arid conditions. Euphytica 34, 641–649.

Jedel, P.E., Helm, J.H., 1995. Agronomic response to seeding rate of 2-rowed and 6-rowed barley cultivars in Central Alberta. Can. J. Plant Sci. 75, 315–320.

Kernich, G.C., Slafer, G.A., Halloran, G.M., 1995. Barley development as affected by rate of change of photoperiod. J. Agric. Sci. 124, 379–388.

Kirby, E.J.M., Appleyard, M., 1987. Cereal Development Guide. NAC Cereal Unit, Stoneleight, UK.

Kirby, E.J.M., Riggs, T.J., 1978. Developmental consequences of two-row and six-row ear type in spring barley. II. Shoot apex leaf and tiller development. J. Agric. Sci. 91, 207–216.

Le Gouis, J., 1992. A comparison between two- and six-row winter barley genotypes for above-ground dry matter production and distribution. Agronomie 12, 163–171.

Le Gouis, J., Delebarre, O., Beghin, D., Heumez, E., Pluchard, P., 1999. Nitrogen uptake and utilisation efficiency of two-row and six-row winter barley cultivars grown at two N levels. Eur. J. Agron. 10, 73–79.

Maidl, F.X., Panse, A., Dennert, J., Ruser, R., Fischbeck, G., 1996. Effect of varied rates and timing on yield, N uptake and fertilizer N use efficiency of a six-row and a two-row winter barley. Eur. J. Agron. 5, 247–257.

Miralles, D.J., Richards, R.A., Slafer, G.A., 2000. Duration of stem elongation period influence the number of fertile florets in wheat and barley. Austr. J. Plant Physiol. 27, 931–940.

Ramos, J.M., García del Moral, L.F., Recalde, L., 1982. The influence of pre- and post-anthesis periods on yields of winter barley varieties in southern Spain. J. Agric. Sci. 99, 521–523.

Ramos, J.M., De la Morena, I., García del Moral, L.F., 1995. Barley response to nitrogen timing in a Mediterranean environment. J. Agric. Sci. 125, 175–182.

Richards, R.A., 1996. Defining selection criteria to improve yield under drought. Plant Growth Reg. 20, 157–166.

Slafer, G.A., Araus, J.L., 1998. Improving wheat responses to abiotic stresses. In: Slinkard, A.E. (Ed.), Proceedings of the Ninth International Wheat Genetics Symposium, vol. 1. University of Saskatchewan, Extension Press, Saskatoon, pp. 201–213.

Slafer, G.A., Kernich, G.C., 1996. Have changes in yield (1900–1992) been accompanied by a decreased yield stability in Australian cereal production? Aust. J. Agric. Res. 47, 323–334.

Slafer, G.A., Miralles, D.J., 1992. Green area duration during the grain filling period of wheat as affected by sowing date, temperature and sink strength. J. Agron. Crop Sci. 168, 191–200.

Slafer, G.A., Savin, R., 1994. Source–sink relationship and grain mass at different positions within the spike in wheat. Field Crops Res. 37, 39–49.

Smith, D.L., Dijak, M., Bulman, P., Ma, B.L., Hamel, C., 1999. Barley: physiology of yield. In: Smith, D.L., Hamel, C. (Eds.), Crop Yield: Physiology and Processes. Springer, Berlin, pp. 67–107.

Steel, R.G.D., Torrie, J.H., 1982. Principles and Procedures of Statistics: A Biometrical Approach, 2nd ed. McGraw-Hill Int. Book Co., Tokyo, Japan.

Villegas, D., Aparicio, N., Nachit, M.M., Araus, J.L., Royo, C., 2000. Photosynthetic and developmental traits associated with genotypic differences in durum wheat yield across the Mediterranean basin. Aust. J. Agric. Res. 51, 891–901.

Wych, R.D., Simmons, S.R., Warner, R.L., Kirby, E.J.M., 1985. Physiology and development. In: Rasmusson, D.C. (Ed.), Barley. ASA–CSSA–SSSA Publishers, Madison, pp. 103–125.

Yates, F., Cochran, W.G., 1938. The analysis of groups of experiments. J. Agric. Sci. 28, 556–580.