Response to F3 bi-directional selection for above ground biomass and its effect on grain yield in F4 to F7-generation of three barley (Hordeum vulgare L.) cross-populations

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Abstract:

Early selection based on above ground biomass was made in the F3 of three barley (Hordeum vulgare L.) populations, and the direct response in biomass and the correlated response in grain yield were assessed in the F4 to F7 generations at the experimental site of the Agricultural Research Station of Sétif, in the High Plateaux of Eastern Algeria. The results indicated that neither the direct response (biomass) nor correlated response (grain yield) were significant because strong genotype x environment interactions (GEI) affected both characters. GEI originated from the traits contributing to biomass, which changed, qualitatively and quantitatively, from one environment to another, making selection for biomass to improve grain yield and yield stability, less efficient. Determination of earliness class which fits best the most frequent environment, followed by selection, within this class type, for above ground biomass seems to be an alternative to reduce the effect of GEI on genetic progress.

Key words: : Barley, Mediterranean climate, Yield correlated response, Genotype x environment interaction.

ملخص

أنجز انتقاء مبني على كمية المادة الخضراء السطحية على ثلاثة أصناف من الشعير من الجيل الثالث. وبعد بلوغ تلك الأصناف الجيل السابع، درست عليها العلاقة بين المادة الخضراء والمحصول من الحبوب. ووجد أن العلاقة ضعيفة، مما يؤكد التأثير الحاسم للبيئة.

الكلمات المفتاحية : شعير، المناخ المتوسطي، المحصول من الحبوب، البيئة.

Résumé

une selection a été effectuée sur la base de la biomasse superficielle produite sur trois variétés d'orge de la génetation F3. Lorsque, ces variétés atteignent le stade F7, la corrélation entre biomasse superficielle et rendement en grain reste faible, ce qui confirme le caractère décisif du facteur environnement.

Mots-clé : : Orge, climat méditerranéen, rendement en grain, environnement.

Introduction

In small grain cereals, selection in early generations such as F2 and F3 is performed on heterogeneous populations, and is usually based on traits which are highly heritable like plant height, diseases reaction, and earliness. At this early stage, selection for yield is of interest but is practiced less frequently because this trait showed generally low heritability (Borghi et al. 1998). Under stress, grain yield variability is usually characterized by a larger environmental component, and early selection for this variable is inefficient (Ceccarelli, 1989; Bouzerzour and Dekhili, 1995). There is an increasing interest in selecting for traits other than yield to improve crop production under harsh and variable environments (Ceccarelli et al. 1991). The main objective of selection in these areas is greater yield stability since high grain yield levels are usually rarely achieved because of high stress frequency (Avecedo et al. 1991).

Among the traits associated with grain yield under spaced planting as well as under normal seeding, harvest index and above ground biomass have been often tentatively used as selection criteria to improve grain yield level and yield stability (Donald and Hamblin, 1976, Mc Vetty and Evans, 1980, Sharma, 1993, Borghi et al. 1998). Harvest index has been more widely used than above ground biomass as selection criterion, mainly in environments where above ground biomass was less subjected to variation (see Hay, 1995 for a review). Under stress conditions such as those experienced by crops grown under Mediterranean-type environments, harvest index has been found to be of limited value as indicator of the yield potential of a selected line (Siddique et al. 1989; Bouzerzour et al. 1998; Borghi et al. 1998). On the contrary, above ground biomass showed a constant relationship with grain yield under most environmental growth conditions (Slaffer and Andrade, 1990, Boukerou and Rasmusson, 1990, Sharma and Smith, 1993, Bouzerzour et al. 1998), and appears as a valuable selection criterion to obtain stable and higher yield. Early selection based on either traits is justified only if there is a high degree of similitude between selected individuals in early generations and their derived relatives in later generations (Whan et al. 1981; Borghi et al. 1998).

The objectives of this study were to evaluate the response of bi-directional selection for above ground biomass in F3 and to determine the correlated response in grain yield in the F4 to F7 generations of three barley (Hordeum vulgare L.) cross-population.

Matériel et méthodes

Experimental details and measurements

Hand hybridization was done at the Agricultural Research Station of Setif (1080 m altitude, 36°9'N and 5°21'E, Algeria) during the 1992/93 cropping season to produce the crosses Alpha/Tichedrett, Saïda/Jaïdor and Lignée686/Rebelle. Tichedrett and Saïda are 6-row barley originating from Algerian landraces; Jaïdor, Rebelle, Lignée 686 and Alpha are modern cultivars were received kindly from ENSA-INRA Montpelier (France). Alpha is a 2-row barley. Local varieties were relatively more adapted but French lines exhibited an acceptable yield potential. The crosses made were

The F1-seed was planted during the 1992/93 season to produce F2-seed which was sown in 1993/94 in a randomized complete block design. Plot size was one single row in F1 and 4 rows in the F2. One single 3 m long row was sown with 15 seeds, with 15 cm as spacing between seeds and 30 cm between adjacent rows. 120 plants were randomly selected from the F2 generation and the corresponding F3 families were evaluated in a randomized complete blocks design with 3 replicates, in the following cropping season. Elementary plot was five rows 3 m long, seeded at a rate of 250 kernels m-2. After harvesting, the 120 F3 lines were sorted according to their above ground biomass yield. The 10 extreme lines were selected and compared along with their respective parents in an F4 to F7-trial per cross-population. Measured variables were above ground biomass, number of days to heading, and grain yield on plot basis. The thousand-kernel weight was derived from the number of seeds produced per plot and the number of kernels per head was calculated from plot yield, 1000-kernel weight and spikes number. Yield components determination was made from a harvested area of 2 rows x 1 m long per replicate.

Data analysis

Data obtained from the different generations were subjected to a classical analysis of variance to assess the genotypic effect per cross-population, according to model (1) for the F3 generation and model (2) for the selected material grown in the F3 to F7 generations

Yijk = mm + Gi + Bk + eik (1)

and Yijk = mm + E j + Gi + GxEij + Bk + eijk (2)

where mm is the overall mean, Ej is the environment effect, Gi is the genotypic effect, Bk is the block effect, GxEij is the interaction genotype x Year (with year confounded with generations) and eijk is the error term (Steel and Torrie, 1980).

Broad sense heritability in F3 generation and over generations (F3 to F7) was calculated according to the variance components method (Comstock and Moll, 1963). The appropriate genetic, genotypic x environment, error and phenotypic variance components were estimated from the expected mean squares of the F3-analysis of variance and the combined analysis of variance of the 5 generations (F3 to F7). Selection differential (SD) in the F3-generation, response to selection (RS) and realized heritability (h_r) in the F4 to F7 generations were estimated according to Sharma and Smith (1986):

SD = HF3 - LF3

RS = HFn -LFn

h_r = 100 [(HFn+1 -LFn+1)/(HF3- LF3)]

where H and L stand for high and low group of F3-selected lines respectively. Correlated response of grain yield to selection based on above ground biomass was also estimated.

Phenotypic correlation coefficients within cross population were calculated between above ground biomass and the other traits for each generation. Since correlation coefficients measure mutual relationships without presumption of causation, path coefficient analysis was utilized to specify the plausible causes and measured their relative importance as independent variables according to the method outlined by Li (1975). In the path model retained, biomass was assumed to be the product of direct and indirect effects of 5 characters namely number of spikes per unit area, number of kernels per spike, thousand kernel weight, plant height and number of days to heading. Inter-generation correlation coefficients were also determined for above ground biomass.

Results and discussion

Genetic variability in the F3-generation for above ground biomass

Analysis of the variance of the F3-data showed highly significant genotypic effect, indicating that there was enough genetic variability within each of the three cross populations allowing selection to be practiced (Table 1).

Table 1 : Mean squares of the analysis of variance of above ground biomass of F3 lines.

		Crosses			
Source of variation	**df**	**I**	**II**	**III**	**EMS**
Genotype	21	90441.0**	85152.2**	125801.7**	ss_e + rss_g
Error	336	8505.6	9334.2	7986.4	ss_e

ns, *,** non significant effect and significant at 5 and 1% respectively; EMS= expected mean squares; ss_e = error variance component, ss_g = genotypic variance component and r = number of replications.

The crossed parents diverged significantly for above ground biomass and the difference was large mainly between the parents of cross I and II and to a lesser extent between those of cross III. The within F3 variability included transgressive lines with a superior biomass yield than the best parent and lines with lower biomass yield than the inferior parent. On average, cross I (between Alpha, a 2-row barley, and the 6-row cultivar Tichedrett) showed the best above ground biomass yield (Table 2). The bi-directional selection differential was significant and varied, as percent of the F3-generation average, from 31.0%, for cross II to 38.1 % for cross III (Table 2). Broad sense heritability estimates, derived from the analysis of variance, were above 80%. These high values associated with a significant selection differential predicted a sizeable genetic gain for above ground biomass in the following generations.

Table 2 : Parents and F2- derived F3 lines above ground biomass means and broad sense heritability.

	Crosses		
Generations	I	II	III
P1	550.0	990.2	945.5
P2	1075.2	565.5	835.3
Maximum (F3)	1248.3	1046.7	1095.2
Minimum (F3)	490.3	450.5	535.0
Average (F3)	967.7	888.3	945.3
H	1032.6	931.9	945.5
L	702.8	656.5	585.3
DS	329.8**	275.4**	360.2**
DS (%)	34.08	31.00	38.10
h_bs	82.80	89.04	93.65

** =selection differential (DS) significant at 1% level, DS (%) = selection differential as % of the generation mean, P1 = Alpha, Saida and Lignée , P2 = Tichedrett, Jaidor and Rebelle for cross I, II and III respectively; H and L are mean values for the High and Low selected group of 10 lines, h_bs = broad sense heritability.

Response of biomass and correlated response of grain yield in the F4 to F7

The combined analysis of variance, over generations (F3 to F7) of the selected lines showed significant generation (confounded with year) and genotype x generation effects. Genotype effect, tested against the genotype x year mean square, was non significant (Table 3). Mean values of above ground biomass and grain yield of the selected high group of lines for the different generations are given in the table 4 along with the response and correlated response to F3-selection, and the realized heritability.

Table 3 : Mean squares of the combined analysis of variance of biomass and grain yield measured in the F3 to F7 generations.

		Crosses			
Source	**df**	**I**	**II**	**III**	**EMS**
			Above ground biomass		
Environment (E)	4	5257820.0**	3653025.5**	2460591.7**	s_e+ rs_GxE +rGs_E
Genotype (G)	21	102678.2ns	47081.2ns	119450.9ns	s_e+ rs_GxE +rEs_G
G x E	84	119093.0**	70918.3**	82916.4**	s_e+ rs_GxE
Error	218	3561.70	5726.00	4621.90	s_e
			Grain yield		
Environment (E)	4	1425826.6**	991624.2**	769066.1**	
Genotype (G)	21	12529.7ns	10958.8ns	27080.3ns	
G x E	84	20832.2**	16043.0**	21550.4**	
Error	218	613.6	1222.8	1202.7	

ns, *,** non significant effect and significant at 5 and 1% respectively; EMS= expected mean squares

Table 4 : Above ground biomass and grain yield means of the F3- derived F4 to F7 selected high group of lines, response to selection (RS), realized heritability (h_r) and correlated response (CR) for the three cross-population.

		Crosses							
Gen.	lines	I	II	III	Gen.	lines	I	II	III
				Above ground biomass					
EF4	H	961.7	881.7	656	F6	H	1008	950.8	992.3
	RS	-37.1ns	-51.6ns	-12.3ns		RS	-140ns	-128.2ns	34.1ns
	h_r	0.0	0.0	0.0		h_r	0.0	0.0	0.0
F5	H	508.1	612.8	525.8	F7	H	495.8	508.2	673.3
	RS	8.8ns	-17.6ns	37.1ns		RS	5.0ns	8.7ns	-33.7ns
	h_r	0.0	0.0	0.0		h_r	0.0	0.0	0.0
				Grain yield					
EF4	H	458.1	447.1	282.3	F6	H	358.4	339.9	432.5
	CR	44.8ns	39.7ns	-15.3ns		CR	-12.0ns	-4.8ns	52.3ns
F5	H	227.8	320.0	237.9	F7	H	131.9	138.3	186.5
	CR	33.1ns	43.5ns	17.9ns		CR	29.5ns	9.9ns	-2.9ns

P1 = Alpha, Saida and Lignee , P2 = Tichedrett, Jaidor and Rebelle for cross I, II and III respectively; H and L are mean values for the High and Low selected group of 10 lines; RS = response to F3-selection, tested against the biomass GxE mean square of the combined ANOVA; h_ r= realized heritability (%), values are shown only when the response to selection was statistically significant, otherwise h_r was set equal to zero. CR = correlated response to F3-selection, tested against grain yield GxE mean square of the combined ANOVA

The response to selection, tested against the mean square of the genotype x environment interaction (GEI), was non significant in the different generations and crosses (Table 4). The correlated response of grain yield was also non significant. Though non significant, negative sign responses and correlated responses were noted. These results indicated that early selection for above ground biomass was not effective in increasing directly biomass and indirectly grain yield, even though the phenotypic correlation coefficients per generation between biomass and grain yield were highly significant and varied from 0.667 to 0.970. The lack of efficiency was due to GEI occurring in later generations. The observed variation in biomass values arose from year to year climatic fluctuations characterizing semi-arid areas in general, and from the differential genotypic sensitivity of the selected material to these environmental changes.

The average ranking over generations of the high F3 lines selected for high biomass indicated however that 9 lines in the cross I, 6 in the cross II and 8 lines out of 10 in the cross III maintained their rank among the ten highest entries. Three lines from cross I (number 1, 5 and 7) and three from cross II (number 1, 2 and 8) remained among the ten best yielding lines even under the worst growing conditions (Table 5). The worst rank of most of the F3-selected lines confirmed the high GEI, which is experienced by the selected material under the growth conditions of the experimental site.

This is also corroborated by the intergeneration correlation coefficients which were generally non significant, except in cross I, where above ground biomass measured in the F3 generation was positively and significantly correlated with biomass measured in the F4 (r= 0.445, P<5%) and in the F7 generations (r=0.593, P<1%), and in cross III, where above ground biomass measured in the F4 (r=0.549, P<5%) and the F5 (r=0.444, P<5%) generations was positively and significantly correlated with that measured in the F6 generation. Though non significant, negative intergeneration correlation coefficients were observed.

The variance components derived from the combined analysis of variance indicated that the genetic component (s_G) was nil for cross I and II and the GEI component in cross III was 10 times larger than the genetic component, indicating that intergeneration biomass variability between the selected lines was mostly environmental of origin. So the presence of GEI affected the efficiency of biomass utilized as early selection criterion. As GEI originated from year to year variation in the contribution of different traits to biomass, we investigated the year to year relationships between biomass and the other traits in cross I only, assuming that this applies to some extent to the other crosses.

Table 5 : Average (A) and worst (W) rank of the 10 high F3-selected lines grown in the F4 to F7 generations.

	Crosses					
	I		II		III	
lines	A	W	A	W	A	W
1	7.2	10 (F6)	5.3	9.5 (F4)	7.7	13 (F6)
2	9.9	12 (F6)	5.2	9 (F7)	9.3	15 (F4)
3	12.0	19 (F6)	9.3	20 (F4)	8.6	14 (F7)
4	7.0	14 (F5)	13.0	20 (F5)	9.2	18 (F4)
5	5.0	6 (F6)	12.5	17 (F5)	6.2	11 (F5)
6	9.6	16 (F6)	13.3	19 (F6)	9.4	17 (F5)
7	7.8	8 (F5)	9.3	20 (F7)	16.2	18 (F5)
8	8.0	16 (F5)	9.3	10 (F6)	9.8	19 (F7)
9	9.5	16 (F4)	10.0	17 (F4)	9.6	16 (F7)
10	6.0	17 (F6)	10.2	15 (F6)	11.0	12 (F5)

Stepwise regression analysis retained the number of spikes which explained 52% of the observed variation in biomass in the F3 generation. This trait remained the main contributing character in the F4 generation, explaining only 27% of the observed variation. This trait played also an important role in the F5 generation explaining 91% of the variation in biomass, while together with kernels/spike and plant height, explained 96% of variation in biomass. In the F6 generation, plant height alone, explained 25% of above ground biomass variability. In the F7, the spike number and kernels per spike, both explained 91% of the observed variation.

These results indicated that traits contributing to above ground biomass of the F3 selected lines differed from one year to another. Since no control was made on the non selected characters, the selected lines obviously differed for these traits. The statement of any non -selected trait may be favored or inhibited, depending on the genotype and growth conditions. This differential statement of the non-selected traits affected biomass yield of the selected lines, changing their ranks compared with the F3, thus leading to the observed GEI.

Path coefficient analysis indicated that the number of spikes and the number of kernels per spike had a positive and variable direct effects upon biomass, depending on the environment. These characters had negative indirect effects via each other, probably because of mutual compensation. Indirect effect of number of spikes via thousand kernel weight was positive and the one of number of kernels per spike via the same trait was negative. These characters had no significant indirect effects via plant height nor number of days to heading (Table 6).

Thousand kernel weight had a direct effect varying from -0.0400 to 0.7057 depending on the environment. The indirect effect via spike number was positive and significant during three generations out of five. The indirect effect via kernels per spike was significant and negative in the F3 and F7 generations only. Plant height showed also variable direct and indirect effects, while days to heading showed direct as well as indirect effects, which varied from significantly negative to significantly positive, depending on the environment (Table 6). These results further indicated that the contribution of the non-selected traits to biomass varied also in size and sign from one environment to another, in agreement with the findings of Ceccarelli et al. (1991)

Table 6 : Path coefficients analysis for 5 variables upon above ground biomass (Y) in 5 consecutive generations of cross-population I

	Generations				
Direct/ indirect effects	**F3**	**F4**	**F5**	**F6**	**F7**
Number of spikes (X1) vs Biomass (Y)					
Edirect effect (P1Y)	0.6440	0.8072	0.6175	0.2788	0.7911
indirect effect via kernels/spike r12P2Y	-0.2484	-0.3342	-0.0307	-0.1071	-0.0226
indirect effect via TKW r13P3Y	0.3020	0.0751	0.0799	-0.0141	-0.0016
indirect effect via PHT r14P4Y	0.0304	-0.0147	0.0672	0.0404	0.1015
indirect effect via DHE r15P5Y	-0.0098	0.0021	-0.0030	0.0372	-0.0364
r1Y (total)	0.7182	0.5355	0.749	0.2352	0.832
Kernels/spike (X2) vs Biomass (Y)					
direct effect (P2Y)	0.6420	0.4493	0.4657	0.3359	0.2384
indirect effect via number of spikes r21P1Y	-0.2492	-0.5997	-0.0407	-0.0270	-0.0751
indirect effect via TKW r23P3Y	-0.5546	-0.0842	-0.0601	-0.0753	0.0326
indirect effect via PHT r24P4Y	-0.0216	0.0367	0.0929	0.0041	-0.0060
indirect effect via DHE r25P5Y	-0.0688	-0.0099	-0.0027	0.0510	-0.0276
r2Y (total)	-0.2522	-0.213	0.457	0.286	0.162
Thousand kernel weight (X3) vs Biomass (Y)					
direct effect (P3Y)	0.7057	0.2505	0.2720	0.1457	-0.0400
indirect effect via number of spike r31P1Y	0.2756	0.2442	0.1815	-0.0270	0.0332
indirect effect via kernels/spike r32P2Y	-0.5046	-0.1512	-0.1029	-0.1736	-0.1943
indirect effect via PHT r34P4Y	0.0427	0.0275	0.0911	0.1117	0.0295
indirect effect via DHE r35P5Y	0.0312	-0.0093	0.0016	0.0393	0.0258
r3Y (total)	0.5506	0.3617	0.4433	0.099	-0.144

Plant height (X4) vs Biomass (Y)					
direct effect (P4Y)	-0.0964	0.0819	0.1645	0.2064	0.2143
indirect effect via number of spike r41P1Y	0.2028	-0.1453	0.2525	0.0546	0.3749
indirect effect via kernels/spike r42P2Y	-0.1438	0.2015	0.2631	0.0067	-0.0066
indirect effect via TKW r43P3Y	0.3126	0.0842	0.1506	0.0788	-0.0055
indirect effect via DHE r45P5Y	0. 2148	-0.0107	-0.0001	0.1260	-0.0487
r4Y (total)	0.4900	0.2116	0.8306	0.4725	0.528
Days to heading (X5) vs Biomass (Y)					
direct effect (P5Y)	-0.1514	-0.0454	-0.0075	0.2659	0.0875
indirect effect via number of spikes r52P1Y	0.0418	-0.0379	0.2519	0.0390	-0.3379
indirect effect via kernels/spike r52P2Y	0.2921	0.0989	0.1713	0.0644	-0.0753
indirect effect via TKW r53P3Y	-0.1453	0.0513	-0.0598	0.0215	-0.0118
indirect effect via PHT r54P4Y	-0.0127	0.0193	0.0031	0.0807	-0.1193
r5Y (total)	0.02450	0.0862	0.359	0.474	-0.454

One of the difficulties of studying the efficiency of selection under moisture stress conditions is that the performance of the selected lines fluctuates from year to year, since a small change in growing conditions produced larger effect on genotypic performances. Among the traits related to grain yield, above ground biomass is often utilized as selection criterion to improve yield stability under stress conditions of Mediterranean continental climate. However a given biomass yield can be achieved through different combination of traits non controlled by selection and the effect of individual trait, within any combination, may change across environments, enhancing biomass and grain yield instability and significant GEI of both characters. This change affected the relationship between relatives, due to their relative ranking changes, but not the relationship between biomass and grain yield which remained positive and significant under stress conditions.

Among the main limitations to selection progress are the low selection differential induced by low genetic variability, the lack of significant correlation between generations or years due to GEI and the use of less adapted germplasm (Ceccarelli et al. 1998). As a conclusion, the results of this study indicated that, under Mediterranean continental climate, the recommended breeding method would be (a) to determine, based on the relative frequency of favorable and unfavorable environments, as far as frost and terminal heat and drought stress are concerned, earliness class which fits best the most frequently occurring environment, (b) to select lines in the early segregating generations, within the desirable earliness class, based on biomass, (c) to increase seed of the selected lines in the following generations, (d) to evaluate these lines in several environments, and (e) to select the most stable lines in grain yield , giving more weight to the performance in the most frequently occurring environments.

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