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Genetic analysis of carbon isotope discrimination and agronomic characters in a bread wheat cross

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Abstract Carbon isotope discrimination (Δ) has been suggested as a selection criterion to improve transpiration efficiency (W) in bread wheat (*Triticum aestivum* L.). Cultivars 'Chinese Spring' with low Δ (high W) and 'Yecora Rojo' with high Δ (low W) were crossed to develop F₁, F₂, BC₁, and BC₂ populations for genetic analysis of Δ and other agronomic characters under well-watered (wet) and water-stressed (dry) field conditions. Significant variation was observed among the generations for Δ only under the wet environment. Generation \times irrigation interactions were not significant for Δ . Generation means analysis indicated that additive gene action is of primary importance in the expression of Δ under nonstress conditions. Dominance gene action was also detected for Δ , and the direction of dominance was toward higher values of Δ . The broad-sense and the narrow-sense heritabilities for Δ were 61% and 57% under the wet conditions, but were 48% and 12% under the droughted conditions, respectively. The narrow-sense heritabilities for grain yield, above-ground dry matter, and harvest index were 36%, 39%, and 60% under the wet conditions and 21%, 44%, and 20% under dry conditions, respectively. The significant additive genetic variation and moderate estimate of the narrow-sense heritability observed for Δ indicated that selection under wet environments should be effective in changing Δ in spring bread wheat.

Key words *Triticum aestivum* L. · Drought resistance
Generation means analysis · Transpiration efficiency
Gene action · Heritability

Introduction

Substantial differences have been found in transpiration efficiency (W=total dry matter/total water transpired) in bread wheat (*Triticum aestivum* L.) (Farquhar and Richards 1984; Condon et al. 1990; Ehdaie et al. 1991). Transpiration efficiency is one of the components of water-use efficiency (WUE=grain yield/total evapotranspiration). Improving W should result in greater WUE, provided there is not a strong negative correlation between W and other components of WUE, i.e., the ratio of water transpired to evapotranspiration and harvest index (Ehdaie and Waines 1993). Increased WUE might result in a greater yield in environments where crop growth is limited by a lack of adequate water. Despite substantial variation in W in wheat, it has not been significantly improved due to the lack of an effective selection method applicable in breeding programs.

Recent studies have demonstrated that there is a significant variation in plant carbon isotope discrimination, Δ , (Farquhar et al. 1989). It has been suggested that Δ is a useful indication of genetic variation in W in wheat (Farquhar and Richards 1984; Condon et al. 1990; Ehdaie et al. 1991). Plants discriminate against the naturally occurring and heavier isotope of carbon [¹³C] during the diffusion and fixation of CO₂ in photosynthesis. The extent of the discrimination is a function of the ratio of the intercellular and atmospheric partial pressure of CO₂ (P_i/P_a) (Farquhar et al. 1982). Based on theory, they suggested that Δ measured in plant dry matter should be positively correlated with the ratio of P_i/P_a and negatively associated with W.

Several pot experiments have demonstrated significant differences among wheat genotypes for Δ and for W, and a negative correlation between the two characters (Farquhar and Richards 1984; Condon et al. 1990; Ehdaie et al. 1991). The genotype \times environment interactions for Δ in wheat were reported to be significant but relatively small compared to genotypic variation (Ehdaie et al. 1991; Condon and Richards 1992; Condon et al. 1992). Estimates of broad-sense heritability for Δ in wheat have been relatively

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large, ranging from 74% to 94% (Ehdaie et al. 1991, 1993) and from 62% to 95% (Condon and Richards 1992), depending on the experimental conditions and on the plant parts sampled. Estimates of broad-sense heritability for Δ in cowpea (*Vigna unguiculata* (L.) Walp.) ranged from 76% to 90% (Hall et al. 1990) and in peanut (*Arachis hypogaea* L.) varied from 53% to 81% (Hubick et al. 1988). Broad-sense heritability is the ratio of genetic variance to phenotypic variance. A quantitative character with high broad-sense heritability may respond to selection. Response to selection depends on the proportion of phenotypic variance attributable to additive variance or narrow-sense heritability (Falconer 1988).

A successful breeding program for improving transpiration efficiency in bread wheat based on selection for low values of Δ requires knowledge of the inheritance of Δ . At present there is no information on gene action or on the narrow-sense heritability of Δ of field grown bread wheat or other crop species. Knowledge of the type and amount of gene action and narrow-sense heritability of Δ will help wheat breeders design effective breeding programs to change transpiration efficiency in wheat.

Materials and methods

Genetic materials and field conditions

In our previous studies, only two spring wheat genotypes exhibited consistent differences in W and Δ (Ehdaie et al. 1991). Therefore, we were limited to two genotypes as parents in this study. The first parent, 'Chinese Spring' (P_1), is a tall, later-maturing, landrace cultivar with relatively high W and low Δ . This cultivar is often used in wheat genetic experiments. The second parent, 'Yecora Rojo' (P_2), is a dwarf, early-maturing, modern California cultivar of CIMMYT origin, with low W and high Δ (Ehdaie et al. 1991).

Crosses between the two genotypes were made in the glasshouse in 1988, and the F_1 was backcrossed in 1989 to each of the parents to produce the first backcross generations BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$). Seed produced by self-pollination of F_1 plants was composited to provide the F_2 generation. Parents, F_1 , F_2 , BC_1 , and BC_2 were planted in two adjacent field experiments on 7 December 1989 on a Ramona Type A sandy loam soil (fine-loamy, mixed, thermic Typic Haploxeralf) at the Moreno Farm of the University of California Agricultural Experiment Station, Moreno Valley, Calif. One of the experiments was irrigated with sprinklers as needed (wet experiment) to minimize water shortage until the plants reached maturity. Irrigation was terminated (dry experiment) in the other experiment 110 days post-sowing, when 50% of plants were heading. The wet experiment received 270 mm of irrigation water, while the dry experiment received 130 mm. The total rainfall during the study was 466 mm. Of this amount, more than half fell during March, but no rain fell during April and May 1990.

A randomized complete block design with four replicates was used in each experiment. In each replicate, seeds were planted in rows 1 m in length. Interrow spacing was 30 cm and interplant spacing was 10 cm, allowing a total of 10 plants per row. In each replicate, the number of rows per plot was 1 for each of the nonsegregating generations (P_1 , P_2 , and F_1), 2 for each backcross generation, and four for the F_2 generation. One row of a check cultivar, 'Ramona 50', was planted alternately among the experimental plots. The land was fallowed in the previous year, and 180 kg ha⁻¹ urea was added to the soil before planting.

All measurements were made on an individual plant basis. The terminal plant from each end of a row was excluded to minimize bor-

der effects. Data were available for only 4 plants in a few rows due to some cases of broken plants at harvest. Plants in the dry experiment were harvested between 28–31 May 1990 and those in the wet experiment between 7–11 June 1990. At harvest, flag leaves were collected for carbon isotope analysis. The flag leaves were dried at 80°C for 2 days and individually ground in a Wiley mill to a fine powder. The molar ratios of carbon isotopes in the flag leaves were determined using a ratio mass spectrometer as described by Hubick et al. (1986). The carbon isotope discrimination (Δ) for each plant was calculated according to the formula given by Hubick et al. (1986), assuming an isotope composition of air relative to the standard Pee Dee Formation of belemnite of -8×10^{-3} at Riverside, Calif. Data also were collected on plant height (PH) expressed as the distance between the ground level and the tip of plants, including awns; number of spikes (NS); grain yield (GY), and above-ground dry matter (AGDM). Harvest index (HI) was calculated as the ratio of GY/AGDM.

Statistical and genetic analyses

Generation means and variances were determined for plants within each experimental unit (e.g., within plot means and variances). Variances for each generation were pooled among the replications as $s^2 = \sum (n_i - 1) s_i^2$ divided by $\sum (n_i - 1)$, where n_i is the number of plants and s_i^2 is the variance for each replicate (Ketata et al. 1976). The parental, F_1 , F_2 , BC_1 , and BC_2 means (a total of six generations) were analyzed according to the weighted generation means analysis of Mather and Jinks (1971) to estimate parameters for the genetic model containing additive and dominance effects. This analysis was conducted for those characters in which significant variation was detected among the genotypes. In an additive-dominance model (Mather and Jinks 1971), the expectations of generation means in terms of m , the mean effect; a , the pooled additive effects; and d , the pooled dominance effects are as follows:

$$\bar{P}_1 = m + a$$

$$\bar{P}_2 = m - a$$

$$\bar{F}_1 = m + d$$

$$\bar{F}_2 = m + \frac{1}{2}d$$

$$\bar{BC}_1 = m + \frac{1}{2}a + \frac{1}{2}d$$

$$\bar{BC}_2 = m - \frac{1}{2}a + \frac{1}{2}d$$

Variation among generations was partitioned into variation due to additive and dominance effects and that due to deviation from the additive-dominance model. This permitted a test of the adequacy of the model and an evaluation of the importance of the additive and dominance gene effects in their contribution to the genetic variation.

Variance components and heritability estimation

Variance components, V_E , V_A , and V_D , representing the environmental, additive genetic, and dominance genetic variances, respectively, were estimated as follows:

$$V_E = 1/4(V_{P_1} + V_{P_2} + 2V_{F_1})$$

$$V_A = 2V_{F_2} - (V_{BC_1} + V_{BC_2})$$

$$V_D = V_{BC_1} + V_{BC_2} - V_{F_2} - V_E$$

where V_{P_1} , V_{P_2} , V_{F_1} , V_{F_2} , V_{BC_1} , and V_{BC_2} represent the variances of the parental, F_1 , F_2 , and the backcross to P_1 and P_2 , respectively. Broad-sense and narrow-sense heritabilities were estimated as $H_b = (V_{F_2} - V_E)/V_{F_2}$ and $H_n = [2V_{F_2} - (V_{BC_1} + V_{BC_2})]/V_{F_2}$, respectively (Warner 1952). Standard error for H_n was calculated according to the formula of Ketata et al. (1976). A standard error for H_b was derived as the square root of the following:

$$V(H_b) = \frac{1}{8V_{F_2}^2} \left(\frac{V_{P_1}^2}{df_{P_1}} + \frac{V_{P_2}^2}{df_{P_2}} + \frac{V_{F_1}^2}{df_{F_1}} + \frac{V_{P_1}^2 + V_{P_2}^2 + V_{F_1}^2}{df_{F_2}} \right)$$

where df_{P_1} , df_{P_2} , df_{F_1} , and df_{F_2} are the degrees of freedom associated with V_{P_1} , V_{P_2} , V_{F_1} , and V_{F_2} , respectively.

Table 1 Characters of spring bread wheat with significant mean squares from the analysis of variance and the combined analysis of parental, F₁, F₂, and backcross generations in a 'Chinese Spring' × 'Yecora Rojo' cross grown under wet and dry field conditions (*PH* plant height; *NS* number of spikes per plant; Δ carbon isotope discrimination of flag leaves; *GY* grain yield per plant; *HI* harvest index; *AGDM* above-ground dry matter per plant)

Source	df	Wet			Dry			
		PH	NS	Δ	PH	NS	GY	HI
Replications	3	4.8	1.2	0.7	42.5	1.1	2.0	0.018
Generations	5	290.1**	2.0*	1.2**	190.5**	0.4*	1.2**	0.014**
Error	15	11.9	0.9	0.3	7.7	0.1	0.3	0.001
Combined analysis								
		PH	NS	GY	AGDM	HI	Δ	
Environments (E)	1	100.4*	30.3**	55.5**	112.2**	0.248**	3.3	
Reps./ E	6	23.7	1.1	1.0	2.6	0.010	0.7	
Generations (G)	5	466.6**	2.0**	0.6	1.6	0.013**	0.7	
G × E	5	14.0	1.3	0.9	4.1	0.004	0.6	
Pooled error	30	9.8	0.5	0.4	2.1	0.002	0.4	

*** Significant at the 0.05 and 0.01 probability levels, respectively

Table 2 Estimates of generation means for different characters under wet field conditions in a spring bread wheat cross

Generation	Plant height (cm)	Spikes/ plant (n)	Grain yield/ plant (g)	Above-ground dry matter/ plant (g)	Harvest index	Carbon isotope discrimina- tion (‰)
P ₁ (Chinese Spring)	58.1a ^a	6.0ab	4.28a	9.98a	0.43a	13.9c
P ₂ (Yecora Rojo)	34.3e	4.1c	3.71a	7.97a	0.47a	15.3a
F ₁	52.3bc	4.8bc	4.15a	9.24a	0.45a	15.4a
F ₂	49.8cd	6.2a	4.33a	10.68a	0.40a	14.8ab
BC ₁	55.4ab	5.9ab	4.17a	10.08a	0.41a	14.5bc
BC ₂	45.8d	4.8abc	4.48a	9.65a	0.46a	14.8ab
Mean	49.3	5.3	4.19	9.60	0.44	14.8

^a Within columns, means followed by the same letter(s) are not significantly different at the 0.05 probability level using LSD test

Results and discussion

Significant differences were found among the generation means for PH, NS, and Δ under wet conditions and for PH, NS, GY, and HI under dry conditions (Table 1). The combined analysis of variance for each trait indicated that drought reduced mean values for all traits except Δ (Table 1). None of the characters showed significant generation × irrigation interactions. Mean values under wet and dry conditions were, respectively, 49.3 and 46.4 cm for PH, 5.3 and 3.7 for NS, 4.2 and 2.0 g for GY, 9.6 and 6.5 g for AGDM, and 0.44 and 0.29 for HI (Tables 2 and 3). The mean values of Δ for the wet and the dry experiments were 14.8‰ and 15.3‰, respectively, but the difference was not significant. Our previous studies also showed no significant differences between mean Δ in wet and dry environments for a set of diverse wheat genotypes grown in the glasshouse and in the field (Ehdaie et al. 1991), and for some of the generations used in the present study grown in the glasshouse (Ehdaie et al. 1993). Farquhar and Richards (1984) and Condon et al. (1990) reported reduced Δ in response to water stress for wheat genotypes grown in a glasshouse.

In the wet experiment, 'Chinese Spring' was taller in height, possessed more spikes per plant, and had a smaller value for Δ than 'Yecora Rojo' (Table 2). 'Chinese Spring' and 'Yecora Rojo' had a similar grain yield, above-ground dry matter yield, and harvest index under wet conditions. In the dry experiment, 'Chinese Spring' was also taller in height than 'Yecora Rojo', but they had a similar number of spikes per plant, above-ground dry matter, and Δ (Table 3). 'Yecora Rojo' outperformed 'Chinese Spring' for grain yield and harvest index when water was limited. These differences could be due to the fact that 'Chinese Spring' was exposed more to drought than 'Yecora Rojo'. In the dry experiment, when water was terminated, 'Yecora Rojo' was at the heading stage while 'Chinese Spring' was about 10 days behind. Genotypes with a longer plant life cycle are more prone to terminal environmental stresses such as drought and heat in semiarid and arid regions, such as those found in Mediterranean-type climates, than those with shorter plant life cycles.

For those characters where significant differences among the generations were detected, a genetic analysis of generation means was warranted and consequently conducted. The additive-dominance model accounted for a major portion of the variation among generations (Table

Table 3 Estimates of generation means for different characters under dry field conditions in a spring bread wheat cross

Generation	Plant height (cm)	Spikes/ plant (n)	Grain yield/ plant (g)	Above-ground dry matter/ plant (g)	Harvest index	Carbon isotope discrimina- tion (‰)
P ₁ (Chinese Spring)	51.5a ^a	3.7ab	1.27c	5.69b	0.21c	15.0a
P ₂ (Yecora Rojo)	34.9c	3.6ab	2.37ab	6.82ab	0.34a	15.1a
F ₁	51.5a	4.0a	2.83a	7.89a	0.35a	15.2a
F ₂	47.7a	3.7ab	1.85bc	6.37b	0.28b	15.5a
BC ₁	51.5a	4.1a	1.67bc	6.31b	0.25bc	15.5a
BC ₂	41.3b	3.2b	2.23ab	6.16b	0.35a	15.5a
Mean	46.4	3.7	2.00	6.50	0.29	15.3

^a Within columns, means followed by the same letter(s) are not significantly different either at the 0.10 (above-ground dry matter per plant) or at the 0.05 probability levels using LSD test

Table 4 Analysis of variance and estimates of gene effects^a in a 'Chinese Spring'×'Yecora Rojo' spring bread wheat cross for plant height (PH), number of spikes per plant (NS), and carbon isotope discrimination of flag leaves (Δ) under wet field conditions and for PH, NS, grain yield (GY), and harvest index (HI) under dry field conditions

Source	df	Wet			Dry			
		PH	NS	Δ	PH	NS	GY	HI
Generations	5	290**	2.85**	1.17**	191**	0.38*	1.24**	0.014**
Genetic model	2	717**	4.62*	2.54**	470**	0.38 ⁺	2.61**	0.035**
Additive effects	1	1314**	9.23**	3.82**	750**	0.45 ⁺	3.07**	0.050**
Dominance effects	1	119**	0.00	1.26*	186**	0.31 ⁺	2.16**	0.020**
Deviations	3	6	1.67	0.26	4	0.38 ⁺	0.33	0.000
Error	15	12	0.92	0.27	8	0.12	0.27	0.001
m		46.4±0.34	5.4±0.19	14.5±0.07	43.2±0.32	3.6±0.09	1.7±0.1	0.26±0.01
a		-11.8±0.34	-1.1±0.18	0.7±0.07	-8.4±0.32	-0.3±0.09	0.5±0.1	0.08±0.01
d		6.4±0.63	0.0±0.00	0.6±0.12	8.1±0.61	0.3±0.16	0.7±0.2	0.08±0.02

^a m mean effect, a pooled additive effects, d pooled dominance effects

⁺, **, *** Significant at the 0.10, 0.05, and 0.01 probability levels, respectively

4). The reduction in sums of squares due to fitting the additive gene effects was highly significant in all cases except for NS in dry conditions; the reduction in sums of squares due to fitting dominance gene effects was significant or highly significant in all cases except for NS in dry conditions (Table 4). In no case were the deviations from the additive-dominance model significantly greater than the error mean square. This indicates that epistasis is not a determining factor in the expression of the characters involved. The analysis in Table 4 indicated that about 65% of the variability in Δ under well-watered conditions was due to additive variance and that 22% was due to dominance variance.

The estimates of gene effects (Table 4) are not biased by linkage relationships, if present, since interallelic interactions were not involved (lack of epistasis). The negative estimates for additive effects, a, found for PH and NS (Table 4) were due to the choice as to which parent was designated P₁ or P₂. Estimates of additive effects were either greater than or equal to dominance effects. Estimates of additive effects were larger than dominance effects for PH and NS, but were similar for Δ under wet conditions, which is in agreement with the glasshouse results reported by Ehdaie et al. (1993) for Δ using the same P₁, P₂, F₁, and F₂

generations used in this study. In dry conditions, estimates of additive and dominance effects were the same for PH, NS, GY, and HI (Table 4).

The direction of dominance, as indicated by the positive sign of d, was toward higher PH, NS, Δ , GY, AGDM, and HI, which is in agreement with reports in spring wheat (Singh and Singh 1978; Singh et al. 1984; Singh et al. 1986; McKendry et al. 1988; Ehdaie et al. 1993). Martin and Thorstenson (1988) compared mean values of Δ of a domesticated tomato (*Lycopersicon esculentum*), a wild tomato (*L. pennellii*), and their F₁ hybrids grown in containers. They reported that the domesticated parent had higher Δ than the wild parent and that the mean Δ of the small number of F₁ hybrids used was in between, but slightly closer to the wild parent, indicating a degree of dominance towards lower Δ . Similarly, Hubick et al. (1988), using pot-grown F₂ progeny of a cross between two peanut cultivars, observed that the distribution was slightly skewed toward the lower values of Δ , which suggested a degree of dominance for low Δ . In cowpea, the Δ values of the F₁ hybrids were closer to the Δ values of the parent with low Δ when grown in pots, but when grown in the field they were closer to Δ values of the parents with high Δ (Ismail and Hall 1993).

The estimates of broad-sense (H_b) and narrow-sense (H_n) heritabilities of all characters are presented in Table 5. In general, estimates of heritabilities were lower under drought conditions than under well-watered conditions. Plant height showed the highest H_b under both wet (91%) and dry (81%) conditions; this trait also exhibited the highest H_n under both wet (85%) and dry (66%) conditions (Table 5). Estimates of H_n reported by Bhatt (1972) for PH ranged from 48% to 72%. In the well-watered conditions, NS, GY, and AGDM showed the lowest H_n (33%, 36%, and 39%, respectively). Estimates of H_n reported by McKendry et al. (1988) ranged from 27% to 39% for GY and from 32% to 65% for AGDM in spring wheat. These differences in estimates of heritability can be attributed to differences in the materials used in each case and in the environments in which the plants were grown.

Carbon isotope discrimination, Δ , had higher H_b (61%) and H_n (57%) than GY and AGDM under well-watered conditions (Table 5). While GY, AGDM, HI, and Δ exhibited reduced but similar H_b under drought, the H_n of Δ was much lower (12%) than those of GY and AGDM (Table 5). The reduction in estimate of H_b for Δ from 61% under wet conditions to 48% under dry conditions was due to a higher environmental variance (V_E) relative to the variance associated with the F_2 generation (V_{F_2}) under drought conditions than under well-watered conditions. Under the dry conditions, the estimate of V_E for Δ , which was calculated as the average of within-plot variances of the nonsegregating generations (P_1 , P_2 , and F_1), was 0.46 compared to 0.86 for V_{F_2} . Under the wet conditions, the estimate of V_E and V_{F_2} for Δ were 0.13 and 0.53, respectively.

The estimate of H_n for Δ was much lower under drought conditions (12%) than under the wet conditions (57%) (Table 5). This was due to the relatively higher estimate of dominance genetic variance compared to the estimate of additive genetic variance and to the higher environmental variance observed for Δ under drought conditions than under the wet conditions. Estimates of additive genetic and dominance genetic variances for Δ under the wet conditions were 0.61 and 0.08, respectively, whereas under the dry conditions the estimates were 0.21 and 1.26, respectively.

Carbon isotope discrimination values of the generations measured under wet field conditions were not correlated

with those measured under dry field conditions. This was due to changes in the generation ranking in Δ under dry field conditions. These differences in generation ranking for Δ under the dry conditions could be due to generation differences in the extent of soil water depletion during anthesis when irrigation was terminated earlier during heading and/or to generation variation in stomatal responses to soil water depletion. In a similar study (Ehdaie et al. 1993), we measured the Δ values of the same P_1 , P_2 , F_1 , and F_2 generations under wet and dry glasshouse conditions. The ranking of these generations for Δ was similar only under wet field and wet glasshouse conditions. Condon and Richards (1992) also concluded that for wheat, assessment of genotypic variation in Δ would be most effective under well-watered conditions using dry matter laid down early in plant development. The correlation coefficients between Δ and AGDM and between Δ and GY of the six generations used in this study under wet field conditions were negative and moderate, -0.62 and -0.47 , respectively, but they were not statistically significant due to the small number of degrees of freedom associated with these coefficients ($df=6-2=4$). These observations indicated that under well-watered environments, generations with lower values for Δ (higher transpiration efficiency) produced more above-ground dry matter and had a higher grain yield than those with higher values for Δ (lower transpiration efficiency). The correlation coefficients between Δ and AGDM and between Δ and GY were not significant under dry field conditions. These observations were consistent with results obtained from a set of spring wheat near-isogenic lines for height examined under dry and wet field conditions (Ehdaie and Waines, unpublished). The near-isogenic lines exhibited negative correlations between Δ and AGDM ($r=-0.59$, $P=0.07$) and between Δ and GY ($r=-0.68$, $P<0.05$) under wet field conditions. The correlations between these traits were also negative but not significant under dry field conditions. Morgan et al. (1993) noted conflicting relationships between Δ and AGDM and GY for a set of diverse winter wheat cultivars grown under irrigated and nonirrigated field conditions. They reported nonsignificant correlations and significant negative and positive correlations between Δ and AGDM and GY depending on the environmental conditions. Ehdaie et al. (1991) reported positive correlations between Δ and AGDM and GY for a set of diverse spring wheat cultivars under dry and wet field conditions. These positive correlations may have been due to genotypic differences in plant growth and maturity. Genotypes with faster growth and earlier maturity use the available water and are exposed relatively less to environmental stresses than the genotypes with slower growth and late maturity. Therefore, the former genotypes usually possess higher biomass and Δ compared to the latter genotypes. Under these circumstances, a positive relationship is observed between Δ and AGDM or GY, especially if the genotypes examined are diverse with respect to plant growth and maturity.

The limited results of this study indicated that about 65% of the variability in Δ under well-watered conditions was due to additive genetic variance and that 22% was due

Table 5 Estimates of broad-sense (H_b) and narrow-sense (H_n) heritabilities (\pm standard error) of different characters of spring bread wheat under wet and dry field conditions (AGDM above-ground dry matter, Δ carbon isotope discrimination of flag leaves)

Character	Wet		Dry	
	$H_b \pm SE$	$H_n \pm SE$	$H_b \pm SE$	$H_n \pm SE$
Plant height	0.91 \pm 0.01	0.85 \pm 0.25	0.81 \pm 0.21	0.66 \pm 0.25
No. of spikes	0.48 \pm 0.10	0.33 \pm 0.38	0.73 \pm 0.04	0.30 \pm 0.34
Grain yield	0.54 \pm 0.06	0.36 \pm 0.33	0.39 \pm 0.08	0.21 \pm 0.35
AGDM	0.61 \pm 0.07	0.39 \pm 0.33	0.52 \pm 0.07	0.44 \pm 0.29
Harvest index	0.62 \pm 0.07	0.60 \pm 0.31	0.48 \pm 0.08	0.20 \pm 0.37
Δ	0.61 \pm 0.06	0.57 \pm 0.30	0.48 \pm 0.07	0.12 \pm 0.38

to dominance variance. The additive and dominance gene effects involved in the expressions of Δ were similar. Carbon isotope discrimination also showed a relatively moderate broad- and narrow-sense heritability (61% and 57%, respectively) under well-watered field conditions. Therefore, it appears from these observations that selection in segregating generations under well-watered environments should also be effective in changing Δ in spring wheat. However, a major concern in the use of Δ as a selection criterion is the cost of sample analysis, which is about \$10.00 per sample. In a large-scale breeding program, many thousands of plants are screened in segregating generations, thereby making the cost of carbon isotope discrimination very expensive. An alternative procedure would be to select for other desirable characters, such as above-ground dry matter and harvest index, and then screen this selected material for discrimination analysis.

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