Emir.J.Agric.Sci.(1999),11:1-20

CARBON ISOTOPE DISCRIMINATION, YIELD AND TRANSPIRATION EFFICIENCY IN BARLEY GROWN IN PLASTIC HOUSE

By A. J. Dakheel * and J. M. Peacock
The International Center for Agricultural Research in The Dry Areas (ICARDA) P.O Box 5466, Aleppo, Syria

ABSTRACT

The relationships among carbon isotope discrimination (Δ), transpiration efficiency (*W*) and yield were investigated in ten barley genotypes grown in a plastic house in pot experiment in northern Syria in two consecutive seasons (1990/91 and 1991/92). Four moisture treatments were used. A non-stressed treatment with soil moisture content near to field capacity (FC), a fully stressed treatment kept at 1/3 FC throughout the life cycle, a pre-heading treatment kept at 1/3 FC before heading and a post-heading treatment kept at 1/3 FC after heading. Soil moisture contents were adjusted daily by weighing the pots and adding water. Δ was measured in the peduncles at physiological maturity. Results show that Δ , *W*, grain yield (GY) and above-ground dry matter production (AGDM) varied significantly with moisture level and genotype. Across moisture levels the relations between Δ and yield (GY and AGDM) were highly significant and positive ($r = 0.85$ and 0.82 respectively, $P < 0.001$). Yield and *W*, and Δ and *W* were negatively and significantly correlated ($r = -0.76$ and -0.85, respectively, $P < 0.001$). However, within individual moisture treatments the strength and slopes of the relationships were inconsistent. The relation between Δ and *W*

---

* *Current address and Corresponding author:*
Department of Plant Production, Faculty of Agricultural Sciences,
United Arab Emirates University-P. O. Box 17555, AL-Ain, UAE.

remained consistently negative, although not significant in all cases. Δ and yield were positively related in the fully stressed treatments during both seasons, while in the variable moisture stress treatments (pre- and post-heading) relations were positive but significant only in the first season. In the second season Δ and yield were negatively, but insignificantly, related. The relation between *W* and yield changed from negative to positive between the two seasons. Stability of genotype ranking in Δ between moisture stressed and unstressed treatments was significant only in the first season. Interseasonal stability of Δ was significant only between the means of the stressed treatments, while Δ measured in the unstressed treatments were poorly correlated.

It is concluded from this study that, first, selection for higher Δ in barley is associated with a high yield potential, under both low and high moisture levels. Second, selection for lower Δ will probably lead to an improvement in transpiration efficiency (*W*), however yield potential might be negatively affected. Third, genotype ranking in Δ is more stable across seasons in moisture stressed rather than unstressed treatments, therefore selection for this trait for moisture stressed areas is more appropriate within the targeted environment.

Key words: ^{13}C discrimination, Δ , *Hordeum vulgare*, selection criterion, water use efficiency.

INTRODUCTION

Yield in a water limited environment is viewed as the product of three factors (Passioura 1977; Condon and Richards 1993) namely: amount of water transpired by the plant (E), water use efficiency (or transpiration efficiency) (the ratio of biomass produced /water consumed by plants, *W*), and the efficiency of allocation of dry matter to harvestable crop products, approximated by the harvest index (HI). Maximizing any of the three factors is expected to improve yield potential given that interactions between the three components are minimum.

Improving crop water use efficiency to improve yield, has received increasing attention with the development of the ^{13}C discrimination theory in C3 plants. The theory predicted that ^{13}C discrimination (Δ), water use efficiency and yield are linked at the leaf level (Farquhar *et al.,* 1982; Farquhar and Richards, 1984). During photosynthesis, C3 plants discriminate against the heavier naturally occurring ^{13}C carbon isotope (Farquhar *et al.,* 1982). The process is dependent on the ratio of intercellular (ci) to atmospheric carbon dioxide (ca) concentration (ci/ca). Discrimination is higher, when stomata are widely open and ci is high. Similarly, but independently, transpiration rate is linked to ci/ca at the leaf level (Farquhar *et al.,* 1982). Higher transpiration efficiency (*W*) (ratio of photosynthesis/ conductance) is associated either with a reduced stomatal conductance or an increase in photosynthesis capacity (Condon and Richards, 1993). Therefore, the theory predicts that an increase in *W* would be associated with a reduced discrimination against ^{13}C (Δ) (Farquhar and Richards, 1984; Ehleringer *et al.,* 1990). Consequently, Δ was proposed to predict variation in transpiration efficiency among genotypes of crop species and subsequently to utilize it in breeding programs (Farquhar and Richards, 1984; Condon *et al.,* 1987). The uniqueness of ^{13}C discrimination, is that it is not only an indirect measure of *W* (which has been shown in many studies), but it also represents an integrated measure of the efficiency of photosynthesis, in response to the prevailing environmental conditions during growth cycle prior to its estimation (Condon *et al.,* 1990; Meinzer *et al.,* 1993).

The objective of this study was to determine the relationship among Δ , transpiration efficiency and yield performance in barley under different moisture regimes.

MATERIALS AND METHODS

Location

The experiments were carried out during two seasons (1990/91 and 1991/92) in a plastic house at Tel Hadya, ICARDA's headquarters and main research site in northern Syria. In the first season planting was done in October 1990, and plants were harvested in May 1991. In the 1991/92 season planting was commenced in December 1991 and were harvested in June 1992.

Plant material

Ten two-rowed barley genotypes with similar phenology were selected. These included five landraces (L), which originated in the Syrian steppe and arid zone (Tadmor, SLB 39-99, SLB 62-35, SLB 62-99, and SLB 8-6), and five improved lines (I), two developed at the Waite Institute in Australia (WI 2198, WI 2198/WI 2291) and three from ICARDA's barley breeding program (Harmal, Roho, and SBON 96).

The ten genotypes differ in grain Δ, as determined previously (Acevedo, 1993) and possess the majority of traits identified as important in adaptation to harsh Mediterranean environments.

Growth conditions

Seeds of each genotype were germinated in petri dishes in an incubator at 20 ^{0}C. Two seedlings of equal size were transplanted into a clay soil and sand mix (2:1 ratio) in a six kg plastic pots. A base fertilizer consisting of 0.42 g of superphosphate, 1.0 g ammonium sulphate, and 0.016 g urea was applied to each pot. The soil was fully irrigated to field capacity and the surface was sealed with aluminum foil leaving two holes for seedlings and a third for watering. A plastic tube (15 cm length and 1 cm diameter) was inserted in the hole and used to add water. A 1/10 Hoagland nutrient solution was used for irrigation the tube was closed with a cork to prevent direct evaporation when not in use.

In both seasons the plastic house temperature was set at a maximum day time /minimum night time regime of 22/5 ^{0}C during the first period of plant growth, and 25/10 ^{0}C from head emergence to maturity. Temperature and relative humidity were monitored with a hygrothermograph and vapor pressure with a ventilated psychrometer.

Moisture treatments

There were four moisture treatments. The first a non-stressed treatment with soil moisture contents near to field capacity (FC) throughout the growth cycle. The second was a fully stressed treatment kept at 1/3 field capacity (1/3 FC). The third treatment was subject to pre-heading moisture stress receiving 1/3 FC, then kept near to FC (1/3 FC-FC). The fourth was a post-heading (terminal) moisture stressed treatment which was kept at 1/3 FC moisture regime from heading until harvest (FC-1/3 FC).

Moisture content of the soil mix at field capacity and permanent wilting point was 30.8 % and 16.7 %, respectively. Soil moisture contents were adjusted daily by weighing the pots and adding water according to the pre-designed moisture treatment. The total amounts of water used in each pot were estimated. Watering was terminated at physiological maturity. Direct soil water evaporation was also calculated using twelve pots without plants, which were randomly distributed throughout the treatments.

Treatments were arranged in a randomized complete block, in a split-plot design, where soil moisture levels were the main plots and genotypes were the subplots. Each treatment was replicated three times giving a total of 120 pots for each experiment.

Plant harvest

At maturity, plants were harvested and separated into heads, leaves, stems, and peduncles. The roots were washed and extracted from the soil using a fine steel mesh sieve. The plant parts were oven dried at 70 ^{O}C for 48 h. Total and above ground biomass were calculated. Seeds were threshed and harvest index estimated as the ratio of seed weight to above ground dry matter. Transpiration efficiency was calculated by dividing total or above ground dry matter by the amount of water transpired by the plants (g/kg).

Isotope discrimination analysis

The peduncles at final harvest in all treatments were used for determination of carbon isotopic composition, they were finely ground, mixed and analyzed. A 2 mg subsample from each sample was combusted separately in an elemental analyzer (Heraeus CHN-O RAPID Elemental Analyzer, Germany). Carbon isotopic composition in the combustion gas was determined by a ratio mass spectrometer (Finnigan MAT, Germany) according to the method described by Wright *et al.* (1988). Δ values were obtained according to Hubick et al. (1986) with the assumption that the isotopic composition of the air relative to the international standard (PDB) is -8.0 . Analysis of samples was completed during 1993 and 1994.

Statistical analysis

Variation among genotypes and moisture treatments and the interactions between the two factors for all variables measured were assessed by analysis of variance for the split-plot design (Steel and Torrie, 1980). Data of each season and the mean of the two seasons were analyzed. Variation within each moisture level was assessed by a one-way analysis of variance. Correlation analysis and regressions between various variables were also performed. The statistical package MSTAT was used in performing the analysis.

RESULTS

Yield response and ^{13}C discrimination

Grain yield (GY), above ground dry matter production (AGDM) and ^{13}C discrimination (Δ) varied significantly among barley genotypes and moisture treatments in both seasons (Table 1). Moisture stress reduced GY and AGDM by 39% and 41% respectively in the fully stressed treatment, and by 34 % and 22% in the terminal (post-heading) moisture stress treatment (Table 2). In the pre-heading stressed treatment grain yield was only reduced by 19.7 % and AGDM was equal or higher than other moisture stress treatments (Table 2). The difference in the effects of post-and pre-heading treatments on grain yield emphasizes the importance of terminal moisture stress during grain filling period in determining final yield potential. Harvest index (HI) did not vary significantly among either moisture treatments or genotypes, with the exception of the terminal (post-heading) stress treatment (Table 2). Therefore, it might be expected that according to the equation given by Passioura (1977) other factors, namely E (amount of water transpired by the plant) and *W* (transpiration efficiency), affected the variation in yield potential among genotypes.

Δ was as expected (Richards and Condon, 1993) lowest at high moisture stress levels (fully moisture stressed treatments).

Across all four moisture treatments (stressed and unstressed) AGDM and GY were correlated positively and highly significant with Δ in both 1991 and 1992 seasons (Table 3). Correlation coefficients were substantially higher when only the high and low .

Table 1. ANOVA summary for above ground dry matter production (AGDM), grain yield (GY), seasonal water transpired (SWTR), transpiration efficiency (*W*), and ^{13}C discrimination (Δ) measured in peduncles at harvest in 10 barley genotypes grown in plastic house under four moisture treatments during 1991 and 1992. * P <0.05; ** P <0.01; *** P <0.001; n.s., not significant .

		Source of variation		
Variable	Season	Moisture (M)	Genotype (G)	MXG
AGDM	1991	***	***	n.s
	1992	***	*	n.s
GY	91	*	***	n.s
	92	**	ns	n.s
W	91	***	***	n.s
	92	*	***	*
Δ	91	***	*	n.s
	92	**	**	n.s
SWTR	91	***	***	**
	92	***	***	n.s

Table 2. Mean values of different plant traits (symbols as in table 1) in 10 barley genotypes grown under four moisture treatments in the plastic house during 1991 and 1992.

Moisture treatment	SWTR g/pot	GY g/pot	AGDM g/pot	Δ (X10^{-3})	*W* g.kg	HI
Non-stressed	6615	21.2	47.8	19.44	3.41	0.45
Stressed	3405	12.96	28.4	18.3	3.91	0.46
Pre-heading stress	4433	17.03	36.7	19.8	3.75	0.46
Post-heading stress	5028	14.03	37.2	19.34	3.3	0.37
LSD	453	2.35	3.3	0.310	0.38	0.03

moisture treatments were considered, or when the pre-heading stress treatment was eliminated (Table 3). In the later moisture treatment there was little variation among genotypes in Δ with the relief of stress during the critical period of grain filling. Mean correlation coefficients between GY and Δ, and AGDM and Δ across the three moisture treatments (FC, 1/3 FC and terminal stress treatments) for the two seasons was 0.87 and 0.82, respectively ($P < 0.001$) (Figure 1).

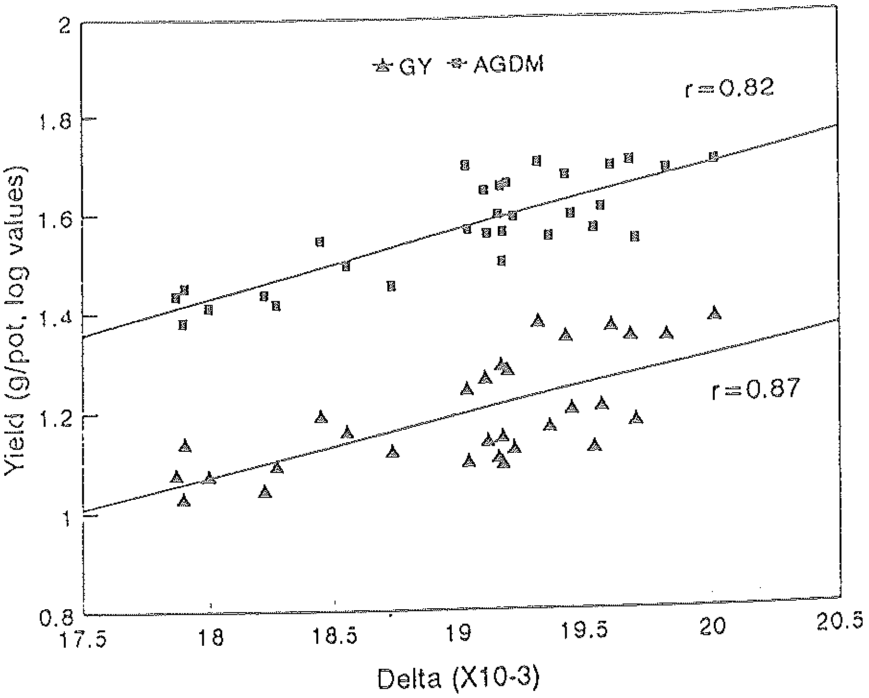

Figure 1. Relation between ^{13}C discrimination (Δ) and grain yield (GY) and above ground dry matter production (AGDM) in ten barley genotypes across the three moisture treatments (FC, 1/3 FC and terminal stress). Values are averages of the two seasons.

Relationship between yield, transpiration efficiency, and Δ

Across moisture treatments yield and transpiration efficiency (*W*) were negatively and significantly related (Table 3). The mean correlation coefficient between AGDM and W of the two seasons was higher ($r = -0.76$) when pre-heading moisture stress treatment was not included (Figure 2).

Table 3. Correlations between grain yield (GY), above ground dry matter production (AGDM), transpiration efficiency (*W*) and ^{13}C discrimination (Δ) in 10 barley genotypes across different moisture treatments, unstressed (FC), and fully stressed (1/3 FC) during two seasons. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., not significant .

Trait	Across four moisture treatments(n=40)				Moisture treatments FC and 1/3 FC (n=20)			
	Δ		*W*		Δ		*W*	
Year	1991	1992	1991	1992	1991	1992	1991	1992
GY (g/pot)	0.75^{***}	0.59^{***}	-0.64^{***}	-0.39^{***}	0.91^{***}	0.85^{***}	-0.70^{***}	-0.79^{***}
AGDM (g/pot)	0.65^{***}	0.63^{***}	-0.54^{***}	-0.61^{***}	0.85^{***}	0.90^{***}	-0.74^{***}	-0.84^{***}
W ($g.kg^{-1}$)	-0.70^{***}	-0.20n.s			-0.78^{***}	-0.85^{***}		

Relationship between yield, transpiration efficiency, and Δ

Across moisture treatments yield and transpiration efficiency (*W*) were negatively and significantly related (Table 3). The mean correlation coefficient between AGDM and W of the two seasons was higher (r =-0.76) when pre-heading moisture stress treatment was not included (Figure 2).

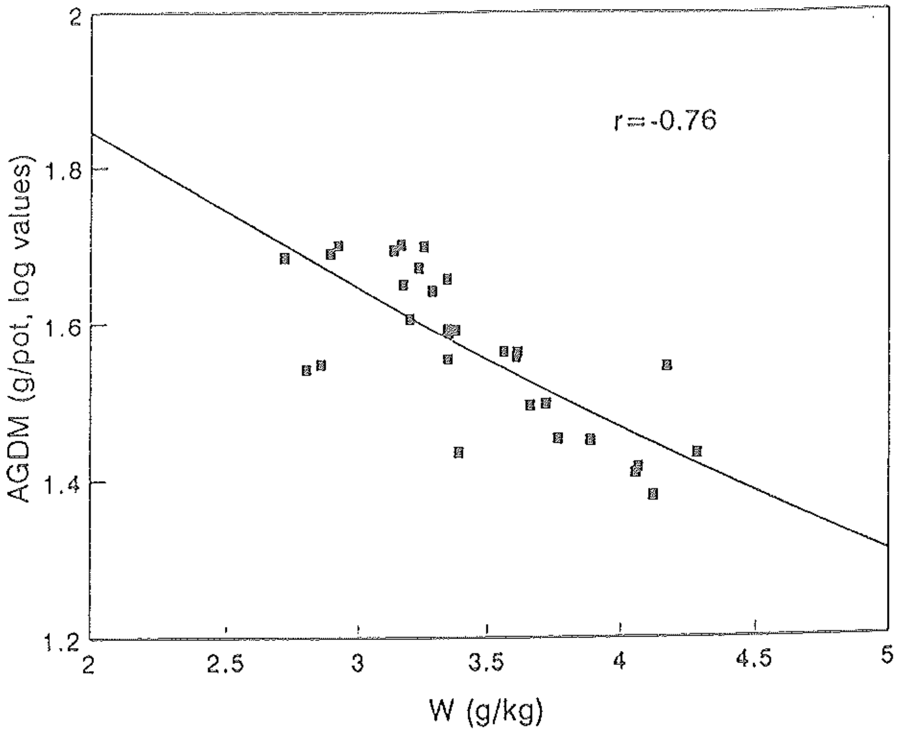

Figure 2. Relation between biological yields (AGDM) and transpiration efficiency (W) in ten barley genotypes across the three moisture treatments (FC, 1/3 FC and terminal stress) Values are averages of the two seasons.

As expected from the theory (Farquhar and Richards, 1984), transpiration efficiency and ^{13}C discrimination (Δ) were negatively and significantly related during both seasons (Table 3). The mean correlation of the two seasons across the three moisture treatments was -0.85 (Figure 3).

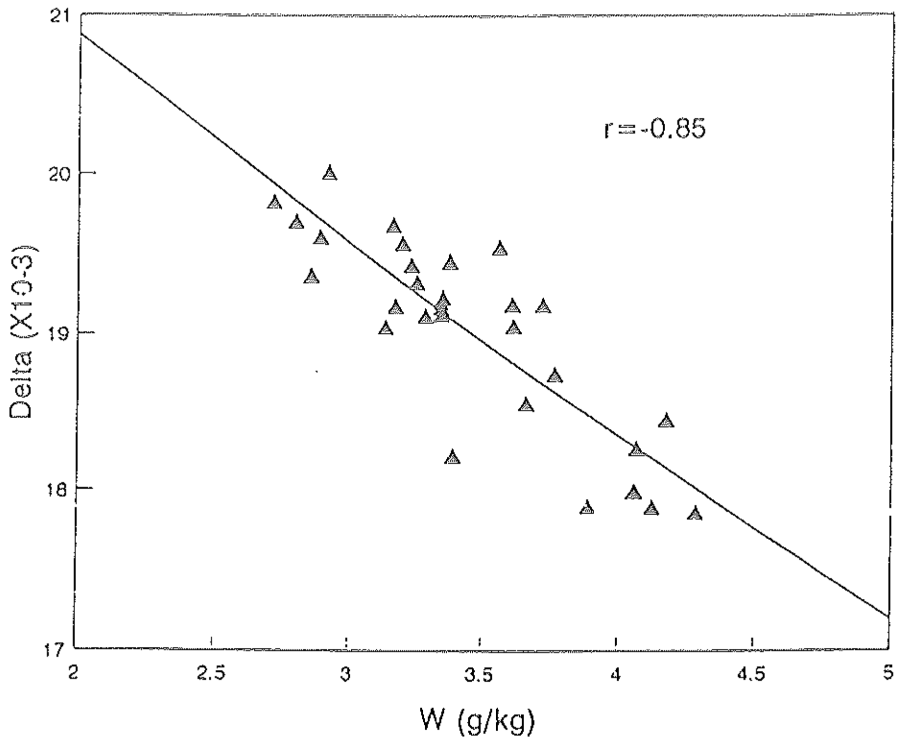

Figure 3. Relation between ^{13}C discrimination (Δ) and transpiration efficiency (W) in ten barley genotypes across the three moisture treatments (FC, 1/3 FC and terminal stress) Values are averages of the two seasons.

Relationship between yield, W and Δ within moisture treatments and seasons

The relationships among yield (GY and AGDM), *W* and Δ appeared to be inconsistent when they were examined within individual moisture treatments or seasons. The relationship between yield and Δ showed a strong positive relation across moisture levels and was positive in the 1991 experiment in the nonstressed (FC) and fully stressed treatments (1/3 FC) (Table 4). In the split moisture stress regimes (post and pre-heading stress) the relations were also positive but weaker (Table 4). Similarly, transpiration efficiency (*W*) was negatively and significantly related to yield in the non-stressed treatment. In the other treatments relationships were also negative but not significant.

Table 4. Correlations between GY, AGDM, *W* and Δ within each moisture treatment for each season in 10 barley genotypes grown under plastic house conditions. * P <0.05; ** P <0.01; *** P <0.001; n.s., not significant

	Moisture treatment							
	FC		1/3 FC		1/3 FC-FC		FC-1/3 FC	
Trait	Δ	*W*	Δ	*W*	Δ	*W*	Δ	*W*
			90/91 season					
GY	0.88***	-0.69*	0.82***	-0.46ns	0.69*	-0.67*	0.59*	-0.42ns
AGDM	0.75**	-0.76**	0.77**	-0.44ns	0.50ns	-0.17ns	0.25ns	-0.46ns
W	-0.83***		-0.81***		-0.84***		-0.74**	
			91/92 season					
GY	-0.36ns	0.22ns	0.35ns	0.36ns	0.14ns	0.41ns	0.45ns	0.57*
AGDM	-0.20ns	0.72**	0.66*	0.20ns	0.40ns	0.41ns	0.45ns	0.72**
W	-0.10ns		-0.69*		-0.45ns		-0.66*	

The relation between yield and Δ in the 1992 experiment was negative but not significant in the unstressed treatment. In the fully stressed treatment (1/3 FC) the relation was positive as in the relation across moisture levels. Contrary to the 1991 season, the slopes of the relation between *W* and yield in the 1992 season were positive in all moisture treatments, but significant in the non-stressed and in terminal moisture stress treatments (Table 4).

Despite these differences in response between the two experiments the slope of the relation between Δ and transpiration efficiency *W* remained negative, although not significant in all cases (Table 4).

Correlations between genotypes response at different moisture levels and seasons

The relation between yield, *W* and Δ in the non-stressed treatment and the mean response over the other three moisture stressed treatments in both seasons are summarized in table (5)$_{13}$In the first experiment correlations were high between C discrimination at high and low moisture levels, and in all other traits (Table 5), while in the second experiment, grain yield (GY) was the only trait which correlated significantly between high and low moisture treatments.

Interseasonal correlations between various traits (*W*, yield and Δ) were high and significant between treatments which were subjected to moisture stress. The unstressed treatments did not correlate significantly between the two seasons with the exception of *W* (Table 6).

Table 5. Correlations of Δ *W*, GY and AGDM between moisture levels in 10 barley genotypes grown under plastic house conditions within each growing season. * P <0.05; ** P <0.01; *** P <0.001; **n.s.,** not significant

	Unstressed treatment (FC)			
	90/91 season			
Mean of all stressed treatments	Δ	*W*	GY	AGDM
Δ	0.94^{***}			
W	-0.66^{*}	0.84^{***}		
GY	0.71^{***}	-0.67^{*}	0.91^{***}	
AGDM	0.45ns	-0.35ns	0.73^{***}	0.85^{***}
	91/92 season			
Δ	-0.41ns			
W	0.14ns	0.44ns		
GY	-0.50ns	-0.26ns	0.83^{***}	
AGDM	-0.50ns	0.01ns	0.10ns	0.10ns

Table 6. Correlation's between the two seasons among moisture stressed and unstressed treatments for Δ , *W* ,GY and AGDM in 10 barley genotypes grown under plastic house conditions. * P <0.05; ** P <0.01; *** P <0.001; **n.s.,** not significant

	90/91 season			
	Δ	GY	AGDM	*W*
		Unstressed		
91/92 season				
Unstressed	-0.43ns	0.32ns	-0.30ns	0.57*
		Stressed		
Stressed	0.58*	0.72*	0.54ns	0.85***

DISCUSSION

The relationship between carbon isotope discrimination (Δ) and yield in crop species has been reported in the literature to vary from strongly negative (Hubick *et al.*, 1986; Wright *et al.*, 1988 and 1994), positive, or to no relation according to species and growth conditions (Craufurd *et al.*, 1991; Condon *et al.*, 1987; Condon and Richards, 1993; Ehdaie *et al.*, 1991; Johnson and Bassett, 1991).

Δ is largely related to the ratio of intercellular to atmospheric carbon dioxide concentration (ci/ca). This ratio is in turn influenced by stomatal conductance and the photosynthesis capacity of the plant. The relationship between yield and Δ is expected to be positive when stomatal conductance increases and photosynthetic capacity remains constant. Such that ci/ca ratio increases and at the same time transpiration efficiency is reduced (Condon *et al.*, 1987). The reverse conditions would lead to a reduction in ci/ca ratio, an increase in *W*, and a negative relationship between yield and Δ (Wright *et al.*, 1994). The two patterns, separately or in combination, were observed in several crop species (Ehleringer *et al.*, 1990; Hubick *et al.*, 1986; Condon *et al.*, 1990).

In this study under the plastic house conditions, the relation between Δ and either grain or dry matter production in barley was strongly positive across all moisture levels. In other studies similar responses were observed in durum wheat (Kirda *et al*, 1992) and in barley (Austin *et al.*, 1990). Such a positive relationship over an increased moisture gradient is expected, since stomatal conductance will increase and so will ci/ca and Δ (Table 3 and Fig. 1). Similarly, transpiration efficiency will decrease and a negative relationship between yield (GY and AGDM) and *W* might also be expected (Table 3 and Figure 2). However, it should be noted that the relationships were inconsistent when they were examined within individual moisture levels. In the first experiment the relationship within each moisture treatment was similar across all moisture levels. Yield correlated highly and positively with Δ and negatively with transpiration efficiency, in the nonstressed and in the fully stressed treatments. While the negative relationships between yield and *W* were weaker in the split moisture treatments (Table 4). In the second experiment the relationship between yield and Δ was significantly positive only in the fully stressed treatment, in the nonstressed moisture regime the relation was weakly negative. Similarly, the relationship between biomass production and W was reversed in the nonstressed treatment and became positive (Table 4).

These differences could be partially related to the differences in environmental conditions inside the plastic house, and by the low differences in yield among moisture treatments in the first experiment. Temperatures were milder in the second experiment, mean maximum temperature was 18.0 °C in comparison with 21.8 °C in the first experiment. Similarly, relative humidity was 80 % and 71 % respectively. Consequently, mean daily seasonal vapor pressure deficit (vpd) was 0.34 kpa in 1992 and 0.53 in 1991, and the growing season was longer in 1992. Similar responses in wheat, grown under plastic house conditions, were observed by Ehdaie *et al.* (1991).

A strong positive relation between Δ and yield during the first season and the higher vpd, especially during the period between heading and maturity (0.71 kpa), suggests that variation in stomatal conductance, rather than photosynthetic capacity, greatly influenced ci/ca ratio and led to the positive relationship. While in the second experiment at a high moisture level, vpd was low, water used in transpiration was high and the negative relation between yield and Δ, indicates that variations in photosynthesis capacity was the controlling factor over the ci/ca variations and caused the negative relationship. Moreover, in the fully stressed moisture treatment, water used in transpiration was similar between the two seasons and regardless of ambient environmental conditions the relation between yield and Δ was positive in both seasons, although weak in 1992 (Table 4). Positive relations between yield and Δ were observed in a close set of barley landraces and improved varieties grown under field conditions in similar Mediterranean environments (Craufurd *et al.*, 1991), also in durum wheat (Kirda *et al.*, 1992) and in bread wheat (Condon *et al.*, 1987).

Contrary to the relation between Δ and yield the relation between Δ and transpiration efficiency (W) was mostly significant and consistently negative as theory predicts (Farquhar and Richards,

1984) under all moisture treatments and during both seasons (Table 4).

An important measure of the suitability of Δ as an indirect selection criterion is the stability of Δ across moisture levels and the relation between Δ and other plant traits under various environmental conditions. In this study, under controlled environmental conditions, the relation between Δ measured at maturity under unstressed and stressed moisture conditions varied. Correlations were high in one season and low during the other. Similarly the relations between Δ measured at high moisture level and yield or *W* at low moisture levels were significant in the first season and weak in the second (Table 5), although grain yield rankings were similar between high and low moisture levels during both seasons.

The stability of Δ , or other traits, measured during the two seasons was also weak between the unstressed moisture treatments. Transpiration efficiency (*W*) was the only trait which was consistent during the two seasons. While among moisture stressed treatments Δ, GY and *W* all correlated significantly across the two seasons (Table 6). Therefore, it is concluded that Δ is more stable across moisture limited environments than unlimited ones.

In conclusion the relationships among yield, transpiration efficiency, and ^{13}C discrimination (Δ) in barley under controlled environmental conditions showed that: First, selection for high Δ is generally associated with higher yield potential under either high or low moisture levels. Second, higher transpiration efficiencies (*W*) were associated with lower Δ and consequently with lower yield potential. This is inconsistent with the results obtained from field studies on the same genotypes where the relations between Δ and W were influenced by variation in temperature and moisture levels (Dakheel *et al.*, 1994). Third, the relation between Δ across moisture levels and seasons was consistent only under moisture stress. Suggesting therefore, that utilizing Δ in selection for dry areas is more appropriate when selection is carried out within the targeted environment. Finally, it is emphasized from the controlled environment, as well as field studies (Dakheel *et al.*, 1994), that the relation between Δ and yield across a moisture gradient does not necessarily reflect the relation observed within individual moisture regimes.

ACKNOWLEDGMENT

This research was supported in part under Grant No. DHR-5542-G-SS-9085-00, Program in Science and Technology Cooperation, Office of the Science Advisor, U. S. Agency for International Development.

REFERENCES

Acevedo, E. (1993). Potential of carbon isotope discrimination as a selection criterion in barley breeding. In 'Stable isotopes and plant carbon-water relations'. (Eds J. R. Ehleringer, A. E. Hall and G. D. Farquhar). pp.399-417. (Academic Press: New York).

Austin, R. B., Craufurd, P. Q., Hall, M. A., Acevedo, E., Silveira, Pinheiro, B., and Ngugi, E. C. K.. (1990). Carbon isotope discrimination as a means of evaluating drought resistance in barley, rice and cowpeas. Bull. Soc. bot. Fr. 137, Actual. bot. 1:21-30.

Condon, A. G., and Richards, R. A. (1993). Exploiting genetic variations in transpiration efficiency in wheat: An agronomic view. In 'Stable isotopes and plant carbon-water relations'. (Eds J. R. Ehleringer, A. E. Hall and G. D. Farquhar) pp.435-450. (Academic Press: New York).

Condon, A. G., Richards, R. A., and Farquhar, G. D. (1987). Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field grown wheat. *Crop Science* 27, 996-1001.

Condon, A. G., Farquhar, G. D., and Richards, R. A. (1990). Genotypic variation in carbon isotope discrimination and transpiration efficiency in wheat. Leaf gas exchange and whole plant studies. *Australian Journal of Plant physiology* 17, 9-22.

Craufurd, P. Q., Austin, R. B., Acevedo, E., and Hall, M. A. (1991). Carbon isotope discrimination and grain yield in barley. *Field Crops Research* 27,301-313.

Dakheel, A. J., Peacock, J. M., Naji, I., and Acevedo, E. (1994). Carbon isotope discrimination and water use efficiency in barley under field conditions. *Aspects of Applied Biology* 38, 173-184.

Ehdaie, B. A., Hall, A. E., Farquhar, G. D., Nguyen, H. T., and Waines J G. (1991). Water-use efficiency and carbon isotope discrimination in wheat. *Crop Science* 31, 1282-1288.

Ehleringer, J. R., White, J. W., Johnson, D. A., and Brick, M. (1990). Carbon isotope discrimination, photosynthetic gas exchange, and transpiration efficiency in beans and range grasses. *Acta Oecologia* 11, 611-625.

Farquhar, G. D., and Richards, R. A. (1984). Isotope composition of plant carbon correlates with water use efficiency of wheat genotypes. *Australian Journal of Plant Physiology* 11, 539-552.

Farquhar, G. D., O'Leary, M. H., and Berry, J. A. (1982). On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* 9, 121-137.

Hubick, K. T., Farquhar, G. D., and Shorter, R. (1986). Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut(Arachis) germplasm. *Australian Journal of Plant Physiology* 13, 803-816.

Johnson, R. C., and Bassett, L. M. (1991). Carbon isotope discrimination and water use efficiency in four cool-season grasses. *Crop Science* 31, 157-162.

Kirda, C., Mohamed, A. R. A. G., Kumarasinghe, K. S., Montenegro, A., and Zapata, F.(1992). Carbon isotope discrimination at vegetative stage as an indicator of yield and water use efficiency of spring wheat (*Triticum turgidum* L. var *durum*). *Plant and Soil* 147, 217-223.

Meinzer, F. C., Goldstein, G., and Grantz, D. A. (1993). Carbon isotope discrimination and gas exchange in coffee during adjustment to different moisture regimes. In 'Stable isotopes and plant carbon-water relations'. (Eds J. R. Ehleringer, A. E. Hall and G. D. Farquhar). pp.327-345. (Academic Press: New York).

Passioura, J. B. (1977). Grain yield, harvest index and water use of wheat. *Journal of.Australian Institute of Agricultural. Sciences*. 43, 117-120.

Richards, R. A., and Condon, A. G. (1993). Challenges ahead in using carbon isotope discrimination in plant-breeding programs. In 'Stable isotopes and plant carbon-water relations'. (Eds J. R. Ehleringer, A. E. Hall and G. D. Farquhar). pp.451-462. (Academic Press: New York).

Steel, R. G. D., and Torrie, J. H. (1980). Principles and Procedures of Statistics: A biometrical approach. (McGraw-Hill: New York).

Wright, G. C., Hubick, K. T., and Farquhar, G. D. (1988). Discrimination in carbon isotopes of leaves correlates with water-use efficiency of field-grown peanut cultivars. *Australian Journal of Plant Physiology* 15, 815-825.

Wright, G. C., Nageswara, Rao. R. C., and Farquhar, G. D. (1994). Water-use efficiency and carbon isotope discrimination in Peanut under water deficit conditions. *Crop Science* 34, 92-97.