

Relations of carbon isotope discrimination and other physiological traits to yield in common bean (*Phaseolus vulgaris*) under rainfed conditions

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SUMMARY

Although direct selection for seed yield under water deficit can result in genetic gains in the common bean (*Phaseolus vulgaris* L.), progress could be enhanced through selection for additional traits that are related to underlying mechanisms of adaptation to water deficit. Carbon isotope discrimination (Δ) has received considerable attention as an indicator of water use efficiency and adaptation to water deficit. To test the utility of Δ as a selection criterion, Δ and other traits were measured in F_2 and F_3 generations of a nine-parent diallel grown under rainfed conditions at two locations in Colombia with contrasting soil types. An irrigated trial was also conducted at one location. Significant ($P < 0.05$) differences among parents, F_2 and F_3 were found for carbon isotope discrimination (Δ), leaf optical density (OD), leaf nitrogen (N) and potassium (K) concentrations, relative duration of pod-filling period (RDPF), shoot dry weight (SDW) and harvest index (HI). Effect of location and water regime and their interactions with genotype were also frequently significant. Heritability estimates, determined by regressing the F_3 on the F_2 , ranged from 0.11 ± 0.11 (S.E.) to 0.33 ± 0.10 for OD, 0.22 ± 0.07 to 0.44 ± 0.09 for N, 0.04 ± 0.05 to 0.29 ± 0.08 for K, 0.40 ± 0.08 to 0.43 ± 0.15 for RDPF and 0.30 ± 0.22 to 1.00 ± 0.24 for SDW. All values for Δ and HI did not differ significantly from zero. Correlations between seed yield and OD and RDPF were negative, whereas those with N, K, SDW, and HI were positive. For all traits, mean square values for general combining ability (GCA) were usually significant and larger than those for specific combining ability (SCA). All significant GCA effects for Δ for 'Rio Tibagi', 'San Cristobal 83' and 'Apetito' were negative, while those for 'Bayo Rio Grande', 'Bayo Criollo del Llano', 'Durango 222' and BAT1224 were positive. Although Δ appears unsuitable as an indirect criterion for selection for yield under water deficit, further study of genotypes exhibiting contrasting values of Δ might reveal differences in mechanisms of adaptation to water deficits, thus leading to other selection criteria or identification of valuable parental lines.

INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) production in many regions occurs under rainfed conditions where water deficit limits yield and causes instability of production. Although agronomic practices are important under water deficit, cultivar improvement is usually seen as the most promising approach to increase yields. Recent studies indicate that direct selection for seed yield in common bean can be effective both for well-watered (Nienhuis & Singh 1988; Singh *et al.* 1990) and deficit conditions (White *et al.* 1994). In the latter study, values for realized gain in seed yield of bulk F_3 populations (after selection among F_2 populations) ranged from 0.4 to 15.7% in four rainfed environments. Nonetheless, yield testing

is difficult and costly, and gains from selection are sometimes low. This situation has led to extensive research on mechanisms of adaptation to water deficit not only in common bean but in many other crops (Blum 1988; Ludlow & Muchow 1990). Such studies hope to detect traits that either are more efficient as selection criteria than yield *per se* or aid in maximizing yield gains when selected simultaneously with yield.

Carbon isotope discrimination (Δ) has received considerable attention as an indicator of water use efficiency (WUE) and adaptation to water deficit (Farquhar & Richards 1984; Hubick *et al.* 1986; Ehleringer *et al.* 1990; Hall *et al.* 1992). Theoretical arguments and studies of actual plant water use have shown that Δ is directly related to the ratio of internal (c_i) and ambient (c_a) CO_2 concentrations in C_3 species

(Farquhar *et al.* 1982, 1989). As a consequence, for constant vapour pressure deficit, the ratio of the rates of carbon assimilation (A) and transpiration (E) is closely associated with Δ , as found in the common bean (Ehleringer *et al.* 1991). In certain situations, Δ is also associated with crop WUE measured as the ratio of crop dry weight to cumulative transpiration (Farquhar & Richards 1984; Ismail & Hall 1992), since discrimination provides an integrated measure of c_i/c_a in C_3 plants. Carbon isotope discrimination was originally quantified as the deviation of the isotopic composition of plant tissue from a standard, but Farquhar & Richards (1984) showed that carbon isotope discrimination is more easily interpreted in relation to WUE if expressed as

$$\Delta = R_a/R_p - 1$$

where R_a and R_p are isotope abundances in the air and in the plant, and Δ is expressed on a 'per mil' (‰) basis. Typically, C_3 plants have Δ values of *c.* 20‰ (Farquhar *et al.* 1989).

At first glance a low value of Δ , implying low c_i/c_a , would appear to be a desirable trait for adaptation to water deficit conditions. In practice, because Δ only reflects one component of crop WUE, and variation in Δ may arise through different mechanisms, relations between Δ and yield under water deficits vary considerably (Ehleringer *et al.* 1990). In field trials of common bean under water deficit, the highest yields among ten genotypes were associated with high values of Δ in a deep mollisol, and with intermediate values of Δ in a shallow oxisol which had a much lower water-holding capacity than the mollisol (White *et al.* 1990).

Values of Δ across seasons or locations with similar patterns of water deficit often show surprising stability, as indicated by correlations among genotypes (Farquhar *et al.* 1989). For the bean genotypes evaluated at Palmira and Quilichao, Colombia, Δ was highly correlated ($r = 0.84$, $P = 0.01$) between the sites (White *et al.* 1990). Hall *et al.* (1990) found that genotype rankings for Δ in cowpea were similar over three years of trials.

The former considerations suggested a need to examine the inheritance of Δ in common bean in different environments, and the effectiveness of Δ as an indirect selection criterion for seed yield. The present study reports patterns of inheritance of Δ at two locations with contrasting soil types. Values of Δ sometimes show stronger relations with shoot dry weight than with seed yield (White *et al.* 1990), so relations with shoot dry weight were also considered. To compare Δ with other traits that might show associations with seed yield, various other traits were also examined. Leaf nitrogen and potassium concentrations and leaf optical density (OD) were included since, in a breeding programme, these could be

determined with similar or lower cost than Δ , and rationales exist for expecting them to vary with adaptation to water deficit. Leaf nitrogen and OD might indicate levels of N reserves available for mobilization to seed, while leaf potassium concentration is sometimes associated with yield under water deficit (Hanway & Johnson 1985). Harvest index and crop phenology were also considered, since these traits often show associations with yield in common bean (Scully *et al.* 1991; White & Izquierdo 1991; White *et al.* 1992).

MATERIALS AND METHODS

The F_2 and F_3 populations from a nine-parent diallel (including parents, but without reciprocals) were grown as bulks under rainfed conditions in three randomized complete blocks at two locations in Colombia (Quilichao and Palmira), with similar climatic conditions, but different soils (Oxisol and Mollisol). At Palmira, irrigated trials were also conducted. The parents were four genotypes adapted to the semi-arid central highlands (HL) of Mexico ('Apetito', 'Bayo Criollo del Llano', 'Bayo Rio Grande' and 'Durango 222'), four genotypes identified as adapted to water deficits at the Colombian sites (BAT477, V8025, 'Rio Tibagi' and 'San Cristobal 83') and considered to represent germplasm adapted to tropical mid-elevations (ME), and one genotype (BAT1224) selected for high yield under irrigation but low yield under water deficit in Colombia. The F_2 and F_3 populations were evaluated in separate years, so results would include effects of season-to-season variation in patterns of water deficit.

Detailed descriptions of genetic materials, levels of water deficit and experimental conditions and procedures are provided elsewhere (White *et al.* 1994). Briefly, trials at both locations were managed using recommended practices to control weeds, diseases and insects. The population was 22 plants/m² after initial thinning. Plots were 5.8 m², permitting a bordered harvested area of 3.6 m². Water deficits were imposed by withholding irrigation after seedling establishment. Mean seed yields under deficit were 580 and 1370 kg/ha for the F_2 and F_3 trials at Quilichao and 700 and 1610 kg/ha at Palmira, as compared to 2370 and 2440 kg/ha for the irrigated F_2 and F_3 trials at Palmira.

Besides data for seed yield, days to maturity and 100-seed weight presented previously (White *et al.* 1994), various leaf traits, shoot dry weight at maturity, relative duration of pod-filling and harvest index (HI) were measured. Leaf Δ and N and K concentrations were determined on bulk samples of 30 central leaflets of fully-expanded trifoliolate leaves taken at *c.* 50 days after planting (early seed filling phase) from separate

Table 1. Combined ANOVA across environments for carbon isotope discrimination (Δ), leaf optical density (OD), leaf N and K concentrations, relative duration of pod filling (RDPF), shoot dry weight (SDW) and harvest index (HI) for F_2 and F_3 populations of common bean from a nine-parent diallel (including parents) grown at Quilichao and Palmira, Colombia and including an irrigated trial at Palmira as a third environment

Source	Mean squares (MS) and variance ratios (VR) for trait																				
	Δ			OD			Leaf N			Leaf K			RDPF			SDW			HI		
	D.F.	MS	VR*	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR		
F_2 population																					
Trial†	2	59.84	20.4	19840	15.5	24.66	86.6	3.321	28.6	404.4	77.4	2115.00	122.6	2873.6	7.8						
Location	1	84.67	28.9	1750	1.4	25.88	90.8	0.248	1.8	559.6	107.0	2299.00	133.3	2303.1	6.3						
Location \times Water regime	1	35.01	11.9	37929	29.7	23.45	82.3	6.393	46.3	249.2	47.7	1931.00	111.9	3444.3	9.4						
Error (a)	6	2.93	—	1278	—	0.28	—	0.116	—	5.2	—	17.25	—	368.2	—						
Population	44	0.32	2.4	344	2.8	0.51	3.7	0.030	1.5	10.9	5.0	2.68	2.7	25.9	1.3						
Population \times Trial	88	0.13	1.3	123	1.2	0.14	1.4	0.020	2.0	2.2	2.2	1.80	1.8	20.0	2.0						
Population \times Location	44	0.12	1.2	85	0.9	0.12	1.2	0.012	1.2	1.9	1.9	2.24	2.2	20.9	2.1						
Population \times Location \times Water regime	44	0.15	1.5	160	1.6	0.15	1.5	0.027	2.7	2.5	2.5	1.36	1.4	19.0	1.9						
Error (b)	264	0.10	—	100	—	0.10	—	0.010	—	1.0	—	1.00	—	10.0	—						
F_3 population																					
Trial	2	15.83	43.0	5651	5.1	63.52	35.5	10.595	49.2	222.2	106.8	49.68	163.4	35.1	1.8						
Location	1	9.89	26.8	4191	3.8	3.47	1.9	0.366	1.7	444.2	213.6	69.88	229.7	2.0	0.1						
Location \times Water regime	1	21.76	59.0	7110	6.4	123.56	69.0	20.824	96.8	0.1	0.1	29.48	96.9	68.3	3.5						
Error (a)	6	0.37	—	1117	—	1.79	—	0.215	—	2.1	—	0.30	—	19.4	—						
Population	44	0.25	1.7	330	2.2	0.56	3.3	0.031	1.3	16.0	9.9	0.30	1.9	9.2	0.8						
Population \times Trial	88	0.14	1.4	152	1.5	0.17	1.7	0.024	2.4	1.6	1.6	0.16	1.6	12.0	1.2						
Population \times Location	44	0.18	1.8	133	1.3	0.22	2.2	0.021	2.1	1.8	1.8	0.12	1.2	11.3	1.1						
Population \times Location \times Water regime	44	0.10	1.0	172	1.7	0.12	1.2	0.027	2.7	1.5	1.5	0.20	2.0	12.8	1.3						
Error (b)	264	0.10	—	100	—	0.10	—	0.010	—	1.0	—	1.00	—	10.0	—						

* Critical values of variance ratios for trial (2 and 6 D.F.) are 5.1 at the 5% level and 10.9 at the 1% level; for location and location \times water regime (1 and 6 D.F.) are 6.0 and 13.7; for population (44 and 88 D.F.) are 1.5 and 1.8; for population \times trial (88 and 264 D.F.) are 1.3 and 1.5; and for population \times location and population \times location \times water regime (44 and 264 D.F.) are 1.4 and 1.6.

† Trials are Quilichao, Palmira-raised and Palmira-irrigated.

Table 2. Mean values of parents and mean, minimum and maximum values among F_2 and F_3 populations of common bean for seven traits measured at Quilichao and Palmira, Colombia

Material		Quilichao		Palmira			
				Rainfed		Irrigated	
		F_2	F_3	F_2	F_3	F_2	F_3
		Carbon isotope discrimination (Δ ; ‰)					
Parents*	ME†	19.45	19.71	17.81	19.57	18.98	20.65
	HL†	19.63	20.14	18.26	19.73	19.06	20.61
	BAT1224	20.16	20.18	18.37	20.09	19.06	21.14
Populations	Mean	19.70	20.07	18.20	19.85	19.12	20.60
	Minimum	18.79	19.76	17.66	19.43	18.40	19.90
	Maximum	20.20	20.62	18.77	20.30	19.61	21.20
s.e.‡	0.20	0.14	0.22	0.31	0.25	0.21	
		Leaf optical density (OD)					
Parents	ME	395	465	443	487	382	467
	HL	423	466	460	502	387	480
	BAT1224	389	478	448	489	387	450
Populations	Mean	408	465	442	485	386	469
	Minimum	383	440	408	445	331	442
	Maximum	436	498	501	508	440	495
s.e.	12	9	17	11	15	8	
		Leaf N (%)					
Parents	ME	4.35	4.62	4.38	3.96	5.10	4.94
	HL	3.63	3.98	3.92	3.44	4.74	4.76
	BAT1224	3.94	4.14	4.26	3.76	5.03	5.03
Populations	Mean	3.85	4.21	4.19	3.70	4.82	4.90
	Minimum	3.20	3.55	3.79	3.37	3.99	4.45
	Maximum	4.48	4.57	4.84	4.29	5.51	5.31
s.e.	0.17	0.13	0.16	0.17	0.23	0.15	
		Leaf K (%)					
Parents	ME	1.78	1.68	1.63	1.43	2.08	2.07
	HL	1.48	1.55	1.34	1.22	2.32	2.17
	BAT1224	1.60	1.54	1.65	1.37	2.22	1.95
Populations	Mean	1.47	1.54	1.42	1.30	2.12	2.09
	Minimum	1.08	1.33	1.22	1.01	1.61	1.78
	Maximum	1.84	1.78	1.84	1.56	2.57	2.43
s.e.	0.16	0.09	0.10	0.08	0.16	0.08	
		Relative duration of pod-filling (RDPF; %)					
Parents	ME	45.8	49.1	48.4	50.1	49.5	49.2
	HL	49.1	51.4	49.8	53.7	54.3	53.5
	BAT1224	46.4	48.0	48.8	48.1	49.3	49.4
Populations	Mean	48.2	50.7	50.1	53.0	52.5	53.0
	Minimum	44.8	47.7	48.2	48.7	49.5	49.2
	Maximum	51.0	52.1	51.3	55.0	56.9	55.0
s.e.	0.6	0.4	0.6	0.7	0.9	0.7	
		Shoot dry weight (SDW; kg/ha)					
Parents	ME	1050	2840	1410	3530	3590	4670
	HL	940	2200	1270	2100	3030	4170
	BAT1224	500	2760	800	1570	3620	5270
Populations	Mean	1010	2550	1470	2950	3530	4610
	Minimum	730	2000	870	1940	2820	3240
	Maximum	1410	3150	2060	4700	4240	5900
s.e.	140	220	230	550	220	380	
		Harvest index (HI; %)					
Parents	ME	61.1	59.1	47.1	58.9	69.3	53.0
	HL	55.8	55.6	30.6	58.7	65.0	50.5
	BAT1224	62.4	57.2	20.2	44.0	68.8	56.3
Populations	Mean	57.9	53.8	46.4	56.5	68.3	54.2
	Minimum	50.3	46.3	26.7	38.9	60.8	45.8
	Maximum	64.7	64.2	67.9	67.8	73.7	66.1
s.e.	2.9	4.0	8.2	8.5	2.3	4.5	

* Values for parents grown in same trials as F_2 or F_3 populations.

† ME = Mean of mid-elevation, tropically adapted parents. HL = Mean of Mexican highland adapted parents.

‡ Standard error is with 88 D.F. and is for parents plus individual populations.

Table 3. Heritability estimated by parent-offspring regression and correlation with seed yield and 100-seed weight for various physiological traits in common bean for populations from a nine-parent diallel grown at Quilichao and Palmira, Colombia

Trait	Trials†	Heritability	Correlation of trait with			
			Seed yield		100-seed weight	
			F ₂	F ₃	F ₂	F ₃
Carbon isotope discrimination (Δ)	Q	0.10 (0.08)*	-0.02‡	-0.38	0.04	0.56
	P _R	0.00 (0.35)	-0.15	0.45	0.37	0.11
	P _I	0.12 (0.12)	0.04	0.19	0.13	-0.25
Leaf optical density (OD)	Q	0.33 (0.10)	-0.22	0.07	0.42	0.44
	P _R	0.11 (0.11)	-0.51	-0.37	0.39	0.30
	P _I	0.13 (0.06)	-0.43	-0.57	0.53	0.40
Leaf N	Q	0.39 (0.06)	0.38	0.20	-0.51	-0.80
	P _R	0.44 (0.09)	0.32	0.67	-0.35	-0.29
	P _I	0.22 (0.07)	0.42	0.37	-0.32	-0.18
Leaf K	Q	0.04 (0.05)	0.27	0.20	-0.20	-0.24
	P _R	0.29 (0.08)	0.03	0.39	-0.18	0.20
	P _I	0.22 (0.07)	0.07	-0.13	0.20	0.37
Relative duration of pod-filling (RDPF)	Q	0.42 (0.05)	-0.21	-0.66	0.58	0.46
	P _R	0.43 (0.15)	0.07	-0.10	0.13	0.34
	P _I	0.40 (0.08)	-0.42	-0.23	0.39	0.42
Shoot dry weight (SDW)	Q	0.30 (0.22)	0.90	0.82	0.30	-0.44
	P _R	1.00 (0.24)	0.83	0.89	-0.33	-0.32
	P _I	0.42 (0.13)	0.90	0.75	-0.41	-0.41
Harvest index (HI)	Q	0.14 (0.10)	0.50	0.41	-0.45	-0.25
	P _R	0.00 (0.07)	0.86	0.26	0.28	-0.29
	P _I	0.00 (0.16)	0.32	0.46	0.08	-0.20

* Values in parentheses indicate standard errors of estimate with D.F. of 34.

† Q = Quilichao; P_R = Palmira-rainfed; P_I = Palmira-irrigated.

‡ Critical values of correlation coefficient are: 0.33 at the 5% level and 0.42 at the 1% level (for $n = 36$).

plants in each plot. Samples were dried at 70 °C for a minimum of 48 h in a forced draught oven, milled and then analysed.

Subsamples for Δ were combusted in a CHN analyser coupled to a Finnegan MAT Delta E isotope ratio mass spectrometer. After combustion, CO₂ was purified before injection into the mass spectrometer to determine the ¹³C/¹²C ratios of the resulting CO₂. To calculate Δ , $\delta^{13}\text{C}$ of air was assumed to be 8‰ on the PDB scale (Mook *et al.* 1983; Farquhar *et al.* 1989). The internal precision of the mass spectrometer was 0.02‰, and replicate analyses of tissues were normally within 0.15‰ of each other.

Leaf N concentrations were determined colorimetrically after Kjeldahl digestion (Salinas & Garcia 1985). Leaf K concentrations were determined using atomic absorption spectrophotometry after acid digestion (Salinas & Garcia 1985). Both N and K concentrations were expressed as fractions of leaf dry weight.

Leaf optical density (OD) measurements were based on OD of 30 leaflets per plot using a hand-held

Chlorophyll Photometer (Design Electronics Ltd, Palmerston North, New Zealand). The instrument is reported to provide readings directly convertible to chlorophyll concentration (Hardacre *et al.* 1984), but in calibration trials with bean, it was found that the relation between OD and chlorophyll concentration varied greatly with cultivar and growing conditions (C. Montes & J. W. White, unpublished). Thus data are reported as leaf OD, with arbitrary units where larger values indicate greater OD.

Shoot dry weight (SDW) was determined at maturity from the central 1.2 m² of the yield plot, following drying as per leaf samples. Relative duration of pod-filling (RDPF) was estimated as the difference between days to flowering and to maturity divided by days to maturity.

In analyses of variance over trials, locations were considered random effects, while water regimes and populations were treated as fixed effects. Data for each trial were weighted in proportion to the inverse of the error mean squares for that trial. Heritability (h^2) was estimated using parent-offspring regressions

Table 4. Mean squares (MS) and variance ratios (VR) for general (GCA) and specific (SCA) combining ability for various traits in common bean measured in a nine-parent diallel grown at Quilichao and Palmira, Colombia

Source	Palmira																		
	Quilichao						Rainfed						Irrigated						
	F ₂		F ₃		F ₃		F ₂		F ₃		F ₃		F ₂		F ₃		F ₃		
D.F.	MS	VR*	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR	MS	VR	
Carbon isotope discrimination (Δ)																			
GCA	8	0.688	5.9	0.578	9.8	0.677	4.8	0.210	0.8	0.639	3.4	0.388	2.9	0.639	3.4	0.388	2.9	0.639	3.4
SCA	36	0.185	1.6	0.076	1.3	0.178	1.3	0.144	0.5	0.227	1.2	0.220	1.7	0.227	1.2	0.220	1.7	0.227	1.2
Error	88	0.116	—	0.059	—	0.141	—	0.280	—	0.187	—	0.133	—	0.187	—	0.133	—	0.187	—
Leaf optical density (OD)																			
GCA	8	2332	5.1	1719	7.7	2597	4.9	1809	3.3	3384	5.0	1309	6.4	3384	5.0	1309	6.4	3384	5.0
SCA	36	405	0.9	240	1.1	649	1.2	548	1.5	1207	1.8	257	1.3	1207	1.8	257	1.3	1207	1.8
Error	88	455	—	223	—	535	—	367	—	677	—	204	—	677	—	204	—	677	—
Leaf N																			
GCA	8	1.476	18.0	1.018	20.8	0.578	7.8	0.727	8.4	0.780	4.8	0.342	5.0	0.780	4.8	0.342	5.0	0.780	4.8
SCA	36	0.069	0.8	0.066	1.3	0.050	0.7	0.047	0.5	0.217	1.3	0.107	1.6	0.217	1.3	0.107	1.6	0.217	1.3
Error	88	0.082	—	0.049	—	0.074	—	0.087	—	0.164	—	0.068	—	0.164	—	0.068	—	0.164	—
Leaf K																			
GCA	8	0.346	4.2	0.045	2.0	0.301	10.0	0.171	9.5	0.333	4.5	0.248	10.8	0.333	4.5	0.248	10.8	0.333	4.5
SCA	36	0.096	1.2	0.032	1.4	0.035	1.2	0.035	1.9	0.138	1.9	0.030	1.3	0.138	1.9	0.030	1.3	0.138	1.9
Error	88	0.082	—	0.023	—	0.030	—	0.018	—	0.074	—	0.023	—	0.074	—	0.023	—	0.074	—
Shoot dry weight (SDW)																			
GCA	8	152523	2.6	994930	6.9	795705	5.2	7265736	8.2	1635292	11.4	2355785	5.6	1635292	11.4	2355785	5.6	1635292	11.4
SCA	36	60761	1.1	135210	0.9	142309	0.9	771720	0.9	207025	1.4	477102	1.1	207025	1.4	477102	1.1	207025	1.4
Error	88	58094	—	143756	—	153689	—	891128	—	143484	—	424254	—	143484	—	424254	—	143484	—
Harvest index (HI)																			
GCA	8	134.0	5.4	102.2	2.1	1546.0	7.7	211.7	1.0	80.7	5.0	137.1	2.2	80.7	5.0	137.1	2.2	80.7	5.0
SCA	36	31.6	1.3	37.3	0.8	190.9	0.9	139.1	0.7	29.4	1.8	51.3	0.8	29.4	1.8	51.3	0.8	29.4	1.8
Error	88	24.7	—	48.9	—	201.9	—	214.0	—	16.2	—	61.5	—	16.2	—	61.5	—	16.2	—

* Critical values for variance ratio with 8 and 88 D.F. are 2.0 at the 5% level and 2.7 at the 1% level, and with 36 and 88 D.F. are 1.6 at the 5% level and 1.9 at the 1% level.

Table 5. General combining ability (GCA) effects for Δ (‰) obtained from a nine-parent diallel of common bean grown at two locations in Colombia

Parent	Origin*	Palmira					
		Quilichao		Rainfed		Irrigated	
		F ₂	F ₃	F ₂	F ₃	F ₂	F ₃
BAT477	ME	0.133	0.033	-0.076	0.032	0.117	0.179
V8025	ME	-0.048	-0.055	-0.030	0.100	-0.052	-0.059
Rio Tibagi	ME	-0.131	-0.242	-0.133	-0.075	-0.093	0.084
San Cristobal 83	ME	-0.134	-0.103	-0.211	0.113	-0.020	-0.083
Apetito	HL	-0.222	-0.041	-0.062	-0.058	-0.274	-0.097
Bayo Criollo del Llano	HL	0.003	0.122	0.105	0.007	0.066	-0.049
Bayo Rio Grande	HL	0.130	-0.022	0.224	-0.027	-0.052	-0.049
Durango 222	HL	0.065	0.188	0.173	-0.126	0.163	-0.080
BAT1224	ME	0.203	0.120	0.011	0.036	0.145	0.155
S.E. (88 D.F.)		0.056	0.040	0.062	0.088	0.071	0.060

* ME = Mid-elevation, tropically adapted parents from Colombia. HL = Mexican highland adapted parents.

(Smith & Kinman 1965). Expected and realized gains were estimated according to Frey & Horner (1955) using a 20% selection pressure. GCA and SCA mean squares and GCA effects of parents were calculated using Method 2, Model I of Griffing (1956). Analyses were conducted using the SAS (1985) and GENSTAT (1987) statistical packages.

RESULTS

All traits except HI showed significant differences among populations (Table 1). Population by trial interactions were significant for leaf N, leaf K, RDPF and SDW in both the F₂ and F₃, but when mean squares were partitioned into interactions of populations with location and with location by water regime (Palmira only) traits varied greatly according to which interaction predominated, and there was little consistency from the F₂ to the F₃ for relative importance of the two interactions. Nonetheless, leaf Δ stood out for having no population \times location \times water regime interaction, while this interaction was significant in both generations for leaf OD, leaf K concentration, and RDPF.

Values of Δ varied from 18.8 to 20.6‰ at Quilichao, 17.7 to 20.3‰ at Palmira under rainfed conditions, and 18.4 to 21.2‰ at Palmira under irrigation (Table 2). Leaf OD increased under water deficit, while N and K concentrations, RDPF and SDW decreased. Parents of HL origin generally showed higher values of Δ under water deficit than did ME parents, except Apetito in the F₃ trials (which gave values of 19.10, 17.77 and 18.32‰ at Quilichao, Palmira-rainfed and Palmira-irrigated, respectively). Leaf N and K concen-

trations, and SDW, tended to be lower for HL than ME parents.

Leaf N concentration and RDPF had significant ($P < 0.05$) heritability estimates for all environments (Table 3). In contrast, estimates for Δ and HI were not significantly different from zero.

Leaf N, SDW and HI showed consistent positive correlations with seed yield (Table 3). For other traits, correlations were either low or varied over environment or generation. Only two of six correlations between Δ and seed yield were significant, and these were of opposite signs. Correlations between Δ and SDW were also low, being of the same magnitude as those for seed yield (data not shown). Leaf OD and N concentration, RDPF and SDW all varied with 100-seed weight (Table 3).

For all traits, GCA mean squares were generally large and significant ($P < 0.05$), while those of SCA were small and often non-significant (Table 4). As reported previously for seed yield (White *et al.* 1994), GCA effects for Δ varied according to whether parents were of mid-elevation or highland origin (Table 5). For example, negative GCA effects for Δ were found for Rio Tibagi and San Cristobal 83 among ME parents, while three of the four HL parents showed only positive GCA effects, the exception being Apetito. For leaf N concentration, ME parents had positive GCA effects, while HL parents consistently showed negative effects. GCA effects of BAT1224 for Δ tended to be large and positive irrespective of location or water regime. In contrast, its GCA effects for SDW were negative under water deficits, but positive under irrigated conditions, following the same pattern as described previously for seed yield (White *et al.* 1994).

DISCUSSION

The significant mean square (MS) values for genotype \times environment interactions for most traits suggest that the performance of parents, F_2 and F_3 varied between the two locations and the rainfed treatments at Palmira. This was also reflected in the estimates of heritability, correlation coefficients and GCA for most traits. Thus, choice of locations and their prevailing water deficit conditions would play an important role in determining breeding strategies.

Our low heritability estimates for Δ contrast with those reported in inheritance studies in other crops including cowpea (Hall *et al.* 1990) and groundnut (Hubick *et al.* 1988). In most inheritance studies, broad sense heritability was estimated, and in the groundnut study, one estimate was based on data for a single season and location. These data would be expected to give higher estimates than in our study, which used estimates from parent-offspring regression from trials grown in separate seasons, resulting in conservative estimates. An additional consideration that would contribute to the low estimates is that our parents were not selected *a priori* for extreme values of Δ . The leaf tissue sampled also may have been a poor indicator of integrated A/E, although the low heritability of Δ contrasted with estimates for leaf N and K, which were determined on the same samples. Moreover, this suggests that, in common bean, Δ is more sensitive to environmental factors than are other traits related to crop growth and yield.

Nonetheless, the significant GCA mean square values for Δ show the importance of additive gene action in its inheritance. This discrepancy with non-significant heritability values could be due to inherent differences into the two models or estimation methods. GCA values were estimated in separate seasons for the F_2 and F_3 , whereas heritability was obtained by regression across the two seasons. Thus the estimate would be free from a genotype \times season effect (Casler 1982) and may be more reliable for selection over seasons with variable patterns of water deficit.

Significant GCA values for Δ of some ME and HL parents were consistent and contrasting across sites. This suggests that some inherent genetic differences are expressed across environments. Similarly, the typically high values of Δ for BAT1224 and its large GCA effects agree with a previous report that this line shows unusually high values of Δ (White *et al.* 1990). Although 'Apetito' is from the Mexican highland state of Jalisco, its values for physiological traits and GCA effects were similar to the small-seeded, mid-elevation, tropical parents, and differed from the other Mexican germplasm. Thus, it appears to be genetically closer to the ME group. Seeds of Apetito are smaller than the other HL parents, and the cultivar also differs in other morphological traits including seed shape and colour and leaf size.

Given the low heritability of Δ , it is not surprising that Δ showed no consistent relation with seed yield or SDW. This result agrees with our previous study where relations between Δ and yield varied between the same sites used in this study (White *et al.* 1990), and coincides with the expectation that variation in Δ may be driven by several factors. These might include efficiency of the root system, leaf movements (Ehleringer *et al.* 1991), stomatal response to water deficit, and leaf photosynthetic capacity, and might affect productivity in different ways depending upon the specific growing environment.

Some researchers have considered the possibility that response of Δ to water deficit might show a closer relation to yield than absolute values of Δ (Hall *et al.* 1990; White *et al.* 1990). The presence of significant genotypic differences for Δ in non-deficit conditions indicates that each genotype has a characteristic baseline level of c_i . Water deficit causes deviation from the baseline, thus a more relevant parameter may be the reduction in Δ from normal to deficit conditions. Analyses of variance for reduction in Δ (calculated as Δ under irrigated conditions $- \Delta$ under deficit conditions) suggested significant differences among populations in the four deficit trials (data not shown). Estimated heritability was 0.14 (± 0.20) at Quilichao and 0.00 (± 0.24) at Palmira. No correlations of reduction in Δ with seed yield or SDW were significant.

Assuming that a useful criterion for indirect selection for yield should have both moderate to high heritability and consistent relations with yield across environments, SDW and leaf N concentration appeared to hold the greatest promise. One might expect leaf OD to be nearly as useful a selection criterion as N concentration, since both may be related to leaf photosynthetic capacity. However, leaf OD was negatively correlated with N concentration in three of the experiments (data not shown), and showed negative rather than positive association with seed yield. Perhaps this is because OD is an indicator of chlorophyll concentration per unit area, the leaf N concentration indicates total N accumulation on a leaf dry weight basis.

Heritability estimates for leaf K and SDW were not significant at Quilichao, whereas values for both environments at Palmira were significant. Presumably, an unidentified factor at Quilichao masked genetic effects, and did not allow expression of genes controlling inheritance of these traits at Quilichao. Similarly, irrigated conditions at Palmira masked genetic effects for leaf OD. Alternatively, for these three traits, genes expressed in one environment perhaps were different from those required for expression of these same traits in other environments.

For other traits, no specific trends in heritability values, correlations with yield, or importance of GCA were noted that varied with water regime. Thus the

described associations seem unlikely to reflect specific adaptations to water deficit or well-watered conditions. Presumably, they involve processes affecting the overall efficiency of the crop.

For the range of parents and experimental conditions examined, Δ was not a promising indicator of adaptation to water deficit in the common bean.

Nonetheless, the consistent high GCA of BAT1224 and contrasting GCA values of ME v. HL parents suggest differences in Δ among genotypes that might merit further study. Of alternative traits, SDW and leaf N concentration appeared the most promising based on heritability, strong GCA effects and correlations with seed yield across trials.

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