

Relationships between productivity and carbon isotope discrimination among dry bean lines and F₂ progeny

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Summary

Common bean (*Phaseolus vulgaris* L.) and tepary bean (*P. acutifolius* Gray) are grown for their edible seed and production is limited by insufficient soil moisture in many parts of the world. Carbon isotope discrimination (Δ) against ¹³CO₂ during photosynthesis has been suggested as a useful selection criterion to improve crop productivity in water-limited environments, however, there is a need to first understand relationships between productivity and Δ in common bean. The objectives of this study were to: 1) evaluate relationships between productivity (as measured by seed yield and biomass) and Δ among diverse dry bean lines and F₂ progeny, 2) evaluate associations for Δ , seed yield and biomass among lines grown in different field environments and 3) estimate narrow sense heritability for Δ , seed yield and yield components. One hundred dry bean lines were evaluated at Yellow Jacket, CO in irrigated and non-irrigated field plots during 1988 and 1989. All significant relationships between seed yield or biomass and Δ were positive. In general, relationship between seed yield and Δ among lines were weak and R² ranged from near zero to 0.29 across years and environments. The correlations for Δ , seed yield and biomass production among lines grown in different environments were all significant and positive ($0.76 > r > 0.36$). Narrow-sense heritability estimates for Δ and seed yield were 0.78 and 0.75, respectively. These results support the positive relationship between productivity and Δ in bean, however, the weak relationships between Δ and seed yield do not suggest that Δ would be a useful sole selection criterion to improve productivity.

Abbreviations: C_a – atmospheric partial pressure of CO₂; C_i – intercellular partial pressure of CO₂; Δ – carbon isotope discrimination; W – transpiration efficiency; WUE – water-use efficiency

Introduction

Crop productivity is limited by insufficient soil water in many regions of the world (Boyer, 1982; McWilliam, 1986). Over half of the world's land surface is arid or exposed to periodic drought conditions. In Latin America, Laing et al. (1984) estimated that over 60% of the common bean (*Phaseolus vulgaris* L.) production areas experience moisture stress some time during the growing season. Dry beans are also produced under rainfed conditions in the arid western

US, where productivity is often limited by insufficient soil water.

Genetic progress from selection for increased crop productivity in water limited environments has been slow (Hurd, 1976; Blum, 1988; Ludlow & Muchow, 1990). Recent studies have shown that selection for seed yield in common bean under rainfed conditions can be effective, however, it requires costly yield testing and gains from selection are modest (Schneider et al., 1997a, 1997b; Singh, 1995; White et al., 1994b). More efficient screening methods and selection cri-

teria are needed to improve productivity of common bean cultivars in water-limited environments.

Carbon isotope discrimination (Δ) has been proposed as an indirect selection criterion to improve drought tolerance in crops because it has been associated with transpiration efficiency at the leaf level (W , g of CO_2 fixed per g of water transpired), water-use efficiency at the field level (WUE , kg of dry matter produced per kg of water transpired) and in some cases productivity (Farquhar & Richards, 1984; Hubick et al., 1986; Condon et al., 1987; Hubick & Farquhar, 1989; Condon et al., 1990; Ehleringer et al., 1990; Hall et al., 1990; Johnson et al., 1990; Read et al., 1991; Ismail & Hall, 1993; Matus et al., 1995; Menendez & Hall, 1995). Theory predicts that discrimination against atmospheric ^{13}C by ribulose biphosphate carboxylase-oxygenase during photosynthesis will increase when intercellular partial pressure of CO_2 (C_i) increases. Because high C_i/C_a ratios (C_a , atmospheric partial pressure of CO_2) result in low W and high Δ values, Δ and W are negatively associated at the leaf level. Further, because plant tissue is used to estimate Δ , it is an integrated measurement of long term W .

Many studies have investigated associations between Δ and W , WUE or productivity with varying results. Johnson et al. (1990) examined the relationships between WUE and Δ for forage yield of range grasses in both greenhouse and field environments. They found a negative correlation between WUE and Δ among two grass species grown in greenhouse pots, however, in a field study, a positive association was found between Δ and forage yield for each of three harvests for one species. Positive associations between Δ and grain yield have also been reported in field-grown wheat (*Triticum aestivum* L.) (Condon et al., 1987; Read et al., 1991), common bean (Ehleringer et al., 1990; White et al., 1990) and lentil (*Lens culinaris* Medikus) (Matus et al., 1995). Several studies reported negative associations between Δ and productivity or W . Hubick & Farquhar (1989) reported a negative association between Δ and W for potted barley (*Hordeum vulgare* L.) and Hubick et al. (1986) reported negative associations between Δ and dry matter production in field-grown peanut (*Arachis hypogea* L.). These reports provide conflicting evidence regarding associations between Δ and W or productivity in crop plants.

Genetic variation for Δ has been shown to exist in both monocot and dicot crop series, including wheat (Farquhar & Richards, 1984), peanut (Hubick et al., 1986), barley (Hubick & Farquhar, 1989), crested

wheatgrass [*Agropyron desertorum* (Fisher ex Link) Schultes] altai wildrye [*Leymus angustus* (Trin.) Pilger] (Johnson et al., 1990), common bean (Ehleringer et al., 1990) and other crops (Matus et al., 1995; Menendez & Hall, 1995).

Heritability estimates for Δ have been reported for several crops. Broad sense heritability for wheat, peanut and lentil genotypes ranged from 27 to 90% (Condon et al., 1987; Hubick et al., 1988; Matus et al., 1995; Menendez & Hall, 1995; Menendez & Hall, 1996). Hall et al. (1990) reported that heritability estimates for cowpea were similar when plants were grown under wet or dry field conditions. Heritability estimates for Δ in common bean based on regression of F_3 on F_2 were not significantly different from zero according to White et al. (1994a).

There is a need to better understand relationships between productivity and Δ in common bean. Most studies that have evaluated relationships between productivity and Δ involved only a limited number of unrelated genotypes. We designed this study to expand the number of genotypes to investigate relationships between productivity and Δ in common bean grown in diverse environments. The objectives of this study were to: 1) evaluate relationships between productivity (as measured by seed yield and biomass) and Δ among a large group of diverse dry bean lines and F_2 progeny, 2) evaluate associations for Δ , seed yield and biomass among lines grown in different field environments and 3) estimate narrow sense heritability for Δ , seed yield and yield components.

Materials and methods

Two experiments, I and II, were conducted at the Southwest Colorado Research Center, Yellow Jacket, CO (37° 30' N, 108° 45' W). The soil type at this site is a deep, silty clay loam (Witt series) with a pH 7.5 and contains approximately 1% organic matter. Dry beans are commercially produced in this region under rain-fed conditions with a long term production average of approximately 450 kg ha⁻¹. Thirty-year mean annual precipitation is 408 mm and the elevation is 1895 m above sea level. Total annual precipitation during 1988 and 1989 at the site was 372 and 193 mm, respectively. The test region normally receives seasonal precipitation in late July and early August due to weather patterns that form in the Gulf of Mexico, therefore, the most severe drought at the test site does not occur late in the growing season as in many areas of the world.

Even though precipitation in 1989 was a 30 year low, non-irrigated field plots did not undergo severe moisture stress during the critical flower and pod fill stages because they received 99 mm of precipitation during late July and early August.

In Experiment I, 100 dry bean lines were evaluated in an irrigated and non-irrigated field environment to study associations between productivity and Δ . In Experiment II, approximately five hundred F_2 plants derived from two sets of a Design I mating scheme (Comstock & Robinson, 1948) were evaluated to study associations between Δ and productivity and estimate narrow sense heritability for Δ , seed yield and yield components.

Experiment I

One hundred dry bean entries (advanced lines and cultivars) from both the Andean and Middle American (MA) centers of domestication (Singh et al., 1991) were grown under irrigated and non-irrigated field conditions during 1988 and 1989. Ninety three of the 100 lines were representative of races Durango and Mesoamerica from the MA gene pool that were selected based upon previous field observations for adaptation to the region. Race Nueva Granada was represented by five entries and races Chile, Peru and Jalisco were not represented. Seed type of entries included 50 Pinto, nine pink, five red kidney, three great northern, two small red, two tepary bean (*Phaseolus acutifolius* Gray) cultivars 'Vepegi' and 'Sonora', one black, one ojo de cabra, one small white and 26 miscellaneous seed types. Seed for most of the tropical lines was obtained from Dr. Shree Singh at the International Center for Tropical Agriculture (CIAT), Cali, Colombia.

The entries were grown in a randomized complete block design (RCBD) with three replicates during both years. The irrigated plots received approximately 300 mm of supplemental water applied with an overhead sprinkler during five irrigations each year. In 1989, the region had undergone a severe drought and prior to planting both the irrigated and non-irrigated plots received 50 mm of supplemental water to provide adequate soil moisture for seed germination and seedling establishment.

The plots were planted with an air-planter on 9 and 7 June in 1988 and 1989, respectively. Each experimental unit consisted of one row, 6.1 m long with rows spaced 0.76 m apart. Seeding rates in the irrigated and non-irrigated environments differed and were repre-

sentative of plant populations used by commercial dry bean producers in the region (Brick & Smith, 1996). Seeding rates must be lower under non-irrigated production because high seeding rates will cause the crop to deplete stored soil moisture too rapidly in the early growth stage and result in crop failure. The seeding rates were 4.3 and 12.5 seeds m^{-1} row in the non-irrigated and irrigated plots, respectively. The seeding rates provided plant populations of 32,800 and 95,250 plants ha^{-1} in the non-irrigated and irrigated plots, respectively. Differences in seeding rates across environments was essential to simulate commercial production, but prevented an appropriate evaluation of interactions between entries and environments.

Leaf samples for isotopic analysis were collected on 28 July in 1988 and 26 July in 1989 in one replicate of both the irrigated and non-irrigated plots. Only one replicate was sampled because isotopic analysis is costly and one replicate was sufficient to fulfill the main research objective to elucidate relationships between productivity and Δ . Three leaflets from a fully expanded leaf located approximately three nodes below the apical meristem were collected and bulked for isotopic analysis. The leaflets were obtained from one plant for isotopic analysis in 1988, and from five plants in 1989. The samples were oven dried and ground to pass through a 40 mesh screen. Ground samples were then combusted using an in-vial technique (Ehleringer & Osmond, 1991). The CO_2 from combustion was measured on a Finnigan MAT delta E mass spectrometer. Carbon isotopic composition is expressed using Δ notation (Farquhar et al., 1989), assuming an isotopic composition of atmospheric CO_2 of $\delta = -8$

Relative maturity for all entries was determined by visual observations. Entries were categorized on 19 August 1988 into maturity groups as follows: 1) early, if one or more of the lower pods had turned brown and one or more of the lower leaves had abscised, 2) medium, if the lower pods had begun to color and the lower leaves had begun to turn yellow but not abscised, 3) late, if the plants had ceased to flower and formed elongated green pods, but had no leaf or pod discoloration and 4) very-late, if the plants were in flower and had formed immature pods 10 to 20 mm in length, with no leaf discoloration.

Data were collected to estimate above-ground biomass by harvesting three adjacent plants at the soil surface from each experimental unit when approximately 50% of the plants in the row had one or more yellow leaves on the plant. This period occurred from early August through early September and coincided with

the period prior to maximum total biomass accumulation for some of the late maturing entries. Biomass samples were oven-dried for 72 hours at 77°C, then weighed to determine dry weight.

Seeds were harvested on entries as they reached harvest maturity which occurred between early and late September among entries. Seed yield was determined by harvesting plants from a 2-m long section of each experimental unit. Plants were pulled, placed in paper bags to air dry, then threshed with a portable thresher. Seed samples were cleaned with an air-screen seed cleaner prior to weighing.

The regression analyses to study the relationships between productivity and Δ used Δ values obtained from leaf tissue in one replicate. One replicate was used for isotopic analysis to reduce the total cost of isotopic analysis and because it was sufficient to fulfill the primary interest to evaluate relationships between productivity and isotope discrimination among genetically diverse bean entries. The lack of replication did not allow us to statistically compare means or interactions for Δ among entries and environments. Mean seed yield and biomass from three replicates were used in the regression analyses to improve the estimate of entry performance.

Experiment II

Two sets of a North Carolina Design I mating scheme (Comstock & Robinson, 1948) were made to estimate narrow-sense heritability for Δ , seed yield and yield components. Fourteen parents were randomly selected among lines representative of the Middle American gene pool evaluated in the 1988 field nursery. The entries were used in the two mating schemes as shown in Table 1. Entries from the Andean gene pool and the two tepary lines were not used as parents to prevent problems associated with recovering viable and fertile progeny. The parents used in the two sets of the mating scheme were grouped according to maturity because plants that differ in maturity can be difficult to mate due to different times of floral initiation. Set 1 was composed of entries in the early to medium maturity and set 2 composed of entries classified as late to very late. Two sets of crosses were made to assure an adequate sample of genotypes to estimate heritability. Each set in the Design I mating scheme consisted of three female parents nested in each of three male parents to produce nine F_2 families, except set 2 which had eight families because one female parent did not produce hybrid progeny.

The origin of lines and cultivars used as parental material are as follows: 'Bill Z' and 'Cahone' are Pinto cultivars released by the Colorado State University Experiment Station, Ft. Collins, CO (Wood et al., 1983, 1989); 'Victor', 'Viva' (Burke, 1982) and 'UNS-117' are pink-seeded, and 'Othello' a Pinto cultivar released by the USDA Agricultural Research Service, Prosser, WA; CO 22625, CZ 35241, CZ 56240, CO 80-1661, CZ 59202 and CZ 81-13183 are advanced Pinto lines from the Colorado State University Dry Bean Breeding Project; and 'San Cristobal' and G-5201 are a black-seeded cultivar and breeding line, respectively adapted to lowland tropical areas.

Crosses were made in a greenhouse during the fall 1988 by hand transfer of pollen to emasculated female parents. The resultant F_1 seed was planted in the greenhouse in January 1989 to produce F_2 seed for each of the 17 families. The success of hybridization among crosses was determined by F_2 testa color when the parents differed in testa color. The F_2 families which could not be confirmed as hybrids based on testa color were confirmed as hybrids based on visual evaluation for phenotypic segregation among plants in the field nursery.

The F_2 seed was planted on 6 June, 1989 at the Southwest Colorado Research Center in a non-irrigated plot as described in experiment I. Seed from each F_2 family was separated into three equal portions to plant three replicates of each family in a RCBD. Each experimental unit consisted of one row 3.3 m long, with rows spaced 0.76 m apart. Mean plant population was 4.3 plants m^{-1} row and all plots were pre-irrigated with 50 mm of supplemental water prior to planting to ensure uniform seed germination as described in Experiment I. Plots did not receive supplemental irrigation during the growing season.

Ten plants in each replicate were labeled to maintain their identity for seed yield and isotopic analysis. Three leaflets from each of the ten plants in each replicate were collected on 26 July, 1989 and analyzed for isotopic composition as in experiment I. Seed yield and yield components were also measured for each F_2 plant. F_2 plants were harvested on 15 September, then placed in paper bags to air dry for four weeks. The pods were subsequently removed, counted and threshed to obtain total pod and seed number, and seed yield. Seed weight was determined by weighing three subsamples of 50 seeds from each plant.

Regression analyses were conducted for data on both single F_2 plants and F_2 population means. Narrow-sense heritability estimates (h^2) were calcu-

Table 1. Origin, seed type of parental lines/cultivars used in two sets of a Design I mating scheme

| Male parent | | | Female parent | | |
|--|---------|-----------|---------------|---------|-----------|
| Line | Race | Seed type | Line | Race | Seed type |
| Set 1 Early and medium maturity parents | | | | | |
| UNS 117 | Durango | Pink | Bill Z | Durango | Pinto |
| | | | CO 80-1661 | Durango | Pinto |
| | | | CZ 56240 | Durango | Pinto |
| Bill Z | Durango | Pinto | Othello | Durango | Pinto |
| | | | UNS-117 | Durango | Pink |
| | | | CZ 81-3183 | Durango | Pinto |
| CO 22625 | Durango | Pinto | Bill Z | Durango | Pinto |
| | | | UNS-117 | Durango | Pink |
| | | | CZ 81-13183 | Durango | Pinto |
| Set 2 Late and very late maturity parents | | | | | |
| Victor | Durango | Pink | San Cristobal | Meso | Black |
| | | | CZ 35241 | Durango | Pinto |
| | | | G-5201 | Meso | Black |
| Cahone | Durango | Pinto | Victor | Durango | Pink |
| | | | Viva | Durango | Pink |
| | | | CZ 59202 | Durango | Pinto |
| G-5201 | Meso | Black | Viva | Durango | Pink |
| | | | CZ 35241 | Durango | Pinto |
| | | | Missing | | |

lated on an entry basis from F_2 populations generated in the two sets of the mating scheme (Table 2). Data from the two sets were combined into one analysis with replicates and crosses nested in sets. In the analysis, variation was divided into sets, replicates in sets, males in sets, females in sets, and pooled to plot error. Confidence intervals for heritability estimates were calculated according to Knapp et al. (1985). Because there were missing plants in some of the F_2 populations the SAS statistical package GLM (SAS Institute Inc., 1995) was used for analyses of variance of unbalanced data.

Results and discussion

Experiment I

Productivity of entries

Substantial variation in seed yield was observed among the 100 entries. All entries produced seed and were reasonable adapted to the test environment because they were selected on the basis of adaptation to

the region from previous field observations. In 1988, seed yield ranged from 238 to 1270 kg ha⁻¹ in the non-irrigated and from 444 to 2502 kg ha⁻¹ in the irrigated environments. Mean seed yields were 755 ± 117 and 1732 ± 247 kg ha⁻¹ in the same respective environments. In 1989, seed yield ranged from 164 to 1637 kg ha⁻¹ in the non-irrigated and 125 to 2812 kg ha⁻¹ in the irrigated environments. Mean seed yields were 1015 ± 151 and 1832 ± 287 kg ha⁻¹, in the same respective environments. The variation observed among entries for productivity was anticipated because the lines were of diverse origin, maturity, and seed size which differed from 15 to 45 g 100⁻¹ seeds. The approximate two fold mean yield difference between the irrigated and non-irrigated environments each year indicated that the irrigated and non-irrigated environments contrasted for available soil moisture.

Entries also varied for above-ground biomass production. In 1988, above-ground biomass ranged from 374 to 1900 kg ha⁻¹ in the non-irrigated and from 483 to 4231 kg ha⁻¹ in the irrigated environments. Mean biomass was 703 ± 108 and 2101 ± 361 kg ha⁻¹ in the same respective environments. In 1989, above-

Table 2. Carbon isotope discrimination (Δ) and ranking among the ten entries with the highest and lowest mean Δ values among 100 dry bean lines grown in irrigated and non-irrigated field environments in 1988 and 1989

| Entry | Maturity/Race ^a | 1988 | | | | 1989 | | | | Mean | |
|------------------|----------------------------|-----------|------|---------------|------|-----------|------|---------------|------|----------|------|
| | | Irrigated | | Non-irrigated | | Irrigated | | Non-irrigated | | Δ | Rank |
| | | Δ | Rank | Δ | Rank | Δ | Rank | Δ | Rank | | |
| | | ‰ | No. | ‰ | No. | ‰ | No. | ‰ | No. | ‰ | No. |
| CZ 81-13183 | M/D | 19.60 | 3 | 19.68 | 3 | 19.92 | 40 | 21.39 | 1 | 20.15 | 1 |
| Victor | L/D | 19.41 | 8 | 19.47 | 5 | 19.97 | 32 | 21.35 | 2 | 20.05 | 2 |
| Othello | E/D | 19.56 | 5 | 19.72 | 1 | 20.23 | 14 | 20.24 | 37 | 19.94 | 3 |
| UNS-117 | M/D | 19.33 | 10 | 19.57 | 4 | 19.92 | 40 | 20.71 | 8 | 19.88 | 4 |
| NW 410 | M/D | 19.69 | 1 | 19.31 | 8 | 19.84 | 46 | 20.24 | 37 | 19.77 | 5 |
| RS 101 | L/D | 18.82 | 33 | 19.22 | 12 | 20.61 | 2 | 20.42 | 19 | 19.77 | 6 |
| Viva | L/D | 19.59 | 4 | 19.17 | 14 | 19.95 | 36 | 20.18 | 42 | 19.72 | 7 |
| Harold | M/D | 19.31 | 11 | 18.08 | 72 | 20.26 | 10 | 21.20 | 3 | 19.71 | 8 |
| GW 612 | M/D | 19.22 | 12 | 19.19 | 13 | 20.26 | 10 | 20.15 | 47 | 19.71 | 9 |
| Arapaho | M/D | 19.14 | 17 | 18.21 | 63 | 20.46 | 5 | 20.94 | 4 | 19.69 | 10 |
| EMP105 | VL/MA | 18.66 | 44 | 17.42 | 93 | 19.15 | 91 | 18.87 | 97 | 18.52 | 91 |
| San Cristobal | VL/MA | 18.00 | 88 | 17.51 | 92 | 19.22 | 87 | 19.27 | 89 | 18.50 | 92 |
| Vepegi | E/Tep | 18.29 | 67 | 17.26 | 96 | 19.37 | 79 | 19.05 | 91 | 18.49 | 93 |
| Rio Tibagi | VL/MA | 17.72 | 91 | 17.58 | 91 | 19.44 | 72 | 18.91 | 95 | 18.41 | 94 |
| A-170 | VL/MA | 17.34 | 97 | 17.88 | 83 | 18.48 | 97 | 19.78 | 66 | 18.37 | 95 |
| G-5059 | VL/MA | 17.39 | 95 | 16.86 | 98 | 19.56 | 66 | 19.41 | 83 | 18.31 | 96 |
| A-59 | VL/MA | 17.60 | 92 | 18.37 | 55 | 18.22 | 98 | 19.00 | 92 | 18.30 | 97 |
| G-4523 | M/NG | 18.36 | 63 | 17.32 | 95 | 18.88 | 93 | 18.54 | 99 | 18.27 | 98 |
| BAT1298 | VL/MA | . | . | 17.18 | 97 | 18.68 | 95 | 18.95 | 94 | 18.27 | 99 |
| A-54 | L/MA | 18.18 | 81 | 16.75 | 99 | 18.09 | 99 | 19.36 | 85 | 18.09 | 100 |
| Mean all entries | | 18.59 | | 18.45 | | 19.69 | | 19.99 | | 1918 | |

^a Plant maturity: E = early, M = medium, L = late, VL = very-late; Race: D = Durango, MA = Mesoamerica, NG = Nueva Granada, Tep = tepary bean.

. denotes missing data.

ground biomass ranged from 353 to 1699 kg ha⁻¹ in the non-irrigated and from 484 to 5743 kg ha⁻¹ in the irrigated environments. Mean biomass was 1175 ± 139 and 2904 ± 517 kg ha⁻¹ in the same respective environments. Similar to seed yield, there was approximately a two fold difference between mean biomass production across the irrigated and non-irrigated environments each year.

Relationships between productivity and Δ

Linear regression analyses were conducted to study the relationships between productivity and Δ in each environment/year. In 1988, the relationships between seed yield and Δ were weak but positive in both the irrigated and non-irrigated environments ($R^2 = 0.08$ and 0.06, respectively, $p < 0.05$ for $b = 0$) (Figure 1A, 1B). The relationships between biomass and Δ were not significant for either environment in 1988 (relationships not shown). In 1989, the R^2 values for the

relationships between seed yield and Δ , and biomass and Δ were higher than in 1988 (Figure 1C, 1D). In 1989, the R^2 values were 0.25 and 0.29 for the relationship between seed yield and Δ ; and 0.17 and 0.13 for the relationship between biomass and Δ in the irrigated and non-irrigated environments, respectively. Mean Δ over entries was also more than one part per mil higher in 1989 than 1988 in both irrigated and non-irrigated environments, however, mean production did not differ ($p < 0.05$) between years. Lack of consistency in relationships between productivity and Δ across environments has also been reported in common bean by White et al. (1994a). A portion of the differences between the relationships observed in 1988 and 1989 may be due to differences in leaf sampling technique for isotopic analysis. In 1988, leaf tissue from only one plant per entry was used for isotopic analysis, while in 1989 leaves from five plants per entry were used for analysis. The larger sample

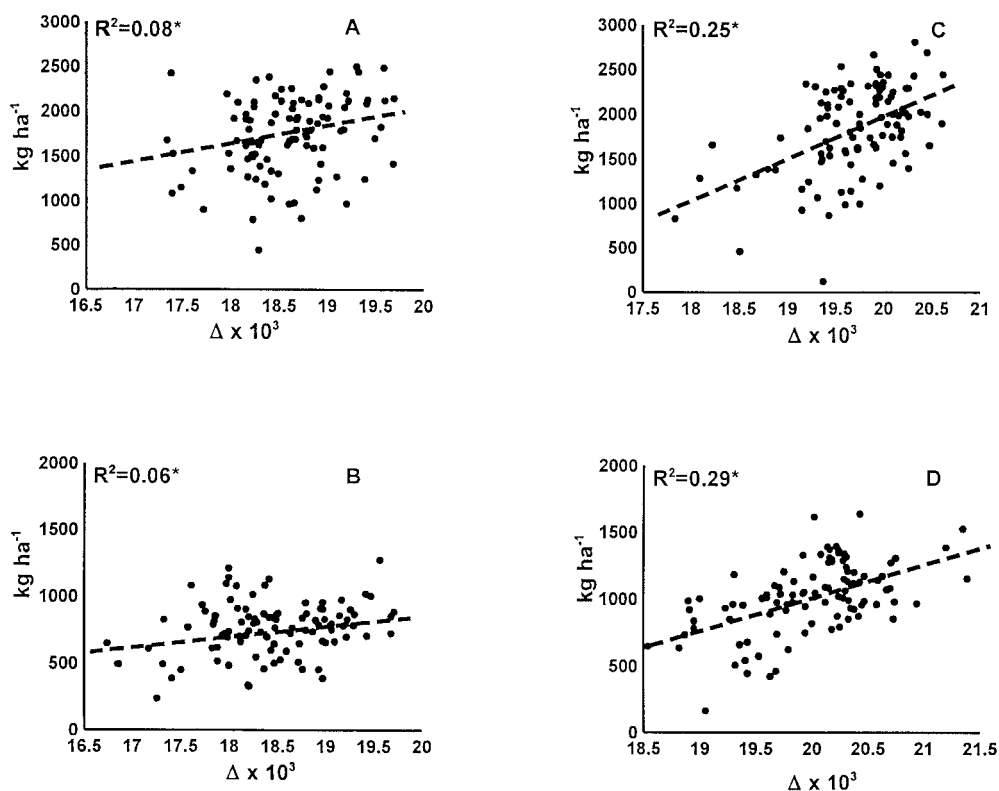


Figure 1. Relationships between seed yield and Δ for dry bean entries in the irrigated 1988 (A), non-irrigated 1988 (B), irrigated 1989 (C), and non-irrigated 1989 (D) field nurseries.

size in 1989 may have provided greater precision to estimate Δ values among entries. Because the sampling procedures were not independently studied over years, there is no conclusive evidence that sampling procedure contributed to the difference.

To determine if relationships between productivity and Δ varied among maturity groups, separate regression analyses were conducted on each maturity group. In general, the relationships between productivity and Δ across maturity groups were poor in 1988 (data not shown). In 1989, the relationships between productivity and Δ for the early maturity group was not significant for either seed yield or biomass (Table 3). In the medium, late and very late maturity groups, eleven of the twelve relationships were positive ($p < 0.05$ for $b = 0$). The relationships for entries which represented the medium to late maturity groups had higher R^2 values and seed yield than the early or very late entries. Three of the four relationships between productivity and Δ for the very-late lines were also positive. Differences in responses among maturity groups were not unexpected because some of the

Table 3. Coefficients of determination (R^2) for the regression of seed yield and above-ground biomass on Δ in the combined analysis and among four maturity groups in 1989

| Maturity | R^2 | | | |
|-----------------------|-----------|--------|---------------|--------|
| | Irrigated | | Non-irrigated | |
| | Biomass | Yield | Biomass | Yield |
| Combined (n ~ 100) | 0.17** | 0.25** | 0.13** | 0.29** |
| Early (n = 12) | 0.03 | 0.04 | 0.17 | 0.25 |
| Medium (n = 36) | 0.35** | 0.33** | 0.14* | 0.28** |
| Late (n = 22) | 0.27* | 0.27* | 0.46** | 0.41** |
| Very Late (n = 30) | 0.26** | 0.31** | 0.02 | 0.15* |

*,** Indicates the slope of the linear regression equation was significantly different from zero at $p \leq 0.05$ and 0.01, respectively.

early and very-late entries had high yield potential, but were unproductive in the test environment due to early leaf senescence or lack of sufficient time for pod fill. Because all significant responses between productivity and Δ were positive, increased productivity does not appear to be related to higher W due to stomatal closure. The positive responses suggest that lines which maintain higher intercellular partial pressure of CO₂ also have higher yield potential, possibly by enhanced soil moisture extraction due to greater root density or efficiency as suggested by White et al. (1990).

Carbon isotope discrimination among lines was negatively associated with maturity classification (1 = early to 4 = very-late). The correlation coefficients between maturity and Δ were -0.40^{**} and -0.54^{**} in the irrigated and non-irrigated environment in 1988, and -0.15 and -0.26^{**} in the irrigated and non-irrigated environments in 1989, respectively. Early and medium maturity lines constituted seven of the ten entries with the highest mean Δ across environments and the late and very-late maturity lines constituted eight of the ten entries with the lowest mean Δ (Table 2). All ten of the entries with the highest mean Δ across environments were from race Durango and eight of the ten lowest mean Δ across environments were from race Mesoamerica (Table 2). The negative associations between Δ and maturity classification and association between origin and Δ suggests that early maturity and race Durango entries had higher intercellular partial pressure of CO₂ than later entries at the time of leaf tissue sampling. Negative associations between maturity and Δ have also been reported in barley (Craufurd et al., 1991), wheat (Ehdaie et al., 1991; Richards & Condon, 1993) and cowpea (Hall et al., 1990; Menendez & Hall, 1995). Menendez & Hall (1995) pointed out that the negative association between earliness and Δ could compromise progress in breeding drought-adapted varieties where early maturity is used as a mechanism to avoid drought stress. However, the positive associations that occurred between productivity and Δ , and the generally higher Δ values for race Durango lines in this study suggest that entries from race Durango have higher yield potential than entries from race Mesoamerica in this test environment.

Correlation analyses were conducted to determine whether values for Δ , seed yield and biomass among entries were correlated across environments. All correlation coefficients were positive ($p < 0.001$) (Table 4). In general, correlation coefficients were highest for seed yield and moderate for Δ and biomass. Values of Δ among entries grown in diverse environments have

Table 4. Correlation coefficients ($96 < n \leq 100$) for the associations among entries for Δ , seed yield and biomass between environments in 1988 and 1989

| Environments | r | | |
|--------------------------------|---------|------------|---------|
| | Delta | Seed yield | Biomass |
| Irrigated vs Non-irr. 1988 | 0.59*** | 0.81*** | 0.41*** |
| Irrigated vs Non-irr. 1989 | 0.42*** | 0.75*** | 0.55*** |
| 1988 Irrigated vs 1989 Irr. | 0.41*** | 0.76*** | 0.49*** |
| 1988 Non-irr. vs 1989 Non-irr. | 0.44*** | 0.72*** | 0.36*** |

*** Indicates a significant r value ($p \leq 0.001$).

also been shown to be correlated in cowpea (Hall et al., 1990) and common bean (White et al., 1990). These results support the findings that many plant traits are correlated across environments and that in general, genotypes retain a level of consistency across environments. However, some entries such as Harold, WY 167 and Co 33142 had rank changes for Δ greater than 64 places across environments. This indicates that while many genotypes maintained a level of consistent rank across environments, not all entries were stable.

Experiment II

Relationships between seed yield and Δ in F₂ progeny

Relationships between seed yield and Δ in two sets of F₂ progeny were evaluated in the non-irrigated 1989 environment. Approximately 500 F₂ plants were evaluated to determine if Δ could have potential for use as a single plant selection criterion in early generation segregating populations. No significant relationship occurred between seed yield and Δ among single F₂ plants in either set (Figure 2A, 2B). The lack of relationships between single plant seed yield and Δ suggest that Δ would not be useful for predicting seed yield among single plants and is likely due to error associated with estimating seed yield and/or Δ on a single plant basis. Relationships between seed yield and Δ among F₂ population means were positive ($p < 0.05$) in both sets (Figure 2C, 2D). Δ explained 52 and 37% of the variation for seed yield in the two sets of the mating scheme, and the R² values were similar to those found in Experiment I during 1989. Even though Δ has been found to explain a significant proportion of the variation in yield in these and other studies, the relationship is likely too weak to suggest use of Δ as a sole indirect selection criterion to improve productivity in dry bean under soil moisture stress. This conclusion is in agreement with White et

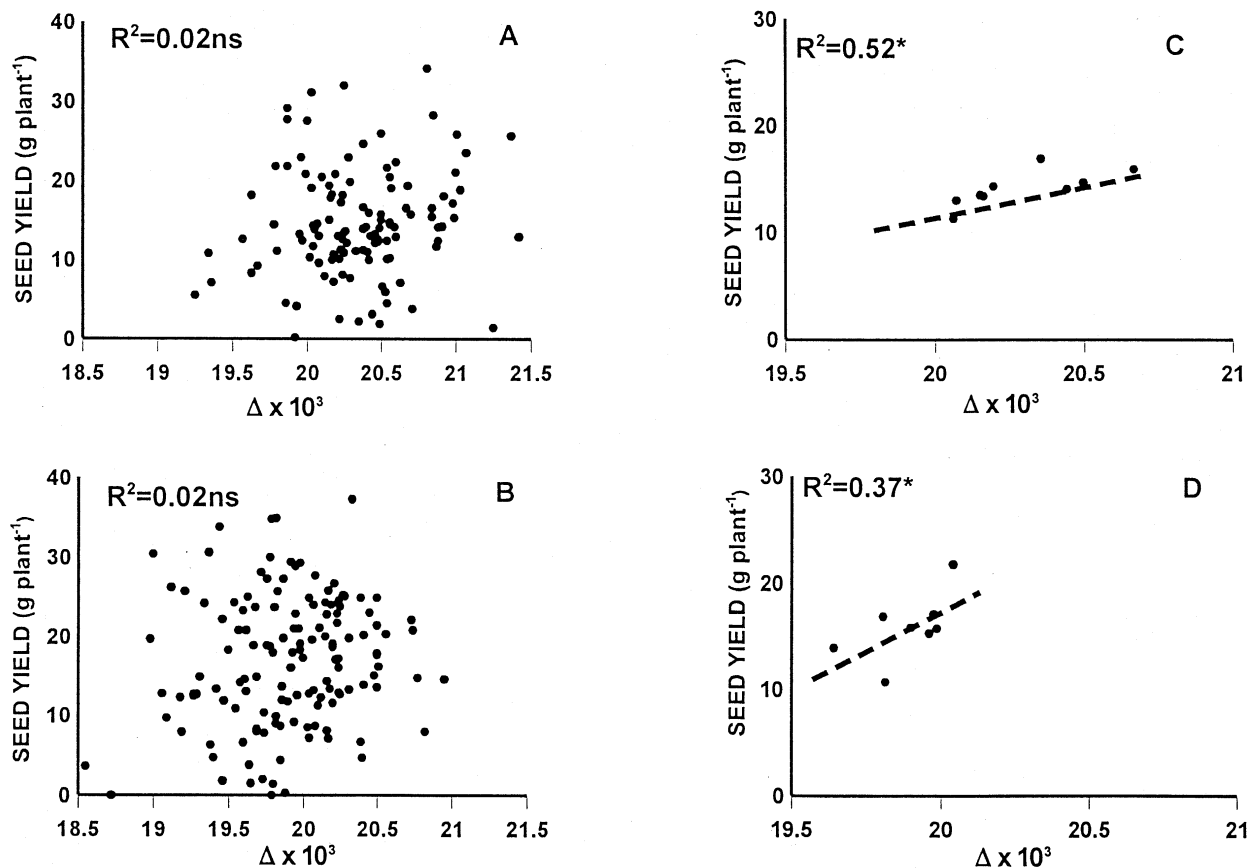


Figure 2. Relationships between seed yield and Δ for single F₂ plants in populations from crossing set 1 (A), set 2 (B), and F₂ population means from set 1 (C) and set 2 (D).

al. (1994a). However, Δ may be useful as one of several selection criteria to choose parents or populations for improved productivity. The positive relationship between seed yield and Δ among F₂ families supports the results from Experiment I and others that seed yield is positively related to Δ in field grown common bean (Ehleringer et al., 1990; White et al., 1990).

Heritability of Δ , seed yield and yield components

Narrow-sense heritability estimates based on entry means were highest for seed weight, intermediate for Δ , seed yield and seed pod⁻¹, and low for pod number. Heritability estimates for Δ , seed yield, pod number, seed number pod⁻¹, and seed weight were 0.77, 0.75, 0.36, 0.74, and 0.95, respectively (Table 5). All estimates were significantly different from zero ($p < 0.10$) except pod number. The heritability estimate for Δ was within the range of estimates reported in cowpea by Hall et al. (1990, $h^2 = 0.35\text{--}0.90$) and wheat

Table 5. Narrow sense heritability (h^2) estimates and upper and lower 90% confidence limits for carbon isotope discrimination, seed yield and yield components

| Trait | h^2 | Upper limit | Lower limit |
|-------------------------|-------|-------------|-------------|
| Δ | 0.77 | 0.95 | 0.19 |
| Seed yield | 0.75 | 0.91 | 0.29 |
| Pod number | 0.36 | 0.71 | 0 |
| Seeds pod ⁻¹ | 0.74 | 0.96 | 0.72 |
| Seed weight | 0.95 | 0.99 | 0.89 |

by Hubick et al. (1988; $h^2 = 0.53\text{--}0.81$), but higher than that reported in common bean by White et al. (1994a; h^2 from 0 to 0.14 ± 0.21). The estimates of White et al. were calculated from parent-offspring regression in trials grown in different seasons, thus accounted for environmental effects and genotype by

environment interactions. Because we did not estimate environmental effects or interactions with entries, our estimate would be expected to be higher than White et al. (1994a). Our estimate for heritability of seed yield ($h^2 = 0.75$) was similar to Singh (1995) for selection of common bean under drought stress in a population derived from crosses between races Durango and Mesoamerica, and Schneider et al. (1997b) for a population derived from crosses between parents from race Durango. These results also indicate that sufficient genetic variation for Δ was present among parents used in this study and that the response to selection for Δ in these families would be similar to seed yield or seed number if environmental or interaction effects had similar effects on progress from selection.

The low heritability estimate for pod number was unexpected, because heritability estimates for pod number have been shown to be high (Coyne, 1965; Bennett et al., 1977; Sarafi, 1978; Nienhuis & Singh, 1988a; Nienhuis & Singh, 1988b). In practice, because pod number is highly heritable, many breeders rely on visual selection for pod number to improve seed yield (Singh, 1991). The low estimate for heritability of pod number in this experiment likely resulted from the lack of genetic variability for pod number among the parents used in the crossing scheme.

The high narrow sense heritability estimate for seed weight (0.95 ± 0.06) suggest that selection for altered seed weight is feasible. However, because seed size in dry beans is an important criterion that defines a market class based upon consumer acceptance, selection for increased seed weight within a market class is not an appropriate selection criterion to develop commercial cultivars. The high heritability estimate for seed number pod^{-1} also suggest that seed number may be a useful selection criterion for increasing seed yield, however, yield component compensation and genotype \times environment interactions often prevent progress from selection exclusively for a single yield component (Adams, 1967; Bennett et al., 1977; Coyne, 1965; Sarafi, 1978).

Conclusions

The weak relationships between productivity and Δ in these studies suggest that Δ is not a useful sole selection criterion to identify highly productive bean lines or early generation plants. At best, Δ only accounted for 29% of yield variation among lines and 52% among F_2 population means. The lack of signifi-

cant relationships between productivity and Δ among individual F_2 plants suggest that Δ was not a good predictor of seed yield on a single plant basis, therefore Δ would not be useful for early generation plant selection. However, Δ may be useful as one of several selection criteria to select productive lines or populations. Because all significant relationships between productivity and Δ among lines were positive, high Δ values were related to high productivity. The positive relationships between productivity and Δ observed in both irrigated and non-irrigated environments suggest that the relationships between productivity and Δ remain positive over a range of field environments.

Differences among relationships between productivity and Δ in the four maturity groups suggests that plant maturity influences this relationship. Plant breeders must consider the time of tissue sampling and associations with plant maturity to adequately evaluate relationships between productivity and Δ . The close associations between Δ values, seed yield and biomass among entries grown in different environments provide justification that these traits are somewhat stable across environments. However, for Δ some entries varied greatly in rank across environments. To better understand specific genotype by environmental interactions, researchers need to make costly replicated measurements across environments. The relatively high narrow-sense heritability estimate for Δ suggest that progress from selection for Δ can be made, however, lack of strong relationships between productivity and Δ preclude the use of Δ as a sole indirect selection criterion to improve seed yield in dry bean. Use of Δ as one of several selection criteria in a selection index may provide breeders with a useful tool to improve productivity across a range of environments.

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