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Consistency of genotypic ranking for carbon isotope discrimination by cowpea grown in tropical and subtropical zones

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Abstract

Measurements of plant composition of stable carbon isotopes ($^{13}C/^{12}C$) can be used to estimate the extent that plants discriminate (Δ) against the heavier carbon isotope. Theoretical and experimental studies have shown that Δ can be negatively correlated with transpiration efficiency (W = seasonal total biomass production/seasonal transpiration) in C_3 plants. Consequently, selection for low Δ (and high W) may be useful in breeding C_3 plants for some water-limited environments. Development of effective breeding methods depends upon the extent of genotype X environment interaction (G XE) as it influences the consistency of genotypic ranking across environments.

Sets of cowpea cultivars and lines were grown under contrasting water supply regimes in subtropical zones in Riverside, California, and Lubbock, Texas, and in tropical zones in Senegal. Leaf carbon isotope composition was measured and significant genotypic differences in Δ were observed in most trials with little G X E for trials within these regions. Genotypic rankings were quite consistent between wetter and drier environments and different years within these regions with significant correlation coefficients for genotypic means in most cases. However, when comparing Δ values between the two subtropical zones (California versus Texas), correlation coefficients for genotypic means only were moderate and not significant. Comparisons of Δ values between the tropical zone (Senegal) and the two subtropical zones indicated no consistency in genotypic ranking, and correlation coefficients for genotypic comparisons were very small.

Apparently, G X E for Δ would not necessarily constrain cowpea breeding programs which aim at developing improved cultivars for specific target production regions, such as semiarid tropical Senegal. However, cowpea performance, with respect to Δ and W, would not be transferable to radically different production zones where attainment of high W may require different sets of genes.

Key words: Cowpea; Transpiration efficiency; Variety trial; *Vigna*

1. Introduction

Yields of crops for water-limited environments would be enhanced if transpiration efficiency (W = seasonal total biomass production/seasonal transpiration) could be increased without associated negative effects. Richards and Condon (1993) provide a discussion of possible associated negative effects, such as slow canopy growth and associated increases in soil evaporation. Direct selection for W in field conditions

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would be very difficult due to the need to extract and measure root biomass, and estimate soil evaporation and total water-use so that transpirational water-use can be estimated. However, theoretical and empirical studies indicate that carbon isotope discrimination (A) may be effective for indirectly selecting for W (i.e., reviews and case studies in Ehleringer et al., 1993), and A can be estimated in field nurseries from measurements of $^{12}C/^{13}C$ in plant tissues. Discrimination against the heavier isotope (^{13}C) occurs during the diffusion and fixation of CO_2. According to the theory for C_3 plants, *A* and W both depend upon the concentration of CO, within leaves (Farquhar et al., 1982). Increases in internal photosynthetic capacity or partial stomatal closure cause decreases in the concentration of CO, within leaves and concomitant increases in W and decreases in *A*. Consistent with this theory, plants growing in the same aerial environment have exhibited a negative linear regression between W and *A* (Farquhar and Richards, 1984). Development of effective breeding methods depends upon the extent of genotype X environment interaction (G X E) for *A* as it influences the consistency of genotypic ranking (Hall et al., 1994). Selection would not be effective if genotypic ranking for a trait were to vary from year to pear for the same genotypes.

Some studies have not detected significant G XE. Sixteen peanut genotypes were evaluated in 10 contrasting subtropical and tropical environments in Queensland, and G X E was not significant for *A*, but was highly significant for kemel yield (Hubick et al., 1988). Studies with 21 or 23 genotypes of barley over 2 years in two environments in the United Kingdbm, and three locations in Syria, gave positive and significant correlations among genotypic values of *A* for 20 out of 25 comparisons with different pairs of environments (Craufurd et al., 199 1).

In other studies, significant G X E has been detected. Studies with about 20 genotypes in a range of field environments across the southern Australian wheatbelt (Condon and Richards, 1992) indicated significant G XE in rnany cases, but it was generally a minor component of variation in *A* compared with the genotypic variation. For common bean (*Phaseolus vulgaris* L.), significant G X E has been observed for genotypes grown under different watering regimes (White, 1993).

Cowpea (*Vigna unguiculata* L. Walp.) is an important crop for rainfed semiarid tropical regions of Africa where water limitations can substantially reduce yield (Hall and Patel, 1987; Thiaw et al., 1993). Studies conducted in southem Califomia have discovered cowpea accessions with significant differences in *A* (Hall et al., 1990) that could confer substantial differences in W (Ismail and Hall, 1992), and genotypic ranking for *A* was consistent over different levels of drought and years (Hall et al., 1992). Consistency of genotypic ranking for *A* over a very wide range of environments has not been evaluated for cowpea or most other crops. Studies were conducted to: (1) determine whether a set of contrasting cowpea genotypes exhibit significant differences and any G XE in *A* measured in leaves of plants grown in two tropical locations in semiarid Senegal; and (2) compare genotypic ranking with values of *A* already obtained for the same genotypes in subtropical regions in southem Califomia (Hall et al., 1992) and the high plains of Texas.

'2. Materials and methods

Experiments were conducted in a semiarid tropical region of Senegal having a single summer rainfall season on the Bambey and Louga research stations of the Institut Senegalais de Recherches Agricoles in 1991 and 1992. These stations have similar air temperatures during the growing season with daily maxima averaging 33°C and daily minima averaging 24°C (Hall and Patel, 1987). Louga is located on the arid boundary of the semiarid zone with an average annual rainfall of 269 mm in recent years compared with 471 mm at Bambey (Hall and Patel, 1987).

During the summer of 199 1, 42 land races, cultivars, and breeding lines of cowpea were grown at Bambey (14°42′N 16°28′W) on a deep, slightly leached, tropical ferruginous soil, called a "Dior" soil, which has a volumetric moisture content at field capacity of 0.16. Fertilizer was broadcast and incorporated at the rate of 150 kg/ha of 6:9:8 (N:P:K). Seed was sown at the beginning of the rainy season on 12 July in rows 50 cm apart with 50 cm between plants for spreading genotypes and 25 cm for erect genotypes, consistent with current recommended practices. The experimental design consisted of four :randomized complete blocks. Individual plots consisted of four rows of plants, 4 m long. Samples consisting of three leaflets were taken from the eighth node of three plants in each plot on the 33th day after sowing. The nine leaflets taken from each plot were pooled and dried, and carbon isotope composition was measured as described in Hall et al. (1992).

During the summer of 1992, nine cowpea genotypes were grown in two experiments at Bambey and Louga (15°36′N 16°13′W). The soil at Louga is sandy with a small clay content (3%) and a volumetric moisture content at field capacity of 0.08. Seeds were sown at the beginning of the rainy season on 17 July in Bambey, and 10 August in Louga, and the plants were grown using the same methods as in 1991, except that individual plots consisted of three rows, 6 m long. Samples consisting of three leaflets were taken from the fifth node of four plants on the 28th day after sowing. The 12 leaflets taken from each plot were pooled, dried, and analyzed for carbon isotope composition as described in Hall et al. (1992). Forage and grain yield were determined on the center row of each plot at the end of the growing season.

Experiments were conducted in the summers of 1988 and 1989 in a semiarid, subtropical region in the high plains of Texas at the research station of Texas Tech University at Brownfield in Terry County in a loamy fine-sand soil. Similar experimental methods were used in both years except that eight cowpea genotypes were evaluated in 1988 and six cowpea genotypes were evaluated in 1989. The experimental design was a split plot with three replications. The main plots were two levels of trickle irrigation and the sub-plots were the different genotypes. Individual plots consisted of four rows, with 75 cm between rows, and 12 m long. A fertilizer application of 50 kg N ha^{-1} and 20 kg P ha^{-1} was made prior to sowing, and additional N was provided in the irrigation water at a rate of 1 kg N ha^{-1} mm^{-1}. A well-watered treatment was established which received maximal water needs every 3 days. A drier treatment was established where plants were provided with maximal water needs for the first 35 days, after which irrigation was terminated. Samples consisting of three leaflets were taken from the eighth node of three plants in each plot on the 60th and 58th day after sowing in 1988 and 1989, respectively. The nine leaflets taken from each plot were pooled and dried, and carbon iso-

Table 1
Carbon isotope discrimination measured in leaves of cowpea genotypes grown at Bambey, Senegal, in 1991. Genotypic effects were very highly significant with an LSD$_{0.05}$ = 0.4‰

Rank	Genotype	A (‰)	Rank	Genotype	A (‰)
1	480	22.3	22	Baye Ngagne	21.7
2	Tn 88-63	22.2	23	Vita 7	21.7
3	Kaedi Gris-blanc	22.2	24	Ndout	21.6
4	4R-0267-1F	22.1	25	CB5	21.6
5	ER-1	22.0	26	Ndiaga Aw	21.6
6	Ndiambour	22.0	27	ER-7	21.5
7	473	21.9	28	Diongama	21.5
8	5x-57	21.9	29	Chino M1	21.5
9	572	21.9	30	CB5-E1	21.4
10	601	21.9	31	Bambey 21	21.4
11	Mougne	21.9	32	8517	21.4
12	482	21.9	33	TVx 1841-01E	21.4
13	Mouride	21.9	34	Prima	21.4
14	514	21.9	35	UCR 237A	21.4
15	TVu 374	21.9	36	CB46	21.3
16	Melakh	21.8	37	TVx 309-1G	21.3
17	475	21.8	38	58-111	21.3
18	TVx 75-4	21.7	39	66-20	21.3
19	590	21.7	40	Bambey 29	21.3
20	TVx 1836-015	21.7	41	Casa 16	21.3
21	484	21.7	42	IAR 16-96	21.1

Table 2
Carbon isotope discrimination measared in leaves of cowpea genotypes grown at Bambey and Louga, Senegal, in 1992

Genotype	Bambey		Louga	
	Rank	Δ (‰)	Rank	Δ (‰)
58-57	(3)	20.2	(1)	22.8
Vita 7	(4)	20.2	(2)	22.7
Bambey 21	(1)	20.3	(3)	21.9
CB5	(2)	20.3	(4)	21.9
4R-0267-1F	(5)	20.1	(5)	21.8
CB46	(6)	20.1	(6)	21.4
Prima	(7)	20.1	(8)	21.0
UCR 237A	(8)	19.8	(7)	21.2
TVx 309-1G	(9)	19.5	(9)	20.9
Mean		20.1		21.7
$LSD_{0.50}$			0.7	
Mean Squares				
Genotype effects		1.53	**	
Location effects		50.72	***	
G X E effects		0.56	ns	
Error		0.51		

LSD tests differences between genotypic means. ** and *** = significant at $P<0.01$ and 0.001, respectively. and ns is not significant at $P=0.38$.

Table 3
Hay and grain yield of cowpea genotypes grown at Bambey, Senegal, in 1992

Genotype	Hay (kg/ha)	Grain (kg/ha)	Total (kg/ha)
58-57	4433	1973	6406
TVx 309-1G	3151	2120	5271
4R-0267-1F	2278	2197	4475
Vita 7	2033	2081	4114
Bambey 21	2291	15.35	3826
UCR 237A	1503	1829	3332
Prima	1847	1105	2952
CB46	1139	1412	2551
CB5	1116	13.54	2520
Mean	2205	17.34	3939
$LSD_{0.05}$	937	406	

tope composition was measured as described in Hall et al. (1992).

Experiments were conducted in the summers of 1987 and 1988 in a semiarid, subtropical region of southem Califomia at the Riverside research station of the University of Califomia. These experiments have been described previously (Hall et al., 1992). In 1987, cowpea genotypes were grown under well-watered and stored-soil-moisture conditions in a split-block design with four replications. The main blocks consisted of weekly, well-watered furrow irrigation and a treatment that received no rain or irrigation after plant establishment. The sub-plots consisted of the different genotypes. In 1988 a third, intermediate irrigation treatment was included that was irrigated on altemate furrows every 3 weeks during the growing season. Samples consisting of three leaflets were taken from the eighth node of three plants in each plot 5.5 and 62 days after sowing in 1987 and 1988, respectively, and processed to determine A as described in Hall et al. (1992).

3. Results

The screening trial with 42 diverse cultivars and lines at Bambey, Senegal, in 1991 received 347 mm of rain. There was little plant-available moisture in the soil at the beginning of the cropping season. This rainfall

Table 4
Cowpea genotypic ranking for carbon isotope discrimination measured in leaves in California and Senegal

Genotype	Riverside, California						Senegal			
	1987		1988				1991	1992		
	Wet[a] Rank	Dry Rank	Wet Rank	Med. Rank	Dry Rank	Mean (‰)	Bambey[b] Rank	Bambey Rank	Louga Rank	Mean (‰)
CB46	1	2	2	1	1	19.8	8	7	6	20.9
Prima	2	1	3	2	2	19.7	6	6	8	20.8
CB5	3	3	1	3	3	19.5	4	2	4	21.2
4R-0267-1F	4	7	4	4	4	19.0	1	5	5	21.4
Bambey 21	5	5	6	5	7	18.8	5	1	3	21.2
58-57	7	4	5	6	5	18.8	2	4	1	21.6
TVx 309-1G	6	6	7	7	6	18.7	9	9	9	20.6
Vita 7	8	8	9	8	8	18.1	3	3	2	21.5
UCR 237A	9	9	8	9	9	17.9	7	8	7	20.8

[a]Wet, Med., and Dry denote well-watered, intermediate, and limited-irrigation treatments, data from Hall et al. (1992).
[b]Bambey and Louga are locations in Senegal with intermediate and limited supplies of rain, respectively.

Table 5
Correlation coefficients for genotypic mean values of carbon isotope discrimination measured in leaves of cowpea

Comparisons	*r*	*n*	*P*
Within regions			
Southern California			
Riverside Wet vs Dry 1987	0.909	9	<0.001
Riverside Wet vs Dry 1988	0.916	9	<0.001
Riverside 1987 vs Riverside 1988	0.994	9	<0.001
Senegal			
Bambey 1992 vs Louga 1992	0.700	9	0.05
Bambey 1991 vs Bambey 1992	0.477	9	ns
High Plains of Texas			
Lubbock Wet vs Dry 1988	0.907	8	0.01
Lubbock Wet vs Dry 1989	0.317	6	ns
Between regions			
Senegal (1991 + 1992) vs Riverside (1987 + 1988)	-0.125	9	ns
Senegal (1991 + 1992) vs Lubbock (1988)	-0.122	6	ns
Senegal (1991 + 1992) vs Lubbock (1989)	-0.098	6	ns
Lubbock (1988) vs Riverside (1987 + 1988)	0.569	8	ns
Lubbock (1989) vs Riverside (1987 + 1988)	0.518	6	os

would have provided about 77% of the maximal water requirement of a medium-cycle cultivar such as 58-57 (Hall and Patel, 1987). Genotypic differences in leaf Δ were very highly significant (Table 1), but the range of values (1.2‰) was smaller than the range obtained at Riverside, California (2.1‰) with a set of 50 genotypes including 13 of the same ones (Hall et al., 1990). Maximum differences in W can be estimated using the following equation:

$$W_1/W_2 = (b-d-\Delta_1)/(b-d-\Delta_2) \qquad (1)$$

where $(b-d)$ are parameters for the inherent discrimination associated with carboxylation (b) and other metabolic processes (d). The value of $(b-d)$ was estimated from the empirical studies of Ismail and Hall (1992) as being 24.3‰. The genotype with the lowest Δ (IAR 16-96) in Table 1 is estimated to have 58% higher W than the genotype with the highest Δ (#480). This is similar to the range of difference in W estimated for the study at Riverside, California (Hall et al., 1990) of 62%.

At Bambey, Senegal (Table 1), there was a tendency for well-adapted local cultivars to have high leaf Δ (e.g., Tn 88-63, Ndiambour, 58-57, Mougne, Mouride, and Melakh) and poorly adapted exotics to have low leaf Δ (e.g., CB46, Prima, 8517, and CB5-E1). For the 13 genotypes included in the trials at both Bambey, Senegal, and Riverside, California, the correlation coefficient for genotypic means was small and nonsignificant ($r=0.295$, $n=13$), and substantial rank changes were present for Chino M1, 4R-0267-1 F, and Vita 7.

The trials with nine cultivars and lines at Bambey and Louga, Senegal, in 1992 received 34 1 and 202 mm of rain, respectively. There was little plant-available moisture in the soil at the beginning of the cropping season in either location. This rainfall would have provided about 75% and 44% of the maximal water requirements of a medium-cycle cultivar, such as 58-57, at Bambey and Louga, respectively (Hall and Patel, 1987). Genotypic differences in leaf A were highly significant, and there were significant effects of location but very little G X E or change in genotypic ranking (Table 2). Total shoot biomass production at Bambey (Table 3) was not correlated with leaf A, but the well-adapted local land race, 58-57, had the greatest shoot biomass production and relatively high leaf A. Two exotic lines, CB46 and Prima, had small shoot biomass production and relatively low leaf A. Contrasting performance was exhibited by TVx 309-1G which had the lowest leaf A, but the second largest shoot biomass production. Grain yields at Louga were very small due to the drought (an average value of 13 1 kg/ha compared with 1734 kg/ha at Bambey:) and genotypic comparisons are not reliable.

In five studies over 2 years at Riverside, California, with different irrigation treatments (Hall et al.. 1992), leaf A values exhibited consistent genotypic ranking (Table 4). The same nine genotypes exhibi ted moderately consistent ranking for leaf A values over three trials in Senegal (Table 4). Four genotypes exhibited substantial changes in ranking across regions: CB46, Prima, 58-57, and Vita 7. Cultivar CB46, which is productive in California, had higb leaf A in Riverside, but low A in Senegal, where it has small yields of grain or hay (Table 3). Genotypes that are well-adapted to Senegal, 58-57 and Vita 7 (Table 3), had high A in Senegal, but low A in California. Two genotypes had consistently low leaf A in both regions: UCR 237A and TVx 309-1G; and the latter can be productive in Senegal (Table 3).

Comparisons of genotypic means using correlation coefficients indicates that genotypic rankings were relatively consistent in trials over different watering regimes and years within regions (Table 5). In contrast, correlation coefficients were very small for comparisons between the tropical and subtropical regions (Table 5) indicating inconsistent genotypic rankings between Senegal and either Riverside, California, or Lubbock, Texas. Correlation coefficients for Riverside versus Lubbock were moderate and were not significant.

4. Discussion

Genotypic differences in leaf A were observed for cowpea cultivars and lines grown in Senegal (Table 1) that were relatively consistent over three trials in contrasting conditions (Table 4). Similar consistency in ranking for leaf A had been reported for southern California (Table 4) and may occur in the high plains of Texas (Table 5). For cowpeaprograms concerned with breeding cultivars for rainfed production in semiarid Senegal, it is not clear whether selection should be for high, intermediate, or low leaf A. The productive and broadly adapted local land race, 58-57, had high leaf A (Tables 2 and 3), as did Tn 88-63 (Table 1) which is well-adapted to dry zones of West Africa. In contrast, TVx 309-1 G had consistently Iow leaf A (Tables 2 and 4), but was productive at Bambey (Table 3).

The major differences in climate between the regions are that semiarid Senegal has higher night temperatures than Lubbock or Riverside: and daytime humidity is higher at Lubbock than Riverside. Substantial changes in genotypic ranking for low leaf A were observed between regions (Tables 4 and 5); although TVx 309-1G and UCR 237A had consistently low Δ in both southem Califomia and Senegal (Table 4). In addition, there was a tendency for well-adapted genotypes to have high leaf A. These data may be explained by the presence of different genes conferring local adaptation in different environments. These genes may cause stomata1 conductance to be 'large, which would then enhance CO_2 assimilation and growth, but cause W to be low and A to be high. Positive correlations between Δ and shoot biomass production that might be caused by genotypic differences in stomatal conductance have been reported for wheat (Condon et al., 1987) and *Phaseolus vulgaris* L. (Ehleringer, 1990). The consistently low A of TVx 309-I G and UCR 237A appear to have different physiological bases (Ismail and Hall, 1993): TVx 309-1G has greater photosynthetic capacity, whereas UCR 237A has smaller stomatal conductance. Apparently, the genes conferring these traits may be consistently expressed in different environments.

The G x E that was observed would not necessarily constrain cowpea breeding programs that aim at developing improved cultivars for specific target production regions, such as semiarid tropical Senegal or subtropical California. Selection for A in one of these regions, however, may not be effective in producing cultivars of cowpea and, possibly, other crops for the other region. Also, Richards and Condon (1993) reported that genotypic ranking of wheat can be different in off-season glasshouse environments compared with commercial field production environments. Use of linked genetic markers to indirectly select for *A* has been proposed (Martin et al., 1984). One advantage of DNA marker selection is that it could be effective in any environment, including off-season nurseries (B. Martin, pers. commun., 1992). This approach would not appear to be more effective than selecting for *A*, at this time, because several markers are needed that may vary depending upon the target production environment. Genotypes with consistently low *A* (e.g., TVx 309-1G) and consistently high *A* (e.g., Tn 88-63) may be useful for selection experiments to determine for rainfed production in semiarid zones whether low, intermediate, or high *A* is adaptive.

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