Genetic Analysis and Interrelationships between Traits for Cooking Time, Water Absorption, and Protein and Tannin Content of Andean Dry Beans

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ABSTRACT. A knowledge of the relative proportion of additive and nonadditive genetic variances for complex traits in a population forms a basis for studying trait inheritance and can be used as a tool in plant breeding. A North Carolina Design II mating scheme was used to determine the inheritance of cooking time, protein and tannin content, and water absorption among 16 genotypes of dry bean (*Phaseolus vulgaris* L.) representative of the Andean Center of Domestication. Heritability and the degree of dominance for the traits were also calculated to provide guidelines for adopting breeding strategies for cultivar development. Thirty-two progeny resulted from the matings and these were assigned to two sets of 16 progeny each. Variances due to general combining ability (GCA) and specific combining ability (SCA) were significant for the traits. The GCA was larger in all cases. Narrow-sense heritability for protein, tannin, water absorption, and cooking time averaged 0.88, 0.91, 0.77, and 0.90, respectively. Degree of dominance estimates indicated that the traits were governed by genes with partial dominance except, in one case, tannin had a degree of dominance value of zero, indicating no dominance. The phenotypic correlation (-0.82) between water absorption and cooking time justifies using the water absorption trait as an indirect selection method for cooking time. With regard to parent selection in crosses, significant differences between GCA females and GCA males suggested cytoplasmic influences on trait expression. Hence, the way a parent is used in a cross (i.e., as female or male) will offset trait segregation. Using fast-cooking bean cultivars in conjunction with fuel-efficient cooking methods may be the best strategy to conserve fuelwood and help reduce the rate of deforestation in East and Central Africa.

Although dry bean (*Phaseolus vulgaris*) is a dietary staple of low- and middle-income families in Africa and Latin America, the crop is underused as a food. The prolonged time required to cook beans to a point at which they are palatable and the protein and starch can be digested often leads to an unfavorable acceptance by consumers in these regions. Also, the fact that bean protein is not as bioavailable as proteins from other plant sources limits the inherent supply of this nutrient to consumers (Bressani, 1973).

Beans are cooked in much of eastern and central Africa over an open wood fire built on the ground (Poulsen, 1978). However, the long cooking time required for beans compared to other foodstuffs,

and the fact that open wood fires are not fuel efficient, exacts a high cost in human and physical resources. The cost is reflected in an excessive use of fuelwood and labor required to gather the wood and tend the fire throughout the cooking period. The important contribution of beans to human nutrition and the large amount of fuelwood required to prepare them for consumption illustrates a strong link between nutritional well-being and fuel supply in this region (Shellie-Dessert and Hosfield, 1990).

Wood is the most widely used household fuel in the developing world and, in Tanzania, accounts for 94% of the total national energy consumption (Eckholm et al., 1984). Of this percentage, 80% is used for cooking. Deforestation has occurred at a rapid rate in the eastern-central region of Africa because of excessive cutting of trees for fuel use (Sirven, 1981). Beans require much more energy (300,000 kJ·g⁻¹) than other staple foods (Brouwer et al., 1989). In Mexico and Guatemala, the consumption of beans has decreased because of the long cooking time required to make beans palatable, render starch and protein digestible, and detoxify antinutrients. The current scarcity of fuelwood in Tanzania has made the reduction in resources to prepare beans for eating an important economic consideration.

The development of bean cultivars with faster cooking times than the cultivars currently grown for consumption might help conserve fuelwood. Shellie-Dessert and Hosfield (1990) described a novel crock-pot-like cooking method that used 40% less fuelwood

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than the traditional open fire cooking method. Using stoves that enclose the fuel source rather than allowing it to burn openly and dissipate most of the heat to an open environment also has been suggested as a means to conserve fuelwood.

In addition to cooking time, water uptake and protein and tannin content of bean seed must be considered by the breeder. Beans are generally soaked before cooking to improve the hydration characteristics of seeds for uniform cooking and to ensure bean tenderness (Hoff and Nelson, 1965). The presence of tannin in beans has been shown to adversely affect the nutrition of animals (Kakade and Evans, 1965; Lindgren, 1975; Rannenkamp, 1977). Tannin is localized in the testa of colored-seeded beans (Ma and Bliss, 1978; Wassimi et al., 1988). The adverse biological effects of tannin in foodstuffs are probably due to its ability to cross-link with protein and other macromolecules through phenolic hydroxyl and other reactive groups characteristic of tannin molecules (Swain, 1965). Since beans are the major source of protein in the diets of rural consumers of Tanzania, and the preferred seed types have red, beige, or brown seedcoats, there is a possibility for impaired protein bioavailability by tannin in these seed types.

Several studies have indicated genetic variability in dry bean for cooking time (Castellanos et al., 1995; Shellie and Hosfield, 1991), water absorption (Shellie and Hosfield, 1991; Castellanos et al., 1995), protein percentage (Bliss and Brown, 1983; Kelly and Bliss, 1975), and tannin content (Ma and Bliss, 1978; Wassimi et al., 1988). The improvement of beans for these traits through breeding should lead to bean cultivars that cook rapidly and have a maintained or increased protein percentage and low tannin content. Different breeding procedures may be necessary to improve each trait if gene action or heritability differs.

A knowledge of the importance of general combining ability (GCA) and specific combining ability (SCA) within a breeding population provides guidance as to whether additive or nonadditive gene action is influencing trait expression. A knowledge of the type of gene action in a population aids the breeder in ascertaining which breeding procedure will efficiently improve the performance of metric traits in a crop (Dudley and Moll, 1969). Since an increase in the use of dry bean in the diets of consumers in Tanzania and other major bean-consuming countries of the region might be achieved by reducing cooking time, this study was undertaken. Specific objectives were to 1) estimate GCA and SCA variances for cooking time, water absorption, and protein and tannin content, 2) estimate the heritability and degree of dominance for the traits and use this information for developing a selection strategy, and 3) calculate correlations between pairs of traits and evaluate whether a particular trait can be used to select for another indirectly.

Materials and Methods

GENETIC MATERIAL. Sixteen genotypes of dry bean that differed morphologically, phenologically, and agronomically (Table 1) were used as parents in the study. Except for 'Sierra', the parents were representative of the Andean gene pool of *P. vulgaris* and represented preferred grain types in eastern and central Africa. 'Sierra' is a high-yielding bean and representative of the Middle-American gene pool with the medium pinto market class seed size (Table 1).

The genotypes were all adapted to the bean production areas of eastern and central Africa. Seeds of the entries are highly favored by consumers in the region because of their meat-like appearance and thick broth and soup quality after cooking. The appearance of the bean complements a stiffened porridge-like staple food prepared from corn called *ugali* in Kiswahili (eastern Africa), *nsima*

in Malawi, *saza* in Zimbabwe, *bogobe* in Botswana, *papa* in South Africa and *fufu* in Nigeria.

PROCEDURES. The 16 genotypes were intermated in 1991 using a North Carolina Design II (Comstock and Robinson, 1948) mating scheme. Eight genotypes were chosen randomly as male parents, and the remaining eight genotypes were used as female parents. The genotypes used as male parents were not crossed to each other, nor were the genotypes used as females crossed to each other. To reduce the number of matings required, two sets were formed. Within each set, each male parent was crossed to four females, resulting in a total of 16 crosses per set.

The 16 parents were increased, and the 32 F_1 populations were advanced in a winter nursery at the Univ. of Puerto Rico substation near Isabela in 1992. The 32 F_2 populations were planted at the Saginaw Valley Bean and Sugarbeet Research Farm, Saginaw, Mich., in a Misteguay silty clay [fine, illitic (calcareous), frigid typic Haplaquolls] in 1992. One-hundred F_2 plants from each cross were selected randomly and threshed, and the seeds were bulked. Because most of the parents were obtained from breeding programs in Tanzania and countries in eastern and central Africa, the F_2 progeny were generally unadapted in Michigan and were not evaluated. The F_3 progeny were grown and evaluated in Tanzania (Morogoro Region) during the annual periods of bimodal rain distribution [short rain (SR) and long rain (LR) growing seasons].

The experiments were planted in the 1993 SR growing season and 1994 LR growing season in a randomized complete-block design with three replications at the Crop Museum (530 masl) and Morning Site (1000 masl) research farms of the Agricultural Univ. of Sokoine. Since there was insufficient F_3 seed to plant the experiment at both locations during the SR growing season, F_4 seed produced from this crop was planted at both locations in March 1994 during the LR period. Hence, generation and season effects were confounded. The confounding was not a major consideration in the study because the comparison of generations (F_3 vs F_4) was only of minor interest.

The 32 progeny were arranged in the field in two sets. The four females and four males used as parents of a particular set were included in the planting arrangement along with the 16 F_3 or F_4 progeny. The 48 entries (parents and progeny) making up the two sets were hand seeded into four-row plots. Rows were 4 m long and spaced 0.5 m apart. The within row spacing was 0.1 m, giving an approximate plant density per plot of 20 plants/m².

TRAIT EVALUATION. Mature plants were harvested by hand from the middle two rows of individual plots when the pods could be threshed. After the seeds were harvested from each plot, they were air dried for 2 weeks. The moisture content of the samples was equilibrated to each other by storing the samples in sealed plastic buckets and held at 20 °C and 70% relative humidity (RH) until evaluated (Shellie, 1990). At the initiation of the soaking and cooking evaluations, it was not possible to determine seed moisture on the samples. However, Dexter et al. (1955) showed that navy bean samples stored at 20 °C and 70% RH equilibrated to 15.2% moisture content.

Protein content was determined on 30 g of bean seeds that were ground to 40- μ m particle size with a Udy Cyclone mill (Boulder, Colo.). Protein percentage was estimated on the bean flour by the micro-Kjedahl method (Association of Official Analytical Chemists, 1975). Percent protein was calculated as percent N $\times$ 6.25.

The vanillin hydrochloric acid method of Burns (1963) was used to estimate tannin content. Since catechin was used as a standard in the tannin assay procedure, tannin content was estimated as catechin equivalent. However, in this report, catechin equivalent will be referred as tannin.

The percent water absorption of the entries was determined on triplicate samples of a known mass of 75 seeds from each plot. Seeds were soaked in distilled water for 12 h at room temperature. The amount of water absorbed was taken as the difference in mass before and after soaking divided by the mass before soaking of the 75 seed sample.

Bean cooking time was estimated with a 25-seed Mattson pin-drop cooker (Jackson and Varriano-Marston, 1981). Cooking time was calculated as the elapsed time from initiation of cooking until the time when 13 of the 25 pins (52%) of the instrument had dropped and penetrated seeds in the cooker. Data were taken on triplicate samples for each plot at each location.

STATISTICAL ANALYSIS. An all-random-effects model was used for analyses of variance (ANOVA) (Searle, 1971). In the Design II ANOVA, the variability due to progeny was broken out as variation due to males within sets, females within sets, and male $\times$ female interaction within sets (Hallauer and Miranda, 1988). Throughout the text, variation due to males within sets, females within sets, and males $\times$ females within sets will be referred to interchangeably as GCA males, GCA females, and SCA variation, respectively (Pixley and Frey, 1991). The F tests were straightforward for all sources of variation in the ANOVA except for the male and female components. Approximate F tests (Satterthwaite, 1946) were constructed based on the mean square expectations and used to test the male and female effects.

Estimates of variance components were calculated by equating terms comprising the expected mean squares to the corresponding observed mean square and solving by appropriate algebraic manipulation (Comstock and Robinson, 1948; Hallauer and Miranda, 1988). The components of genetic variance were estimated according to expectations provided by Cockerham (1956) as

$$\sigma_m^2 = \sigma_f^2 = \text{cov HS} = (1/4)\sigma_A^2, \text{ and} \\ \sigma_{mf}^2 = \text{Cov FS} - \text{Cov HS}_m - \text{Cov HS}_f = (1/4)\sigma_D^2$$

where σ_A^2 ; σ_D^2 ; σ_m^2 ; σ_f^2 ; and σ_{mf}^2 are the additive and dominance variance and the variance due to GCA males, GCA females, and SCA, respectively. The Cov HS and Cov FS are the covariances of

half-sib and full-sib progeny.

The degree of dominance (d) governing the genes for trait expression was estimated by

$$d = (2\sigma_{mf}^2/\sigma_m^2)^{1/2}.$$

Narrow-sense heritability was estimated from the components of variance values pertaining to a Design II mating scheme as

$$h^2_N = \sigma_A^2 / \sigma_{ph}^2$$

where σ_A^2 is the additive genetic variance and σ_{ph}^2 is the phenotypic variance. The approximate standard error of the narrow-sense heritability estimate was calculated as

$$SE(h^2) = SE(S^2_f) / S^2_{pfm}$$

where S^2_f is the variance components due to progeny and S^2_{pfm} is the total phenotypic variance of progeny estimated from variance components (Dickerson, 1969). Phenotypic correlations between cooking time and percent protein, tannin content, and water absorption were calculated using the GENSTAT 5 program (GENSTAT 5, 1989).

Results and Discussion

Although the sixteen parents represented a large proportion of the most widely grown cultivars in the region, they cannot be considered a random sample in the strictest sense. Baker (1978) raised concerns as to the use of random sample terminology for the most commonly encountered type of parental set, i.e., a set of unrelated lines that derive from broadly diverse genetic backgrounds. In his view (Baker, 1978), for one to assume that parents used in an experiment are a random sample of some reference population, the parents must be produced by random mating followed by nonselective inbreeding. Random mating followed by inbreeding was not performed on the parents used in this study; hence, the 16 genetic lines are the population about which inferences are made.

Significant effects across two locations in Tanzania were de-

Table 1. Description, and combined means across two locations and growing seasons (1993, 1994) in the Morogoro Region, Tanzania for chemical contents, water absorption, cooking time and maturity of 16 dry bean accessions used as parents in a North Carolina Design II mating scheme.

Entry	Maturity (d)	Protein content (g·kg ⁻¹)	Tannin content (mg/100 g)	100-Seed mass (g)	Water absorption (g·kg ⁻¹)	Cooking time (min)
Var 11	72	245	335	36	1061	26
Nyirakizungu	71	250	308	40	941	31
Lyamungu	82	220	337	35	786	42
Kilyumukwe	75	253	409	47	699	47
Yellow eye	69	241	353	37	819	36
UAC 221	80	258	499	45	543	52
TMO 959	82	192	388	35	765	44
Kalima	72	205	318	45	992	28
CIAT 3005	76	209	479	37	589	50
PI 605623	81	254	323	48	1030	28
GLPX 1125	74	260	423	45	649	49
Jacob's Cattle	71	216	337	46	818	34
Montcalm	70	246	418	44	675	47
NY 99	79	233	402	33	733	46
Sierra	69	219	352	29	860	35
Diacol Calima	73	253	365	45	805	37
Mean	75	234	380	41	758	39
LSD (0.05)	4	30	23	1	20	2
CV (%)	4	11	5	4	2	4

tested for the protein content and water absorption traits in the SR and LR growing seasons and for tannin content only in the SR season (Table 2). Variability between locations led to significant location interactions for some traits. A significant male $\times$ location interaction was noted for protein content in the SR season and tannin content in the LR season. Significant variability between sets was observed for water absorption and cooking time (Table 2). Another explanation for these differences could be sampling error.

The increased variability due to GCA in the LR season (F_4) compared to the SR season (F_3) was most likely caused by the effect inbreeding has on additive and dominance variance. As inbreeding progresses, the proportion of the total variance, which is additive, increases and the dominance portion decreases until at the limit there is no dominance variance among homozygous lines (Falconer, 1981).

Mean squares for GCA males and GCA females were highly significant for all four traits in both growing seasons (Table 2). A Design II mating scheme provides two independent estimates of GCA—one due to female and one due to male parents (Hallauer and Miranda, 1988). Except for cooking time in the SR season, the mean squares for GCA females were larger than for GCA males. The differences between the two GCA estimates reflected the variability for traits among the parents per se and suggested significant maternal and nonmaternal reciprocal influences on trait expression (Cockerham, 1963). Another explanation for these differences could be sampling error.

Despite the difference in level of inbreeding between the genotypes grown in the SR (F_3) and LR (F_4) growing seasons, the magnitude of the main-effect mean squares between the two generations was in good agreement (Table 2). The most notable

exceptions were the GCA male and GCA female mean squares for tannin content and cooking time and the location mean square for tannin content and water absorption. The GCA female mean square for cooking time was about 12 times greater in the LR than the SR season.

Means and ranges for progeny grown in the SR and LR were similar in magnitude for all traits (Table 3). However, there was less variability in protein content in the LR than the SR season. But the range in cooking time was greater in the LR (16 min) than the SR (10 min) growing season. The variability noted for cooking time should be sufficient to develop bean cultivars from these parents that cook rapidly and therefore conserve fuel wood.

The genotypic variance observed among progeny of the 16 parents for protein and tannin content, water absorption, and cooking time was due to additive and dominance genetic effects, with the additive portion being larger in all cases (Table 4). Hence, additive gene action was the major contributor to progeny variation. Wassimi et al. (1988) showed a 4:1 ratio of GCA to SCA for bean protein content among F_3 matings from a diallel cross.

Heritability estimates for protein and tannin content and water absorption in the SR and LR growing seasons were high (Table 4). The H^2_N for protein and tannin content ranged from 0.71 to 0.91 in both growing seasons, but values for the respective traits were lower—0.71 and 0.77—in SR. In the LR growing season, H^2_N for water absorption was similar (0.77) to that of the SR growing season. The H^2_N for cooking time was 0.97 and 0.90 in the SR and LR growing seasons, respectively. Except for tannin content in the LR growing season, the four traits showed degrees of dominance <1.0 but >0.0 (Table 4), indicating that these traits were governed by genes with partial dominance.

Table 2. Mean squares from analyses of variance combined across two locations in Tanzania for protein, tannin, water absorption, and cooking time of dry bean progeny grown during the short-rains (1993) and long-rains (1994) seasons.

Source of variation	df	Growing season ²	Protein content	Tannin content	Water absorption	Cooking time
Location, L	1	SR	339*	324*	383*	278
		LR	273*	511	275*	213
Sets, S	1	SR	6	94	2663*	1117*
		LR	9	77	2770*	1281*
S (L)	2	SR	1	0	1	0
		LR	0	1	1	5
Replications (S) (L)	8	SR	0	1	1	3
		LR	1	3	2	1
Males (S), M	6	SR	16**	31**	315**	62**
		LR	21**	15**	322**	114**
Females (S), F	6	SR	40**	326**	1358**	21**
		LR	50**	164**	1310**	248**
M $\times$ F(S)	18	SR	1**	3**	23**	1
		LR	1	8**	24**	5**
M(S) $\times$ L	6	SR	4**	1	0	4
		LR	1	17**	1	1
F(S) $\times$ L	6	SR	0	0	1	0
		LR	1	7	0	2
L(S) (M) (F)	18	SR	0**y	1	1	1
		LR	1	9	1	1
Error	120	SR	0*	1	1	2
		LR	1	2	1	2
Total	191					

²SR = short rains, LR = long rains.

*Small positive value (<0.5) that was significant.

**Small positive value <0.5 .

*,**Significant at $P = 0.05$ or 0.01 , respectively.

Table 3. Means and ranges for protein, tannin, water absorption and cooking time combined across two locations in Tanzania, for dry bean progeny grown during the short-rains (1993) and long-rains (1994) growing seasons.

	Growing season ²	Protein (g·kg ⁻¹)	Tannin (mg/100 g)	Water absorption (g·kg ⁻¹)	Cooking time (min)
Mean	SR	234	399	817	38
	LR	244	373	823	38
Range	SR	197–340	338–471	648–955	33–43
	LR	205–265	336–438	677–975	31–47
CV (%)	SR	17	2	3	5
	LR	5	8	1	3

²SR = short rains, LR = long rains.

Phenotypic correlations between cooking time and water absorption were -0.78^* and -0.87^* , in the SR and LR seasons, respectively (Table 5). These values showed a consistency across growing seasons. Several studies have indicated an inverse relationship between cooking time and water absorption (Castellanos et al., 1995; Edminster et al., 1990; Shellie and Hosfield, 1991). The magnitude of correlations between cooking time and water absorption determined in the current study agreed with Castellanos et al. (1995), who obtained correlations on nonscarified seed of -0.69^{**} to -0.81^{**} for cooking time and water absorption after an 18-h soak. However, the magnitude of the correlations between cooking time and water absorption we observed differed from that reported (-0.37^*) by Shellie and Hosfield (1991), who removed seed that did not imbibe water during soaking (hard shell) from the experiment. These authors suggested that removing hard shell beans from the cooking evaluation probably biased the correlation values downwards. Similar results were observed by Castellanos et al. (1995). These researchers found a nonsignificant correlation between cooking time and water absorption of scarified seed.

Since fast-cooking beans imbibed more water than slow-cooking ones, as indicated by the negative correlations, water absorption should be a useful predictor of cooking time in these beans. Selection based on the water absorption of a breeding line as an indirect estimation of its cooking time is rapid and saves resources. The phenotypic correlations between protein and tannin content and between cooking time and protein content were nonsignificant (Table 5), but the correlations between cooking time and tannin were positive and significant in both locations, suggesting that, in this study, beans with low tannin content cooked faster than beans with high tannin content.

BREEDING IMPLICATIONS. Significant variability in protein and

tannin content, water absorption, and cooking time among the matings in the present study suggest that these traits can be altered by selection. The magnitude of GCA to SCA genetic variation in the families derived from mating of the 16 parents indicates that progress can be expected as materials are advanced and inbred. Since all the traits had high narrow-sense heritabilities (0.71 to 0.97), a combination of early generation selection or pedigree selection would be preferable. Should a combination of inbreeding methods be used for trait improvement, the breeder could begin selection in the F_2 for traits such as seed size and color on a single plant basis. After two generations of inbreeding, the breeder could select the best F_2 -derived F_4 lines and evaluate these on a row basis for water uptake and cooking time. The genotypes 'Var 11', PI 605623, and 'Kalima' would be useful parents to improve cooking time (Table 1). Selected individuals could be intermated, and one cycle of recurrent selection included to increase the gene frequencies of favorable alleles if limited variability is detected for specific traits in the $F_{2.4}$ lines. For those traits such as water absorption and cooking time, which exhibited high heritability, pedigree selection could be continued between selected $F_{2.4}$ lines derived from the second recurrent selection cycle. Additive genetic variance should increase among families. Additional selection among these lines for yield-related traits could be practiced at the F_6 , when the individual lines are nearly homozygous. The selected F_6 lines would be replicated and grown in different locations over years. Since water absorption and cooking time are best evaluated on a row rather than a plant basis, desirable seed traits like size and color can be fixed before evaluation for the other quality traits, thus improving the efficiency of the procedure.

USE OF CORRELATED RESPONSES IN BREEDING STRATEGY. The significant and positive correlation (0.77^* and 0.68^*) obtained in

Table 4. Estimates of additive and dominance variance, narrow sense heritability, and the degree of dominance combined across two locations in Tanzania for protein content, tannin content, water absorption, and cooking time traits measured on dry bean progeny grown during the short-rains (1993) and long-rains (1994) growing seasons.

Character	Growing season ²	σ^2_A ^y	σ^2_D ^x	$H^2_{(N)}$ ^w	Degree of dominance
Protein (g·kg ⁻¹)	SR	2.1	0.2	0.71 ± 0.22	0.4
	LR	3.2	0.4	0.88 ± 0.04	0.2
Tannin (mg/100 g)	SR	4.8	1.4	0.77 ± 0.03	0.8
	LR	26.2	2.7	0.91 ± 0.11	0.0
Water absorption (g·kg ⁻¹)	SR	48.9	14.5	0.77 ± 0.05	0.8
	LR	49.6	15.2	0.77 ± 0.04	0.8
Cooking time (min)	SR	9.5	0.3	0.97 ± 0.10	0.2
	LR	18.1	2.7	0.90 ± 0.02	0.5

²SR = short rains, LR = long rains.

^y σ^2_A = additive genetic variance.

^x σ^2_D = dominance genetic variance.

^w $H^2_{(N)}$ = narrow sense heritability.

Table 5. Phenotypic correlation coefficients in two growing seasons and combined across two locations in Tanzania between protein, tannin, water absorption and cooking time.

Trait ^a	Protein content	Tannin content	Water absorption	Cooking time
Protein (g·kg ⁻¹)	---	-0.06	0.04	-0.12
Tannin (mg/100 g)	-0.08	---	0.87*	0.77*
Water absorption (g·kg ⁻¹)	-0.05	-0.81*	---	-0.78*
Cooking time (min)	-0.03	0.68*	-0.87*	---

^aBold = short rains growing seasons; nonbold = long rains growing season.

*Significant at $P < 0.05$.

this study between tannin content and cooking time indicated that beans low in tannin cooked faster than beans with high tannin. Selecting faster-cooking genotypes during the inbreeding process of cultivar development should indirectly lead to cultivars with reduced tannin content. The potential of intermating fast-cooking genotypes, e.g., 'Var 11' and 'Kalima', with 'Nyirakizungu', a genotype with relatively high protein, low tannin, and acceptable cooking time, may prove fruitful in providing appropriate recombinants to improve all three quality traits simultaneously and lead to the development of rapid-cooking cultivars with low tannin and high protein content. Although this strategy may lead to improved nutritional quality through an increase in protein contents and decrease in tannin contents, the breeder must not lose sight of regional preferences for production, marketing, and consumption. In Tanzania, farmers prefer to grow cultivars with large red or red-mottled seed types.

POTENTIAL IMPACT ON FUELWOOD CONSERVATION. Data from this study suggests that cooking time in populations developed from the 16 parents can be shortened through selection. Hence, the breeding and use of fast-cooking dry bean cultivars derived from intermating these parents could help slow the rapid deforestation that has gripped parts of eastern and central Africa. We did not measure fuelwood usage corresponding to cooking beans. However, in a study conducted in Rwanda, Shellie-Dessert and Hosfield (1990) estimated an annual savings of 150,000 Mg of wood by the country's 1.1 million rural households if they produced and consumed fast-cooking cultivars instead of the traditional ones. This estimate was based on a 24-min reduction in cooking time by using 'Calima', a fast-cooking cultivar introduced to the National Bean Program by the International Center for Tropical Agriculture (CIAT), Cali, Colombia. Perhaps the best strategy to conserve fuelwood associated with cooking beans in Tanzania and other countries in the region is to find more fuel-efficient cooking methods such as the haybasket procedure (Shellie-Dessert and Hosfield, 1990) in conjunction with the use of fast-cooking cultivars.

Literature Cited

- Association of Official Analytical Chemists 1975. Official methods of analysis. 12th ed. AOAC, Washington, D.C.
- Baker, R.J. 1978. Issues in diallel analysis. *Crop Sci.* 18:533-536.
- Bliss, F.A. and J.W.S. Brown. 1983. Breeding common bean for improved quantity and quality of seed protein. *Plant Breed. Rev.* 1:59-102.
- Bressani, R. 1973. Legumes in human diets and how they might be improved, p. 15-42. In: M. Milner (ed.). *Nutritional improvement of food legumes by breeding*. Proc. Symp. sponsored by PAG, Rome, 3-5 July 1972) Protein Advisory Group, United Nations, New York.
- Brouwer, I.D., L.M. Nederveen, A.P. den Hartog, and A.H.C. Vlasveld. 1989. Nutritional impacts of an increasing fuelwood shortage in rural households in developing countries. *Prog. Food Nutr. Sci.* 13:349-361.
- Burns, R.E. 1963. Method of tannin analysis for forage crop evaluation. *Tech. Bul. N.S. 32*. Georgia Agr. Expt. Sta., Athens.
- Castellanos, J.Z., H. Guzman-Maldonado, J.A. Acosta-Gallegos, and J.D. Kelly. 1995. Effects of hardshell character on cooking time of common beans grown in the semiarid highlands of Mexico. *J. Sci. Food Agr.* 69:437-443.
- Cockerham, C.C. 1956. Analysis of quantitative gene action. *Brookhaven Symposia Biol.* 9:53-68.
- Cockerham, C.C. 1963. Estimation of genetic variances, p. 53-94. In: W.D. Hanson and H.F. Robinson (eds.). *Statistical genetics and plant breeding*. Natl. Acad. Sci. Natl. Res. Council Publ. 982
- Comstock, R.E. and H.F. Robinson. 1948. The components of genetic variation in population of biparental progenies and their use in estimating average degree of dominance. *Biometrics* 4:254-266.
- Dexter, S.T., A.L. Andersen, P.L. Pfahler, and E.J. Benne. 1955. Responses of white pea beans to various humidities and temperatures of storage. *Agron. J.* 47:246-250.
- Dickerson, G.E. 1969. Techniques for research in quantitative animal genetics. In *techniques and procedures in animal science research*. Amer. Soc. Animal Sci. p. 36-79.
- Dudley, J.W. and R.H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. *Crop Sci.* 9:257-262.
- Eckholm, E., G. Foley, G. Barnard, and L. Timberlake. 1984. Fuelwood: The energy crisis that won't go away. *Intl. Inst. Env. Dev.*, Washington, D.C.
- Edmister, J.A., W.M. Breene, and A. Serugendo. 1990. Influence of temperature, water activity and time on cookability and color of a stored Rwandan dry bean (*Phaseolus vulgaris* L.). *J. Stored Prod Res* 26:121-126.
- Falconer, D.S. 1981. *Introduction to quantitative genetics*. 2nd ed. Longman, New York.
- GENSTAT 5. 1989. A statistical software program from Rothamsted Expt. Sta., Harpenden, Hertfordshire, England AL5 2JQ.
- Hallauer, A.R. and J.B. Miranda. 1988. *Quantitative genetics in maize breeding*. Iowa State Univ. Press, Ames.
- Hoff, J.E. and P.E. Nelson. 1965. An investigation of accelerated water-uptake in dry pea beans. *Agr. Expt. Sta., Purdue Univ., West Lafayette, Ind., Res. Prog. Rpt.* 211.
- Jackson, G.M. and E. Varriano-Marston. 1981. Hard-to-cook phenomenon in beans: effect of accelerated storage on water absorption and cooking time. *J. Food Sci.* 46:799-803.
- Kakade, M.L. and R.J. Evans. 1965. Toxic factors in beans: Growth inhibition of rats fed navy bean fractions. *Agr. Food Chem.* 13:450-452.
- Kelly, J.D. and F.A. Bliss. 1975. Heritability estimates of percentage seed protein and available methionine and correlations with yield in dry beans. *Crop Sci.* 15:753-757.
- Lindgren, E. 1975. The nutritive value of peas and field beans for hens. *Swed. J. Agr. Res.* 5:159-161.
- Ma, Y. and F.A. Bliss. 1978. Tannin content and inheritance in common bean. *Crop Sci.* 18:201-204.
- Pixley, K.V. and K.J. Frey. 1991. Combining ability for test weight and agronomic traits of oat. *Crop Sci.* 31:1448-1451
- Poulsen, G. 1978. Man and tree in tropical Africa: Three essays on the role of trees in the African environment. *Intl. Develop. Res. Centre*, Ottawa, Canada. p. 31.
- Rannenkamp, R.R. 1977. The effect of tannins on nutritional quality of dry beans, *Phaseolus vulgaris* L. PhD thesis. Purdue Univ., West Lafayette, Ind.
- Satterthwaite, F.E. 1946. An approximate distribution of estimates of

- variance components. *Biometrics* 2:110–114.
- Searle, S.R. 1971. Topics in variance component estimation. *Biometrics* 27:1–74.
- Shellie, K.C. 1990. Food quality and fuelwood conservation of selected common bean (*Phaseolus vulgaris* L.), cultivars and land races in Rwanda. PhD thesis. Michigan State Univ., East Lansing.
- Shellie, K.C. and G.L. Hosfield. 1991. Genotype $\times$ environmental effects on food quality of common bean: Resource-efficient testing procedures. *J. Amer. Soc. Hort. Sci.* 116:732–736.
- Shellie-Dessert, K.C. and G.L. Hosfield. 1990. Implications of genetic variability for dry bean cooking time and novel cooking methods for fuelwood conservation in Rwanda. *Ecol. Food Nutr.* 24:195–211.
- Sirven, P. 1981. Le role des centres urbains dans la deforestation de la campagne Rwandaise, p. 243–254. In: *Energie dans les Communautes Rurals des Pays du Tiers Monde*.
- Swain, T. 1965. The tannins, p. 552–580. In: J. Bonner and J.E. Varner (eds.). *Plant biochemistry*. Academic Press, New York.
- Wassimi, N.N., G.L. Hosfield, and M.A. Uebersax. 1988. Combining ability of tannin content and protein characteristics of raw and cooked dry beans. *Crop Sci.* 28:452–458.