Navy Bean Canning Quality: Correlations, Heritability Estimates, and Randomly Amplified Polymorphic DNA Markers Associated with Component Traits

Kimberly J. Walters¹

Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824

George L. Hosfield²

Sugarbeet and Bean Research Unit; U.S. Dept. of Agriculture, Agricultural Research Service and Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824

Mark A. Uebersax³

Department of Food Science and Human Nutrition, Michigan State University, East Lansing, MI 48824

James D. Kelly³

Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824

ADDITIONAL INDEX WORDS. *Phaseolus vulgaris*, polymerase chain reaction, marker assisted selection, quantitative trait loci

ABSTRACT. Three populations of navy bean (*Phaseolus vulgaris* L.), consisting of recombinant inbred lines, were grown at two locations for 2 years and were used to study canning quality. The traits measured included visual appeal (VIS), texture (TXT), and washed drained mass (WDM). Genotype mean squares were significant for all three traits across populations, although location and year mean squares were higher. We found a positive correlation ($r = 0.19$ to 0.66) between VIS and TXT and a negative correlation ($r = -0.26$ to -0.66) between VIS and WDM and between TXT and WDM ($r = -0.53$ to -0.83) in all three populations. Heritability estimates were calculated for VIS, TXT, and WDM, and these values were moderate to high (0.48 to 0.78). Random amplified polymorphic DNA markers associated with quantitative trait loci (QTL) for the same canning quality traits were identified and studied in each population. Marker-QTL associations were established using the general linear models procedure with significance set at $P = 0.05$. Location and population specificity was common among the marker-QTL associations identified. Coefficient of determination (R^2) values for groups of markers used in multiple regression analyses ranged from 0.2 to 0.52 for VIS, 0.11 to 0.38 for TXT, and 0.25 to 0.38 for WDM. Markers were identified that were associated with multiple traits and those associations supported correlations between phenotypic traits. MAS would offer no advantage over phenotypic selection for the improvement of negatively associated traits.

Acceptable canning quality in dry bean is desired by consumers, processors, and plant breeders, but what constitutes "acceptable" can vary with different end-users. Consumers are most aware of texture, wholeness, and overall visual appearance of processed beans (Wassimi et al., 1990). Although processors are constrained by consumer expectations, they also seek beans that lend themselves to ease of preparation, greater processing efficiency, and higher processor yield. To this end, processors are seeking beans that exhibit rapid and uniform seed expansion during blanching (Hosfield, 1991) and beans that have intact seed coats coupled with high water-holding capacity. Washed drained mass (WDM) is the measurement used by processors to indicate the swelling capacity and water entrainment of beans (Hosfield, 1991) and is a direct measure of processor yield. Developing cultivars that meet consumer and processor expectations provide a difficult challenge for the plant breeder.

Canning quality traits exhibit quantitative inheritance with continuous variation between phenotypes (Hosfield et al., 1984). Although canning quality traits are modulated by the environment, there is a lack of agreement concerning the significance of environmental effects in the literature. Several reports suggest significant genotype $\times$ location ($g \times l$) or genotype $\times$ year ($g \times y$) interactions (Ghaderi et al., 1984; Hosfield, et al., 1984), while other studies found these interactions to be nonsignificant (Wassimi et al., 1990; Shellie and Hosfield, 1991). In addition, practical breeding experience indicates that, although variation for canning quality occurs over locations and years, the rankings among breeding lines and cultivars may be consistent from location to location (Kelly et al., 1994). Determining the significance of $g \times e$ and $g \times y$ effects is critical to the development of appropriate and efficient breeding strategies.

Although research and experience suggests that the environment can influence canning quality, there is no information on the heritability of individual canning quality traits. In addition, limited research has been conducted to evaluate correlations between canning quality traits in navy bean. Ghaderi, et al. (1984) examined interrelationships between canning quality traits in navy and pinto bean and found that, with few exceptions, associations among quality characters were low. Knowledge of the relationships between canning quality traits and their heritabilities determines the methodologies used when breeding for canning quality in navy bean, including strategies for indirect selection.

Ruengsakulrach et al. (1991) proposed a method of indirect

Received for publication 13 May 1996. Accepted for publication 16 Jan. 1997. This paper is part of a thesis submitted by Kimberly J. Walters in partial fulfillment of the requirements for a MS degree at Michigan State Univ. Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable. Partial support for this research was provided by the Quaker Oats Company. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Graduate student.

²Research geneticist and adjunct professor; to whom reprint requests should be addressed.

³Professor.

selection for canning quality based on pasting characteristics of bean flour. The benefit of this selection procedure is that it allows for selection in early generations. However, bean processing quality estimated by using whole bean flour is based entirely on the functional differences in bean chemical composition and, in part, microstructure (Ruengsakulrach et al., 1994). Physical traits would have to be assessed separately when enough material was available for canning. Indirect selection using linked markers, marker assisted selection (MAS), has received attention as a method for increasing selection efficiency within breeding programs. If a trait is difficult and expensive to evaluate, under polygenic control, or highly influenced by the environment, MAS may be more efficient than traditional selection methods based on phenotype (Dudley, 1993). Evaluating a large number of canned bean samples is time consuming, expensive, and may lack the precision to detect small quality differences. Therefore, MAS may be a useful strategy to indirectly select for canning quality in navy bean in earlier generations.

Several studies have already identified molecular markers associated with quantitative trait loci (QTL) in various crops (Mansur et al., 1996; Thomas et al., 1996; Tuinstra et al., 1996; Veldboom and Lee, 1996). RAPD markers have been used to tag loci linked to qualitative traits and QTL in common bean (Haley et al., 1993, 1994b; Miklas et al., 1993, 1996) and are being used for selection purposes (Kelly, 1995). In addition to their use for tagging loci in common bean, RAPD markers have revealed useful levels of polymorphism between commercially adapted genotypes of the same market class (Haley et al., 1994a) and are more abundant than isozymes or restriction fragment polymorphisms (RFLP). For these reasons, RAPDs may be useful in identifying QTL controlling canning quality traits in navy beans.

The objectives of our research were 1) to assess the significance of genotypic and environmental effects on three canning quality traits [visual appeal (VIS), texture (TXT) and WDM], 2) to examine interrelationships between pairs of traits, 3) to estimate heritabilities of the traits, and 4) to identify RAPD markers associated with QTL controlling these traits. A additional objective was to discuss the results in terms of breeding strategies to improve canning quality in navy bean.

Materials and Methods

PLANT MATERIALS. Parental genotypes represented commercial navy bean cultivars and Michigan State University breeding lines and were chosen for their extremes in canning quality. 'Seafarer' and N81099 exhibited desirable canning quality over 10 years, whereas 'Cumulus' and N84004 consistently exhibited poor canning quality. Fifty single plants from each of three populations derived from biparental crosses were advanced via single seed descent to the F_6 . Population one (P1) consisted of progeny from 'Seafarer'/N84004, population two (P2) was derived from N81099/N84004, and population three (P3) was derived from N81099/Cumulus. Single plants were selected from within each F_6 line and the $F_{6,7}$ seed was increased at a winter nursery in Puerto Rico. A sample of seed from each F_6 plant selected also was grown in the greenhouse for DNA isolation from leaf tissue. Lines were lost during selfing due to failure of germination and poor adaptation to growing conditions in Michigan and in the winter nursery. Final populations consisted of 27, 37, and 26 recombinant inbred lines (RILs) in P1, P2, and P3, respectively. The $F_{6,8}$ and $F_{6,9}$ RILs and the respective parents for each population were grown in lattice designs with three replications at two locations in Michigan during Summer 1993 and 1994.

PROCESSING PROCEDURES AND QUALITY EVALUATIONS. Duplicate samples from each plot for each RIL and parent were taken from two replications at each location and were evaluated for canning quality traits at soaked and cooked stages of processing. Before samples were processed, they were hand-cleaned and seed moisture percentage was determined on 250 g of beans. Bean samples with a fresh-mass equivalent of 100 g total solids were placed in nylon mesh bags and soaked in water (100 ppm Ca) for 60 min (30 min at 21 °C followed by 30 min at 87 °C). The soaking procedure produced well-hydrated beans with minimum damage, similar to beans soaked continuously in the high-temperature systems common throughout the U.S. canning industry (Hosfield and Uebersax, 1980). Soaked bean samples were weighed and emptied into no. 303 tin cans (100 × 75 mm) that were subsequently filled with boiling brine [142.0 g sucrose, 113.4 g of table salt (NaCl)] added to 9.1 kg of tap water containing 0.025 mol·L⁻¹ (100 ppm) Ca ion. Cans were sealed and cooked in a retort without agitation for 45 min at 116 °C and 10.4 × 10⁴ Pa (15 lb/inch²). After cooking, cans were cooled under cold running tap water and stored for a minimum of 2 weeks at room temperature.

Cooked beans were evaluated for WDM and cooked bean TXT. WDM (in grams) was calculated by draining and weighing cooked bean samples (Hosfield and Uebersax, 1980). Texture was measured using a Kramer Shear Press and peak forces were reported as Newtons per 100 grams. The visual appeal (VIS score) of processed beans was determined subjectively by a panel of 10 judges trained to distinguish quality attributes. A 7-point Hedonic scale was used (1 = very undesirable, 4 = neither desirable nor undesirable, 7 = very desirable), and the VIS score was averaged across judges for each sample.

DNA EXTRACTION AND RAPD PROTOCOL. One young trifoliate leaf was harvested from each of six plants of each parent and $F_{6,7}$ RIL. Tissue was lyophilized, ground, and stored at -80 °C. DNA was extracted using a modification of the protocol outlined by Saghai-Marooft et al. (1984). Chloroform : isoamyl alcohol (24:1) was used in place of chloroform : octanol. RNAase A was added before a second chloroform : isoamyl alcohol extraction, and DNA was resuspended in Tris-EDTA buffer (TE_{0.1}). DNA that was recalcitrant to amplification by the polymerase chain reaction (PCR) was dissolved in a high-salt solution and re-precipitated in ethanol to remove polysaccharides (Fang et al., 1992). The PCR procedure reported by Haley et al. (1994a) was followed with minor modifications to the reaction volume and cycling profile. About 19 ng of genomic DNA template and 19 ng single decamer primer were used in a 19 µl reaction. Amplification was performed in a DNA thermal cycler (model 480; Perkin Elmer Cetus, Norwalk, Conn.) programmed for three cycles of 1 min at 94 °C, 1 min at 35 °C, and 2 min at 72 °C, 34 cycles of 10 s at 94 °C, 20 s at 40 °C, and 2 min at 72 °C (the final step extended by 1 s for each of the 34 cycles) and then one final extension cycle of 5 min at 72 °C. From the 390 random decamer primers (Operon Technologies, Alameda, Calif.) screened, those primers yielding polymorphisms between N84004 and 'Seafarer' (31 primers), N81099, and N84004 (36 primers) and N81099 and 'Cumulus' (34 primers) were screened against the respective populations and scored for the presence or absence of the band.

STATISTICAL ANALYSIS. Simple correlations were computed for the following pairs of traits: VIS : WDM, VIS : TXT, and WDM : TXT. Heritability estimates were calculated on an entry mean basis for VIS, TXT, and WDM by population as described by Allard (1960). Standard errors were calculated as suggested by Hallauer and Miranda (1981), modified to include interactions involving years.

Histograms were constructed to determine the frequency distribution of each canning quality trait and χ^2 tests were used to determine if the polymorphic markers fit the expected 1:1 segregation ratio. Markers that did not fit the expected ratio were not used in future analyses. Each of the measured traits was analyzed by the analysis of variance procedure with a factorial arrangement of treatments. Data from individual RAPDs were then analyzed against each of the measured traits (VIS, TXT, and WDM) using the statistical program SAS proc glm (SAS Institute, 1988). Analyses were performed using various data sets: each location in each year, individual location data combined over years, location data combined within each year, and data combined over locations and years. The probability level for acceptance of marker-QTL association was $P < 0.05$. In each population, markers were selected for multiple regression analyses if their individual coefficient of determination (R^2) was relatively high or they were significantly associated with a trait when different data sets were used for the analysis. The coefficient of determination (R^2) resulting from the multiple regression analysis indicated the level of phenotypic variation accounted for by the selected markers.

Results

Frequency distributions (not shown) for VIS, TXT, and WDM were determined for each population. The distributions approximated the normal distribution expected for quantitative traits in the absence of any data transformation. Thus, there was no need to transform the data. Genotypic mean squares from the combined analyses of variance (ANOVA) were highly significant for the three traits despite significant environmental effects (Table 1). Location and year mean squares were higher than genotypic mean squares and also were highly significant with a few exceptions. In most cases when a location and year mean square for a trait was significant the first- and second-order interaction mean squares for the trait were also significant (Table 1). All three populations showed similar levels of significance for individual traits and interactions.

Experimental variability was investigated further by examining variance component estimates (Table 2). The main interest was to examine the relative importance (percentage) of the genotypic (g),

genotype $\times$ year (g $\times$ y), genotype $\times$ location (g $\times$ l) and genotype $\times$ year $\times$ location (g $\times$ y $\times$ l) components. Except for VIS in P1, the variance component for genotypes (g) accounted for $>20\%$ of the total variance and ranged from 16% to 38% (Table 2). The significant second-order interaction of genotypes, years, and locations for VIS and TXT in P2 and P3 and WDM in P1 and P3 demonstrated that location and year caused changes in the relationships among the lines for these traits (Tables 1 and 2). However, except for VIS in P2, the genotypic variance component exceeded that of the first- and second-order interaction variance components.

The phenotypic correlation coefficients (Table 3) between pairs of traits (VIS and WDM, VIS and TXT, and TXT and WDM) were variable from population to population and year to year. Nevertheless, except for the VIS : WDM correlation coefficient in P2 for 1994, all of the correlations were significant or highly significant. The correlations between VIS and TXT were always positive and ranged from 0.19 to 0.66 across populations. The correlations between VIS : WDM and TXT : WDM were negative in all cases and ranged from -0.26 to -0.66 and from -0.53 to -0.83 for the pairs of traits, respectively.

Heritability estimates from combined data were 0.59 for VIS, 0.64 for TXT, and 0.67 for WDM and were considered moderate in value (Table 4). All three traits (VIS, TXT, and WDM) had consistent heritability estimates across the three populations. These estimates are the first heritability values presented for canning quality traits in dry bean.

Of 390 random primers tested, 8% were polymorphic in P1 and 9% were polymorphic in P2 and P3. However, significant genotypic variation permitted the identification of several markers associated with each trait ($p < 0.05$) in each of the three populations (not shown). The R^2 values calculated from multiple regression analyses using selected markers for each trait ranged from 0.11 to 0.52 depending on the trait and the population considered (Table 5). Location specificity was evident because only a small percentage of the markers were associated with traits at both locations (11% for VIS, 19% for TXT, and 18% for WDM; data not shown). Many of the marker-trait associations also were population specific although a few markers were significantly associated with a canning quality trait in multiple populations (Table 6). There were

Table 1. Mean squares, experimental means, and coefficients of variability (CV) from combined analysis of variance in three populations (P1, P2, P3) of processed navy bean grown over 2 years at two locations in Michigan.

Source	df ¹	Population								
		Trait ²								
		VIS			TXT			WDM		
		P1	P2	P3	P1 ³	P2 ⁴	P3 ⁵	P1	P2	P3
Year (Y)	1	0.04	1.1	10 ^{**}	2 ^{**}	10 ^{**}	31 ^{**}	621 ^{**}	183 [*]	823 ^{**}
Location (L)	1	82 ^{**}	23 ^{**}	0.04	3 ^{**}	18 ^{**}	23 ^{**}	28,755 ^{**}	26,712 ^{**}	18,452 ^{**}
Y $\times$ L	1	0.8	5.6 ^{**}	1 [*]	0.8 ^{**}	3 ^{**}	7.5 ^{**}	1,193 ^{**}	468 ^{**}	8,975 ^{**}
Genotype (G)	29, 39, 29	2.7 ^{**}	2.0 ^{**}	3.0 ^{**}	0.06 ^{**}	0.4 ^{**}	1.1 ^{**}	186 ^{**}	177 ^{**}	284 ^{**}
G $\times$ Y	29, 39, 29	1.2 [*]	0.5 [*]	0.9 ^{**}	0.01 ^{**}	0.06 ^{**}	0.4 ^{**}	35 ^{**}	65 [*]	80 ^{**}
G $\times$ L	29, 39, 29	0.9	0.9 ^{**}	0.7 ^{**}	0.02 ^{**}	0.08	0.2 ^{**}	43 ^{**}	55	89 ^{**}
G $\times$ Y $\times$ L	29, 39, 29	0.7	0.8 ^{**}	0.6 ^{**}	0.005 ^{**}	0.07 ^{**}	0.2 ^{**}	27 ^{**}	52	75 ^{**}
Error	119, 159, 129	0.7	0.3	0.2	0.006	0.03	0.06	14	39	30
Experiment mean		3.6	3.3	2.9	620	588	674	297	298	293
CV (%)		22.5	16.7	16.8	12.7	8.6	11.3	1.3	2.1	1.9

²VIS (1–7); TXT (N·100 g⁻¹); WDM (g).

³Multiple values correspond to P1, P2, and P3 respectively

⁴Mean square values are $\times 10^{-6}$.

⁵Mean square values are $\times 10^{-5}$.

^{*}Significant at $P = 0.05$ and 0.01, respectively.

also markers significantly associated with more than one trait. One marker (OQ11 in P3) was significantly associated with VIS ($R^2 = 0.17$), WDM ($R^2 = 0.27$), and TXT ($R^2 = 0.25$), and it supported the observation of a negative relationship between VIS and WDM. Selection for high VIS required the presence of the OQ11 band, whereas selection for high WDM required the absence of the OQ11 band. OQ11 also was polymorphic in P1 and P2 but was not associated with VIS, TXT, or WDM except in P2 at one location. The marker ON18b from P2 was significantly associated with VIS ($R^2 = 0.20$) and TXT ($R^2 = 0.11$), and the association supported the observed positive correlation between the two traits. Selection for high VIS and a high TXT value required the absence of the ON18b marker band. ON18b was monomorphic in P1 and in P3. Marker OF5 was associated with TXT in P1 ($R^2 = 0.29$) and P3 ($R^2 = 0.14$) but was monomorphic in P2.

Discussion

Canning quality of dry bean is viewed by breeders as a "super" trait because no single variable can adequately describe a sample (Hosfield and Uebersax, 1990). In view of their inherent complexity, super traits are difficult to improve. At best, the breeder seeks to dissect the super trait into a number of component characters that can be individually measured and selected. Based on knowledge of consumer and processor acceptability criteria for visual, soaking, and cooking properties of dry beans, tests have been developed, that measure distinct properties of seeds that are intrinsically

Table 2. Estimates of variance components scaled to sum to 100 for visual appeal (VIS), texture (TXT) and washed drained mass (WDM) in three populations (P1, P2, P3) of processed navy bean grown over 2 years at two locations in Michigan.

Trait	Component ^a					Total
	g	g × y	g × l	g × y × l	e	
VIS						
P1	16	13	5	1	65	1.0
P2	23	0 ^b	3	34	40	0.8
P3	32	12	5	21	30	0.8
TXT						
P1	27	13	19	0 ^b	41	15 × 10 ⁻³
P2	30	0 ^b	29	19	22	8.6 × 10 ⁻³
P3	31	20	9	18	22	26 × 10 ⁻³
WDM						
P1	38	5	9	16	32	44
P2	22	5	2	9	62	64
P3	30	1	5	27	37	81

^ag = genotype, y = years, l = location, e = error.

^bSmall negative values or zero estimates of variance components.

Table 3. Correlation coefficients between canning quality traits in three populations of navy bean grown over 2 years at two locations in Michigan.

Trait pair correlated ^a	Correlation coefficients (r)								
	Population								
	1			2			3		
	Combined	1993	1994	Combined	1993	1994	Combined	1993	1994
vis:txt	0.49**	0.66**	0.46**	0.22**	0.33**	0.19*	0.42**	0.43**	0.29**
vis:WDM	-0.58**	-0.66**	-0.51**	-0.26**	-0.49**	-0.08 ^{NS}	-0.33**	-0.39**	-0.45**
WDM:txt	-0.83**	-0.81**	-0.67**	-0.56**	-0.81**	-0.53**	-0.79**	-0.71**	-0.59**

^aVIS (visual appeal); WDM (washed drained mass); TXT (texture).

^{NS}, *, ** Nonsignificant or significant at $P = 0.05$ or 0.01 , respectively.

related to canning quality (Hosfield et al., 1984). Among the traits that are measured, VIS, TXT, and WDM are the most important.

Relationships between various canning quality traits will not only influence which markers can be used most effectively for MAS but also which traits will be best suited for improvement by traditional selection. However, limited research has been conducted to evaluate relationships between various canning quality traits in navy bean. The negative correlation between WDM and TXT supports the observations of Ghaderi et al. (1984), who also found a negative correlation between TXT and WDM ($r = -0.49$). However, the positive correlation between VIS and TXT and the negative correlation between VIS and WDM have not been reported previously and have important breeding implications. Because of the cost and time involved in evaluating several canning quality traits simultaneously among numerous breeding lines, bean breeders make their initial selections based on visual criteria (VIS). Breeders also give considerable attention to VIS because of the scrutiny of this trait by processors and consumers. In addition to VIS, WDM also must be considered during selection due to processor requirements for this trait. Beans with higher WDMs give higher processor yields (Wassimi et al, 1990), and any beans that fall below accepted values for this trait may be rejected. However, based on the correlations between traits reported in this study, selection for VIS would lead to lines with acceptable TXT but low WDMs. Although one can expect WDM values to be lower in lines selected for high VIS scores, it is still important to look for outliers that not only have high VIS scores but also have acceptable WDMs. Markers, such as OQ11, for which the presence of the band is associated with high VIS scores and the absence of the band is associated with high WDM will not be useful to identify such outliers. Breeding lines that have high VIS scores but deviate substantially from accepted values for WDM would not be good candidates for release as cultivars since they would not meet processor standards.

Individually measured characters or components of canning quality are heritable but behave as quantitatively inherited traits (Wassimi et al., 1990). The environment has substantially influenced canning quality components in dry bean and can complicate the measurement of these traits. Ghaderi et al. (1984) found significant genotype × location (g × l) interactions for clumps and splits, two components of VIS, among genotypes of the navy and pinto market class and a significant g × l interaction for WDM in pinto but not navy beans. Hosfield et al. (1984) showed year effects to be important in canning quality traits of tropical black beans.

Since environmental influences on canning quality traits in dry bean appear substantial, one expects low heritability estimates for traits. In our study, heritability estimates for VIS, TXT, and WDM were moderate in value, despite, in most cases, significant first- and second-order interactions involving years and locations. The

heritability estimates obtained in conjunction with the relative magnitude of the genotypic variance component in relation to the first- and second-order interaction components suggest that progress for improving canning quality traits can be made by selection. However, it is important to remember that these traits are components of canning quality and may be physically, chemically, or developmentally interrelated. Thus, the improve-

ment of one trait may hinder the improvement of other traits, resulting in less progress than expected based on gain from selection estimates. This situation is analogous to yield component compensation when breeding for yield (Adams, 1967).

Environment-specific marker-QTL associations have been identified (Bubeck et al., 1993; Paterson et al., 1991) therefore, it is important to determine the stability of marker QTL associations across multiple locations. The location specificity of markers for the canning quality traits evaluated in this study was not unexpected. It is common for the canning quality of a genotype to vary from location to location (Ghaderi et al., 1984), and the analysis of variance indicated that location $\times$ genotype interactions were significant for many of the traits in each population. Markers for QTL that function consistently at a number of locations would be preferred for MAS; however, location-specific markers may also be useful. Testing at several locations is commonly practiced to identify genotypes that perform well over a range of environments. By pyramiding location-specific markers into one genotype, it may be possible to achieve the same phenotypic results at a faster rate (Paterson et al., 1991).

The usefulness of marker-QTL associations is also affected by population specificity since marker studies using only one population may also lead to a poor choice of markers for MAS. Population-specific marker-QTL associations were prevalent in this study and were of two different types. Some markers were population specific simply because they were monomorphic among the parents and the progeny in all but one population. Other markers were polymorphic in multiple populations but were not significantly associated with the same trait in more than one population. This latter case may be due to small population sizes, which were unavoidable in this study due to the loss of maladapted lines and the high cost associated with canning many individual samples of beans. Small population sizes are a limitation of this study but may be less serious due to the relatedness of the populations. Breeding lines N84004 and N81099 were each parents in two of the three populations. Marker-QTL associations that are not population specific would allow markers to be used in all populations. However, in a bean breeding program, lines that exhibit superior canning quality are often used repeatedly in

crosses designed to combine canning quality with other desirable traits. Population-specific markers could be used to facilitate this breeding strategy. For example, marker OA18 was associated with high VIS scores and marker OF5 was associated with high TXT values in P1 ('Seafarer'/N84004). Since each of these markers was present in 'Seafarer', these markers could be used to select for improved canning quality among progeny from crosses between 'Seafarer' and various breeding lines. When used in this fashion, population-specific markers may have long-term utility in a breeding program.

Navy bean is one of the most important market classes of dry bean in the United States with >95% of the production commercially canned. Canning characteristics of "navies" largely influ-

Table 4. Heritability estimates for visual appeal (VIS), texture (TXT) and washed drained mass (WDM) traits in three populations (P1, P2, and P3) of processed navy beans grown over 2 years at two Michigan locations.

Trait	P1	SE	P2	SE	P3	SE	Mean across
							populations
VIS	0.48	0.23	0.62	0.17	0.66	0.26	0.59
TXT	0.56	0.26	0.78	0.23	0.59	0.28	0.64
WDM	0.72	0.26	0.62	0.25	0.67	0.28	0.67

Table 5. Proportion of phenotypic variation accounted for by selected markers using multiple regression. Visual appeal (VIS), texture (TXT), and washed drained mass (WDM) were evaluated in three populations of processed navy beans grown over 2 years and two locations in Michigan.

Trait	Population					
	1		2		3	
	R ^{2z}	No. markers	R ²	No. markers	R ²	No. markers
VIS	0.20	1	0.45	6	0.52	4
TXT	0.22	3	0.11	3	0.38	5
WDM	0.25	6	---	0	0.38	3

^zCoefficient of determination. Data combined over years and locations.

Table 6. Probability values for markers significantly associated with multiple populations, multiple traits within a population or multiple locations within a population (P = population).

Marker	P1						P2						P3					
	Trait						Trait						Trait					
	VIS		TXT		WDM		VIS		TXT		WDM		VIS		TXT		WDM	
	Location		Location		Location		Location		Location		Location		Location		Location		Location	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
OA18	0.04	0.03	NS	NS	0.03	NS	---	---	---	---	---	---	---	---	---	---	---	---
OF5	NS	NS	0.02	0.004	NS	NS	---	---	---	---	---	---	NS	NS	NS	0.05	NS	0.03
OG4	NS	NS	NS	0.02	NS	NS	---	---	---	---	---	---	NS	NS	NS	0.01	NS	0.03
OI2	NS	NS	0.05	NS	0.04	NS	0.02	0.01	NS	NS	NS	NS	---	---	---	---	---	---
OM10	NS	NS	NS	NS	0.02	0.02	NS	NS	NS	NS	NS	NS	---	---	---	---	---	---
OM11	---	---	---	---	---	---	0.02	0.05	NS	NS	NS	NS	0.001	NS	NS	NS	NS	NS
OP5	NS	NS	NS	0.003	NS	0.04	---	---	---	---	---	---	NS	NS	NS	0.01	0.05	0.01
ON18b	---	---	---	---	---	---	NS	0.004	NS	0.04	NS	NS	NS	NS	NS	NS	NS	NS
OQ11	NS	NS	NS	NS	NS	NS	NS	0.01	NS	NS	NS	NS	0.02	0.03	0.03	0.003	0.004	0.03
OX3	---	---	---	---	---	---	NS	NS	NS	NS	NS	NS	0.002	NS	NS	NS	NS	NS
OY4b	NS	NS	0.04	0.02	0.02	0.004	---	---	---	---	---	---	NS	0.04	NS	NS	NS	0.04
OAA1	NS	NS	NS	NS	0.02	0.008	NS	NS	NS	NS	NS	NS	---	---	---	---	---	---

^zMonomorphic.

NS Nonsignificant at $P \leq 0.05$.

ence final product acceptability. Thus, the canning industry has established a definite set of standards that are rigorously adhered to when a cultivar is considered for processing. Poor canning quality in navy bean is often the characteristic that prevents a high yielding and agronomically superior breeding line from becoming a cultivar. The importance of consumer and processor requirements in navy bean makes the improvement of canning quality an important breeding objective for this market class. Since canning quality is a difficult and expensive trait to select, breeders are interested in alternatives to the traditional selection strategies. Indirect selection methods may be useful to improve individual canning quality traits. However, direct selection methods would appear to offer greater opportunity to improve negatively correlated canning quality traits than more rigid indirect selection methods such as MAS.

Literature Cited

- Adams, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop Sci.* 7:505–510.
- Allard, R.W. 1960. Principles of plant breeding. Wiley, New York.
- Bubeck, D., M. Goodman, W. Beavis, and D. Grant. 1993. Quantitative trait loci controlling resistance to gray leaf spot in maize. *Crop Sci.* 33:838–847.
- Dudley, J.W. 1993. Molecular markers in plant improvement: Manipulation of genes affecting quantitative traits. *Crop Sci.* 33:660–668.
- Fang, G., S. Hammar, and R. Grumet. 1992. A quick and inexpensive method for removing polysaccharides from plant genomic DNA. *BioFeedback* 13:52–55.
- Ghaderi, A., G.L. Hosfield, M.W. Adams and M.A. Uebersax. 1984. Variability in culinary quality, component interrelationships, and breeding implications in navy and pinto beans. *J. Amer. Soc. Hort. Sci.* 109:85–90.
- Haley, S.D., P.N. Miklas, J.R. Stavely, J. Byrum, and J.D. Kelly. 1993. Identification of RAPD markers linked to a major rust resistance gene block in common bean. *Theor. Appl. Genet.* 86:505–512.
- Haley, S.D., P.N. Miklas, L. Afanador, and J.D. Kelly. 1994a. Random amplified polymorphic DNA (RAPD) marker variability between and within gene pools of common bean. *J. Amer. Soc. Hort. Sci.* 119:122–125.
- Haley, S.D., L. Afanador, and J.D. Kelly. 1994b. Identification and application of a random amplified polymorphic DNA marker for the I gene (potyvirus resistance) in common bean. *Phytopathology* 84:157–160.
- Hallauer, A. and J. Miranda. 1981. Quantitative genetics in maize breeding. Iowa State University Press, Ames.
- Hosfield, G.L. 1991. Genetic control of production and food quality factors in dry bean. *Food Technol.* 45:98–103.
- Hosfield, G.L. and M.A. Uebersax. 1980. Variability in physico-chemical properties and nutritional components of tropical and domestic dry bean germplasm. *J. Amer. Soc. Hort. Sci.* 105:246–252.
- Hosfield, G.L. and M.A. Uebersax. 1990. The definition and measurement of culinary quality in dry bean. *Michigan Dry Bean Dig.* 14:20–27.
- Hosfield, G.L., M.A. Uebersax, and T.G. Isleib. 1984. Seasonal and genotypic effects on yield and physico-chemical seed characteristics related to food quality in dry, edible beans. *J. Amer. Soc. Hort. Sci.* 109:182–189.
- Kelly, J.D. 1995. Use of random amplified polymorphic DNA markers in breeding for major gene resistance to plant pathogens. *HortScience.* 30:461–465.
- Kelly, J.D., G.L. Hosfield, G.V. Varner, M.A. Uebersax, M.E. Brothers and J. Taylor. 1994. Registration of 'Huron' navy bean. *Crop Sci.* 34:1408.
- Mansur, L., J. Orf, K. Chase, T. Jarvik, P. Cregan and K. Lark. 1996. Genetic mapping of agronomic traits using recombinant inbred lines of soybean. *Crop Sci.* 36:1327–1336.
- Miklas, P.N., J.R. Stavely, and J.D. Kelly. 1993. Identification and potential use of a molecular marker for rust resistance in common bean. *Theor. Appl. Genet.* 85:745–749.
- Miklas, P., E. Johnson, V. Stone, J. Beaver, C. Montoya and M. Zapata. 1996. Selective mapping of QTL conditioning disease resistance in common bean. *Crop Sci.* 36:1344–1351.
- Paterson, A.H., S. Damon, J.D. Hewitt, D. Zamir, H.D. Rabinowitch, S.E. Lincoln, E.S. Lander, and S.D. Tanksley. 1991. Mendelian factors underlying quantitative traits in tomato: comparison across species, generations and environments. *Genetics* 127:181–197.
- Ruengsakulrach, S., N. Srisuma, M.A. Uebersax and G.L. Hosfield. 1994. Early generation screening of navy bean breeding lines by canning quality assessment and pasting characteristics of bean flour. *J. Food Quality* 17:321–333.
- Saghai-Marouf, M.A., K.M. Soliman, R.A. Jorgensen, and R.W. Allard. 1984. Ribosomal DNA spacer-length polymorphisms in barley: Mendelian inheritance, chromosomal location, and population dynamics. *Proc. Natl. Acad. Sci.* 81:8014–8018.
- Shellie, K.C. and G.L. Hosfield. 1991. Genotype x environmental effects on food quality of common bean: resource-efficient testing procedures. *J. Amer. Soc. Hort. Sci.* 116:732–736.
- Thomas, W., W. Powell, J. Swanston, R. Ellis, K. Chalmers, U. Barua, P. Jack, V. Lea, B. Forster, R. Waugh and D. Smith. 1996. Quantitative trait loci for germination and malting quality characters in a spring barley cross. *Crop Sci.* 36:265–273.
- Tuinstra, M., E. Grote, P. Goldsbrough and G. Ejeta. 1996. Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. *Crop Sci.* 36:1337–1344.
- Veldboom, L. and M. Lee. 1996. Genetic mapping of quantitative trait loci in maize in stress and nonstress environments: I. grain yield and yield components. *Crop Sci.* 36:1310–1319.
- Wassimi, N.N., G.L. Hosfield, and M.A. Uebersax. 1990. Inheritance of physico-chemical seed characters related to culinary quality in dry bean. *J. Amer. Soc. Hort. Sci.* 115:492–499.